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ORIGINAL PAPER

Potential spread of the invasive North American termite, *Reticulitermes flavipes*, and the impact of climate warming

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Abstract *Reticulitermes flavipes* is an invasive termite from North America that is found in several European countries, including France from north to south. It feeds on several timber species and can cause major damage when it infests lumber. Termites are urban pests: they are often found in and around towns and their expansion is closely linked to human activity. Although, by law, termite infestations must be reported and treated, *R. flavipes* continues to spread. To better identify areas that may soon be colonized, it is crucial to understand the mechanisms underlying the termite's spread at a fine spatial scale. However, the complexity of the species' dispersal dynamics (i.e., via swarming, budding, or human-mediated transport of infested material) and social organization render this process difficult. The goal of our study was to determine *R. flavipes*' potential to expand its current range within a region of France: Centre-Val de Loire. We focused on one administrative department within the region—Indre and Loire—where infestations are common and data on termite presence date back to the 1980s. We developed a spatiotemporal model to study the growth and dispersal of termite colonies within favorable habitat. Habitat favorability was defined based on the density of urbanization and annual mean minimum temperature. First, we modeled temporal population dynamics, using biological parameters describing the transitions between life stages/castes within colonies; we could thus estimate alates production. Then, using this information, we modeled termite dispersal within favorable habitat, and determined the termite's potential spread. We validated the results by comparing the model's output with actual data on the termite's range expansion between 1985 (when the termite was first observed in the region) and 2013. Finally, the model was used to predict the termite's future spread given climate warming for the period from 2013 to 2030. The results show that an increase in temperature should increase the amount of favorable habitat and, as a consequence, termites could continue to spread within this region. In addition to continuing current control efforts, it will be necessary to enact preventative strategies in newly favorable habitat. In these areas, monitoring efforts should therefore be intensified, as they might be able to slow down the termite's spread and limit its impact.

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Introduction

When seeking to understand biological invasions, it is crucial to characterize the interactions between invasive species and their biotic and abiotic environments. Different factors predispose a species to invading new habitats and, conversely, new habitats could be predisposed to invasions, as may be the case in anthropogenic landscapes (e.g., agricultural or forestry systems and urban areas) (Epanchin-Niell and Wilen 2014). However, a species goes through different phases between the time it arrives and the time it begins to spread, and different outcomes may result depending on environmental conditions (Facon et al. 2006).

Insects comprise the world's most diverse taxon and are also responsible for the majority of animal invasions worldwide. Their size means they are easily transported accidentally, and the probability of establishment increases with propagule pressure, which is perhaps the most important determinant of establishment success (Liebhold et al. 2016; Su 2013). This is especially true in the case of social insects (ants, bees, wasps, and termites), which are highly successful at invading new habitats thanks to their flexible social organization (Chapman and Bourke 2001; Scaduto et al. 2012). Interestingly, due to various ecological factors, colonies can vary in the number and relatedness of reproductives and dispersal modes (i.e., swarming vs. budding); such variation has direct consequences on colony density and species spread. It has been observed that accidentally introduced species spread faster than intentionally introduced species (Roques et al. 2016); all non-native social insect species have been introduced accidently, with the exception of the honeybee. In this area of research, ants have been a focal study taxon because they have succeeded in colonizing nearly all of Europe. They are generally ecologically dominant, and invasive ants are better than native ants at discovering resources (Bertelsmeier et al. 2015). Variation among colonies may be mediated by different ecological factors, such as anthropogenic disturbance, competition, food scarcity, and climate change. Even if there are some cases where climate change decreases the area suitable for species, it is often benefic for invasive species. Indeed, climate change could affect biological invasions by increasing habitat favorability, improving species survival, and facilitating species reproduction, and thus promoting population persistence (Walther et al. 2009). Consequently, it is essential to study the invasion dynamics of social insects and the effects of climate change if we wish to better understand the potential for non-native species to spread (Kenis et al. 2008). Furthermore, invasive social insects, such as certain termites, are of major economic importance (Alvarez 2016; Clément et al. 2001; Evans et al. 2013; Haury et al. 2015; Scaduto et al. 2012).

