Simulating the Spread of an Invasive Termite in an Urban Environment Using a Stochastic Individual-Based Model

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Abstract

Invasive termites are destructive insect pests that cause billions of dollars in property damage every year. Termite species can be transported overseas by maritime vessels. However, only if the climatic conditions are suitable will the introduced species flourish. Models predicting the areas of infestation following initial introduction of an invasive species could help regulatory agencies develop successful early detection, quarantine, or eradication efforts. At present, no model has been developed to estimate the geographic spread of a termite infestation from a set of surveyed locations. In the current study, we used actual field data as a starting point, and relevant information on termite species to develop a spatially-explicit stochastic individual-based simulation to predict areas potentially infested by an invasive termite, *Nasutitermes corniger* (Motschulsky), in Dania Beach, FL. The Monte Carlo technique is used to assess outcome uncertainty. A set of model realizations describing potential areas of infestation were considered in a sensitivity analysis, which showed that the model results had greatest sensitivity to number of alates released from nest, alate survival, maximum pheromone attraction distance between heterosexual pairs, and mean flight distance. Results showed that the areas predicted as infested in all simulation runs of a baseline model cover the spatial extent of all locations recently discovered. The model presented in this study could be applied to any invasive termite species after proper calibration of parameters. The simulation herein can be used by regulatory authorities to define most probable quarantine and survey zones.

Keywords: Monte Carlo simulation, invasive species, individual-based approach, spatial stochastic simulation, habitat suitability
1. Introduction

The primary anthropogenic means by which termites are transported between continents and islands is by maritime vessel (Scheffrahn and Crowe 2011). Over a dozen exotic termite species have become established worldwide (Evans 2011), of which six can be found in Florida (Scheffrahn et al. 2002).

Termites are destructive insect pests that cause billions of dollars in property damage every year (Edwards and Mill 1986). Once a species is established, the natural dispersal of termite colonies proceeds slowly. Termite colonies typically require 4-6 years to mature, and once the first group of alates (winged reproductives) leaves the colony, they are unable to fly more than a few hundred meters from the parent colony (Husseneder et al. 2006; Messenger and Mullins 2005; Mill 1983). Anthropogenic or “vehicular” dispersal is far more rapid and can be measured in km/h. However, such long distance movements lack predictability. Specifically, the nesting core of a termite colony (reproductives, brood, and most foragers) must be moved intact and both a water and food source must be associated with the core during movement (Hochmair and Scheffrahn 2010).

The inherent complexity of a physical environment limits the applicability of mathematical models for realistic dispersal modeling of invasive species, and practical predictions are difficult to obtain (Pitt 2008). Analytical methods commonly used to model dispersal in the past and in some cases up to the present include: (i) simple reaction-diffusion models (Fisher 1937), which ignore any spatial interaction between individuals and do not consider single dispersal events; (ii) mixed diffusion-population growth models, which include a per capita growth parameter (Okubo 1980; Skellam 1951) or several demographic variables (Van Den Bosch et al. 1990); and
(iii) integro-differential equation models, which separate population dynamics and dispersal into two stages (Neubert et al. 1995). More recently, computer-intensive approaches, such as spatially-explicit population models (SEPMs), have been able to incorporate both ecological/biological information at a population level with underlying habitat differences (Wiegand et al. 2004).

Computer simulations seek to imitate the dynamics of various real world processes (Steyaert 1993) rather than solving sets of equations. Simulation models are either deterministic or stochastic. The first model type gives a fixed output for a given set of input data and model parameters while the second model type includes at least one stochastic process and provides a probabilistic outcome (Law and Kelton 1982). The intrinsic dynamic component of a computer simulation provides the ability to estimate the rate at which an invading species is likely to occupy suitable areas. However, such models may represent a poor choice in cases where established populations are restricted to distinct areas of suitable habitat, since assuming universal dispersal abilities may not reflect the ability of a species to move from a current location to another potentially suitable habitat (Peterson et al. 2002). Whereas simulating the spread of invasive species beyond a decade into the future may decrease the reliability of the model outcome (Pitt et al. 2011), it should be noted that the invasive plant used by Pitt et al. (2011) has a much faster dispersal capacity compared to termites.

