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

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32 **Abstract**

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

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52 Keywords: Monte Carlo simulation, invasive species, individual-based approach, spatial
53 stochastic simulation, habitat suitability

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55 **1. Introduction**

56

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

61 Termites are destructive insect pests that cause billions of dollars in property damage every
62 year (Edwards and Mill 1986). Once a species is established, the natural dispersal of termite
63 colonies proceeds slowly. Termite colonies typically require 4-6 years to mature, and once the
64 first group of alates (winged reproductives) leaves the colony, they are unable to fly more than a
65 few hundred meters from the parent colony (Husseneder et al. 2006; Messenger and Mullins
66 2005; Mill 1983). Anthropogenic or “vehicular” dispersal is far more rapid and can be measured
67 in km/h. However, such long distance movements lack predictability. Specifically, the nesting
68 core of a termite colony (reproductives, brood, and most foragers) must be moved intact and both
69 a water and food source must be associated with the core during movement (Hochmair and
70 Scheffrahn 2010).

71 The inherent complexity of a physical environment limits the applicability of mathematical
72 models for realistic dispersal modeling of invasive species, and practical predictions are difficult
73 to obtain (Pitt 2008). Analytical methods commonly used to model dispersal in the past and in
74 some cases up to the present include: (i) simple reaction-diffusion models (Fisher 1937), which
75 ignore any spatial interaction between individuals and do not consider single dispersal events;
76 (ii) mixed diffusion-population growth models, which include a per capita growth parameter
77 (Okubo 1980; Skellam 1951) or several demographic variables (Van Den Bosch et al. 1990); and

78 (iii) integro-differential equation models, which separate population dynamics and dispersal into
79 two stages (Neubert et al. 1995). More recently, computer-intensive approaches, such as
80 spatially-explicit population models (SEPMs), have been able to incorporate both
81 ecological/biological information at a population level with underlying habitat differences
82 (Wiegand et al. 2004).

83 Computer simulations seek to imitate the dynamics of various real world processes (Steyaert
84 1993) rather than solving sets of equations. Simulation models are either deterministic or
85 stochastic. The first model type gives a fixed output for a given set of input data and model
86 parameters while the second model type includes at least one stochastic process and provides a
87 probabilistic outcome (Law and Kelton 1982). The intrinsic dynamic component of a computer
88 simulation provides the ability to estimate the rate at which an invading species is likely to
89 occupy suitable areas. However, such models may represent a poor choice in cases where
90 established populations are restricted to distinct areas of suitable habitat, since assuming
91 universal dispersal abilities may not reflect the ability of a species to move from a current
92 location to another potentially suitable habitat (Peterson et al. 2002). Whereas simulating the
93 spread of invasive species beyond a decade into the future may decrease the reliability of the
94 model outcome (Pitt et al. 2011), it should be noted that the invasive plant used by Pitt et al.
95 (2011) has a much faster dispersal capacity compared to termites.

96 Individual-based models (IBMs) are able to incorporate several rules describing the
97 interactions between individual units considering each one of them as different, both
98 physiologically and behaviorally (Huston et al. 1988). The complexity of the rules increases with
99 the total number of parameters involved in describing them. However, complexity often comes at
100 the expense of generality, which makes it necessary to select the most appropriate modeling

101 approach on a case by case basis. Small spatial scales, such as urban environments, are
102 particularly suitable for the development of IBMs, because they are complex enough to require
103 simulation but not so large as to be unmanageable for an IBM. Also, IBMs are able to represent
104 individuals explicitly and incorporate biologically relevant rules that have a strong influence on
105 the dynamics of an invasion (Pitt 2008).

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

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

123 dispersal, as it would assist them in targeting specific areas for survey, eradication, or quarantine
124 efforts.

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

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

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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

169 their continuous spatial location specified in a Cartesian plane coordinate system. Alates are also
170 characterized by their sex (M-F), and colonies by their age (in years). We use a reference spatial
171 grid to represent the distribution of all areas occupied by one or more termite colonies at each
172 time step. The grid is set to an extent of 10 km x 10 km over the urban area of Dania Beach, FL,
173 with a resolution of 100 x 100 meters. We believe that the chosen resolution is suitable for a few
174 reasons such as the uncertainty associated with the precise locations of surveyed
175 colonies/individuals, the approximate maximum extent of a colony's foraging territory (Collins
176 1981), and because it is a suitable scale of surveillance and pest control management. In order for
177 the simulation to be more realistic, we also consider the local urban environment and exclude
178 areas that are unsuitable for the establishment of a new colony, such as roads, highways, non-
179 wooded fields, and water bodies. Each area with wood sources (e.g., buildings, trees, boats,
180 debris, etc.) has potential for colonization. We believe that for the chosen temporal resolution (10
181 years) the choice of a static habitat suitability layer does not introduce any relevant bias in the
182 results. However, should the model be run over a much longer time span, we recommend
183 considering a different strategy. The temporal scale is discrete and one time step represents 1
184 year. The model is run from 2003 (year of the first complete survey of infested locations) to
185 2012.

