Please address correspondence to:
Dr. Rudolf H. Scheffrahn
University of Florida
Fort Lauderdale Research and Education Center
3205 College Avenue, Davie, Florida, U.S.A. 33314
Phone: 954-577-6312, FAX: 954-475-4125
E-mail: rhsc@ufl.edu

Financial contact for invoice: Same

Proliferation of the invasive termite *Coptotermes gestroi* (Isoptera: Rhinotermitidae) on Grand Cayman and overall termite diversity of the Cayman Islands

Rudolf H. **Scheffrahn**[1]*, Hartwig H. **Hochmair**[1], Francesco **Tonini**[2], Jan **Křeček**[1], Nan-Yao **Su**[1], Peter **Fitzgerald**[3], Kieran **Hendricken**[3], James A. **Chase**[4], John **Mangold**[4], and Jeremy **Olynik**[5]

[1] University of Florida, Fort Lauderdale Research and Education Center
Davie, Florida 3314, USA

[2] North Carolina State University, Center for Geospatial Analytics, Raleigh, North Carolina 27695, USA

[3] Pestkil, Grand Cayman KY1-1106, Cayman Islands

[4] Terminix International, Memphis, Tennessee 38120, USA

[5] Cayman Islands Government, Department of Environment, Grand Cayman KY1-1002, Cayman Islands

*Corresponding author; E-mail: rhsc@ufl.edu

Abstract

The Asian subterranean termite, *Coptotermes gestroi*, was discovered on Grand Cayman Island in 2000 and, by 2014, had been recorded from 102 land-based localities. These data were used in a hierarchical cluster analysis to identify homogeneous clusters of sites to estimate separate introduction points on the island. Results suggest four different introductions of *C. gestroi* to Grand Cayman by boat and one by land transport from other previously infested parts of the island. The infestations by boat could either be primary introductions (originating from another island) or secondary introductions (originating from other previously infested parts of Grand Cayman). An individual-based model was used to simulate non-anthropogenic spread of *C. gestroi* over Grand Cayman from 2014 to 2050. The model predicts that by 2050, most of the western part of Grand Cayman will likely be heavily infested by *C. gestroi*, while patches of unsuitable habitat restrict the expansion of the species over the central and eastern parts of the island. In the absence of further human introductions, it will likely take a century for *C. gestroi* to saturate the island by natural dispersal only. Based on detailed termite diversity surveys, we provide updated records for 14 termite species, collectively, on Grand Cayman, Little Cayman, and Cayman Brac.

Key Words: *Coptotermes gestroi*; cluster analysis; individual based spread model; Little Cayman; Cayman Brac

Resumen

[to be added after review].

Palabras Clave: [to be added after review]

The diversity and distribution of termites on the Caribbean mainland and West Indian islands have received renewed attention during the past 20 years (e.g., Scheffrahn and Křeček 1999, Scheffrahn et al. 1994, 2003, 2005, 2006). The great majority of these termite species are non-pestiferous endemics that support ecosystem stability by contributing to cellulose decomposition, soil enrichment, and diet for other animals (Jouquet et al. 2011). Species of the Caribbean genera *Heterotermes* and *Nasutitermes*, however, cause significant damage to wood in service, and *Neotermes* spp. are known to occasionally damage tree crops (Constantino 2002). Two exotic species pose the greatest threat of structural damage in the West Indies (Scheffrahn et al. 2006) and beyond (Constantino 2002). The West Indian drywood termite, *Cryptotermes brevis* (Walker), is a long-established and broadly distributed pest in the New World owing to five centuries of anthropogenic spread from its endemic Chilean/Peruvian origin (Scheffrahn et al. 2009). The Asian subterranean termite, *Coptotermes gestroi* (Wasmann), on the other hand, is a more recent Caribbean invader first reported on Barbados in 1937 (Adamson 1938). Since then, boat infestations (Scheffrahn & Crowe 2011) have facilitated the spread of *C. gestroi* along the coasts of tropical Florida (Hochmair & Scheffrahn 2010) and numerous West Indian islands (Fig. 1).

Grand Cayman Island, along with Cayman Brac and Little Cayman, are British Overseas Territories. Grand Cayman is best known as a tourist destination and banking center with a high standard of living. The island has a commercial seaport in George Town, and in line with its strong local economy and resort destination status, the island is a noteworthy Caribbean yachting center with ample dockage and boat servicing facilities. Several waterfront neighborhoods have their own private marine dockage. As part of a prosperous resort-driven economy, pest control services on Grand Cayman are available for treatment of household and structural pests including termites. Until 2000, no *C. gestroi* populations were known on Grand Cayman (data herein). Therefore, the first land-based infestation on the island provided a unique opportunity to track the establishment and proliferation of *C. gestroi* on a single island.

The Cayman Islands also have a unique natural ecology which invites ongoing studies in biodiversity and conservation (Oldfield & Sheppard 1997). The first records of termites from the Cayman Islands were offered only recently by the late Smithsonian taxonomist, Margaret S. Collins (Scheffrahn et al. 1994) who, on occasion, visited the islands. Dr. Collins' encouragement to investigate the Caymanian termite fauna prompted the first West Indian study of *C. gestroi* on Little Cayman (Su et al. 2000) and the taxonomy of the genus *Cryptotermes* (Scheffrahn & Křeček 1999) and *Procryptotermes* (Scheffrahn & Křeček 2001) occurring on these islands.

In this paper, we analyze 14 years of spatial occurrences of *C. gestroi* on Grand Cayman to estimate marine and overland introduction sites and predict the future distribution range of this pest. We also provide new termite records from field surveys of all three islands.

Materials and Methods

ESTABLISHMENT OF C. *gestroi* ON GRAND CAYMAN

In July 2000, one of us (PF) collected the first sample of *C. gestroi* at Rum Point on Grand Cayman. From then on, PF and KH, working as Pestkil Ltd., a principle Caymanian termite inspection and pest control service provider, amassed *C. gestroi* samples or records from customer inspection calls and termite treatments. Samples were sent to RHS to confirm identification. Although two other pest control companies operate on Grand Cayman, Pestkil has ca. 85% of the termite inspection and control market (PF pers. comm.). The spatial distribution of the *C. gestroi* localities was used to estimate the number of both boat and overland introduction sites. Termite collection dates, however, could not be used to determine colonization dates because termite discovery dates may lag actual colonization by several years. Grand Cayman Island is divided into five districts. The 1999 annual average household income ranged between $58,635 Cayman Is. dollars (Bodden Town in central south) and CID $47,673 (at East End), indicating a lower income toward the east. This discrepancy could cause some sampling bias since residents in the east may be less likely to call a pest control company than those in other parts of the island. However, it must be noted that in the wealthier district (Bodden Town), not a single termite incident was reported, and that the remaining districts have more comparable average annual household incomes, ranging between CI$ 47,673 and CI$ 54,430.

To determine the likelihood of boat versus overland introduction modes for *C. gestroi*, we followed the procedure of Hochmair & Scheffrahn (2010) which assessed the spatial association of marine dockage with land-borne infestations of *Coptotermes* spp. in southeastern Florida. We applied hierarchical cluster analysis to identify homogeneous clusters of Grand Cayman termite localities based on their easting and northing coordinates, and then assessed whether these clusters were located near marine dockage. If so, these clusters could indicate separate points of introduction by boat. Clusters can indicate both primary and secondary introductions. A primary introduction describes an infestation from other islands or the mainland and subsequent establishment of a base population. A secondary introduction is established by local dispersal flights of termites from a base population. For an island, the suspected source of a primary introduction is boat traffic, whereas a secondary introductions can be established by boat (most likely if an infestation occurs close to dockage), or by land transport (most likely if an infestation is distant from nearest dockage). Different clusters near boat dockage can either stem from different primary introductions to the island, or be the result of fewer primary introductions (possibly even one) and subsequent distribution by local boat traffic (Scheffrahn 2013). The question of primary, secondary or multiple same-site introductions can be determined through genetic analysis of termite samples. This was not possible in this study because samples were not available from all the observed locations where locality data were reported.

