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Geography, opportunity and bridgeheads facilitate termite invasions to the United States

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Abstract With the ever-increasing rate of globalization, port of entry data can be an important source of information for the introduction and spread of invasive species on a worldwide scale. Using a comprehensive dataset spanning records from 1923 to 2017, termite interceptions at US ports of entry were analyzed. We identified 906 non-native interceptions originating from outside the US, including four families, 32 genera and 75 different termite species. Non-native termites originated from 88 different countries and were intercepted in 29 different states. There was a strong regional bias, with termite-rich areas closest to the US—Central America, South America and the Caribbean—the greatest exporters of termite species to the US. Among the 75 non-native termites intercepted, 12 had already become established outside of their native range, with eight appearing to utilize bridgeheads to expand their global distribution. Additionally, the establishment probability of a species was positively influenced by the number of interceptions, as three of the most common non-native species intercepted at ports of entry are currently established within the US—*Nasutitermes corniger*, *Cryptotermes brevis* and *Coptotermes formosanus*. Our results reveal important insights into the global dispersal of invasive termites and contribute further evidence towards the importance of trade, increased propagule pressure and the bridgehead effect as drivers of global invasion rates.

Keywords Invasive species · Termites · Bridgehead effect · Propagule pressure

Introduction

The worldwide trend towards globalization has promoted the accidental transfer of animal and plant species throughout the world (Westphal et al. 2008; Banks et al. 2015). Introduction rates of alien species have been shown to match up remarkably well with modern, human-mediated events (Bertelsmeier et al. 2017); therefore, alien species range expansion appears to be a trademark of the Anthropocene (Capinha et al. 2015; Lewis and Maslin 2015). The rate at which these alien species are spreading to novel countries is still increasing (Seebens et al. 2017, 2018) and may continue to rise for the foreseeable future (Seebens et al. 2015), despite focused efforts to mitigate invasions over the last half-century (Hulme 2009). Even though many species do not succeed in

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establishing, those that persist and then spread from their initial introduction point can become invasive species (i.e., harmful alien species) (Tobin 2018). The detrimental impacts of invasive species are well documented (Simberloff et al. 2013; Bradshaw et al. 2016), and pose a tremendous threat to biodiversity, agriculture and general human health. As prevention of their introduction or rapid response treatment programs remain the most cost-effective approach of reducing their impacts (Finnoff et al. 2007; Keller et al. 2007; Reaser et al. 2020), it is important to fully understand the pathways by which they are spreading in order to prevent invasions or generate early detections.

Recently, port of entry data have been utilized to elucidate patterns in the spread of alien species in a wide variety of organisms, including beetles (Haack 2001), mosquitoes (Derraik 2004), ants (Suarez et al. 2005; Bertelsmeier et al. 2018; Suhr et al. 2019), lizards (Chapple et al. 2013) and general plant pests (McCullough et al. 2006). The data specifically refer to interceptions of pest species at a country's various ports of entry (e.g., airports, seaports or land borders), and has the potential to reveal novel insights into invasion pathways. Records of port of entry interceptions in the US date back to the early 1900s, when the USDA Animal and Plant Health Inspection Service (APHIS) first began publishing annual lists of the intercepted pest species (e.g., USDA (1942)). The primary data compiled for each interception include the name of the pest species, date of the interception, country of origin, US port of entry and item on which the pest was found (e.g., trade commodity, packaging). Therefore, this historical port of entry dataset offers a robust opportunity to identify patterns in species invasion pathways. For example, Bertelsmeier et al. (2018) utilized 100 years' worth of port of entry records to find that invasive ants more frequently originated from countries where the ant had previously invaded and established, a phenomenon known as the 'bridgehead effect' (Lombaert et al. 2010). This phenomenon has been found to play a role in the invasions of several different organisms (Lombaert et al. 2010; van Boheemen et al. 2017; Javal et al. 2019), with Ascunce et al. (2011) the first to describe this phenomenon in a eusocial organism, in the spread of the red imported fire ant *Solenopsis invicta* out of South America. Given the recent finding that the bridgehead effect appears prevalent in many ant invasions, bridgeheads may also play a vital role in the invasions of other eusocial organisms.

Termites are a group of eusocial insects that consume the cellulose and lignocellulose found in dead wood, grass, microepiphytes, leaf litter, and cultivated fungi (Hartke and Baer 2011). They perform beneficial ecosystem services in their natural environments, primarily improving soil quality (Black and Okwakol 1997; Dawes 2010), and thereby productivity (Nash and Whitford 1995), of an ecosystem, making them critical members of their community (Holt and Coventry 1990; Whitford 1991). However, the services they perform that make them key members of their natural environments render them destructive in urban environments, as they can heavily infest man-made structures (Rust and Su 2012). Of the approximately 3000 described termite species, 80 are currently designated as serious urban pests (Rust and Su 2012) and 28 species have become established in countries outside their native range (i.e., alien species) (Evans et al. 2013). Worldwide, urban pest termites necessitate expensive repairs, prevention and control efforts by humans (Ghaly and Edwards 2011; Scharf 2015), with recent damage estimates approaching $40 billion annually (Rust and Su 2012). Invasive termites threaten to exacerbate these costs within the US, as two of the most destructive urban termite pests in the world are now established there (Evans et al. 2013; Chouvenc et al. 2016)—the Formosan subterranean termite *Coptotermes formosanus* and the Asian subterranean termite *C. gestroi*. Moreover, invasive termites could become the cause of more traditional negative invasive effects, as their expansion out of urban environments is occurring in the southeastern US (Evans et al. 2019). To mitigate and possibly prevent costs associated with future invasive termite establishments, a more thorough knowledge of their pathways into the US is necessary. We used almost 100 years of port of entry data of non-native termites to the US to analyze and elucidate their invasion pathways.