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187 **2.1.3. Process overview and scheduling.**

188

189 Dispersal of alates is the key process in the spread of colonies, and we simulate the dispersal
190 as a single annual event. The consequence may be an increased chance for alates to find a mate
191 and form a new colony. However, this represents a necessary simplification, since typical termite

192 dispersal is formed by a major exodus that may be preceded and/or followed by smaller flights,
193 of unknown magnitude and timing. Many termite species initiate dispersal flights in the early
194 stages of the wet season and are triggered by environmental factors (Jones et al. 1988; Martius
195 2003; Nutting 1969). Dispersal flights are the only means by which new colonies can form
196 beyond the foraging territory of the mother colony. Although the model simplifies the temporal
197 scale of the real phenomenon, single massive dispersal flights are common because: (i) alates are
198 less vulnerable as prey, as they can overwhelm predators by large numbers (Nutting 1969); and
199 (ii) there are higher odds of finding and choosing a mate.

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201 **2.1.4. Design Concepts.**

202

203 *2.1.4.1. Sensing.* Dispersing alates (reproductives) can sense and respond to pheromones in
204 order to find potential mates of the opposite sex that have dispersed by chance to the nearby
205 sites.

206 *2.1.4.2. Interaction.* Male and female alates interact to form new colonies.

207 *2.1.4.3. Stochasticity.* Both distance and direction of dispersal by alates are determined
208 stochastically from a probability distribution (see Section 2.1.7.4). The sex (male or female) of
209 a particular alate is random.

210 *2.1.4.4. Collectives.* Individual alates are followed during dispersal, but after a colony is
211 formed by two alates of the opposite sex, the colony is followed as whole rather than at the
212 resolution of individuals.

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214 **2.1.5. Initialization.**

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

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218 **Figure 1–caption at the end of file**

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220 At the initial state, i.e. time $t=1$, the spatial locations of all surveyed termite colonies are stored in

221 a dataset and assigned a random age between 0 and the maximum lifespan decided by the user.

222 The initialization process is the same in all simulation runs. Surveyed colonies can be imported

223 from an external data file containing their geographic coordinates, e.g. recorded with a GPS

224 device. In most cases, the collected samples do not identify different termite colonies, as they are

225 taken opportunistically with the goal of spotting an infestation. Therefore, different termite

226 locations may or may not belong to the same colony.

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228 **2.1.6. Input Data.**

229

230 Table 1 shows seven main parameters of the implemented dispersal model and their baseline

231 values, i.e. the values assigned for the baseline simulation, which are based either on related

232 literature findings (see Section 2.3) or the opinion of termite experts. More specific information

233 for the particular location modeled, Dania Beach, FL, is described in Section 3.

234

235 **Table 1-end of file**

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237 **2.1.7. Submodels.**

238

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

243

244 **Figure 2–caption at the end of file**

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246 2.1.7.1. *Habitat Suitability*. The habitat suitability submodel checks the suitability of the
247 underlying environment for all termite individuals after dispersal. If an individual alate falls
248 within an unsuitable habitat, as defined by the user, then it is eliminated. In order to include the
249 local landscape in the simulation model and identify areas unsuitable for the establishment of
250 new termite colonies, we combine the following vector-type spatial layers in a GIS (using
251 ESRI’s ArcMap 10.0). A surface water layer published in 2006 was obtained from the Broward
252 County GIS data online repository (Lelis 2006). We used 2011 NAVTEQ NAVSTREETS street
253 data for the street network layer and created a 10 m buffer around each line segment to model the
254 approximate coverage of roads. Further, we extracted the Fort Lauderdale Airport area and its
255 runways from the 2010 TomTom (formerly TeleAtlas) Multinet Dataset.

256 Because *N. corniger*, like other invasive termite species, needs a wood source as food, we
257 added all agricultural field polygons to the collection of unsuitable areas. These polygons were
258 extracted from a 2010 land use layer at the parcel level, which was obtained from the University
259 of Florida GeoPlan Center. The original land use layer was compiled by the the Florida
260 Department of Transportation and contains 99 land use classes which have been collapsed into

261 15 classes by the GeoPlan Center (University of Florida Geoplan Center 2010). Using the union
262 overlay operation in ArcMap, we combined all the GIS layers listed above into a single layer
263 denoting unsuitable habitat areas in which colonies are not able to survive.

264 *2.1.7.2. Alate Dispersal.* The dynamics and speed of termite dispersal by natural means are
265 controlled by several behavioral characteristics affecting the successful creation of new colonies.
266 We identified and included such behavioral characteristics in the form of model parameters to
267 better simulate the real process. A new colony begins with a male-female (i.e. king and queen)
268 couple of unwinged alates building and sealing the nuptial chamber in a proper substrate, usually
269 soil or wood. After a termite colony matures, which requires about 4 years, alates are produced.
270 All alates change their behavior in response to: (i) changes of habitat, i.e. they may fall into an
271 unsuitable patch of land and therefore are not able to find a location to form an incipient colony;
272 (ii) their proximity to a heterosexual mate. Alates do not adjust their behavior over time as a
273 consequence of their experience, since they only serve the purpose of expanding the colony with
274 a one-time flight after which they either die or find a mate and become the king/queen of a new
275 colony. Although they have eyes, alates are probably not able to predict which location will be
276 suitable once in flight. Dispersal flights typically occur at dusk or at night after a light rain and
277 during calm weather conditions. It is known that alates are attracted by lights, as found in mark-
278 recapture studies (Messenger and Mullins 2005). Sex pheromones have two main roles: a close-
279 range attraction and contact attraction. The former is used to unite sexual partners, the latter is
280 used to maintain the contact during the tandem behavior (Nutting 1969). Alates do not release
281 pheromones during the flight and therefore their flight behavior is not influenced by it. The
282 processes that are modeled assuming they are stochastic, i.e., random, are the flight distance,

283 flight direction, and the sex of each individual. The model output is used to spot which areas
284 have been occupied and how often throughout all 100 runs.