Hierarchical cluster analysis starts with each termite collection point as a separate cluster, and then combines clusters sequentially, reducing the number of clusters with each step, until only one cluster is left. The method applies measures of dissimilarities between cases (i.e. points) when forming the clusters. In our approach, dissimilarity was expressed as the squared Euclidean distance between observed points to give greater weight on points that are further apart compared to the simple Euclidean distance. One can choose from a variety of hierarchical clustering analysis methods. Each of them includes rules that govern between which points distances are measured to determine cluster membership. Five cluster analysis methods were tested, i.e., Ward’s method, Average Linkage between groups, Average Linkage within groups, Centroid Linkage, and Single Linkage.

Although infestation points can be grouped into clusters, not every cluster might originate from a boat infestation. In order to determine the potential association of each cluster with a boat dockage, we first identified dockage locations on Grand Cayman that allow inter-island boat traffic. To do so the island outline polygon was overlaid with 100 m grid cells. Using the background satellite imagery provided in ESRI’s ArcGIS 10.3, cells which contained a boat dockage suitable for boats of 10 m length or more (boats large enough to reach out-island destinations) were visually identified and marked (shown as blue squares in Figs. 2 and 3). Furthermore, a set of 102 points were randomly placed in built areas suitable for termite habitat (Fig. 3), which is where termites are typically collected by pest control companies, as opposed to undeveloped areas where no damage is caused by termite infestation.

The generation of the suitability layer based on several source files is described in more detail in the spread model section below. For the generation of the random point layer, which reflects typical termite collection locations of pest treatment companies under assumed randomness, buildings were identified from the ArcGIS imagery background layer, followed by clipping suitable habitat areas to the vicinity of identified buildings. Next, distances were measured between termite localities in all clusters and the nearest marine docks (using the Spatial Join function in ArcGIS), and compared to distances obtained between random points (located in developed areas) and nearest dockages. Before this, dockage grid cells were substituted by their cell center points, which the distances were measured to. Statistical comparison of distances to dockages between the different termite location clusters and the random point set was then used to assess which cluster could originate from infestation by inter-island boat traffic, and which from infestation by land transport or local boat traffic. In addition a Monte Carlo simulation was run that repeatedly generated sets of 102 random points and computed the mean nearest neighbor (nn) distances for each of the generated point patterns. This distribution of mean nn distances was then compared to the mean nn distance obtained for observed termite sites. This was done to determine whether observed collection sites are spatially clustered differently than potential termite collection sites (i.e. built areas within suitable habitats), illustrating the effect of boat dockage on the spatial distribution of identified termite locations.

SPREAD MODEL FOR C. gestroi ON GRAND CAYMAN

In order to account for the local landscape within the simulation model and identify areas unsuitable for the establishment of colonies of *C. gestroi*, a combination of the following vector-type spatial layers was created using ArcMap. A 2006 land cover classification, developed by the Department of Environment was obtained. The classification was broken down into four classes: dry forest, dry shrub land, wetlands, and man-modified. The latter type includes land that has been modified in any way at any time in the past. It includes pasture, agricultural land, secondary forest, built up areas, and road allowances. The wetland class is comprised of various wetland types, such as permanently flooded grasslands, tidally flooded mangrove shrub land/forest, seasonally flooded mangrove shrub land/forest, and seasonally flooded forest. For the purpose of this study, we considered all non-forested wetland areas as unsuitable for the establishment of *C. gestroi* colonies, regardless of the aforementioned subdivision. Dry shrub land was also considered unsuitable for *C. gestroi* which nests in larger trees and building voids (Kirton & Brown 2003). We used OpenStreetMap street data (http://www.openstreetmap.org/) for the street network layer, integrated with some manual additions to include segments that were missing, and created a 10-m buffer around each line segment to model the approximate coverage of roads. Furthermore, we manually digitized bare land areas and airport grounds to combine them with the other unsuitable layers. Fig. 4 shows all the individual vector-type layers combined to obtain a single unsuitable habitat polygon layer to use in the simulation model.

The individual-based model by Tonini et al. (2013) was used in order to simulate the spread of *C. gestroi* over Grand Cayman from 2014 to 2050. The values used in the model for the main ecological parameters (Tonini et al. 2013) are shown in Table 1. Because of the stochastic nature of the model used, 100 replications were run in order to account for the uncertainty associated with the outcome of a stochastic simulation. A spatial grid with resolution of 100 x 100 m was created to be overlaid at the end of the simulation with all other replications for a given year. The set of *C. gestroi* localities were grouped in each grid cell according to the chosen value for the DEN (Maximum density of colonies per hectare) parameter, and the centers of the cells infested by at least one colony were used as a starting point for the simulation.

TERMITE DIVERSITY STUDIES ON THE CAYMAN ISLANDS

In 1996, JK surveyed termites on Grand Cayman (83 colony samples) and Little Cayman Islands (73 samples) followed by a further survey of Grand Cayman in 1999 by JC and JM (223 samples), and a survey of Cayman Brac in 1999 by JC, JM, and RHS (200 samples). A few additional samples, including *Cr. brevis*, were collected on Grand Cayman by RHS in 2013. Termites were collected along roadsides and trails in as many geographically and ecologically diverse habitats as time and accessibility permitted. Termites were collected from all possible microhabitats from which colonies with brood or foragers were accessible including sound dry or decomposing wood, arboreal and epigeal nests (*Nasutitermes* and *Microcerotermes*, respectively), and in soil underneath stones and logs. Each locality (Fig. 5) is defined as map-deduced latitude/longitude position from which we searched for termites on foot, typically only a hundred meters in any direction. Specimens were aspirated and immediately transferred to vials containing 85% ethanol. Upon completion of expeditions, samples were cleaned, identified, labeled, and deposited in the University of Florida Termite Collection, Davie, Florida.

Results and Discussion

ESTABLISHMENT OF C. *gestroi* ON GRAND CAYMAN

Between 2000 and July 2014, Pestkil recorded 102 ground-based *C. gestroi* infestations on Grand Cayman. In July 2012, a single water-based *C. gestroi* colony was discovered on a yacht docked at a waterfront house in the Governor's Harbor neighborhood. The Single Linkage, Average Linkage between groups, and Centroid clustering methods identified the isolated termite sighting at Rum Point (located at the center north of the island, Fig. 2) as its own cluster using the smallest number of total clusters in the solution (three), whereas the two other methods (Ward's method and Average Linkage within groups) require a larger cluster number to classify this point as a separate cluster. Retaining the location at Rum Point as a separate cluster of introduction due to its far distance to the remaining termite collection points seemed to be a desirable solution. Hence the first three clustering methods would be viable options. Point assignments to clusters are identical between these three methods for the two, three, and five-cluster solutions, but slightly different for the four-cluster solution. For the illustration of the steps of the clustering process and further exploratory analysis the results of the Single Linkage method are used.