The genus *Reticulitermes* (Rhinotermitidae) contains well-known subterranean termite pest species (Evans et al. 2013). They are efficient at recycling organic compounds (i.e., the cellulose in dead wood) in natural ecosystems, mainly temperate forests, but they are highly destructive when they feed on trees in urban habitats and the wood found in buildings. Anthropogenic forces, such as the transport of soil, lumber, and paper, and ever increasing urban development have helped to create favorable, artificial habitat, characterized by warmer temperatures, higher humidity levels, and ad libitum food. Because subterranean termites have a cryptic lifestyle, their breeding structure is still poorly understood. According to Buchli (1958), who originally described reproduction in this taxon, and Scharf et al. (2003) (see Fig. 1), a single pair of primary reproductives (alates) founds a colony after swarming and, generally, disperses over a long distance. Such a colony will have a simple structure: one queen, an unrelated king, and their offspring. In *Reticulitermes* termites, primary reproductives are often supplemented or replaced entirely by secondary reproductives (kept at the larval stage) that develop from short-winged nymphs (brachypterous or nymphoid neotenics) or from workers (apterous or ergatoid neotenics). Since these neotenics cannot fly, they must mate locally and can only disperse over short distances by budding. They may also be carried short or long distances by human-mediated transport. These colony propagules can become autonomous and create new colonies. While colonies with neotenics are generally extended colonies, they can also fuse to form

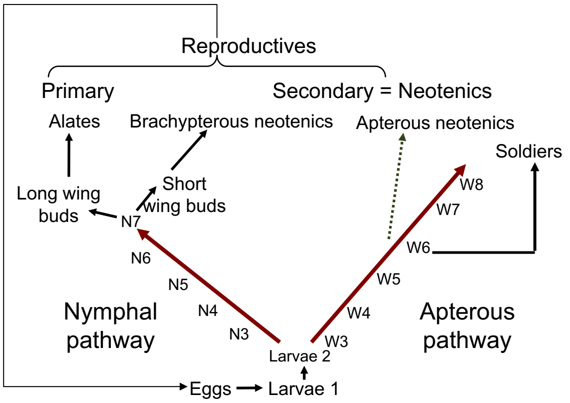


Fig. 1 The two main developmental pathways and the castes produced from the first two undifferentiated larval instars. Workers can remain true workers or, alternatively, can become soldiers or apterous neotenics. Nymphs can develop into (1) nymphs with long wing buds or alates (primary reproductives) or (2) nymphs with short wing buds that become brachypterous neotenics (from Buchli 1958; Scharf et al. 2003)

mixed colonies (Perdereau et al. 2010). This breeding flexibility probably facilitates their invasion and colonization of new habitats. Indeed, controlling *Reticulitermes* species is very difficult given their complex life history. But control is more efficient when the density of the invader is low. So if new colonies could be early detected then control could give better results.

Reticulitermes flavipes is an invasive species that has been introduced to several parts of North America, South America, and Europe. In the Americas, *R. flavipes* occurs outside its native range (i.e., the eastern US) (Ripa and Castro 2000; Austin et al. 2005; Su et al. 2006; Scaduto et al. 2012; Dedeine et al. 2016). In Europe, *R. flavipes* is found throughout France and has been observed in Austria [where it was first described by Kollar (1837)], Germany, and Italy (Weidner 1937; Clément et al. 2001; Ghesini et al. 2010). Recently, a study of *R. flavipes* genetics using samples collected in the termite's native and invasive ranges in both the Americas and Europe continents revealed that French populations were likely founded by termites from the region in and around New Orleans, Louisiana (Perdereau et al. 2013). The study also suggested these termites arrived directly from Louisiana, at the end of the seventeenth century at the earliest, which was when trade was initiated between France and the area that became New Orleans. French populations exhibit two colony-level traits that are shared by the Louisiana population—namely a propensity for colony fusion and the formation of large colonies containing numerous neotenics. Therefore, it could be said that the source population was preadapted for invasion. Indeed, these traits may have enhanced the colonization success of *R. flavipes* in France by helping the species establish itself, reproduce rapidly following introduction, and spread via human-mediated dispersal (Perdereau et al. 2015).