Methods

Data acquisition, standardization and filtration

Termite interceptions were acquired from USDA APHIS through their (1) published annual reports and (2) current computerized database, resulting in a catalog of interceptions spanning almost 100 years, from 1924 to 2017. Country and termite species names have fluctuated greatly over the past century, so the data were standardized to facilitate downstream analysis. Country names were changed to align with recognized countries as of 2019, and termite species names were changed to align with the current taxonomy, reflecting both updates of genus/species names (Krishna et al. 2013) and synonymies of two or more species (Austin et al. 2005; Scheffrahn et al. 2005, 2015). Additionally, Hawaii was listed in the USDA records as a port of origin for some interceptions. Given its statehood, we chose to treat Hawaii solely as a member of the US and therefore excluded interceptions originating from Hawaii from all analyses except for the bridgehead analysis, as Hawaii could potentially act as an important bridgehead for alien termites (see "Bridgehead" section). However, US territories such as American Samoa, Guam, Puerto Rico and the US Virgin Islands were treated as foreign countries given their closer associations with their geographic neighbors—Oceania for American Samoa and Guam and the Caribbean for Puerto Rico and the US Virgin Islands.

Non-native termites were the focus of this study, so only non-native termite interceptions were analyzed. Non-native termites were assigned to one of two groups, when applicable: (1) alien—non-native and established somewhere outside of their native range or (2) invasive—harmful alien species. The port of entry records did not designate whether the pests intercepted were native or non-native to the US, so designations were performed primarily based on the distributions given in Krishna et al. (2013). Additionally, data from Evans et al. (2013) were used to determine whether the non-native termite species intercepted had established a population outside of its native range (i.e., alien). Finally, species recognized as pests of significant economic importance by Rust and Su (2012) were designated as invasive for this study, as the detrimental impacts of alien termites primarily occur in the urban environment. All of the following analyses were conducted in R (R Core Team 2019).

Sources of termites

To identify countries and regions acting as major source of interceptions, we analyzed the total number of non-native termite interceptions originating from each country. Countries were also assigned to one of eight world regions to identify trends among larger land masses—(1) Africa, (2) Asia, (3) Caribbean, (4) Central America, (5) Europe, (6) North America, (7) Oceania or (8) South America. Exact assignments for each country are available in the supplementary material. Trade and distance data were also analyzed in conjunction with the region and country data in order to ascertain the most important factors influencing interception rates. Trade data (i.e., value of imports) was obtained from the World Bank and dated back to 1991 (https://wits.worldbank.org/). Three trade categories were tested for a link with interceptions—(1) overall (i.e., all imports), (2) wood and (3) vegetables (the latter two reflect the goods most commonly associated with the termite interceptions). The monetary value for all three import categories was adjusted for inflation to reflect the value as of 2017, the last date for which data were collected. The geographical distance between a country and the US was measured as the distance between the capital of the country and the capital of the US state to which the country had introduced termites most frequently. When two or more US states were tied as a country's most frequent destination, the state which had intercepted more total termites was chosen. Additionally, a Poisson GLM was created to elucidate the individual and interactive effects of trade and distance on interceptions. As the trade data only went back to 1991, interception and distance data prior to this date were also excluded.

Propagule pressure

Propagule pressure refers to the number of individuals colonizing a new locality and the rate at which this colonizing force arrives to the locality (Lockwood et al. 2005; Simberloff 2009), with increases in propagule pressure found to enhance colonization success in many organisms (Veltman et al. 1996; Petri et al. 2003; Suarez et al. 2005; Woodford et al. 2013). There are currently five alien termites present in the United States—*Coptotermes formosanus, C. gestroi, Cryptotermes brevis, Nasutitermes corniger* (Evans et al. 2013) and a yet unidentified species of *Heterotermes* (Scheffrahn and Su 1995; Szalanski et al. 2004)—all with multiple documented interceptions over the last 90 years. This highlights the role of opportunity (i.e., increased propagule pressure) for a non-native termite in becoming established in a novel country. To identify the influence propagule pressure has on the spread of non-native termites to the US, we first modeled the establishment probability at the species level using a binomial generalized linear model (GLM). We then constructed two Poisson GLMs to identify the relationship between the number of world regions a species inhabits with its number of both overall interceptions and secondary interceptions. All three models were tested for significance against their null equivalents (i.e., y $\sim$ 1) using a Chi squared test.

Bridgehead interceptions

Given that the bridgehead effect appears widespread among invasive species, including invasive ants, a similar investigation is warranted for invasive termites. For all invasive termites intercepted, we calculated the proportion of primary interceptions (interceptions from countries within their native range) and secondary interceptions (interceptions from countries outside their native range). Additionally, interceptions originating from Hawaii were included as foreign introduction events in order to evaluate the potential bridgehead status of the state, as there are no termites native to the islands (Tong et al. 2017). Therefore, each interception originating from Hawaii was considered a secondary interception. Six alien termites are present in Hawaii, including three of the four already established on the US mainland (*C. formosanus*, *C. gestroi* and *Cr. brevis*) (Tong et al. 2017).