285 *2.1.7.3. Colony Formation.* The colony formation subprocess loops through each grid cell
286 that is occupied by at least two individuals and, subsequently, through each individual. This
287 process is necessary to check if a reproductive is able to find a heterosexual neighbor and form a
288 nuptial pair, where the neighborhood is defined by a circular buffer with the pre-set pheromone
289 attraction radius. If two candidate alates are matched, a new colony is created and assigned
290 spatial coordinates of the mid point between the two individuals. The process stops for a
291 particular grid cell as soon as the maximum density of colonies per hectare is reached. At the end
292 of the present subprocess, if one or more pairs of individuals are matched, new colonies are
293 created and their spatial location is saved.

294 *2.1.7.4. Colony Aging and Alate Production.* Each time step, the age of every existing colony
295 is increased by one (aging submodel). If this value exceeds the maximum lifespan defined by the
296 user, then the colony is eliminated from the map. After the aging subprocess, alates are generated
297 by each existing colony based on colony age (dispersal subprocess). Older colonies generate
298 more alates, which increase the overall chances for an individual reproductive to find a mate, a
299 suitable nesting site, and a location farther away from the mother colony. The dispersal
300 subprocess also executes the following: (i) random creation of male and female individuals by
301 sampling from a Binomial distribution, $\text{Bin}(n,p)$, where n is the number of alates to be generated
302 and p is the probability of drawing a male, (ii) random sampling of flight directions (in radians)
303 from a uniform distribution, $\text{Unif}[0, 2\pi]$, (iii) random sampling of flight distances (Euclidean)
304 from a negative exponential distribution, $\text{Exp}(\lambda)$, with mean $1/\lambda$ (where $\lambda = \text{rate}$), and (iv)

305 calculation of new spatial locations X and Y (Easting and Northing) of alates derived from basic
306 trigonometric equations, using both the simulated flight direction and flight distances.

307 *2.1.7.5. Updating the Distribution of Colonies on the Landscape.* The final subprocess
308 (stacking colonies subprocess) stacks all new colonies created during the previous process
309 (colony formation) with the existing ones in a dataset. Before moving to the next time step, all
310 colonies can be saved to an external shapefile as points and further converted to a geo-referenced
311 raster grid. The raster grid allows us to overlay modeling results from multiple simulations and to
312 compute a final occupancy envelope. At the following time step, new alates are generated which
313 fly out from all mature colonies, i.e., colonies old enough to produce alates.

314

315 **2.2. Sensitivity Analysis**

316

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

324

325 **2.3. Model Parameterization**

326

327 We used basic data relevant to several termite species in order to parameterize the model.
328 Unfortunately, there is not sufficient data to calibrate the model directly against *N. corniger* at
329 the Dania Beach site. The age of colonies at the first production of alates, which varies between
330 different termite species, can be derived from related literature studies. Typically, a colony takes
331 four to six years from its creation to reach maturity and start the production of alates (Collins
332 1981). In this paper, we set the baseline value of the age of first production to 4 years. Lifespan
333 estimates are approximations because they only reflect laboratory conditions. Estimated maxima
334 ranged from 15 years old in *Macrotermes bellicosus* (Keller 1998) to 20 years in
335 *Pseudacanthotermes spiniger* and *P. militaris* (Connétable et al. 2012). In this work, we set an
336 age threshold of 20 years, after which a colony dies.

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

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

344 Literature sources treating the topic of alate predation or alate flight success rate are scant.
345 Both predation and injuries typically occur as alates start leaving the nest (i.e. pre-flight), in
346 flight (bats and birds), and as soon as they alight on the ground or on a tree (i.e. post-flight) to
347 search for a mate. Empirical observation of alates of a different invasive termite species,
348 *Cryptotermes brevis*, found an approximate survival rate of 1%, excluding predation (Scheffrahn
349 et al. 2001). Factors affecting the outcome and the success of the dispersal flight include

350 environmental conditions, number of alates, sex ratio, proportion of alates eaten by predators,
351 and efficiency of the post-flight mating behavior (Noirot 1990; Nutting 1969). A recent field
352 study for two termite species showed that, despite the presence of 40 mature colonies over an
353 area of one hectare producing approximately one million alates every year, no new colonies were
354 found (Connétable et al. 2012). In this paper, we set the baseline value of the overall survival rate
355 to 0.01 (1%). We consider this to be a realistic estimate considering all the aforementioned
356 factors (Scheffrahn, personal communication).

357 Although sex ratios of termite alates are variable, they tend towards parity (Jones et al. 1988).
358 In *N. corniger*, individual colonies produced alates whose sex ratio was around 1:1 (Darlington
359 1986; Thorne 1983). Therefore, we set the baseline value of the prevalence of male alates in the
360 colony to 0.5 (50%).