Mechanistic models are an essential tool when seeking to understand the spread of invasive species (Facon et al. 2015). The aim of this study was to use *R. flavipes* as a model species with which to explore the introduction and dispersal dynamics of an insect pest at the regional scale. First, we used geographic information to define habitat favorable to the termite. Then, we built a mathematical model that consisted of two parts: a temporal model based on colony-level dynamics representing species growth at the regional level (i.e., within the Centre-Val de Loire region of France) and a spatial model that represented the termite's spread within the administrative department of Indre and Loire; the department's main city, Tours (N 47.39379° E 0.68801°), has high infestation levels. The temporal model allowed us to estimate the annual production of primary and secondary reproductives (alates vs. neotenics, respectively), information we could then use in the spatial model to describe termite dispersal and thus spread. We also utilized the spatial model to predict potential termite spread through 2030 given normal conditions versus climate warming.

Methods

Data collected

Our data consisted of official declarations of termite presence made to the region's prefectures (department-level administrative centers) and research results from our various collaborators on the TermiCentre Project.

Defining favorable termite habitat in the Centre-Val de Loire region

Our spatial analysis used grid cells of 100 m × 100 m. Our data consisted of 509 survey points whose locations were provided by GPS coordinates, zip codes, or cadastral reference numbers. When surveys are from zip code or cadastral reference, we take the point at the center of the area. The mean area of a zip code in France is 5600 km^2 and the mean area of cadastral reference is 6700 km^2 in the department of Indre et Loire. Certain locations may have been surveyed twice if an infestation was monitored following treatment. To correct this, 189 points were eliminated because they corresponded to repeated measures. The surveys identified 320 locations of termite infestation.

Spatial pattern of infestation

First, we determined whether these points exhibited a random or non-random distribution pattern. A non-random pattern could suggest that the infestations were clustered, which could occur due to favorable habitat conditions. The Clark and Evans aggregation index (1954) is a simple way of quantifying the spatial pattern exhibited by presence/absence data. We found that the mean nearest-neighbor distance between infestation points was 598 m; this is significantly different from the mean distance of 5106 m that would be expected for randomly distributed points (z-score $= -30.166$; $p < 0.000001$), which meant that the points were clustered. Indeed, they formed two main groups, one in/near Tours (N 47.39379° E 0.68801°) and another in/near Richelieu (N 47.01667° E 0.31667°). In literature, the railroad tracks are suspected, as the road or navigation tracks, to be the way by which the termites arrived on new places (Ewart et al. 2017). The purpose of the spatial analysis is to test this hypothesis in the study region. The specificity of the railways is not only to provide a means of bringing termites, but also a way to set up them locally, which is not the case of the roads. We also exclude navigation transportation, which is no longer active on the Loire river since a long time in the region Centre-Val de Loire. During a transport of infested ground or wood, termites have the opportunity to stay near by the wooden sleepers, sometimes stored directly on the ground beside the railways, when replaced by sleepers in concrete: this has often been observed in St-Pierre-des Corps near Tours, one of the most important railways hubs in France. Presence of termites in proximity of railways and railways stations has been frequently observed in France and in particular in Paris in France (Baudouin et al. submitted). We therefore hypothesized that there must be spatial variables promoting clustering and examined evidence for the following explanations:

- the proximity of railroad tracks: while the tracks themselves do not directly promote termite survival, they are associated with infestations because they may enhance termite transport. Termite persistence post arrival depends on local habitat features. As a result, we also needed to look at environmental factors that could promote termite spread within the region (see below). Source of information: BD Topo® and National Institute of Geographic and Forest Information (IGN).
- the presence of buildings; source: BD Topo®, IGN
- the presence of urban green areas; source: Tour Urbanism Agency and OpenStreetMap
- climate: Climatic data come from monthly weather records of 130 stations on the Centre Val de Loire region and neighboring departments. Minimal and maximal temperatures as well as minimal and maximal humidity are stated each month during 22 years (1991–2013). We calculate the annual means of minimal and maximal temperature as well as minimal and maximal humidity. Then we interpolate these data with an Inverse Distance Weighting method (IDW) by using the software ArcGIS 10.2. Then we obtain minimal and maximal temperature and minimal and maximal humidity on each cell of the Region. Source: Météo France

Methodology

Spatial analyses can be used to examine the relationship between spatial patterns and variables of interest and thus help characterize underlying mechanisms. Since we did not have the degree of infestation, we looked at infestation frequency across grid space. Therefore, in our analysis, we used the estimated number of infestation points per grid cell.