Results

We identified 906 non-native termite interceptions originating from outside the US from the last 100 years of USDA records. On an annual basis, the number of non-native termite interceptions increased until reaching a peak in the late 1970s, at which point a steady decline has occurred until the present day (Fig. 1a). Also, in 1984 the USDA began including the month associated with the interceptions, enabling the possible identification of seasonal effects upon interceptions. However, seasonal effects appear negligible for termites, as only 2 months had significantly different means (June–December; $p = 0.0232$; Supplementary Fig. 1).

All interceptions were identified to at least the family level, with 904 and 620 further down to genera and species, respectively. In total, four families, 32 genera and 75 species were represented in the data. *Nasutitermes corniger* (119 interceptions), *Cryptotermes brevis* (61), *N. ephratae* (52), *Coptotermes formosanus* (45) and *Kalotermes flavicollis* (38) were the five most commonly intercepted termites. *Nasutitermes* was the most abundant (384) and rich (11 species) genus intercepted, followed by *Coptotermes* (173) and *Cryptotermes* (70) in abundance and *Neotermes* (seven species) and *Incisitermes* (six species) in richness. At the family level, Termitidae was the most abundant (447) and rich (38 species) family intercepted, due in large part to the high number of *Nasutitermes* spp. interceptions, followed by Rhinotermitidae in abundance (273 interceptions from 14 species) and Kalotermitidae in richness (181 interceptions from 22 species). Stolotermitidae ranked last in both respects (five interceptions represented by one species) (Supplementary Table 1).

Sources and destinations of termites

Of the eight world regions defined in the study, Central America (256), South America (157), the Caribbean (142) and Asia (140) were the greatest contributors of non-native termites to the US (Fig. 1b; Table 1). Interceptions originated from 88 countries across the world (Fig. 2a), arriving at ports of entry in 29 different states and Washington DC (Fig. 2b). By country, the top five exporters of termites to the US were Honduras (71), Costa Rica (49), Mexico (48), Brazil (45) and Panama (43), and the five states intercepting the most termites were Florida (232), New York (104), California (95), Louisiana (82) and Texas (70) (full breakdowns by both origin and destination available in Supplementary Tables 2 & 3, respectively). Additionally, a geographical bias in interceptions appears to be present within the US. In the southern and eastern portions of the US, interceptions primarily originated from the Caribbean, Central America and South America, while interceptions in the west primarily originated from Asia, North America (Mexico) and Oceania (Fig. 3). As the results above allude to, a significant negative relationship was found between the distance from the US to the

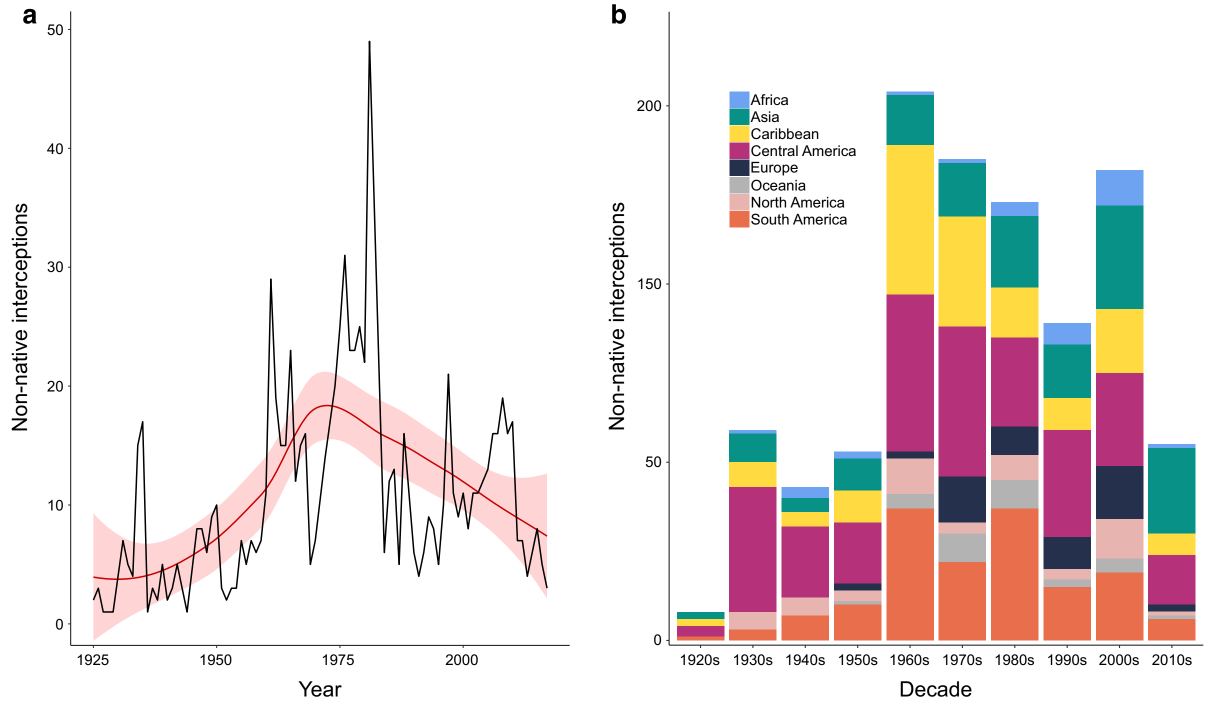


Fig. 1 **a** Time series of non-native termite interceptions from 1925 to 2017 and **b** time series of interceptions for each world region from 1925 to 2017 (interceptions of unknown origin not pictured)

originating country and the overall number of interceptions from that country ($r = -0.36$; $p = 0.0014$; Fig. 4a). Also, a significant positive correlation was found between the overall number of interceptions from a country and the number of unique non-native termite species ($r = 0.86$; $p < 2.2 \times 10^{-16}$; Fig. 4b), suggesting increased diversity from a country is most likely a result of increased interceptions rather than a reflection of the diversity of termite fauna existing within a country.