Starting with the set of 102 observed points the hierarchical cluster process undergoes 101 cluster fusion stages. The last 8 fusion steps in the agglomeration schedule with their characteristics are listed in Table 2. The dissimilarity measure describes the squared Euclidean distance between points or centers of clusters being joined in a fusion step. A sudden increase in the dissimilarity value suggests natural cutting points to determine the best number of clusters before two very dissimilar clusters are combined. Table 3 shows that, based on this criterion, the two-cluster solution is best due to the sudden increase in dissimilarity in the last stage. This can also be observed in Figure 6 where a natural break at the two-cluster solution is clearly discernible.

Figure 2a shows the two spatial regions resulting from the two-cluster solution. It separates termite collection points in the western half of the island from those in the east. Large boat dockages are only present in the western half of the island. Considering the large gaps between observed termite points in the western half of the island and the availability of boat dockage in various portions of that cluster makes it, however, unlikely that the termite infestation started from only one single point within this cluster and then dispersed from there. If that was the case, one could expect a more even coverage of infestation points in the affected areas without the large observed gaps in-between (Tonini et al. 2013).

A more realistic scenario provides the four-cluster solution, which reflects another natural cutting point shown in Figure 6. In this four-cluster solution, the different point clusters follow generally the clustered pattern of marine dockage locations (Fig. 2c) at least for the western half of the island. Therefore, this solution gives three point clusters near boat dockages, one of which is the isolated spot at Rum Point. It suggests three separate points of infestation through boat traffic and the subsequent spread of termites to the other points of each cluster. The five cluster solution (Fig. 2d) splits the cluster along the Seven Mile Beach to the west into two clusters. Each of these two new clusters (the larger one to the north and the smaller one to the south) has nearby marine docks, which makes separate introductions in those two clusters plausible. The five cluster solution would therefore suggest four different introductions of *C. gestroi* to the island by boat, with at least one of them being a primary introduction.

One isolated cluster of termite sites, located to the south-east of the island, visually stands out since it is far from marine dockages on the island. Due to a lack of dockage in the south-east of the island this introduction occurred most likely overland, e.g. by transportation of infested timber, originating from an established population on the western half of the island. There is, however, the possibility that infestations even in this cluster stem from introduction by boat, e.g. when an infested boat anchored in close proximity to land and termite alates were flying out that day towards land. Given that termites are weak flyers which avoid dispersal flights in windy conditions (which are often found on the open sea), this scenario is very unlikely. The termite discovery dates of this isolated cluster (years 2011 and 2014) are later than termite discovery dates of clusters in the western part of the island, which are, when using the four-cluster solution from Figure 2c, 2001-2014 (cluster 1), 2003-2014 (cluster 2), and 2001 (cluster 4). This suggests that the south-eastern cluster was established (probably by land transport) after the other clusters, and thus originating from one of the other termite populations on the island. The clusters in the western portion of the island, due to their close proximity to marine dockages, can be assumed to originate from boat traffic between Grand Cayman Island and other Caribbean islands (primary introduction), or from already infested areas on Grand Cayman Island (secondary introduction). To verify the potential of infestation of the three westernmost clusters by inter-island boat traffic statistically, distances between termite sightings in all clusters and the nearest marine dock were measured. The point pattern from the four cluster solution was used for this task (Fig. 2c) instead of the five cluster solution to retain larger cluster sizes for statistical testing. Together with a set of 102 random points placed around built areas this resulted in five sets of distances to the nearest marine dockage, i.e., one for each of the four clusters, and one for the random point set (Fig. 3).

Figure 7 visualizes how the distances to the nearest marine dockage are distributed for the previously described point sets. The horizontal line in the middle of each box indicates the median of distances for clusters 1 through 4 and the random point set, respectively. Visual inspection suggest shortest distances to marine dockage for clusters 1 (South Bay), 2 (Seven Mile Beach), and 3 (Rum Point), and largest distances for cluster 4 (South-east of island). Distances for the random point set are mostly found in-between. Descriptive statistics for distances associated with the five point sets are provided in Table 3. Sizes of the four cluster point sets vary between 90 (cluster 2), and 1 (single observation at Rum Point in cluster 3). Since sample sizes are small, a nonparametric test was used to check for significant differences between distances to the nearest marine dockage. Results show that the distances to nearest docks associated with clusters 1 and 2 are significantly shorter than the distance for the random point set (Mann-Whitney, n_1=5, n_R=102, Z=-2.568, p=<0.02, 2-tailed; and Mann-Whitney, n_2=90, n_R=102, Z=-5.934, p=<0.0001, 2-tailed). For cluster 3, which consists of only one point with a distance to the nearest marine dockage of 151 m, the difference to the median distance for the random point set is not significant at a 5% level of significance (Mann-Whitney, n_3=1, n_R=102, Z=-1.614, p=0.078), which is due to the low power of the test given the small sample size. The fact that the observed distances for these three clusters are shorter than distances for random points gives statistical evidence that infestations in these clusters are associated with (intra- or inter-island) boat traffic. Further, results show that the median distance to the nearest marine dock associated with cluster 4 is significantly larger than the distances for the random points (Mann-Whitney, n_4=6, n_R=102, Z=-3.943, p=<0.0001), suggesting that these termite infestations were not introduced by inter-island boat traffic but by either local boat traffic originating from another locality on Grand Cayman island, or more likely, by land transport, given the newly constructed condominiums in that cluster region.

One might argue that observed clusters are not solely based on boat and overland introduction sites but caused by the patchiness of potential collection areas, i.e. built areas. To analyze whether the pattern of observed infestation points differs from built areas we first computed the mean nn distance for the 102 observed termite locations, which was 250.0m. This was followed by a Monte Carlo procedure with 100 realizations of generating 102 points that were randomly placed inside the built area polygons, followed by a mean nn computation for each generated point pattern. This resulted in the distribution of mean nn distances under the null hypothesis of termite locations being randomly distributed within built areas. Figure 8 plots the distribution of mean nn distances based on the Monte Carlo simulation (M=561.7m, SD=54.83m) and the mean nn distance of the observed termite distribution pattern (250.0m). The result indicates significant clustering of termite locations when controlling for patchiness of built areas ($p<0.01$), and therefore a different cluster pattern between observation sites and built areas.

SPREAD MODEL FOR C. gestroi ON GRAND CAYMAN

The outcomes of all model replications are grouped and visualized by three color-coded occupancy envelopes as described in Tonini et al. (2013). The “>0%” (yellow) occupancy envelope shows all areas predicted to be infested in one or more model replications. The “>=50%” (orange) occupancy shows all areas predicted to be infested by at least half of all simulation runs. Finally, the "100%" (red) occupancy envelope shows areas that are predicted as infested by all model replications. Figure 9 shows the results of the simulation in 2050.

A visual inspection of the results suggests that the termite spread will proceed fairly slowly over the suitable areas in the island if no additional anthropogenic transport occurs. By 2050, most of the western part of Grand Cayman will likely be infested by *C. gestroi*, while patches of unsuitable habitat restrict the expansion of the species over the central and eastern parts. In the absence of human movement, it will likely take a century for *C. gestroi* to saturate the island by natural means.