Individual-based models (IBMs) are able to incorporate several rules describing the interactions between individual units considering each one of them as different, both physiologically and behaviorally (Huston et al. 1988). The complexity of the rules increases with the total number of parameters involved in describing them. However, complexity often comes at the expense of generality, which makes it necessary to select the most appropriate modeling
approach on a case by case basis. Small spatial scales, such as urban environments, are particularly suitable for the development of IBMs, because they are complex enough to require simulation but not so large as to be unmanageable for an IBM. Also, IBMs are able to represent individuals explicitly and incorporate biologically relevant rules that have a strong influence on the dynamics of an invasion (Pitt 2008).

In this paper, we develop a computer simulation using a spatially-explicit stochastic individual-based modeling approach and use hindcasting in order to predict which areas would have been infested by an arboreal invasive termite, *Nasutitermes corniger* (Motschulsky), had no eradication plan been implemented at a particular location, Dania Beach, FL. The methodology presented herein is appropriate for more general application, such as predicting the future geographical spread or studying a different termite species after appropriate adjustments in the model parameters.

Individual-based simulations consider the individual organism to be a logical basic unit for modeling ecological phenomena (Grimm and Railsback 2005). We ran each model from 2003, the year in which a first complete survey of infested locations had been conducted over the study area, until 2012. The model outcome is the predicted areas of infestation at any time step, indicating the spatial extent and dynamic evolution of the invasion. Beginning in 2003, local authorities have been trying to eradicate this pest from the original survey area. However, between 2006 and 2011, extended survey procedures had to be stopped due to discontinued funds. A new recent survey conducted in 2012 found newly infested locations in areas not spotted originally and therefore not included in the eradication plan. We believe that state or local regulatory agencies can benefit from a model that predicts the rate and direction of termite
dispersal, as it would assist them in targeting specific areas for survey, eradication, or quarantine efforts.

In the literature, only two computer simulation models have been applied to a termite species: one has been developed to determine per-capita wood consumption rates of termite workers (Morales Ramos and Rojas 2005), while the other explored termite foraging behavior underneath the soil (Lee et al. 2008). To date, no computer simulation models have been published that investigate the geographic spread of a termite infestation from a set of surveyed locations. Unlike some other recently developed spatial simulation models found in the literature for other insects (Carrasco et al. 2010; Pitt 2009) the human-mediated dispersal component is not included because of its unpredictability and lack of calibration data. Although samples collected over the past 10 years do not reflect the true (i.e. natural) expansion of the species, and were collected mainly for the purpose of verifying the success of the eradication effort, it is nevertheless possible to use the newly infested locations (2012) to ground truth our simulation model.

We herein describe the parameters and methods used to develop the computer simulation. Results are presented together with a discussion on the relative importance of each biological parameter included in the model, followed by conclusions.
2. Materials and Methods

2.1. Model Design

The simulation algorithm is implemented using a set of R functions (R Development Core Team 2011) and we provide free source code. The model description follows the ODD (Overview, Design concepts, Details) protocol (Grimm et al. 2006; Grimm et al. 2010) in order to make the model's logic as clear as possible.

2.1.1 Purpose of Model.

We developed a spatial, stochastic computer simulation with the purpose of gaining a deeper understanding of the rate and direction of a termite invasion by natural means over a realistic landscape, such as an urban environment. In this study, the model is also used to determine how a new invasive species in South Florida, *N. corniger*, could have expanded from a set of surveyed locations up to the present, if no eradication plan had been implemented throughout the years. The developed simulation model may assist state or local regulatory agencies in targeting specific areas for survey, eradication, or quarantine efforts.

2.1.2. Entities, State Variables and Scales.

The basic entities of the model are individual termite alates (dispersing propagules) and all the individual colonies they are generated from. Both alates and colonies are characterized by
their continuous spatial location specified in a Cartesian plane coordinate system. Alates are also characterized by their sex (M-F), and colonies by their age (in years). We use a reference spatial grid to represent the distribution of all areas occupied by one or more termite colonies at each time step. The grid is set to an extent of 10 km x 10 km over the urban area of Dania Beach, FL, with a resolution of 100 x 100 meters. We believe that the chosen resolution is suitable for a few reasons such as the uncertainty associated with the precise locations of surveyed colonies/individuals, the approximate maximum extent of a colony’s foraging territory (Collins 1981), and because it is a suitable scale of surveillance and pest control management. In order for the simulation to be more realistic, we also consider the local urban environment and exclude areas that are unsuitable for the establishment of a new colony, such as roads, highways, non-wooded fields, and water bodies. Each area with wood sources (e.g., buildings, trees, boats, debris, etc.) has potential for colonization. We believe that for the chosen temporal resolution (10 years) the choice of a static habitat suitability layer does not introduce any relevant bias in the results. However, should the model be run over a much longer time span, we recommend considering a different strategy. The temporal scale is discrete and one time step represents 1 year. The model is run from 2003 (year of the first complete survey of infested locations) to 2012.