361 Field studies aiming to precisely assess the size of an alate crop in individual colonies are
362 rare. Several colonies of *N. corniger* have been compared and a noticeable variation in
363 production of alates was found. Mature colonies, whose population size ranges between 50,000-
364 400,000 individuals, produced 5,000-25,000 alates (Thorne 1983). The production of alates
365 likely depends on factors such as availability of food resources, health of queen(s), colony age,
366 and colony-specific history. All factors are not easily assessed during the short time frame given
367 in field sampling. In another invasive termite, *Coptotermes formosanus*, the alate production of a
368 single colony was over 68,000. In this case, sex ratio was 1:3 (F:M) (Su and Scheffrahn 1987).
369 In the baseline simulation model, we used a “Low Profile” age-related alate production, defined
370 as follows: (i) no production of alates until a colony reaches 4 years of age, (ii) 1,000 alates
371 between 4 and 9 years of age, (iii) 10,000 alates between 10 and 14 years of age, and (iv)
372 100,000 alates between 15 years and the age at which a colony dies. Opposed to this profile, we

373 also defined a “High Profile” scenario, with a greater production of alates at an earlier age: (i) no
374 production of alates until a colony reaches 4 years of age, (ii) 10,000 alates between 4 and 9
375 years of age, (iii) 50,000 alates between 10 and 14 years of age, and (iv) 100,000 alates between
376 15 years and the age at which a colony dies. This alternative scenario is tested in our sensitivity
377 analysis (see Section 4). Although these “profiles” may be an oversimplification, it is likely to
378 match an average magnitude that is otherwise impossible to calibrate with precise empirical data
379 (Scheffrahn personal communication).

380 Termite alates are weak, erratic fliers. On average, alates are capable of flying a few hundred
381 meters on their own (Nutting 1969). Flight distances have not specifically been estimated for *N.*
382 *corniger*. However, it is possible to estimate this model parameter based on findings for other
383 termite species. Mark-recapture studies using light traps gave the first empirical measurements of
384 termite flight skills. A maximum distance of 892 m has been recorded for *C. formosanus*
385 (Messenger and Mullins 2005). In an endemic habitat, alates may fly far enough to ensure that a
386 mixture of different colonies is created with swarm aggregation (Husseneder et al. 2006).
387 However, for an exotic population to spread, alates fly into uncolonized areas lacking
388 conspecifics with which to mate. Recently, a new maximum distance record of about 1.3 km has
389 been recorded by Mullins and Messenger in New Orleans, LA (Mullins, personal
390 communication). Alates of *Odontotermes formosanus* were capable of flying between 120 and
391 743 m (Hu et al. 2007). Other studies recorded only a few dispersal flights covering about 300 m
392 for termite species belonging to the Termitidae family (Mill 1983), to which *N. corniger* belongs,
393 or 460 m for *C. formosanus* (Ikehara 1966). In this study, we decided to sample dispersal flight
394 distances from an exponential distribution. This allows for both short and rare longer dispersal
395 events. In a unique mark-recapture study recently completed in New Orleans, LA, data collected

396 for alates of *C. formosanus* confirmed the “exponential” shape of the empirical histogram
397 derived from several recorded flight distances (Mullins, unpublished data). We estimated the
398 mean of the exponential distribution based on the aforementioned empirical data and literature
399 findings. The baseline value used as a mean dispersal distance for the simulation model was set
400 to 200 m.

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

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3. Application of Model to Specific Study Area and Data

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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).

441 Fig. 3 shows the known infested area in 2003, with a zoom over the recorded GPS locations
442 of all sampled termites. The total area covers less than 0.25 km² and consists of commercial,
443 residential, marina, and vacant wooded properties.

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445 **Figure 3–caption at the end of file**

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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.

Figure4–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

487 represented by both highways and the airport ground on the shape of the predicted surfaces in the
488 East-North East directions. Finally, a few isolated spots are predicted by the “>0%” envelope
489 across the study area. However, these spots may have been predicted by a single simulation run
490 out of 100 and we believe they should not be looked at as a threat.

491 The contribution of each model parameter to the final outcome of the computer simulation is
492 assessed with a sensitivity analysis. This is typically done by slightly changing the value of a
493 given model parameter while keeping the other model parameters constant. Based on the change
494 in output one can estimate how the uncertainty in the model output can be apportioned to
495 uncertainty in that parameter. We evaluate the importance of each parameter through a set of
496 metrics, which are: covered area, absolute area growth, relative area growth. All measures are
497 expressed as Monte Carlo (or multi-run) averages, i.e., as arithmetic means of all 100 simulation
498 runs. For six out of the seven parameters selected for the sensitivity analysis, as introduced in
499 Table 1, we ran the simulation with two alternative values, giving a total of 12 alternative model
500 realizations in addition to the baseline simulation. Further, a single change of value was tested
501 for variable SCR because we were only interested in observing the effect of a different age
502 dependent reproduction structure and did not have empirical data to justify more realistic
503 alternative scenarios on that parameter. Detailed results from the global sensitivity analysis are
504 shown in Supp. Table S1 (found in the online version). Relative and absolute growth rates in the
505 table refer to changes in area compared to the previous year. Here, for the sake of brevity, we
506 report the sensitivity analysis results using line charts and selecting the average predicted area of
507 infestation through time as a representative measure of changed parameter settings. Fig. 5 shows
508 the charts for the seven tested parameters. Each chart also contains a line of the baseline model
509 as a reference.