TERMITE DIVERSITY STUDIES ON THE CAYMAN ISLANDS

A total of 14 termite species are now collectively known from the Cayman Islands (Table 4). As a result of our surveys, three new species of drywood termites were added to the Caymanian fauna, *Cryptotermes nitens* (Scheffrahn & Křeček 1999), *Cr. spathifrons* (Scheffrahn & Křeček 1999), and *Procryptotermes edwardsi* (Scheffrahn & Křeček 2001). We now also report 15 new island records and revise their nomenclature (Table 4). Nomenclatural changes since Scheffrahn et al. (1994) are from the following subsequent synonymies: *Nasutitermes costalis* = *Na. corniger* (Scheffrahn et al. 2006) and *C. havilandi* = *C. gestroi* (Kirton and Brown 2003), *Inicisitermes tabogae* = *I. schwarzi* (James et al., 2013), and *Termes melindae* = *T. hispaniolae* (unpublished data, Scheffrahn). *Incisitermes milleri* was listed as *I. sp.* while *P. edwardsi* was incorrectly recorded as *P. corniceps* in Scheffrahn et al. (1994).

The Cayman Islands termite fauna has a close affinity with Cuba and Central America but with some exceptions. The endemic drywood species, *Cr. nitens* is known only from the

Cayman Islands and Jamaica (Scheffrahn & Křeček, 1999). An undescribed species of *Heterotermes* on Grand Cayman has a disjunctive range of populations in Jamaica, Grand Turk, Bonaire, and Florida suggesting it is been recently introduced to some of these localities (Szalanski et al. 2004). *Nasutitermes nigriceps* occurs also in Jamaica and Central America, but is replaced on Cuba by *Na. rippertii*. As on most small West Indian islands, no soil-feeding species occur on the Caymans Islands.

The occurrence of *Microcerotermes* c.f. *arboreus* is the most interesting biogeographical anomaly of the Cayman island termite fauna. Although *Microcerotermes* spp. are widespread throughout the Caribbean mainland, the Caymanian records for this genus are unique among all other West Indian islands with the exception of the continental islands of Trinidad and Tobago (Figure 10). This genus is in dire need of revision and we cannot be certain that the species from the Caymans is conspecific with the *M. arboreus* as described by Emerson (1925).

Acknowledgments

Many thanks to Tiago Carrijo for reviewing this paper and to Terminix International for partial support of travel expenses.

References Cited

Adamson AM. 1938. Notes on termites destructive to buildings in the Lesser Antilles. Tropical Agriculture (Trinidad) 15: 220–224.

Constantino R. 2002. The pest termites of South America: taxonomy, distribution and status. Journal of Applied Entomology 126: 355-365.

Emerson AE. 1925. The termites of Kartabo, Bartica District, British Guiana. Zoologica 6: 291-459.

James ER, Burki F, Harper JT, Scheffrahn RH, Keeling PJ. 2013. Molecular characterization of parabasalian symbionts *Coronympha clevelandii* and *Trichonympha subquasilla* from the Hawaiian lowland tree termite *Incisitermes immigrans*. Journal of Eukaryotic Microbiology 60: 313-316.

Jouquet P, Traoré S, Choosai C, Hartmann C, Bignell DE. 2011. Influence of termites on ecosystem functioning. Ecosystem services provided by termites. European Journal of Soil Biology 47: 215-222.

Hochmair HH, Scheffrahn RH. 2010. Spatial association of marine dockage with land-borne infestations of invasive termites (Isoptera: Rhinotermitidae: *Coptotermes*) in urban South Florida. Journal of Economic Entomology 103: 1338-1346.

Kirton LG, Brown VK. 2003. The taxonomic status of pest species of Coptotermes in Southeast Asia: Resolving the paradox in the pest status of the termites, *Coptotermes gestroi*, *C. havilandi* and *C. travians* (Isoptera: Rhinotermitidae). Sociobiology 42: 43-63.

Oldfield S, Sheppard C. 1997. Conservation of biodiversity and research needs in the UK Dependent Territories. Journal of Applied Ecology 34: 1111-1121.

Scheffrahn RH. 2013. Overview and current status of non-native termites (Isoptera) in Florida. Florida Entomologist 96: 781-788.

Scheffrahn RH, Crowe W. 2011. Ship-borne termite (Isoptera) border interceptions in Australia and onboard infestations in Florida, 1986-2009. Florida Entomologist, 94: 57-63.

Scheffrahn RH, Darlington JPEC, Collins MS, Křeček J, Su N-Y. 1994. Termites (Isoptera: Kalotermitidae, Rhinotermitidae, Termitidae) of the West Indies. Sociobiology 24: 213-238.

Scheffrahn RH, Křeček J. 1999. Termites of the genus *Cryptotermes* Banks (Isoptera: Kalotermitidae) from the West Indies. Insecta Mundi 13: 111-171.

Scheffrahn RH, Křeček J. 2001. New World revision of the termite genus *Procryptotermes* (Isoptera: Kalotermitidae). Annals of the Entomological Society of America 94: 530-539.

Scheffrahn RH, Jones SC, Křeček J, Chase JA, Mangold JR, Su N-Y. 2003. Taxonomy, distribution, and notes on the termites (Isoptera: Kalotermitidae, Rhinotermitidae, Termitidae) of Puerto Rico and the US Virgin Islands. Annals of the Entomological Society of America 96: 181-201.

Scheffrahn RH, Křeček J, Ripa R, Luppichini P. 2009. Endemic origin and vast anthropogenic dispersal of the West Indian drywood termite. Biological Invasions 11: 787-799.

Scheffrahn RH, Křeček J, Szalanski AL, Austin, JW. 2005. Synonymy of neotropical arboreal termites *Nasutitermes corniger* and *N. costalis* (Isoptera: Termitidae: Nasutitermitinae), with evidence from morphology, genetics, and biogeography. Annals of the Entomological Society of America 98: 273-281.

Scheffrahn RH, Křeček J, Chase JA, Maharajh B, Mangold JR. 2006. Taxonomy, biogeography, and notes on termites (Isoptera: Kalotermitidae, Rhinotermitidae, Termitidae) of the Bahamas and Turks and Caicos Islands. Annals of the Entomological Society of America 99: 463-486.

Scheffrahn RH, Křeček J, Maharajh B, Chase JA, Mangold JR, Moreno J, Herrera, B. 2005. Survey of the termites (Isoptera: Kalotermitidae, Rhinotermitidae, Termitidae) of Nicaragua. Florida Entomologist 88: 549-552.

Su N-Y, Ban PM, Scheffrahn RH. 2000. Control of *Coptotermes havilandi* (Isoptera: Rhinotermitidae) with hexaflumuron baits and a sensor incorporated into a monitoring and baiting program. Journal of Economic Entomology 93: 415-421.

Szalanski AL, Scheffrahn RH, Austin JW, Křeček J, Su N-Y. 2004. Molecular phylogeny and biogeography of *Heterotermes* (Isoptera: Rhinotermitidae) in the West Indies. Annals of the Entomological Society of America 97: 556-566.

Tonini F, Hochmair HH, Scheffrahn RH, Deangelis DL. 2013. Simulating the spread of an invasive termite in an urban environment using a stochastic individual-based model. Environmental Entomology 42: 412-423.

Table 1. Definition of all parameters used for the spread simulation model of *C. gestroi* over Grand Cayman island and their values.

Parameter	Definition	Values
AFP	Colony age at first production of alates	4 yr
PHR	Maximum pheromone attraction distance	3 m
DEN	Maximum density of colonies per hectare	1
SURV	Overall survival rate of alates*	0.01 (1%)*
MAR	Prevalence of male alates in the colony	0.5 (50%)
SCR	Scenario of amount of alates generated by a colony	1,000 for colony age $4 \leq$ yr < 9 10,000 for colony age $9 \leq$ yr < 14 100,000 for colony age ≥ 14 yr
DIST	Mean dispersal flight distance	200 m

* Overall percentage of alates surviving all phases of a dispersal flight

Table 2. Agglomeration schedule for the last 8 stages of hierarchical clustering for *C. gestroi* over Grand Cayman island using the Single Linkage method.