2.1.3. Process overview and scheduling.

Dispersal of alates is the key process in the spread of colonies, and we simulate the dispersal as a single annual event. The consequence may be an increased chance for alates to find a mate and form a new colony. However, this represents a necessary simplification, since typical termite
dispersal is formed by a major exodus that may be preceded and/or followed by smaller flights, of unknown magnitude and timing. Many termite species initiate dispersal flights in the early stages of the wet season and are triggered by environmental factors (Jones et al. 1988; Martius 2003; Nutting 1969). Dispersal flights are the only means by which new colonies can form beyond the foraging territory of the mother colony. Although the model simplifies the temporal scale of the real phenomenon, single massive dispersal flights are common because: (i) alates are less vulnerable as prey, as they can overwhelm predators by large numbers (Nutting 1969); and (ii) there are higher odds of finding and choosing a mate.

2.1.4. Design Concepts.

2.1.4.1. Sensing. Dispersing alates (reproductives) can sense and respond to pheromones in order to find potential mates of the opposite sex that have dispersed by chance to the nearby sites.

2.1.4.2. Interaction. Male and female alates interact to form new colonies.

2.1.4.3. Stochasticity. Both distance and direction of dispersal by alates are determined stochastically from a probability distribution (see Section 2.1.7.4). The sex (male or female) of a particular alate is random.

2.1.4.4. Collectives. Individual alates are followed during dispersal, but after a colony is formed by two alates of the opposite sex, the colony is followed as whole rather than at the resolution of individuals.

2.1.5. Initialization.
Fig. 1 shows a schematic representation of the steps involved for the model initialization.

Figure 1—caption at the end of file

At the initial state, i.e. time t=1, the spatial locations of all surveyed termite colonies are stored in a dataset and assigned a random age between 0 and the maximum lifespan decided by the user. The initialization process is the same in all simulation runs. Surveyed colonies can be imported from an external data file containing their geographic coordinates, e.g. recorded with a GPS device. In most cases, the collected samples do not identify different termite colonies, as they are taken opportunistically with the goal of spotting an infestation. Therefore, different termite locations may or may not belong to the same colony.

2.1.6. Input Data.

Table 1 shows seven main parameters of the implemented dispersal model and their baseline values, i.e. the values assigned for the baseline simulation, which are based either on related literature findings (see Section 2.3) or the opinion of termite experts. More specific information for the particular location modeled, Dania Beach, FL, is described in Section 3.

2.1.7. Submodels.
The simulation algorithm is composed of several modules ordered in a sequential manner and imitates the steps taken by a group of individual alates from the dispersal to the inception of a new colony. Figure 2 shows an overview of the main subprocesses and steps involved in the simulation at any generic time step. Each subprocess is discussed in detail below.

Figure 2–caption at the end of file

2.1.7.1. Habitat Suitability. The habitat suitability submodel checks the suitability of the underlying environment for all termite individuals after dispersal. If an individual alate falls within an unsuitable habitat, as defined by the user, then it is eliminated. In order to include the local landscape in the simulation model and identify areas unsuitable for the establishment of new termite colonies, we combine the following vector-type spatial layers in a GIS (using ESRI’s ArcMap 10.0). A surface water layer published in 2006 was obtained from the Broward County GIS data online repository (Lelis 2006). We used 2011 NAVTEQ NAVSTREETS street data for the street network layer and created a 10 m buffer around each line segment to model the approximate coverage of roads. Further, we extracted the Fort Lauderdale Airport area and its runways from the 2010 TomTom (formerly TeleAtlas) Multinet Dataset.

Because *N. corniger*, like other invasive termite species, needs a wood source as food, we added all agricultural field polygons to the collection of unsuitable areas. These polygons were extracted from a 2010 land use layer at the parcel level, which was obtained from the University of Florida GeoPlan Center. The original land use layer was compiled by the Florida Department of Transportation and contains 99 land use classes which have been collapsed into
15 classes by the GeoPlan Center (University of Florida Geoplan Center 2010). Using the union overlay operation in ArcMap, we combined all the GIS layers listed above into a single layer denoting unsuitable habitat areas in which colonies are not able to survive.