To examine the influence of railroad tracks, we obtained the distances between infestation points and the nearest railroad tracks. We then examined the relationship between the distance magnitude and rank; geographers frequently use this approach to analyze urban population size and rank (Pumain 2012). The rank-size method allows describing inequalities in the repartition of a spatial phenomenon. For a set of locations ranked according to a statistical variable, this method analyzes the correlation between the rank and the value taken by the variable. In the absence of an effect, we would expect the relationship to be linear. When there is a breaking in the relation, there is a spatial discontinuity. So, if railroad tracks help explain the presence of termite infestations, then the curve should not follow a rank-size rule, a form of Zipf's law (Pumain 2012).

The other variables described actual habitat features and were dealt with differently. For each grid cell, we had the number of infestation points and a value for the variables listed above, namely the presence of buildings, the presence of urban green spaces, annual mean minimum and maximum temperature, and annual mean minimum and maximum relative humidity. We analyzed differences in variable values for infested versus uninfested grid cells for the region as a whole. In these analyses, the data were classified using the mean and the standard deviation of the distribution. When the confidence intervals for the mean variable values for the infested units and uninfested units did not overlap, we considered the variable to be significantly associated with infestation. The lower boundary of the class where there is an over-representation of infested units compared to uninfested units defined the minimum variable value at which conditions were considered to be favorable to termites. Using only the infested grid cells, we calculated Pearson's correlation coefficients for the factors we had identified as important ones.

The geographic and statistical analyses were performed using ArcGIS 10.2 and XLSTAT 2014.

Termite spread

New colonies, and thus the spatial propagation of termites, can result from the dispersal of alates from their parent colonies. New colonies can also result from the dispersal of neotenics; neotenics can actively leave their parent colonies accompanied by workers (i.e., budding) or be part of a colony fragment that is passively carried away by human transport (see Fig. 1 for an illustration of termite developmental pathways). Therefore, to estimate termite spread, we must know how many alates are produced by a colony each year. Our overall model has two parts. In the first part, colony temporal dynamics, namely the number of individuals in each life stage/caste, including alates, are modeled as a function of colony age. The second part describes colony spatial dynamics and includes dispersal, mating, and the creation of new colonies within favorable habitat.

Both parts of the model were developed in R (R Development Core Team 2014).

Temporal dynamics

We developed a compartmental model comprising six classes that correspond to the termite's six life stages/castes (L: larvae, W: workers, S: soldiers, Ny: nymphs, Ne: neotenics, and A: alates). Changes in the classes over time, represented in Fig. 2, are driven by six discrete equations (Eq. 1). We used time steps of 1 year; the model covered a maximum of 20 years, which is the theoretical maximum age of a primary pair (Buchli 1958). We modeled both types of reproduction: primary reproduction by the king and queen and secondary reproduction by neotenics. Primary and secondary reproduction rates, B_1 and b_{Ne}, are non-linearly dependent on colony age. In theory, a colony may start producing neotenics 3 years after foundation (Feytaud 1946; Thorne 1998). Each class has its own mortality rate, m_L, m_W, m_{Ny}, m_S, m_{Ne}, and m_A, which depends on the life expectancy for individuals in that class. Each year, a proportion p of larvae becomes either workers, at rate α, or nymphs, at rate $1-\alpha$. A proportion r of workers becomes either neotenics, at rate γ, or soldiers, at rate $1-\gamma$. A proportion q of nymphs becomes either alates, at rate β, or neotenics, at rate $1-\beta$. At the end of a given year, all alates leave the colony to swarm and found colonies of their own. Furthermore, some neotenics leave the colony and found new colonies by budding.

The system of discrete equations is as follows:

$$\begin{aligned}
L(t+1) &= B_1(t) + (1-p)(1-m_L)L(t) \\
&\quad + b_{Ne}(t)Ne(t)(1-m_{Ne}) \\
W(t+1) &= (1-r)(1-m_W)W(t) + \alpha p(1-m_L)L(t) \\
Ny(t+1) &= (1-q(t))\left(1-m_{Ny}\right)Ny(t) \\
&\quad + (1-\alpha)p(1-m_L)L(t) \\
S(t+1) &= (1-m_S)S(t) + r(1-\gamma)(1-m_W)W(t) \\
A(t+1) &= q(t)\beta(t)\left(1-m_{Ny}\right)Ny(t) \\
Ne(t+1) &= (1-m_{Ne})Ne(t) + q(t)(1-\beta(t)) \\
&\quad \left(1-m_{Ny}\right)Ny(t) + r\gamma(1-m_W)W(t)
\end{aligned} \tag{1}$$