510

511

Figure 5–caption at the end of file

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513 The parameters that have the largest overall influence on the model outcome, considering all
514 evaluation metrics, are SCR (scenario of amount of alates generated by a colony), SURV (overall
515 survival rate of alates), PHR (maximum pheromone attraction distance), and DIST (mean
516 dispersal flight distance). The parameter MAR (prevalence of male alates in the colony) has the
517 smallest effect. Both AFP (age of first production of alates) and DEN (density of colonies /ha)
518 have a relatively small effect. When SCR is set to "High Profile" there is a large and sudden
519 increase in the predicted infested area after the first four years, as described in Section 2.3. A
520 higher number of alates is produced after reaching the age of first production and this increase is
521 far more rapid compared to the "Low Profile" used in the baseline model. The PHR parameter
522 has a large effect as it sets the rule for the maximum distance within which alates can find a
523 mate. When the radial distance is reduced by two meters, the final predicted area is reduced to
524 less than half of its corresponding baseline value. The SURV parameter controls the percentage
525 of alates that are able to survive predation and find a mate. Therefore, the higher the percentage,
526 the higher the chance to create new colonies at any time step. In general, the effect of a change in
527 a model parameter accumulates over time. As an example, Fig. 6 (b-c) shows the effect of a
528 change in the SURV parameter on the predicted area of infestation in the study area. For the sake
529 of clarity, we only show the “100%” occupancy envelope.

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Figure 6–caption at the end of file

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533 To corroborate our simulation model, we include all newly infested sites that were
534 discovered in 2012. Figure 7 (right image) shows the infested areas predicted by the baseline
535 simulation model with all three occupancy envelopes using 2003 sample sites as seed points (left
536 image).

537

538 **Figure 7–caption at the end of file**

539

540 The “100%” occupancy envelope overlaps well with the 2012 empirical locations, while the
541 “>0%” and “>=50%” envelopes overestimate termite spread.

542 The main goal of this paper was to develop a stochastic individual-based simulation model
543 that would give regulatory agencies a tool to anticipate possible areas of infestation and, at the
544 same time, optimize the allocation of human and financial resources toward an eradication effort.
545 Model output may be used by either local authorities or pest control agencies to draw one or
546 more areas of intervention instead of randomly inspecting an unknown perimeter with
547 subsequent waste of resources. For example, a greater amount of economic resources could be
548 assigned to those zones encompassed by the “100%” predicted envelope. We used hindcasting in
549 order to predict which areas in Dania Beach, FL, would have been infested up to the present if no
550 eradication plan had ever been implemented. The model presented in this study is a generic
551 model for termites and can be applied to any species after proper calibration of all the
552 parameters. We tried to capture the complexity of a termite invasion and make the model more
553 realistic by including several of the ecological-biological characteristics that control the
554 dynamics and speed of their natural dispersal.

555 Some limitations of the model we presented include the precision of the estimates used to
556 parameterize it. In some cases, parameters had to be estimated based on literature findings on
557 termite species that are not the same as the one modeled. Unfortunately, this was necessary
558 whenever an empirical estimate could not be found for *N. corniger*. Although the lack of precise
559 estimates for *N. corniger* may affect the final outcome of the model, all values reflect a general
560 tendency shared by most termite species. The precision of the model presented in this study will
561 greatly benefit from newer and better empirical estimations for the species being modeled.
562 Whenever calibration data are missing or scant, we suggest a consultation with a termite expert.
563 Future research may expand from our work and implement a micro-level simulation model to
564 simulate multiple dispersal steps within a single year. Moreover, future implementations may
565 include, among other parameters, prevailing breeze direction and distance from city street lights
566 for nocturnal dispersing species. The Monte Carlo technique is used to assess the uncertainty
567 associated with the stochastic outcome of each model and to obtain an approximation of the
568 answer to the problem. We decided to use occupancy envelopes in order to estimate areas of
569 infestation with different likelihoods. Although the nature of the available data does not allow
570 the use of a traditional model validation technique, the comparison with field samples via
571 hindcasting provides at least some support to our conclusions. Results show that the areas
572 predicted as infested in all simulation runs by our baseline model match all empirical sample
573 locations well.

574 A sensitivity analysis was used to check for the importance of each model parameter,
575 indicating that in particular, the parameters settings for the amount of alates generated by a
576 colony, overall survival rate of alates, maximum pheromone attraction distance, and mean
577 dispersal flight distance heavily influenced the final outcome of the model. We believe this study

578 is potentially beneficial to termite science, pest control agencies, and to a general audience. The
579 simulation model was implemented using the open source R programming language. The
580 functions are freely available to the users and flexible to facilitate use in different future
581 applications. The source code can be found at [https://github.com/f-tonini/Termite-Dispersal-](https://github.com/f-tonini/Termite-Dispersal-Simulation)
582 [Simulation.](https://github.com/f-tonini/Termite-Dispersal-Simulation)

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602

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605 to improve the quality of the paper.

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

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

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

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801 **Figure Captions:**

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

805

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

808

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

812

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

818

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

822

823 **Fig. 6.** Model sensitivity to the SURV parameter. (a) Baseline simulation model. (b) SURV =
824 .005 (0.5%) (c) SURV = .02 (2%). Available in color online.

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826 **Fig. 7.** Model evaluation. Original and predicted infested areas by *N. corniger*, with 2003 and
827 2012 sampled termite locations. Available in color online.