2.1.7.2. Alate Dispersal. The dynamics and speed of termite dispersal by natural means are controlled by several behavioral characteristics affecting the successful creation of new colonies. We identified and included such behavioral characteristics in the form of model parameters to better simulate the real process. A new colony begins with a male-female (i.e. king and queen) couple of unwinged alates building and sealing the nuptial chamber in a proper substrate, usually soil or wood. After a termite colony matures, which requires about 4 years, alates are produced. All alates change their behavior in response to: (i) changes of habitat, i.e. they may fall into an unsuitable patch of land and therefore are not able to find a location to form an incipient colony; (ii) their proximity to a heterosexual mate. Alates do not adjust their behavior over time as a consequence of their experience, since they only serve the purpose of expanding the colony with a one-time flight after which they either die or find a mate and become the king/queen of a new colony. Although they have eyes, alates are probably not able to predict which location will be suitable once in flight. Dispersal flights typically occur at dusk or at night after a light rain and during calm weather conditions. It is known that alates are attracted by lights, as found in mark-recapture studies (Messenger and Mullins 2005). Sex pheromones have two main roles: a close-range attraction and contact attraction. The former is used to unite sexual partners, the latter is used to maintain the contact during the tandem behavior (Nutting 1969). Alates do not release pheromones during the flight and therefore their flight behavior is not influenced by it. The processes that are modeled assuming they are stochastic, i.e., random, are the flight distance,
flight direction, and the sex of each individual. The model output is used to spot which areas have been occupied and how often throughout all 100 runs.

2.1.7.3. Colony Formation. The colony formation subprocess loops through each grid cell that is occupied by at least two individuals and, subsequently, through each individual. This process is necessary to check if a reproductive is able to find a heterosexual neighbor and form a nuptial pair, where the neighborhood is defined by a circular buffer with the pre-set pheromone attraction radius. If two candidate alates are matched, a new colony is created and assigned spatial coordinates of the mid point between the two individuals. The process stops for a particular grid cell as soon as the maximum density of colonies per hectare is reached. At the end of the present subprocess, if one or more pairs of individuals are matched, new colonies are created and their spatial location is saved.

2.1.7.4. Colony Aging and Alate Production. Each time step, the age of every existing colony is increased by one (aging submodel). If this value exceeds the maximum lifespan defined by the user, then the colony is eliminated from the map. After the aging subprocess, alates are generated by each existing colony based on colony age (dispersal subprocess). Older colonies generate more alates, which increase the overall chances for an individual reproductive to find a mate, a suitable nesting site, and a location farther away from the mother colony. The dispersal subprocess also executes the following: (i) random creation of male and female individuals by sampling from a Binomial distribution, Bin(n, p), where n is the number of alates to be generated and p is the probability of drawing a male, (ii) random sampling of flight directions (in radians) from a uniform distribution, Unif[0, 2π], (iii) random sampling of flight distances (Euclidean) from a negative exponential distribution, Exp(λ), with mean 1/λ (where λ = rate), and (iv)
calculation of new spatial locations X and Y (Easting and Northing) of alates derived from basic trigonometric equations, using both the simulated flight direction and flight distances.

2.1.7.5. Updating the Distribution of Colonies on the Landscape. The final subprocess (stacking colonies subprocess) stacks all new colonies created during the previous process (colony formation) with the existing ones in a dataset. Before moving to the next time step, all colonies can be saved to an external shapefile as points and further converted to a geo-referenced raster grid. The raster grid allows us to overlay modeling results from multiple simulations and to compute a final occupancy envelope. At the following time step, new alates are generated which fly out from all mature colonies, i.e., colonies old enough to produce alates.

2.2. Sensitivity Analysis

We ran a sensitivity analysis to assess the contribution of each parameter to the model outcome. The uncertainty associated with the outcome of a stochastic simulation was estimated through the Monte Carlo technique and 100 simulation runs. We chose this number as a compromise between short computational time and high precision of confidence intervals around the mean predicted area of infestation. A set of model realizations describing the effect of changes in parameter values on potential areas of infestation were also considered in a sensitivity analysis.

2.3. Model Parameterization
We used basic data relevant to several termite species in order to parameterize the model. Unfortunately, there is not sufficient data to calibrate the model directly against *N. corniger* at the Dania Beach site. The age of colonies at the first production of alates, which varies between different termite species, can be derived from related literature studies. Typically, a colony takes four to six years from its creation to reach maturity and start the production of alates (Collins 1981). In this paper, we set the baseline value of the age of first production to 4 years. Lifespan estimates are approximations because they only reflect laboratory conditions. Estimated maxima ranged from 15 years old in *Macrotermes bellicosus* (Keller 1998) to 20 years in *Pseudacanthotermes spiniger* and *P. militaris* (Connétable et al. 2012). In this work, we set an age threshold of 20 years, after which a colony dies.