Trade was both individually and interactively evaluated to elucidate its possible connection with interceptions. First, the three trade categories (overall, wood and vegetable) were plotted against interceptions, and after the removal of any outliers, only vegetable trade remained significant ($r = 0.46$; $p = 3.3 \times 10^{-5}$; Fig. 4c). A GLM was then constructed to test for an interaction effect between trade and distance, and as the two individual trade categories better correlated with interceptions than overall trade (Supplementary Fig. 2), overall trade was excluded from the model. However, distance and vegetable trade remained the only significant factors, with no interactions significant (Supplementary Table 4).

Propagule pressure and bridgehead interceptions

The binomial GLM identified a significant association between the number of times a non-native termite was intercepted and the likelihood of its establishment, with increased interceptions resulting in a higher probability of establishment ($\chi^2 = 16$; $df = 73$; $p = 7.8 \times 10^{-5}$; Fig. 5a). Additionally, the Poisson GLM's revealed that species inhabiting more world regions were more likely to be intercepted at US ports of entry ($\chi^2 = 631$; $df = 73$; $p < 2.2 \times 10^{-16}$; Fig. 5b), and also more likely to be secondarily intercepted ($\chi^2 = 407$; $df = 73$; $p < 2.2 \times 10^{-16}$; Fig. 5c). Overall, these results suggest that greater propagule pressure increases the chance of a successful invasion.

We found 67 interceptions that originated from Hawaii to add to the above interceptions for our bridgehead analysis, with 64 identified down to species—the majority belonging to *Cr. brevis* (36) and *C. formosanus* (21) (Supplementary Table 5).

Table 1 Interceptions of non-native termites broken down by world region and country. For each world region, the three countries contributing the most termites to interceptions are listed, with the two most commonly intercepted non-native termite species also noted. A full breakdown by both world region and destination is available in the supplementary material (Supplementary Tables 2 & 3, respectively)

World Region	Unique species	Interceptions to species/total[a]	Locality (interceptions to species/total interceptions)	Species (interceptions)
Central America	19	172/256 (67.2%)	Honduras (46/71)	*Nasutitermes corniger* (20)
				N. ephratae (12)
			Costa Rica (30/49)	*N. corniger* (10)
				N. ephratae (8)
			Panama (35/43)	*N. corniger* (12)
				N. ephratae (9)
South America	30	107/157 (68.2%)	Brazil (30/45)	*Coptotermes testaceus* (6)
				N. corniger (6)
			Colombia (26/31)	*Heterotermes tenuis* (7)
				N. corniger (4)
			Chile (17/19)	*Neotermes chilensis* (12)
				Porotermes quadricollis (5)
Caribbean	18	124/142 (87.3%)	Bahamas (22/24)	*N. rippertii* (11)
				Cryptotermes brevis (3)
			Jamaica (16/17)	*H. convexinotatus* (5)
				N. corniger & *N. nigriceps* (3)
			Puerto Rico (13/16)	*N. corniger* (7)
				Cr. brevis (3)
Asia	22	72/140 (51.4%)	China (13/27)	*C. formosanus* (8)
				Cr. brevis (2)
			Philippines (11/21)	*N. luzonicus* (3)
				8 others (1)
			Japan (15/18)	*C. formosanus* (8)
				Reticulitermes speratus (5)

[a] Interceptions to species refers to interceptions identified down to the species level, while the total reflects all interceptions originating from a country, including interceptions identified to the species level, or down to only the genus or family levels (see "Results" section)

Evans et al. (2013) reported that 25 termites are both non-native to the US and established outside of their native range across the world, of which 12 were intercepted at US ports of entry. Of these 12, 11 were deemed pests of significant economic importance by Rust and Su (2012) and therefore could be classified as invasive for this study as potentially harmful to their invaded environments. Ideally, we would have compared invasive termites to non-invasive species, but as there was only a single non-invasive species, such a comparison would be inappropriate. Instead, we compared the number of interceptions that were primary versus those that were secondary among the alien species to determine the prevalence of bridgehead invasions across the alien termites. Overall, 48% of the interceptions of alien species were primary and 46% were secondary (Fig. 6a; Supplementary Table 6), with secondary interceptions largely