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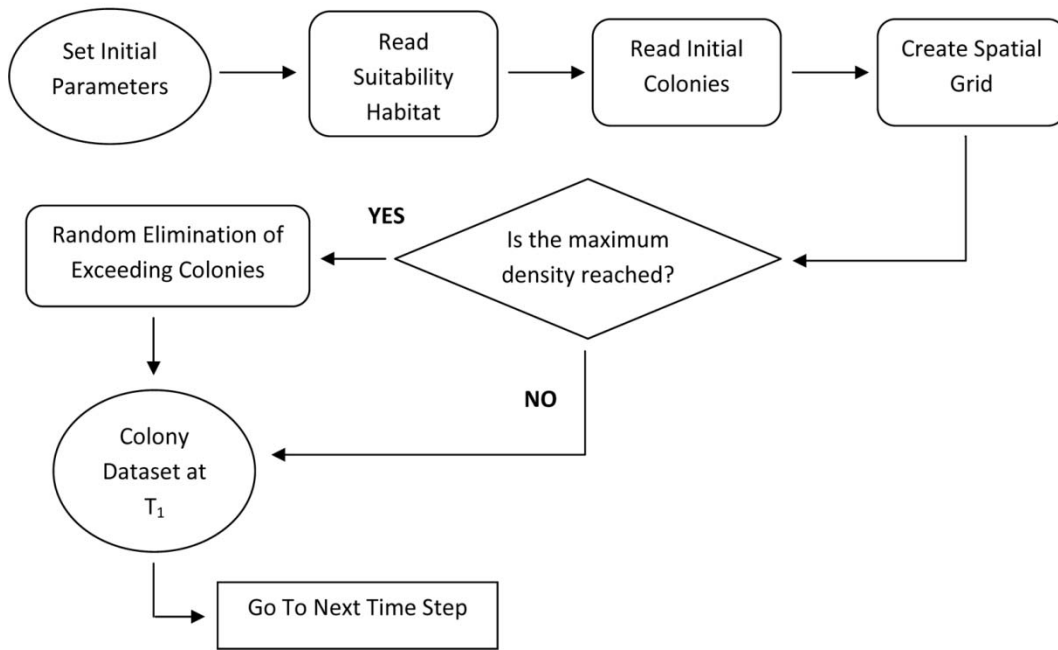
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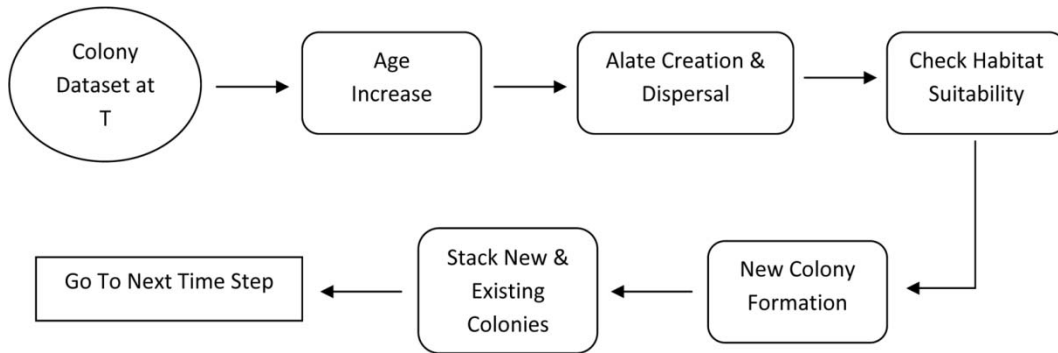
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First Time Step T_1