The maximum distance of pheromone attraction currently reported is 2.5-3 m by males (Leuthold and Bruinsma 1977). Here, we set the baseline value for the model at 3 meters.

The density of termite colonies over a certain patch of land is related to its specific biology, ecology and behavior (Adams and Levings 1987). No specific literature sources studied the density of *N. corniger*'s colonies within an urban environment. However, a study found a density of approximately 7 colonies per hectare in a primary forest in Panama (Thorne 1982), which we use as a baseline value in our model.

Literature sources treating the topic of alate predation or alate flight success rate are scant. Both predation and injuries typically occur as alates start leaving the nest (i.e. pre-flight), in flight (bats and birds), and as soon as they alight on the ground or on a tree (i.e. post-flight) to search for a mate. Empirical observation of alates of a different invasive termite species, *Cryptotermes brevis*, found an approximate survival rate of 1%, excluding predation (Scheffrahn et al. 2001). Factors affecting the outcome and the success of the dispersal flight include
environmental conditions, number of alates, sex ratio, proportion of alates eaten by predators, and efficiency of the post-flight mating behavior (Noirot 1990; Nutting 1969). A recent field study for two termite species showed that, despite the presence of 40 mature colonies over an area of one hectare producing approximately one million alates every year, no new colonies were found (Connéttable et al. 2012). In this paper, we set the baseline value of the overall survival rate to 0.01 (1%). We consider this to be a realistic estimate considering all the aforementioned factors (Scheffrahn, personal communication).

Although sex ratios of termite alates are variable, they tend towards parity (Jones et al. 1988). In *N. corniger*, individual colonies produced alates whose sex ratio was around 1:1 (Darlington 1986; Thorne 1983). Therefore, we set the baseline value of the prevalence of male alates in the colony to 0.5 (50%).

Field studies aiming to precisely assess the size of an alate crop in individual colonies are rare. Several colonies of *N. corniger* have been compared and a noticeable variation in production of alates was found. Mature colonies, whose population size ranges between 50,000-400,000 individuals, produced 5,000-25,000 alates (Thorne 1983). The production of alates likely depends on factors such as availability of food resources, health of queen(s), colony age, and colony-specific history. All factors are not easily assessed during the short time frame given in field sampling. In another invasive termite, *Coptotermes formosanus*, the alate production of a single colony was over 68,000. In this case, sex ratio was 1:3 (F:M) (Su and Scheffrahn 1987). In the baseline simulation model, we used a “Low Profile” age-related alate production, defined as follows: (i) no production of alates until a colony reaches 4 years of age, (ii) 1,000 alates between 4 and 9 years of age, (iii) 10,000 alates between 10 and 14 years of age, and (iv) 100,000 alates between 15 years and the age at which a colony dies. Opposed to this profile, we
also defined a “High Profile” scenario, with a greater production of alates at an earlier age: (i) no production of alates until a colony reaches 4 years of age, (ii) 10,000 alates between 4 and 9 years of age, (iii) 50,000 alates between 10 and 14 years of age, and (iv) 100,000 alates between 15 years and the age at which a colony dies. This alternative scenario is tested in our sensitivity analysis (see Section 4). Although these “profiles” may be an oversimplification, it is likely to match an average magnitude that is otherwise impossible to calibrate with precise empirical data (Scheffrahn personal communication).

Termite alates are weak, erratic fliers. On average, alates are capable of flying a few hundred meters on their own (Nutting 1969). Flight distances have not specifically been estimated for \textit{N. corniger}. However, it is possible to estimate this model parameter based on findings for other termite species. Mark-recapture studies using light traps gave the first empirical measurements of termite flight skills. A maximum distance of 892 m has been recorded for \textit{C. formosanus} (Messenger and Mullins 2005). In an endemic habitat, alates may fly far enough to ensure that a mixture of different colonies is created with swarm aggregation (Husseneder et al. 2006). However, for an exotic population to spread, alates fly into uncolonized areas lacking conspecifics with which to mate. Recently, a new maximum distance record of about 1.3 km has been recorded by Mullins and Messenger in New Orleans, LA (Mullins, personal communication). Alates of \textit{Odontotermes formosanus} were capable of flying between 120 and 743 m (Hu et al. 2007). Other studies recorded only a few dispersal flights covering about 300 m for termite species belonging to the Termitidae family (Mill 1983), to which \textit{N. corniger} belongs, or 460 m for \textit{C. formosanus} (Ikehara 1966). In this study, we decided to sample dispersal flight distances from an exponential distribution. This allows for both short and rare longer dispersal events. In a unique mark-recapture study recently completed in New Orleans, LA, data collected
for alates of *C. formosanus* confirmed the “exponential” shape of the empirical histogram derived from several recorded flight distances (Mullins, unpublished data). We estimated the mean of the exponential distribution based on the aforementioned empirical data and literature findings. The baseline value used as a mean dispersal distance for the simulation model was set to 200 m.