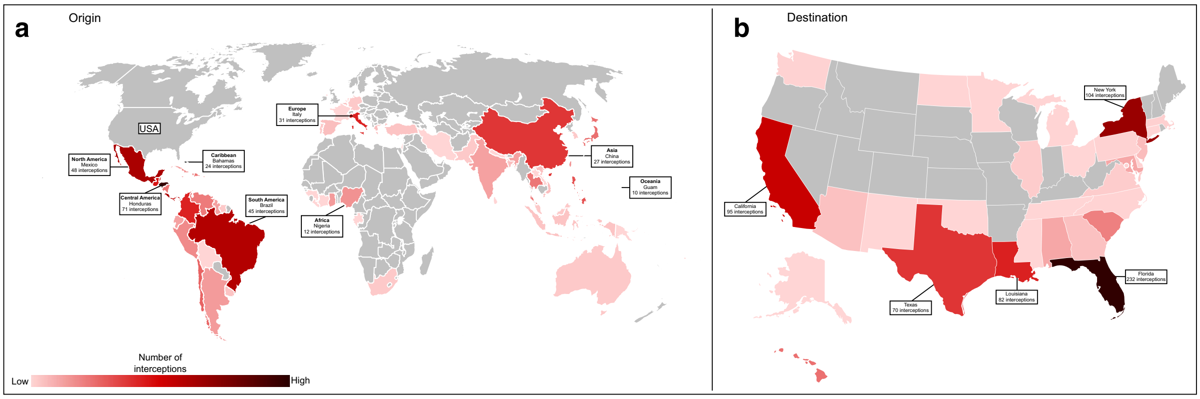


Fig. 2 **a** Origin of non-native termites intercepted at US ports of entry, with the country supplying the most termites in each of the eight world regions highlighted and **b** US interceptions of non-native termites grouped by state, with the five states intercepting the greatest number highlighted

originating from two regions: Hawaii (37%) and the Caribbean (27%) (Fig. 6b). There were also significant differences among these 12 species in their proportion of primary versus secondary interceptions ($\chi^2 = 201$; $df = 11$; $p < 0.001$), indicating certain species more frequently spread through bridgeheads than others. These differences appear linked with the geographical distribution of the alien species, with those inhabiting more world regions more likely to be secondarily intercepted ($\chi^2 = 110$; $df = 10$; $p < 2.2 \times 10^{-16}$; Supplementary Fig. 3).

Discussion

Given their prominent pest status within the urban environment, termites are associated with substantial negative economic consequences. Continued urbanization (Seto et al. 2011) and globalization (Hulme 2009) of the planet threaten to exacerbate these consequences across the world through expansion of their primary pest habitat and increased ability to disperse between these habitats, respectively. Additionally, the cryptic nesting habits of termites create difficulty in both eradication and assessing successful eradication once they become established (Evans et al. 2013; Thorne et al. 2019); in fact, only two known successful eradications of introduced termites have ever occurred (Bain and Jenkin 1983; Mitchell 2002). Furthermore, as re-introduction and re-establishment may be likely without sufficient knowledge of invasion pathways, identifying these pathways and important source locations of invaders are necessary to increase likelihoods of both invasion prevention and early detection (Finnoff et al. 2007; Keller et al. 2007; Reaser et al. 2020). Our results indicate a geographical bias is present in the number of interceptions, as the three closest geographic regions to the US were also the three regions from where non-native termites originated the most. Also, as evidenced in Fig. 2, different regions of the US do not receive the same proportions of non-native termites from the rest of the world, suggesting each state has a unique intake rate based on their individual trading profile. Therefore, shipments from our geographic neighbors require heightened vigilance, and each state (or region) should develop its own risk management plan for potential termite invaders, rather than a one-size-fits-all approach blanketing the entire US.

The 28 alien termite species collectively share three traits: (1) wood-eaters, (2) wood-nesters and (3) readily generate secondary reproductives (Evans et al. 2013). The first two shared characteristics strongly suggest the importance of trade as a dispersal mechanism, given wood is a commonly traded commodity and a heavily utilized packing material (e.g., crating, pallets). Indeed, we found overall trade to be a significantly positive factor in explaining the number of non-native termite interceptions coming from a country; however, this correlation was only slightly positive, perhaps due to regional biases in trading profiles (see above). The third characteristic refers to the eusocial nature of termites, in that a reproductive division of labor exists within colonies so that only