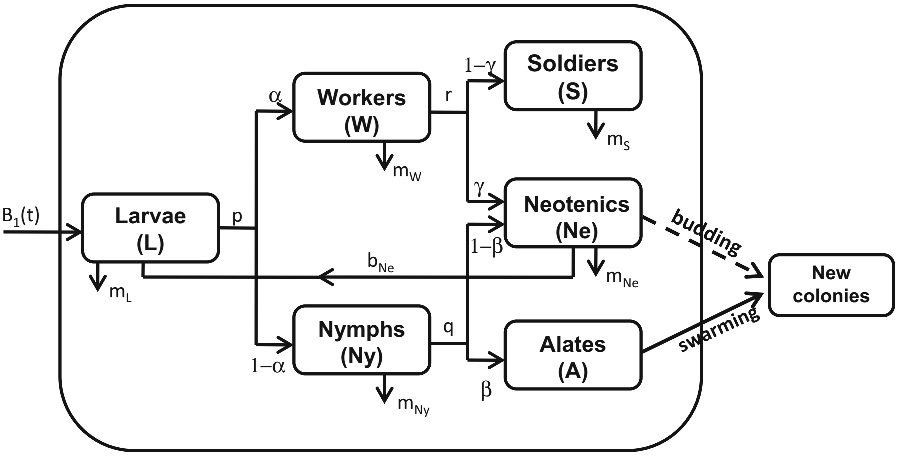


Fig. 2 Schematic of compartments and transitions in the temporal model of colony dynamics

Table 1 List of parameters used in the temporal model

Parameters	Description	Values
p	Proportion of larvae that become workers or nymphs	0.5
α	Proportion of larvae that has leaved larvae stage and become workers	0.2
$1-\alpha$	Proportion of larvae that has leaved larvae stage and become nymphs	0.8
r	Proportion of workers that become neotenics or soldiers	0.3
γ	Proportion of workers that has leaved worker stage and become neotenics	0.3
$1-\gamma$	Proportion of workers that has leaved worker stage and become soldiers	0.7
q	Proportion of nymphs that become alates or neotenics	0.8
β	Proportion of nymphs that has leaved nymphs stage and become alates	$\begin{cases} \beta = 0 \text{ for } t \leq 3 \\ \beta = 0.5 \text{ for } t \geq 4 \end{cases}$
$1-\beta$	Proportion of nymphs that has leaved nymphs stage and become neotenics	$\begin{cases} 1-\beta = 1 \text{ for } t \leq 3 \\ 1-\beta = 0.5 \text{ for } t \geq 4 \end{cases}$
m_L	Larva mortality rate	0.1 ind/year (life expectancy = 10 years)
m_{Ny}	Nymph mortality rate	0.1 ind/year
m_W	Worker mortality rate	0.1 ind/year
m_S	Soldier mortality rate	0.17 ind/year (life expectancy = 6 years)
m_{Ne}	Neotenic mortality rate	0.17 ind/year
b_{Ne}	Neotenic reproduction rate	$b_{Ne}(t) = 4000 - 250(t-4)$ ind/yr

The above parameters were estimated based on our personal knowledge of *R. flavipes* biology. It is important to note that parameter estimation is made challenging by the cryptic lifestyle and extreme life-cycle plasticity of *Reticulitermes* species in general and *R. flavipes* in particular.

The description and values of all the parameters used in the temporal model are provided in Table 1. Parameter values are based on our own research observations.

Larvae are produced by one of two ways: via the reproduction of primary queens or via the reproduction of female neotenics. Primary reproduction by the royal couple (the colony's only adults) depends on colony age. The function describing the number of larvae produced by a couple over time is detailed in Table 2.