Two factors that affect alate dispersal distance during the swarm season are wind velocity and light intensity. In most cases, the flight is only initiated if the wind velocity stays below 3.5 km/h (Leong et al. 1983). Moreover, termites are extremely prone to injuries, hence windless or low wind conditions are preferred. Given the impossibility of forecasting wind direction, wind speed, and light intensity in a multi-year simulation model, we assume alates can fly in any direction and sample all angles (in radians) from a uniform distribution. Moreover, we are using the present model within an urban environment, where light intensity is quite uniformly distributed and therefore we believe it will not affect the model outcome.
3. Application of Model to Specific Study Area and Data

*N. corniger* was first reported in Florida in May 2001, in Dania Beach, Broward County, FL (Scheffrahn et al. 2002). The discovery represents the first record of a non-endemic and land-based establishment of a higher termite (Family Termitidae) in the continental U.S. It is likely that the infestation was the result of dockside flights from an infested boat or shipping container, probably a decade before the discovery, but no specific source was identified (Scheffrahn et al. 2002). Starting in early 2003, a previously delineated area was targeted for a deliberate eradication campaign of this invasive pest. In January 2003, an area-wide visual survey was conducted for nests, foraging tubes, foraging sites, and debris harboring living *N. corniger*. However, most *N. corniger* nest locations were cryptic and even an exhaustive survey is likely to miss some infested locations, especially in the case of young colonies. In 2006, survey work was discontinued due to budget cuts before being re-activated in 2011 (Scheffrahn, unpublished data).

Exact sample locations were recorded using a GPS device and later imported into a database. A total area of 200 acres (approximately 81 ha) was surveyed, 20% of which had active infestations. Several epigeal nests of different diameters were found at the base of both live and dead trees, in tree cavities above ground, and foraging tubes extended upward of 10 m on trees and palms (Scheffrahn et al. 2002). The maximum separation between active sites in north-south and east-west direction was approximately 1 km. A newly funded 2011-2012 survey revealed new infested locations. No pest reoccurrence was observed within the areas originally surveyed between 2003 and 2006 (Scheffrahn, unpublished data).
Fig. 3 shows the known infested area in 2003, with a zoom over the recorded GPS locations of all sampled termites. The total area covers less than 0.25 km$^2$ and consists of commercial, residential, marina, and vacant wooded properties.

**Figure 3–caption at the end of file**
4. Results and Discussion

The stochastic outcome of 100 computer simulations can be grouped and represented by different occupancy envelopes. A “>0%” occupancy envelope groups all areas predicted as occupied by the model in at least one simulation run. Similarly, a “>=50%” occupancy groups all areas predicted as occupied in at least half of all runs. Finally, the “100%” occupancy envelope groups areas that are predicted as infested in all runs.

Fig. 4 shows a snapshot of the spatial expansion of *N. corniger* through time as predicted by the baseline simulation model, with color coding to represent the different occupancy envelopes.

**Figure 4—caption at the end of file**

Between 2003 and 2004 in the model there was a larger expansion in the areas surrounding the first surveyed locations compared to all other time frames. There are two reasons for that: (1) alates fly in all directions and therefore, if the habitat is suitable, fill in all the voids; (2) After 2004, most of the areas toward the center of invasion had already been invaded and therefore occupied by at least one colony. Moreover, both the “>0%” and “>=50%” occupancy envelopes were representing only areas that were not occupied in all simulation runs, hence they overestimate the predicted area and show a much larger extent than was likely to have been invaded. Areas covered by the "100%" envelope can be used to plan a first survey and either quarantine or eradicate the infestation. The other envelopes, instead, can be used as a "worst-case scenario", thus used as a maximum perimeter to plan a more effective eradication program.