Stage	**Clusters**	**Dissimilarity**
94	8	1.142
95	7	1.482
96	6	1.896
97	5	2.088
98	4	2.949
99	3	17.083
100	2	67.783
101	1	364.919

Table 3. Descriptive statistics of shortest distance sets to nearest marine docks (in meters) for locations of *C. gestroi* over Grand Cayman island and random points.

	Cluster 1	Cluster 2	Cluster 3	Cluster 4	Random
n	5	90	1	6	102
Mean	528	1048	151	18729	3228
Std-dev	527	1030	-	301	4023
Median	302	627	151	18733	2210

Table 4. Localities for termites from the Cayman Islands and surrounding areas.

	Cr. brevis	*Cr. cavifrons*	*Cr. nitens*	*Cr. spathifrons*	*I. milleri*[a]	*I. schwarzi*[b]	*Ne. castaneus*	*P. edwardsi*[c]	*C. gestroi*[d]	*H.* n.sp.	*M.* c.f. *arboreus*	*Na. corniger*[e]	*Na. nigriceps*	*T. hispaniolae*[f]
Cayman Brac	X	X	X[g]		X[g]	X	X[g]	X[g]	X[g]		X			X[g]
Grand Cayman	X	X	X[g]		X[g]	X	X		X[g]	X	X	X	X	X
Little Cayman	X[h]	X	X[g]	X[g]	X[g]	X	X[g]	X[g]	X		X			X[g]
Cuba	X	X		X	X	X	X	X	X			X		X
Jamaica	X	X	X		X	X	X	X	X	X		X	X	X
Mainland Caribbean	X	X			X	X	X		X		X	X	X	X
Florida	X	X			X	X	X		X			X		

[a-f] Corrected species designations from Scheffrahn et al. (1994)

[g] Island species records from this study

[h] Not recorded but presence highly likely

FIGURE CAPTIONS

Fig. 1. *Coptotermes gestroi* localities in the greater Caribbean Basin (Source: UF Termite Collection).

Fig. 2. Hierarchical cluster analysis with two (a), three (b), four (c), and five (d) clusters for *C. gestroi* over Grand Cayman Island.

Fig. 3. Collection localities for *C. gestroi* over Grand Cayman Island and 102 random points.

Fig. 4. Vector-type layers used to obtain a surface of unsuitable habitat for *C. gestroi* on Grand Cayman Island.

Fig. 5. Termite sampling localities from UF termite collection (For purposes of space, the geographic positions of Little Cayman and Cayman Brac not related to that of Grand Cayman).

Fig. 6. Plot for the Single Linkage Clustering method for *C. gestroi* over Grand Cayman Island.

Fig. 7. Plot for the Single Linkage Clustering method for distances to the nearest marine dockage *C. gestroi* over Grand Cayman Island.

Fig. 8. Distribution of mean nearest neighbor distance obtained from Monte-Carlo simulation with 102 randomized points placed in built areas within suitable habitats.

Fig. 9. Areas predicted as infested by the simulation model for *C. gestroi* over Grand Cayman Island. Sampled termite locations in 2014 are mapped (points). Yellow, orange, and red cells indicate the > 0%, ≥ 50%, and 100% occupancy envelopes, respectively.

Fig. 10. Caribbean basin survey localities for all termites (blue dots) and for *Microcerotermes* spp. only (orange dots) (Source: UF Termite Collection).

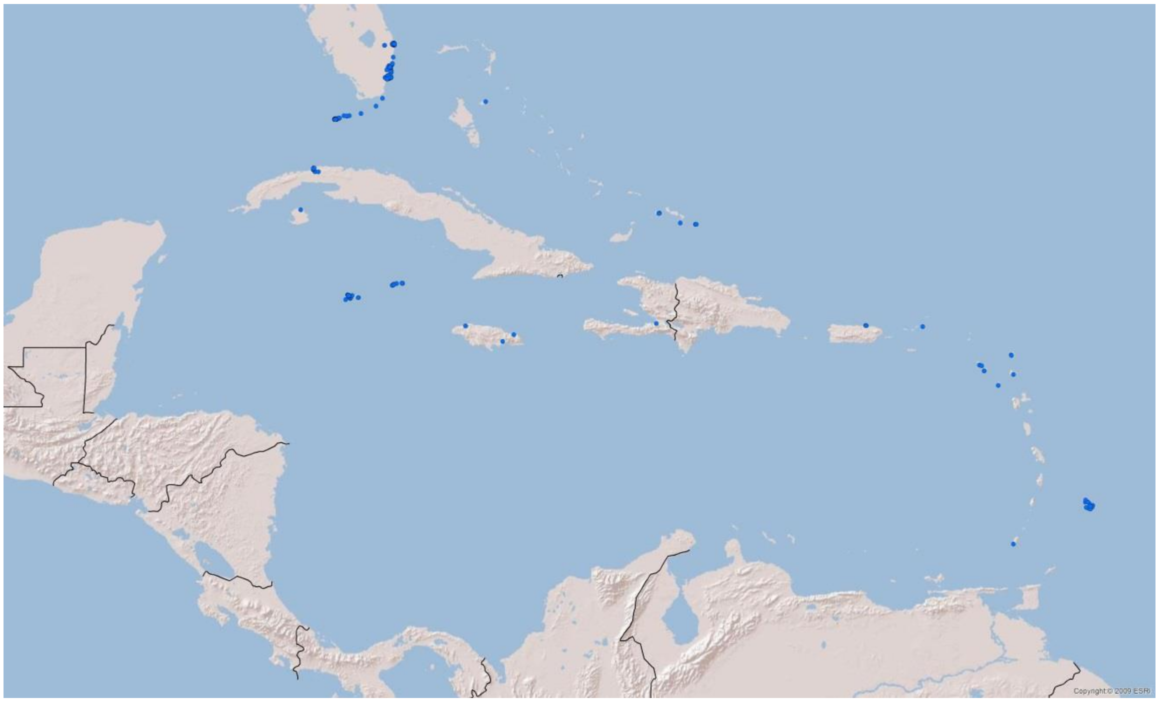

Fig. 1. *Coptotermes gestroi* localities in the greater Caribbean Basin (Source: UF Termite Collection).