Table 2 Values of the primary reproduction rate

t (year)	1	2	3	4	5	6	$7 \leq t \leq 19$	$t \geq 20$
$B_1(t)$	250	700	1560	2420	3280	4140	5000	0

Table 3 List of parameters used in the spatial model

Parameter	Description	Value	Source
R_L	Radial rate of colony spread as a function of the colony age (a)	1 m/year if $a \leq 5$ years 10 m/year if $a > 5$ years	Thorne et al. (1999), Vargo and Husseneder (2008), Perdereau et al. (2011) best judgment
K	Carrying capacity (maximal density of colonies)	2/cell of 100 m × 100 m	Data
SR	Sex ratio	0.5	Tonini et al. (2013); best judgment
$Surv$	Alate survival rate	0.01	Tonini et al. (2013); best judgment
$1/\lambda$	Alate mean dispersal rate	458 m	Shelton et al. (2006)
R_A	Pheromonal attraction distance	10 m	Best judgment
P_{LDD}	Annual probability of colony long-distance dispersal	0.1	Data
R_{LDD}	Maximum distance for human-mediated dispersal	10,000 m	Data; best judgment

Neotenics begin producing larvae after 3 years at a rate b_{Ne} that decreases over time. Nymphs begin producing neotenics after 3 years and thus $q = 0$ for $t < 3$ and $q = 0.8$ for $t \geq 3$. Nymphs produce alates after 4 years.

Spatial dynamics In the spatial dynamics model, the termite's spread (in terms of colony density, *N*) took place over a fine-resolution grid (cells of 100 m × 100 m) that covered a small part of the study region—the French administrative department of Indre and Loire (around 6000 km^2 in size). Termite spatial dynamics were described using a stochastic individual-based model that includes dispersal. The model takes into account: (1) the local dispersal of colonies by budding; (2) the shorter-distance dispersal of colonies by swarming; and (3) the long-distance dispersal of colonies by human-mediated transport.

(1) Local dispersal: Each colony spreads at a radial expansion rate of R_L meters per year, which depends on colony age (Table 3). The radius of the spatial distribution of a colony of age a is then given by: $\sum_{i=1}^{a} R_L(i)$. We then identified the grid cells covered by the colony. Termites can only spread into favorable habitat in which colony density is below the carrying capacity, *K*, which is expressed in numbers of colonies per km^2. If the carrying capacity was already reached on some grid cells, then this colony was not allowed to spread in this grid cell. Here, the individuals are colonies.

(2) Shorter-distance dispersal: This part of the model was derived from a model developed for another invasive termite, *Nasutitermes corniger* (Tonini et al. 2013). However, we estimated *R. flavipes*-specific parameter values when possible and obtained alate numbers from our temporal dynamics model. Alates can disperse from their parent colonies, mate, and found new colonies. From the temporal dynamics model, we obtained the number of alates produced by a given colony based on its age. Using the sex ratio, *SR*, alate sex (male or female) is randomly assigned. Then, based on the alate survival rate, *Surv*, a certain number of surviving alates are randomly chosen. The departure point for all the alates produced by a given colony is randomly chosen within the colony. Then, the arrival point of each alate is

simulated. The direction is randomly chosen using a uniform distribution, Unif[0,2π], and the distance is randomly chosen using a negative exponential distribution Exp(λ) with a mean dispersal distance of 1/λ (in meters). Then, a female can found a new colony if: (i) at least one male is located within the pheromonal attraction distance, R_A(m); (ii) the female is located within favorable habitat; and (iii) colony density does not exceed carrying capacity, *K*. Here, the individuals are alates.

(3) Long-distance, human-mediated dispersal: We first estimated the yearly probability of a long-distance, human-mediated dispersal event originating from each infestation point, P_{LDD}. Then, for each modeling year, the number of such events is given by multiplying this probability and the total number of infested grid cells, and then rounding this number to the nearest unit. For each long-distance dispersal event, the grid cell of origin is sampled among the cells already infested. Both the direction and the distance from the center of the origin cell are randomly chosen using uniform distributions (Unif[0,2π] and Unif[0,R_{LDD}], respectively). If the colony is transported to favorable habitat, then a new colony is established and the corresponding grid cell is considered as infested.

These parameters were estimated using published data on *R. flavipes* (1/λ), published data on *Reticulitermes* species (R_L), and occurrence data collected specifically for this study (*K*, P_{LDD}, R_{LDD}). We also used values obtained for *N. corniger*, such as those employed by Tonini et al. (2013), when estimates were unavailable for *R. flavipes*, but only when they were consistent with our knowledge of *R. flavipes* (*SR*, *Surv*) and our best judgment (R_L, R_A, R_{LDD}) (see Table 3). With regards to the parameters estimated from occurrence data, carrying capacity *K* was obtained from maximum colony density for the study area (observed in 2013), and P_{LDD} and R_{LDD}, the parameters describing human-mediated dispersal, came from the termite's distribution in 2013 and were determined based on our best judgment.