Overall the expansion seems to proceed slowly and it is possible to observe some barrier effect.
represented by both highways and the airport ground on the shape of the predicted surfaces in the East-North East directions. Finally, a few isolated spots are predicted by the “>0%” envelope across the study area. However, these spots may have been predicted by a single simulation run out of 100 and we believe they should not be looked at as a threat.

The contribution of each model parameter to the final outcome of the computer simulation is assessed with a sensitivity analysis. This is typically done by slightly changing the value of a given model parameter while keeping the other model parameters constant. Based on the change in output one can estimate how the uncertainty in the model output can be apportioned to uncertainty in that parameter. We evaluate the importance of each parameter through a set of metrics, which are: covered area, absolute area growth, relative area growth. All measures are expressed as Monte Carlo (or multi-run) averages, i.e., as arithmetic means of all 100 simulation runs. For six out of the seven parameters selected for the sensitivity analysis, as introduced in Table 1, we ran the simulation with two alternative values, giving a total of 12 alternative model realizations in addition to the baseline simulation. Further, a single change of value was tested for variable SCR because we were only interested in observing the effect of a different age dependent reproduction structure and did not have empirical data to justify more realistic alternative scenarios on that parameter. Detailed results from the global sensitivity analysis are shown in Supp. Table S1 (found in the online version). Relative and absolute growth rates in the table refer to changes in area compared to the previous year. Here, for the sake of brevity, we report the sensitivity analysis results using line charts and selecting the average predicted area of infestation through time as a representative measure of changed parameter settings. Fig. 5 shows the charts for the seven tested parameters. Each chart also contains a line of the baseline model as a reference.
The parameters that have the largest overall influence on the model outcome, considering all evaluation metrics, are SCR (scenario of amount of alates generated by a colony), SURV (overall survival rate of alates), PHR (maximum pheromone attraction distance), and DIST (mean dispersal flight distance). The parameter MAR (prevalence of male alates in the colony) has the smallest effect. Both AFP (age of first production of alates) and DEN (density of colonies /ha) have a relatively small effect. When SCR is set to "High Profile" there is a large and sudden increase in the predicted infested area after the first four years, as described in Section 2.3. A higher number of alates is produced after reaching the age of first production and this increase is far more rapid compared to the "Low Profile" used in the baseline model. The PHR parameter has a large effect as it sets the rule for the maximum distance within which alates can find a mate. When the radial distance is reduced by two meters, the final predicted area is reduced to less than half of its corresponding baseline value. The SURV parameter controls the percentage of alates that are able to survive predation and find a mate. Therefore, the higher the percentage, the higher the chance to create new colonies at any time step. In general, the effect of a change in a model parameter accumulates over time. As an example, Fig. 6 (b-c) shows the effect of a change in the SURV parameter on the predicted area of infestation in the study area. For the sake of clarity, we only show the “100%” occupancy envelope.
To corroborate our simulation model, we include all newly infested sites that were discovered in 2012. Figure 7 (right image) shows the infested areas predicted by the baseline simulation model with all three occupancy envelopes using 2003 sample sites as seed points (left image).

Figure 7–caption at the end of file

The “100%” occupancy envelope overlaps well with the 2012 empirical locations, while the “>0%” and “>=50%” envelopes overestimate termite spread.

The main goal of this paper was to develop a stochastic individual-based simulation model that would give regulatory agencies a tool to anticipate possible areas of infestation and, at the same time, optimize the allocation of human and financial resources toward an eradication effort. Model output may be used by either local authorities or pest control agencies to draw one or more areas of intervention instead of randomly inspecting an unknown perimeter with subsequent waste of resources. For example, a greater amount of economic resources could be assigned to those zones encompassed by the “100%” predicted envelope. We used hindcasting in order to predict which areas in Dania Beach, FL, would have been infested up to the present if no eradication plan had ever been implemented. The model presented in this study is a generic model for termites and can be applied to any species after proper calibration of all the parameters. We tried to capture the complexity of a termite invasion and make the model more realistic by including several of the ecological-biological characteristics that control the dynamics and speed of their natural dispersal.
Some limitations of the model we presented include the precision of the estimates used to parameterize it. In some cases, parameters had to be estimated based on literature findings on termite species that are not the same as the one modeled. Unfortunately, this was necessary whenever an empirical estimate could not be found for *N. corniger*. Although the lack of precise estimates for *N. corniger* may affect the final outcome of the model, all values reflect a general tendency shared by most termite species. The precision of the model presented in this study will greatly benefit from newer and better empirical estimations for the species being modeled. Whenever calibration data are missing or scant, we suggest a consultation with a termite expert. Future research may expand from our work and implement a micro-level simulation model to simulate multiple dispersal steps within a single year. Moreover, future implementations may include, among other parameters, prevailing breeze direction and distance from city street lights for nocturnal dispersing species. The Monte Carlo technique is used to assess the uncertainty associated with the stochastic outcome of each model and to obtain an approximation of the answer to the problem. We decided to use occupancy envelopes in order to estimate areas of infestation with different likelihoods. Although the nature of the available data does not allow the use of a traditional model validation technique, the comparison with field samples via hindcasting provides at least some support to our conclusions. Results show that the areas predicted as infested in all simulation runs by our baseline model match all empirical sample locations well.