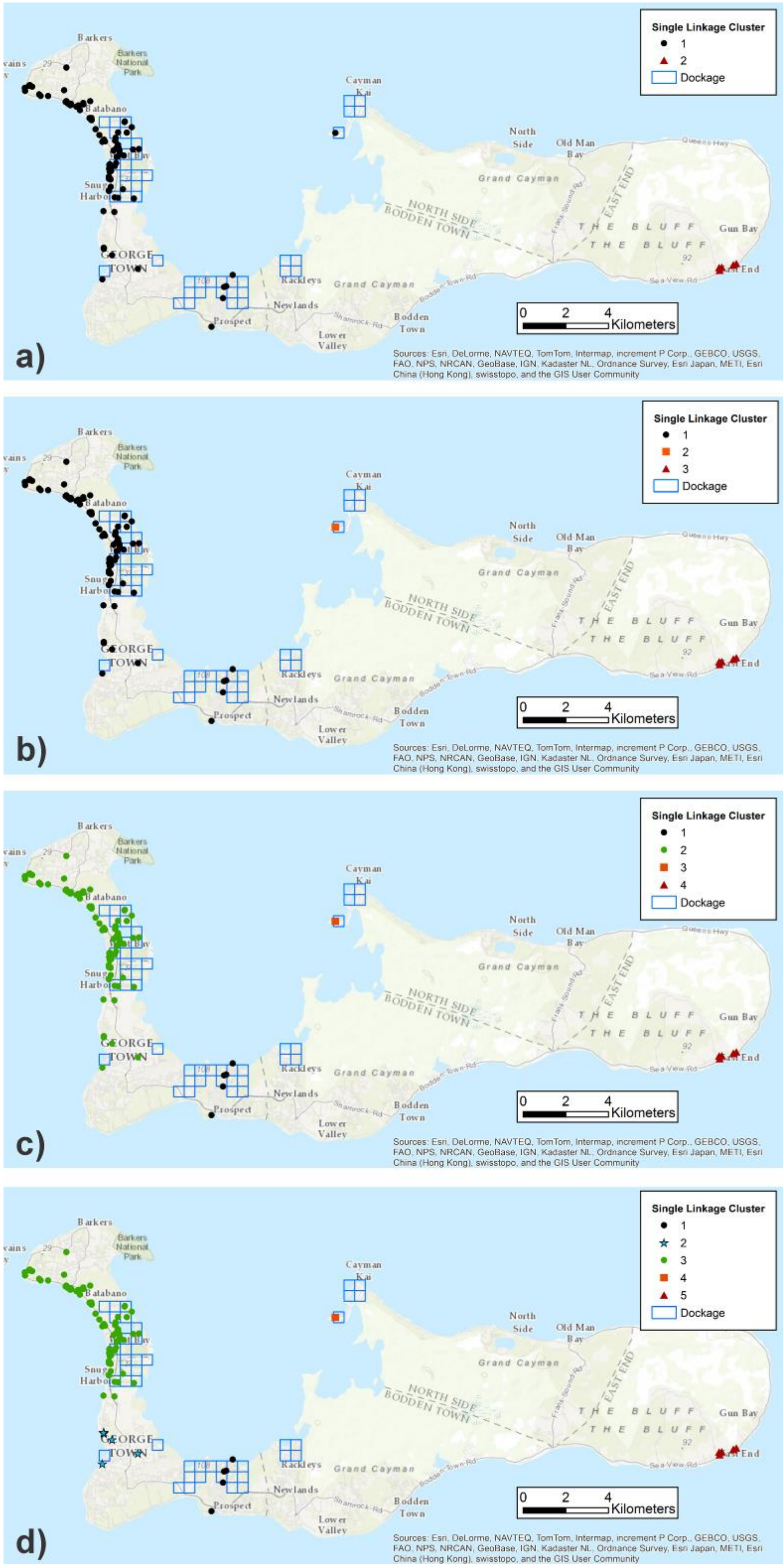

Fig. 2. Hierarchical cluster analysis with two (a), three (b), four (c), and five (d) clusters for *C. gestroi* over Grand Cayman Island.

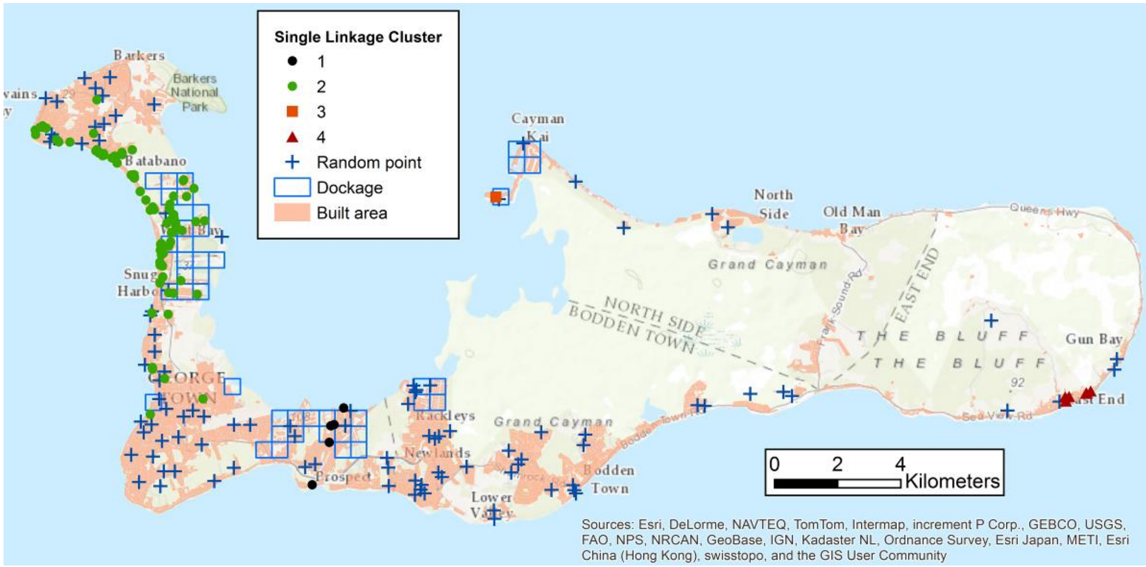

Fig. 3. Collection localities for *C. gestroi* over Grand Cayman Island and 102 random points.

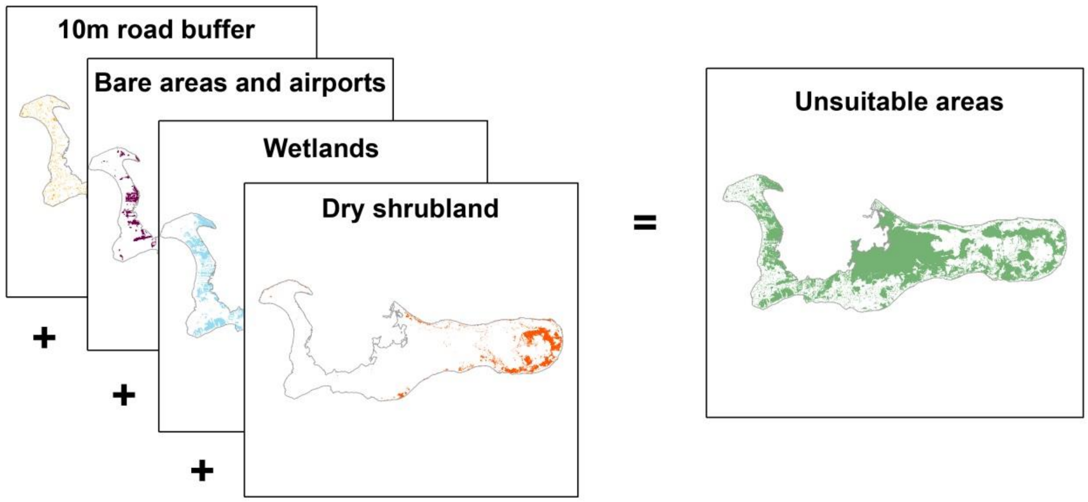

Fig. 4. Vector-type layers used to obtain a surface of unsuitable habitat for *C. gestroi* on Grand Cayman Island.