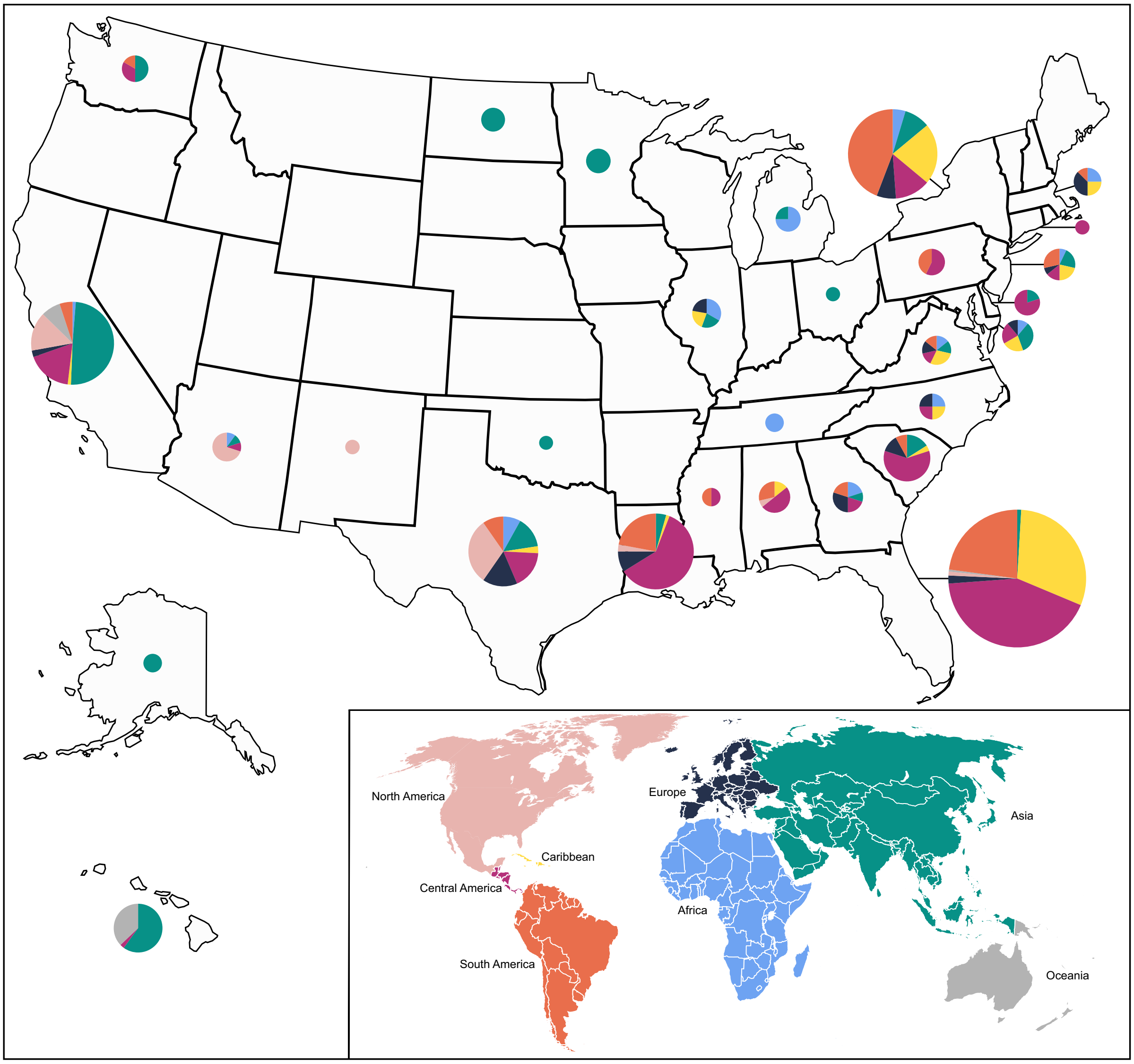


Fig. 3 The proportion of interceptions in each state from the eight world regions defined in the study (shown in the bottom right); the size of each pie chart is proportional to the number of interceptions received

certain members of the colony reproduce (Vargo 2019). Secondary reproductives are members of the colony which develop and become reproductively active within a pre-existing colony. In lower termites (e.g., Kalotermitidae, Rhinotermitidae), secondary reproductives develop from nymphs or workers (Myles 1999), and in rarer cases soldiers (Thorne et al. 2003). In higher termites (e.g., Termitidae), they can develop from nymphs or alates (adultoids) (Noirot 1985). These secondary reproductives are able to supplement the reproductive output of the primary reproductives (i.e., the founding queen and king), or replace their output in the event of their death (Vargo 2019). Taken together, termite species that live and nest in wood, as well as readily generate secondary reproductives have great invasive potential, as any piece of wood serving as a nest or foraging site can potentially be a viable propagule (Lockwood et al. 2005; Simberloff 2009), provided individuals are present who have the potential to develop into secondary reproductives. Worryingly, groups of termites that share these three traits make up the bulk of

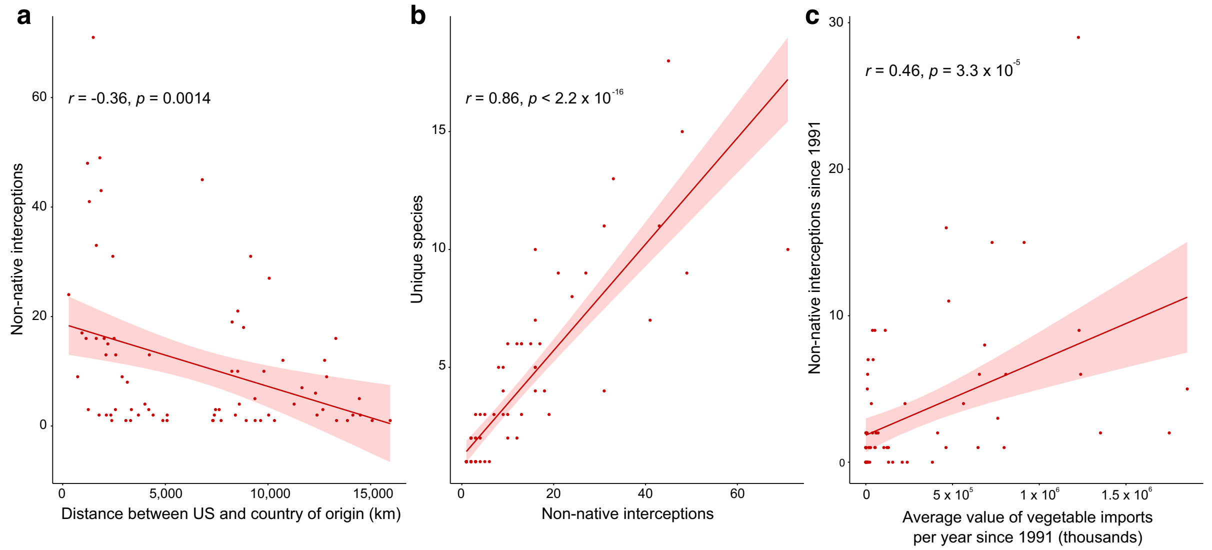


Fig. 4 **a** The negative significant relationship between the distance from the US to the originating country and the overall number of interceptions from that country; **b** positive significant relationship between the number of interceptions from a country with the number of unique termite species it exports; and **c** positive significant relationship between the average value of vegetable imports and the number of interceptions since 1991