A sensitivity analysis was used to check for the importance of each model parameter, indicating that in particular, the parameters settings for the amount of alates generated by a colony, overall survival rate of alates, maximum pheromone attraction distance, and mean dispersal flight distance heavily influenced the final outcome of the model. We believe this study
is potentially beneficial to termite science, pest control agencies, and to a general audience. The simulation model was implemented using the open source R programming language. The functions are freely available to the users and flexible to facilitate use in different future applications. The source code can be found at https://github.com/f-tonini/Termite-Dispersal-Simulation.
Acknowledgements

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Table 1. Model parameters: abbreviations, definitions, and their baseline values.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Definition</th>
<th>Baseline Value</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>AFP</td>
<td>Colony age at first production of alates</td>
<td>4 yrs</td>
<td>(Collins 1981)</td>
</tr>
<tr>
<td>PHR</td>
<td>Maximum pheromone attraction distance</td>
<td>3 m</td>
<td>(Leuthold and Bruinsma 1977)</td>
</tr>
<tr>
<td>DEN</td>
<td>Maximum density of colonies per hectare</td>
<td>7</td>
<td>(Thorne 1982)</td>
</tr>
<tr>
<td>SURV</td>
<td>Overall survival rate of alates*</td>
<td>0.01 (1%)</td>
<td>(Scheffrahn et al. 2001)</td>
</tr>
<tr>
<td>MAR</td>
<td>Prevalence of male alates in the colony</td>
<td>0.5 (50%)</td>
<td>(Darlington 1986; Thorne 1983)</td>
</tr>
<tr>
<td>SCR</td>
<td>Scenario of amount of alates generated by a colony</td>
<td>Low Profile (see Section 2.3)</td>
<td>(Scheffrahn, personal communication)</td>
</tr>
<tr>
<td>DIST</td>
<td>Mean dispersal flight distance</td>
<td>200 m</td>
<td>(Mullins, unpublished work, Scheffrahn, personal communication)</td>
</tr>
</tbody>
</table>

* Overall percentage of alates surviving all phases of a dispersal flight
Figure Captions:

**Fig. 1.** Structure of the initialization steps involved in the simulation model.

**Fig. 2.** Core subprocesses involved in the individual-based simulation algorithm at any generic time step.

**Fig. 3.** Location of samples of *N. corniger* collected during a field survey in 2003. The background satellite image on the top-right corner was taken from a set of historical images in Google Earth. Available in color online.

**Fig. 4.** Snapshot of the areas predicted as infested by the baseline dispersal simulation model. Yellow, orange, and red cells indicate the >0%, >50%, and 100% occupancy envelopes, respectively. Top-left map: dots represent samples of *N. corniger* collected during a field survey in 2003, while green cells indicate the approximate areas of initial infestation. Available in color online.

**Fig. 5.** Sensitivity analysis charts. Each of the seven parameters is compared to the baseline simulation model (blue line). Red and green lines represent the models with a small change in a given parameter, leaving all the other variables unaltered. Available in color online.

**Fig. 6.** Model sensitivity to the SURV parameter. (a) Baseline simulation model. (b) SURV = .005 (0.5%) (c) SURV = .02 (2%). Available in color online.

**Fig. 7.** Model evaluation. Original and predicted infested areas by *N. corniger*, with 2003 and 2012 sampled termite locations. Available in color online.
First Time Step $T_1$

1. Set Initial Parameters
2. Read Suitability Habitat
3. Read Initial Colonies
4. Create Spatial Grid

Random Elimination of Exceeding Colonies

Is the maximum density reached?

YES

NO

Colony Dataset at $T_1$

Go To Next Time Step
Generic Time Step T (for $T > T_1$)

Colony Dataset at T → Age Increase → Alate Creation & Dispersal → Check Habitat Suitability

Go To Next Time Step → Stack New & Existing Colonies → New Colony Formation