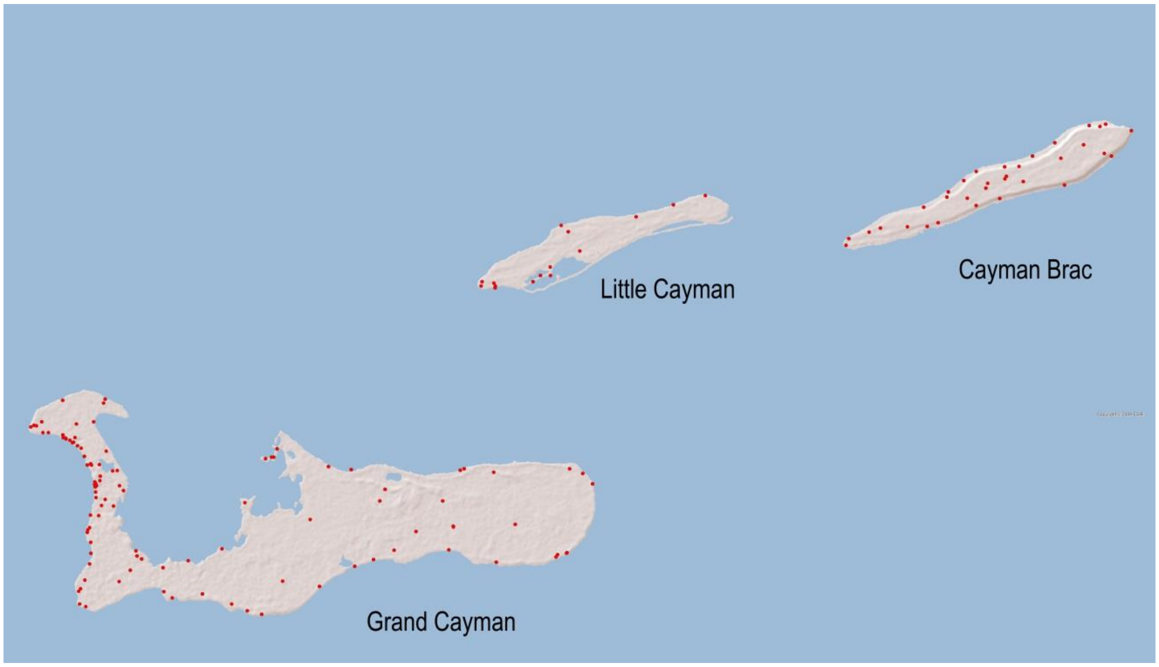

Fig. 5. Termite sampling localities from UF termite collection (For purposes of space, the geographic positions of Little Cayman and Cayman Brac not related to that of Grand Cayman).

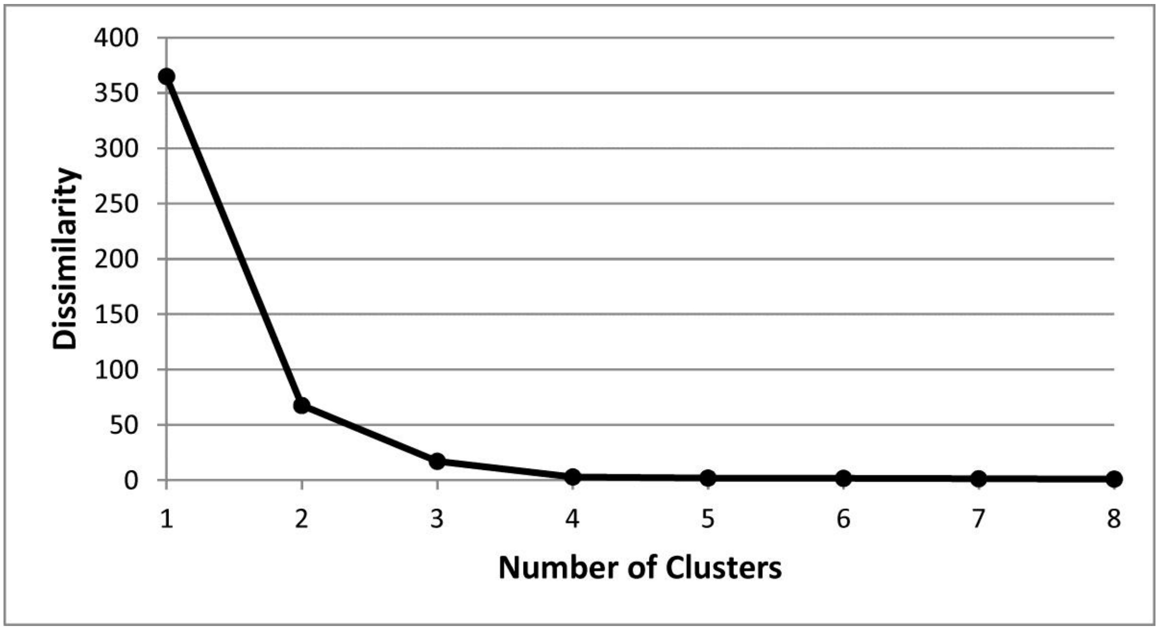

Fig. 6. Plot for the Single Linkage Clustering method for *C. gestroi* over Grand Cayman Island.

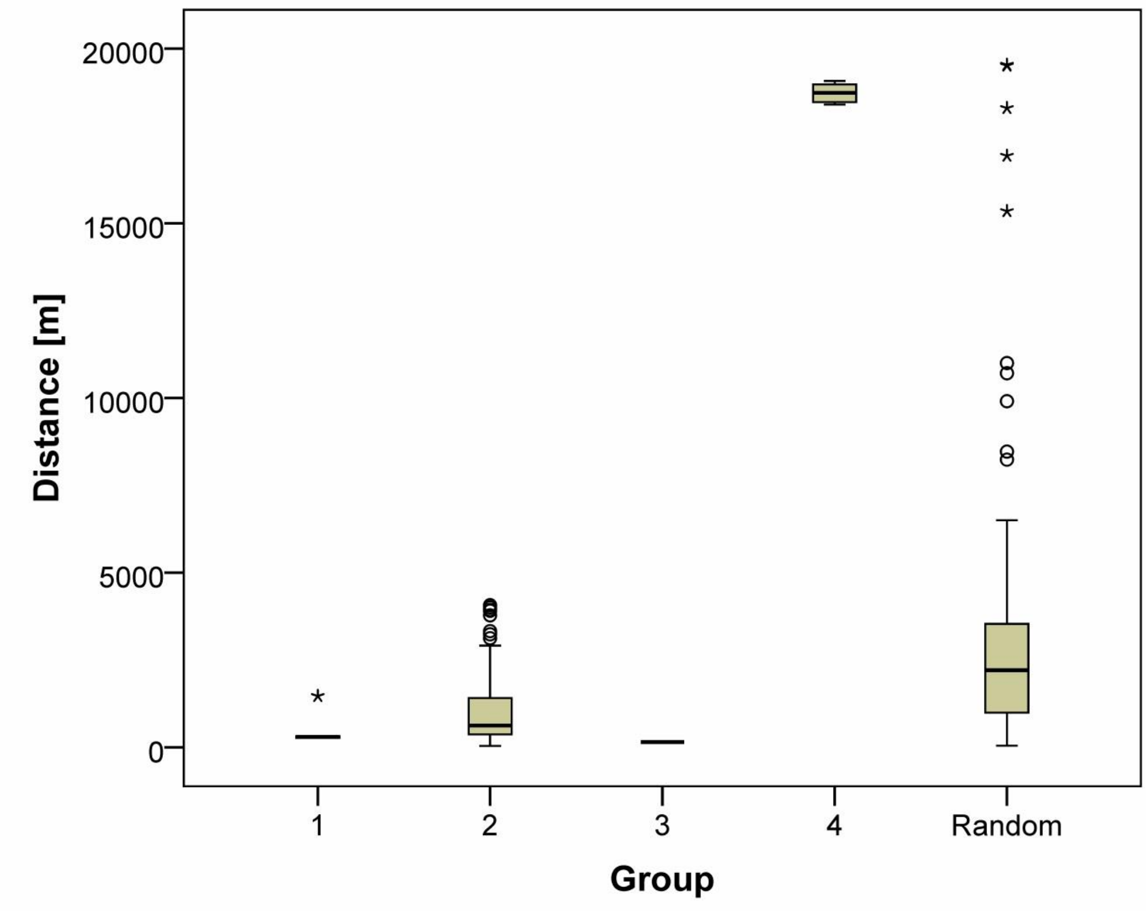

Fig. 7. Plot for the Single Linkage Clustering method for distances to the nearest marine dockage *C. gestroi* over Grand Cayman Island.