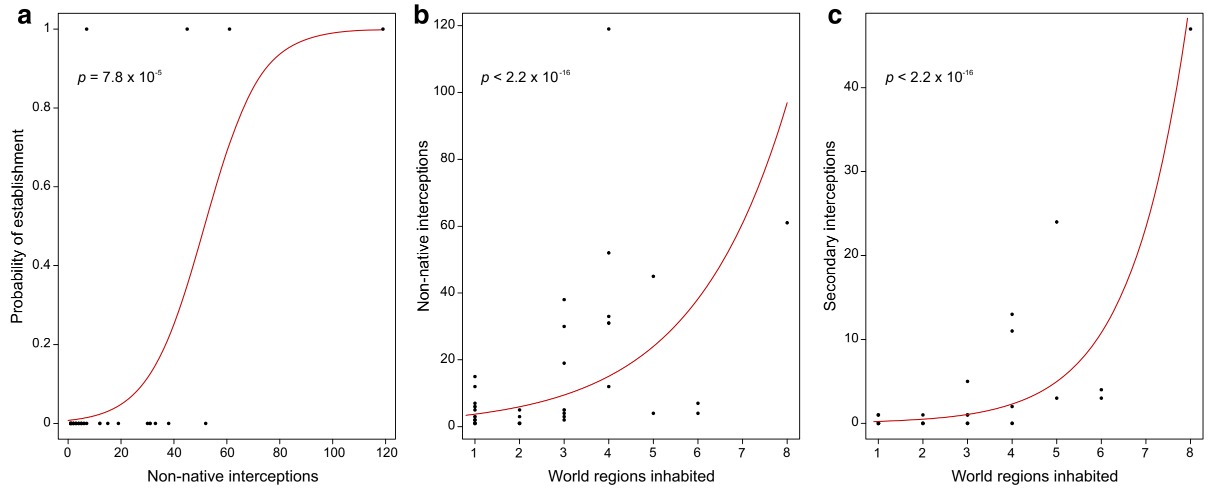
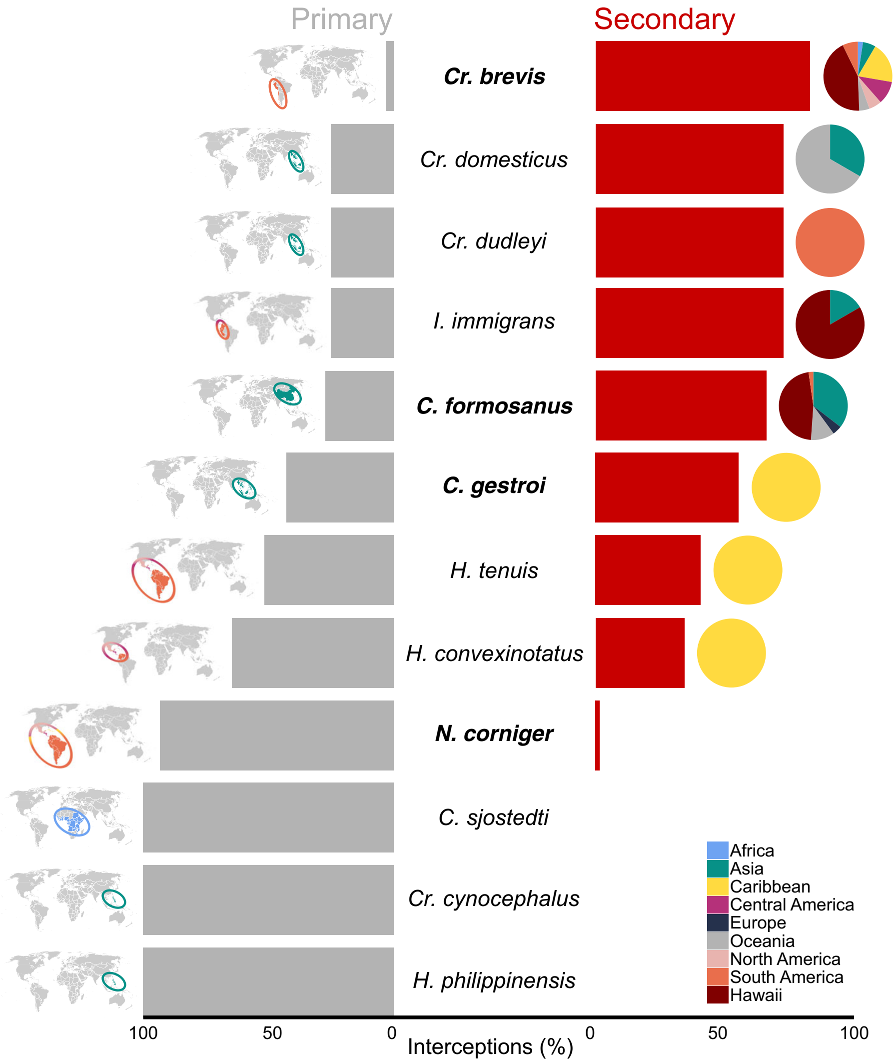