The description and values of the parameters used in the spatial model are provided in Table 3.

The termite's rate of spread was estimated from biological data. Colonies start producing neotenics after 3 years (Thorne et al. 1999). The mean foraging distance for *R. flavipes* colonies is 114.62 m in forested habitat on Oléron Island in France (Perdereau et al. 2011) and total foraging area can span up to 90,000 m^2 (Dronnet et al. 2005; Vargo and Husseneder 2008). We therefore considered that, through 5 years of age, colonies spread locally at a rate of 1 m/year; subsequently, they spread at a rate of 10 m/year.

The maximum colony density reported by Tonini et al. (2013)—7 colonies per hectare—seems relatively high compared to what has been observed in France for *R. flavipes*, where maximum colony density ranges from 0.5 (in urban areas) to 4 (in forested areas) (Dronnet et al. 2005). Therefore, we used a mean density of 2 colonies per hectare in the model.

With regards to the sex ratio, recent research has found it is equal (1:1) within *R. flavipes* populations in France (F. Dedeine personal communication). For alate survival rate, we used the value of 1% in Tonini et al. (2013) for consistency's sake.

Alate mean dispersal capacity was estimated using data for alates flown on flight mills (Shelton et al. 2006): the maximum flight distance for female *R. flavipes* alates was 458.3 m.

The pheromone attraction distance used by Tonini et al. (2013)—3 m—is too low for *R. flavipes*, which appears to detect pheromones at distances of 10 to 30 m. We ultimately used 10 m in our model. In Rhinotermitidae, the encounter rate of alates is also primarily density dependent.

Based on the study region's invasion history and recent results, human-mediated dispersal might explain around 10% of the area infested. Therefore, the probability of a long-distance dispersal event from each infested area was considered to be 0.1. The number of long-distance dispersal events was then calculated by multiplying this probability by the number of infested cells. Therefore, a higher number of infestation points means there is a greater probability of accidentally transporting infested material over a long distance. Based on the data for the study region, we considered the maximum transport distance to be around 10 km.

We assumed that colony longevity was infinite. Since the spatial model is stochastic, we ran it several times to gain a better representation of the termite's potential spread. For the period from 1985 to 2013, we ran the model 25 times, for 2013 to 2030 we ran the model 16 times. For the predictions with climate change, we ran it five times. Indeed, computation time increases exponentially with the number of colonies and there are much more colonies with + 1 °C and + 2 °C than without climate change.

Potential spread under normal conditions and given climate warming

Potential spread

In the study region, three main locations have been infested since the 1980s (Fondettes: N 47.40000° E 0.60000°; Richelieu: N 47.01667° E 0.31667; and Chouzé-sur-Loire: N 47.25000° E 0.13333°). Therefore, in the model's initial conditions, we treated these three points as having been infested since 1985. We then ran the model for the period from 1985 to 2013 and compared the output with actual observations from 2013 to validate the results. We ran the model 25 times and determined how well the results converged.

Then, we ran the model for the period from 2013 to 2030. The colonies and favorable habitat present in 2013 were the starting point for future spread. Colony age was the years since colony detection. Although this approach may not have provided an entirely accurate estimate of age, it was the best we could do. Since computation time was relatively long (e.g., it took almost 1 month for a single model run) and variance among runs was relatively low, we ran the model 16 separate times.

Potential effects of climate warming

One of the major consequences of climate change is increased environmental temperatures. Since higher temperatures are an important feature of favorable termite habitat, climate change could act to expand the amount of favorable habitat, thus contributing to the termite's spread. We modeled the effects of the temperature increase on the termite's spread; we ran the model five times. Since the model resolution was too small (100 m × 100 m) compared to the resolution of available climate projections (8 km × 8 km at best in France), we arbitrary considered a 1 °C increase in temperature, which is within the range of temperature increase predicted in France by 2021–2050 (Ouzeau et al. 2014).

Results

Favorable termite habitat in the Centre-Val de Loire region

Railroad tracks We determined how well the nearest-distance data followed the rank-size rule. For the region as a whole, the coefficient of determination, R^2, was 0.466. Consequently, the distance to the nearest railroad tracks explained about 50% of the variance in the occurrence of infestation points. The coefficient value closest to 1 corresponded to a distance of 211 m ($R^2 = 0.997$; Andrieu et al. 2017). These results suggest that railroads have helped spread *R. flavipes* throughout the Centre-Val de Loire region. However, it is important to note that 19% of the infestation points were found more than one km from railroad tracks, indicating there is a strong chance that other transport mechanisms are at play.