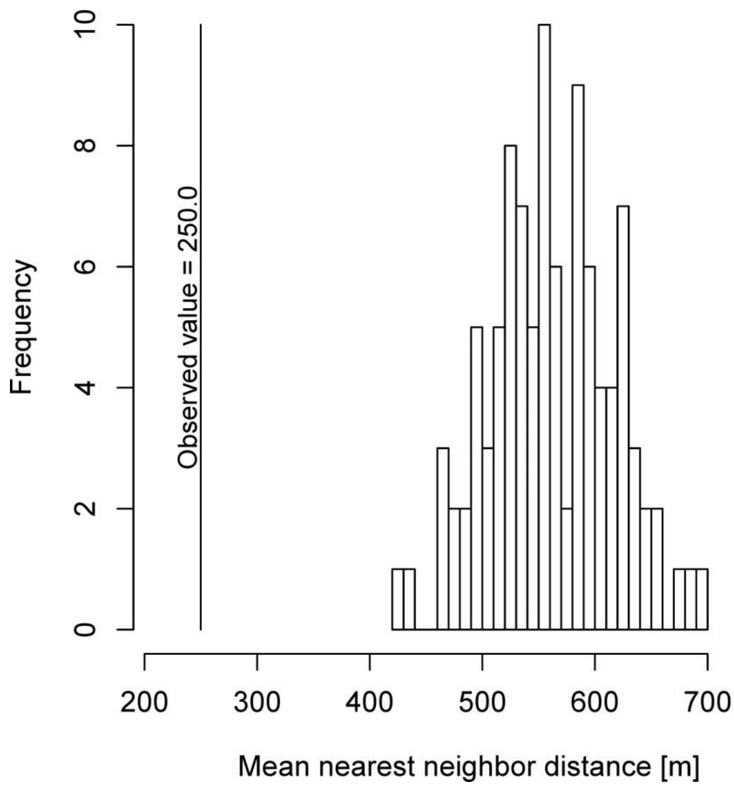

Fig. 8. Distribution of mean nearest neighbor distance obtained from Monte-Carlo simulation with 102 randomized points placed in built areas within suitable habitats.

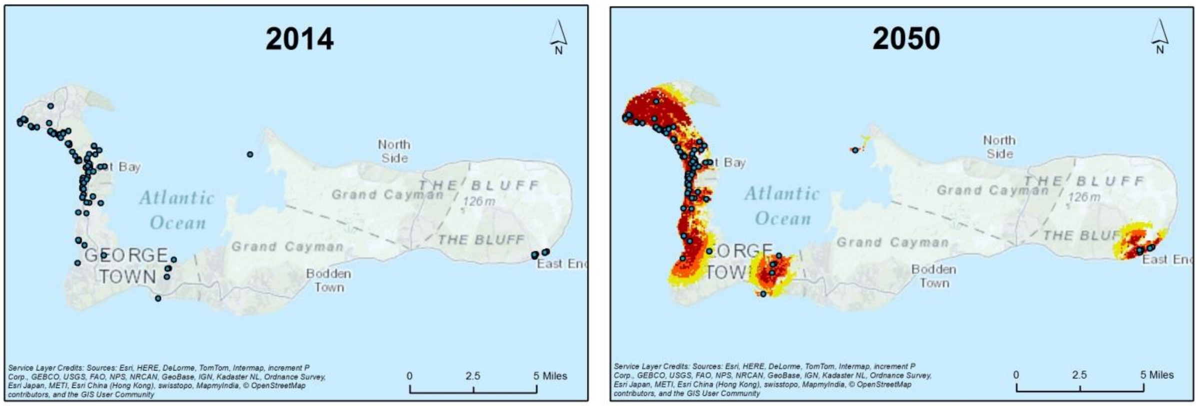

Fig. 9. Areas predicted as infested by the simulation model for *C. gestroi* over Grand Cayman Island. Sampled termite locations in 2014 are mapped (points). Yellow, orange, and red cells indicate the > 0%, ≥ 50%, and 100% occupancy envelopes, respectively.

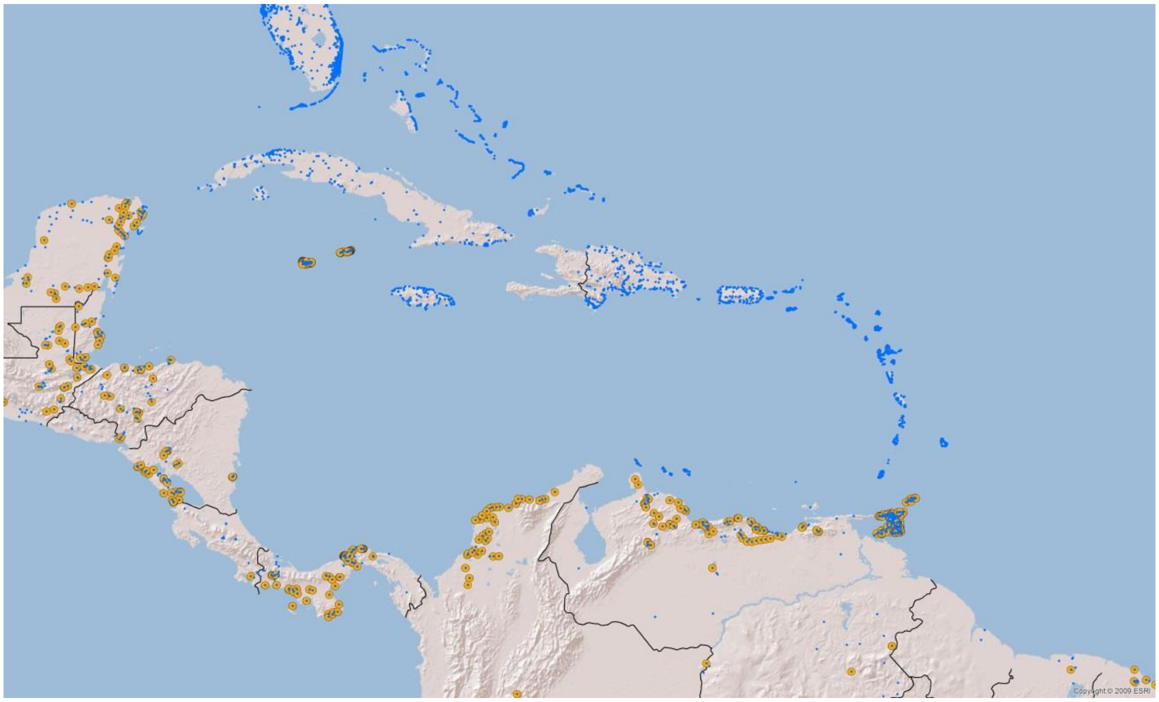

Fig. 10. Caribbean basin survey localities for all termites (blue dots) and for *Microcerotermes* spp. only (orange dots) (Source: UF Termite Collection).