Fig. 5 The relationship between **a** the number of interceptions of a species with its establishment probability, modeled using a binomial GLM; **b** the number of world regions a species inhabits with its interceptions, modeled using a Poisson GLM; and **c** the number of world regions a species inhabits with its secondary interceptions, modeled using a Poisson GLM. For **a**, the black dots at 0 represent species which have not become established within the US, while the black dots at 1 represent species established within the US

the interceptions, including Kalotermitidae, *Coptotermes* spp., *Heterotermes* spp., *Nasutitermes* spp. and *Reticulitermes* spp. (Myles 1999). Given the significant trends for species inhabiting more world regions to be introduced more often leading to increased propagule pressure, more non-native termites threaten to become established within the US in the near future. Termites not yet established within the US that share the three invader traits and had a high number of interceptions include *N. ephratae* (52 interceptions/4 world regions), *K. flavicollis* (38 interceptions/3 world

Fig. 6 The primary and secondary interception percentages of alien termites from this study, with the primary percentage bar to the left of the species name and the secondary percentage bar to the right. The maps to the left of the primary interception bars represent the native world region of each termite, with the countries the termite is native to colored. The pie charts to the right of the secondary interception bars represent the interception makeup of species secondarily intercepted at least 25% of the time. The color code indicates the world region of origin for the secondarily intercepted species. The bolded names represent species already established within the US. The percentage of unknown interceptions (i.e., port of origin unknown) is not pictured, so bars may not add up to 100%



regions) and *N. nigriceps* (33 interceptions/4 world regions).

The recently termed 'bridgehead effect' also appears to be playing a significant role in the dispersal of some invasive termites to the US. For instance, *Cr. brevis* appears to disperse primarily via bridgeheads; it was intercepted from seven of the eight world regions and 96.5% (n = 83) of its known interceptions (i.e., when originating port could be determined) were secondary. *C. formosanus* was also commonly intercepted from bridgeheads, with interceptions originating from four of the eight world regions and 71% (n = 45) of its known interceptions were secondary. However, other species mainly originated from their native countries, chiefly *N. corniger*, with 98.2% (n = 111) of its known interception coming from its native range. To a large extent, this was influenced by its vast native range which encompasses four world regions, stretching from Brazil to southern Mexico and including the Caribbean (Evans et al. 2013). Therefore, bridgeheads could be expected to play a larger role for species with narrower native ranges, as they gain increased access to human transport networks through establishment in other countries (Westphal et al. 2008; Hulme 2009; Banks et al. 2015).

The status of the bridgehead effect as an important feature of future studies on invasion processes and dynamics was recently noted (Ricciardi et al. 2017), and several mechanisms have been suggested as the main driving force behind the effect (Bertelsmeier and

Keller 2018). One popular explanation put forward in many studies (Grapputo et al. 2005; Miller et al. 2005; Lombaert et al. 2010; Zepeda-Paulo et al. 2010; De Kort et al. 2016) suggests that introduced populations acquire traits that confer greater invasiveness, making them more likely than their native counterparts to further disperse throughout the world. However, non-evolutionary mechanisms could also explain the propensity of introduced populations to become sources of future invasions. For one, many species attain far greater densities in their invaded ranges than in their native range (Elton 1958; Torchin et al. 2001; Parker et al. 2013), for several possible reasons [e.g., enemy release, increased resource availability (Catford et al. 2009)]. Increased densities will subsequently lead to increased opportunities for the species to spread again. Two, as the spread of alien species is often linked with human transport and trade networks, introduced populations will likely be located in prime locations to further spread (i.e., transport hubs) (Westphal et al. 2008; Banks et al. 2015). Increased globalization has facilitated an increased connectedness of hubs around the world (Banks et al. 2015), possibly enabling bridgehead populations to piggyback off this network. This explanation seems most likely for termites, since a positive association between trade and interceptions was identified, as well the status of wood as a global trade commodity and packing material. Given the lack of direct empirical evidence for adaptive evolution of introduced populations (i.e., evolution of invasiveness), the most influential mechanism driving the bridgehead effect cannot be precisely known (Bertelsmeier and Keller 2018). Regardless of the mechanism, US port of entry interceptions indicate that as many as eight alien termites may have utilized bridgeheads to successfully invade the US.

Conclusion

Here, we performed a quantitative assessment of US port of entry interceptions for non-native termites, unlocking insights about their global dispersal patterns. With almost 100 years' worth of data, we identified factors which also play crucial roles in the general invasion dynamics of other species, including geographical distance, propagule pressure and bridgeheads. Specifically, interceptions were found to originate more often from world regions closest to a state, increased propagule pressure results in a higher likelihood of becoming intercepted and thereby established, and bridgeheads likely play a role in termite invasions to the US. By shedding light on the influential factors affecting termite spread to the US, this study provides further evidence towards the importance of bridgeheads and increased propagule pressure as significant drivers of global invasion rates in general. Moreover, direct empirical work is recommended in the field of bridgehead biology to determine if true adaptive evolution is the main driving force behind invasions generated from bridgehead populations. As introductions arising from these populations are more probable than introductions originating from native populations (Bertelsmeier and Keller 2018), careful surveillance of bridgeheads is warranted.

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Compliance with ethical standards

Conflict of interest We declare we have no competing interests.

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