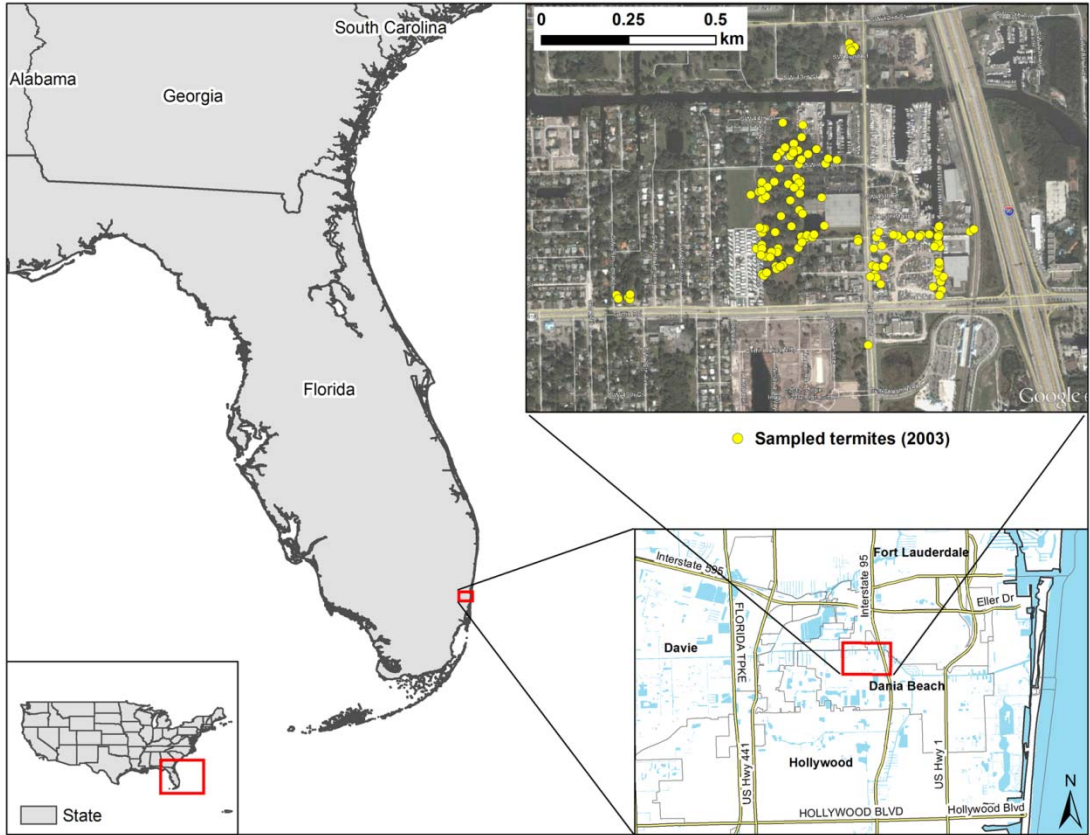


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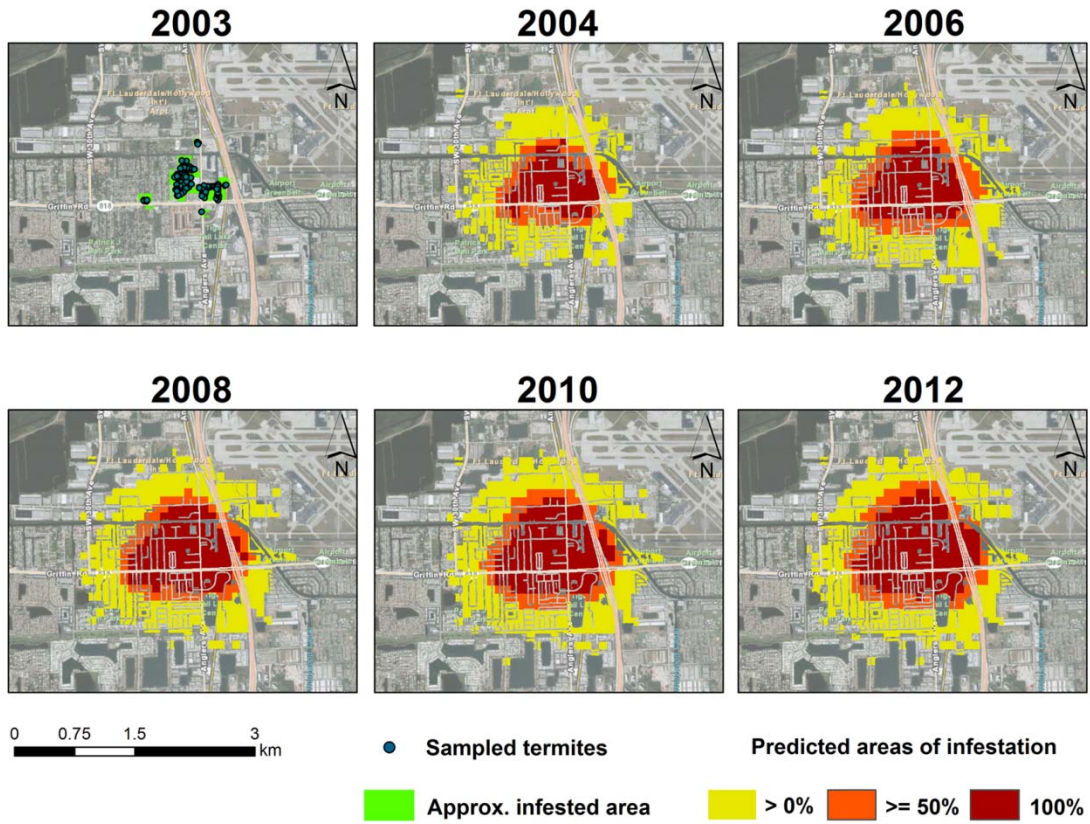
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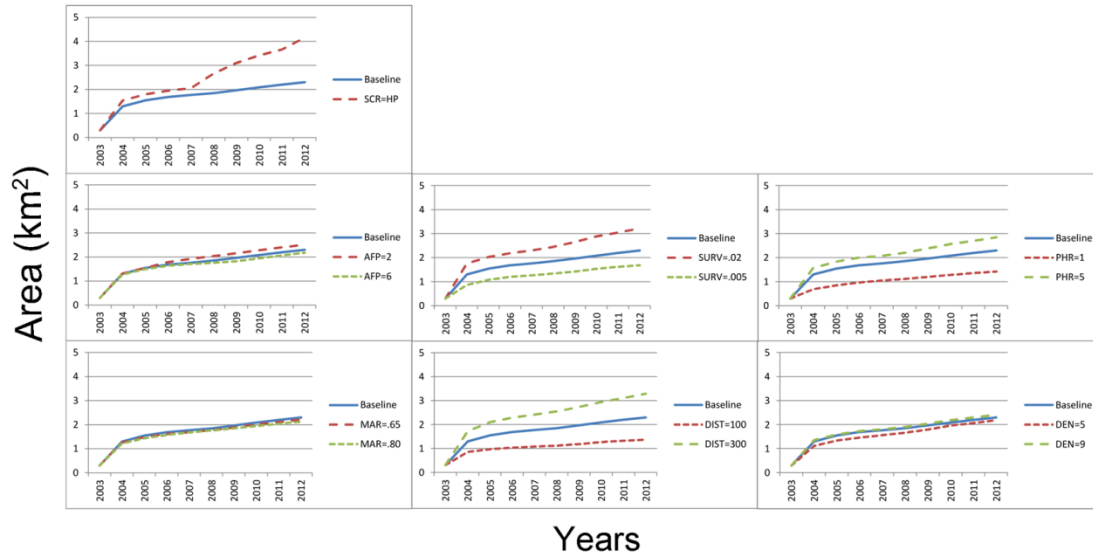
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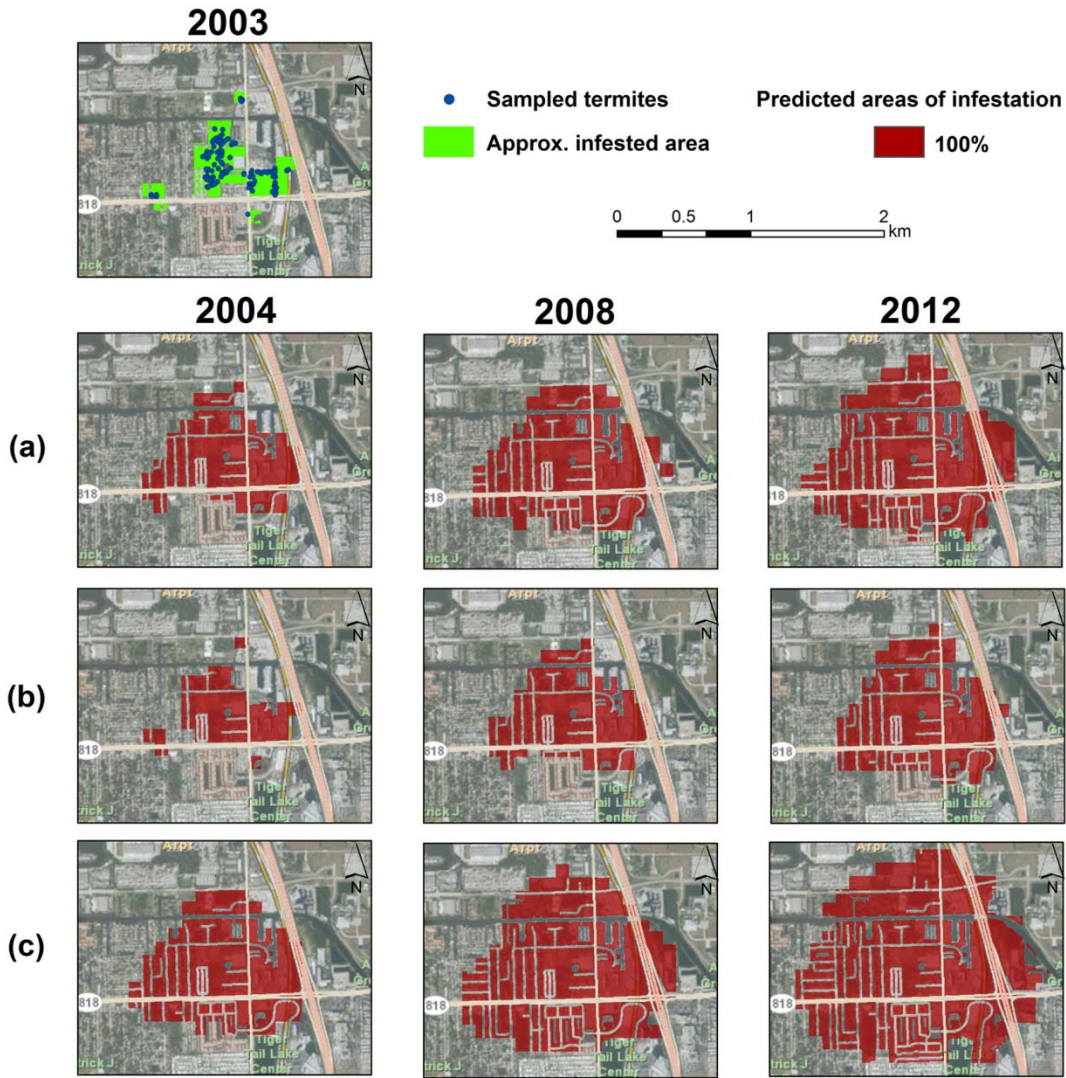
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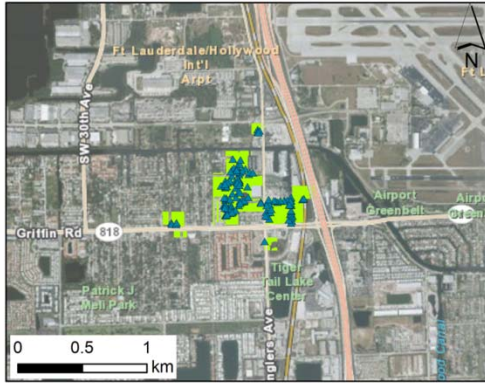


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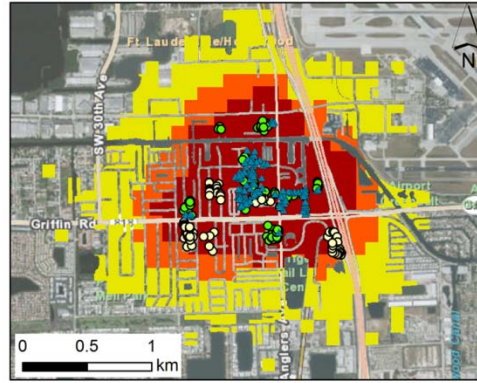


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2003



2012



- Approx. infested area**
- Sampled termites (2003)**

Predicted areas of infestation

- > 0%**
- >= 50%**
- 100%**
- Sampled termites (2012)**
- Sampled termites (2004-2011)**