Presence of buildings The degree of urbanization was strongly associated with infestation. While 93.8% of infested grid cells were found in partially or completely developed areas, this percentage was just 11.3% for uninfested grid cells (Antier et al. 2014). The results show that built-up areas above 10 m^2 are favorable to termites (Antier et al. 2014).

Presence of urban green spaces There was no clear relationship between urban green spaces and termite infestations. Indeed, 0.2% of infested grid cells versus 4.1% of uninfested grid cells were found in urban green spaces, an insignificant difference. Consequently, this variable cannot help explain the occurrence of termite infestations.

Annual mean minimum temperature This variable was clearly associated with termite infestations. Annual mean minimum temperature was significantly different between infested and uninfested grid cells (Fisher's test, p value = 0.009). It would appear that termites are sensitive to extremely low temperatures: a habitat is favorable when its mean annual mimimum temperature is above 1.7 °C (see Table 4).

Annual mean maximum temperature and annual mean minimum and maximum relative humidity None of these factors were significantly associated with termite infestations (Fisher test: maximum temperature_p value = 0.067; minimum relative humidity_*p* value = 0.095; maximum relative humidity_*p* value = 0.059).

Defining favorable habitat

The results of the Pearson's correlation coefficients between variables restrained for the infested grid cells do not allow us to identify important correlations. Since there was no correlation, there was no need to proceed to a principal components analysis. We defined habitat favorability using decision-making tools commonly employed in land development planning and satellite imagery analysis (Caloz and Collet 2011). The combined effect of the two variables was expressed by assigning a 0 to unfavorable conditions and a 1 to favorable conditions; the two numbers were then summed. As shown in Table 5, there are 2 × 2 combinations possible when starting from the hypothesis that railroad tracks helped spread the termite within the region.

The percentage of infested grid cells in function of the four termites' settling conditions is logically coherent. The value 0.5% in the last condition, a priori unfavorable, results of the spatial resolution of 1 hectare. Twelve grid cells are infested whereas they have a built-up area under 10 m^2. But these grid cells are nearby some grid cells with a more important percentage of developed area.

Termite-free habitats

Based on data from the field, we removed all grid cells that were found in completely forested habitat (BD Forest®, IGN) and that were covered by water (lakes or rivers; BD Topo®, IGN). The reason of no termite settling in these areas is based on the temperature being too cold in forests of the studied Region, see information available to us.

We obtained a final map of favorable habitat (Fig. 3).

This map shows the potential of expansion of termites in case of improvement of their environment. The extent of this expansion is explained by the small variability of the climatic parameter on this region. Compared to the favorable area estimated by the present conditions, in blue on the map, the increase of 1 °C multiplies the area by 4.5 (Andrieu et al. 2017). Some of the favorable zones seem to be incoherent with the termites' natural ability of expansion because they are very distant from each other. These separate spots are developed area. Since human activity is a long distance spread's factor, it is not abnormal to obtain this kind of expansion. Thus, this result indirectly integrates the anthropogenic effect of potential infestation.

Table 4 Number and percentage of infested and uninfested grid cells per minimum temperature class (the temperatures at which termite infestations were common are italic)

Temperature class (in °C)	Number of infested grid cells	Number of uninfested grid cells	% of infested grid cells	% of uninfested grid cells	Relative difference
− 0.97 to − 0.83	0	2592	0	0.08	− 100.00
− 0.83 to − 0.51	0	26,208	0	0.78	− 100.00
− 0.51 to − 0.19	0	80,277	0	2.39	− 100.00
− 0.19 to 0.14	1	191,148	0.51	5.70	− 91.00
0.14–0.46	0	472,241	0	14.08	− 100.00
0.46–0.78	3	717,849	1.54	21.40	− 92.81
0.78–1.1	0	527,812	0	15.74	− 100.00
1.1–1.42	5	567,212	2.56	16.91	− 84.84
1.42–1.74	5	367,337	2.56	10.95	− 76.59
1.74–2.06	*84*	*271,495*	*43.08*	*8.09*	*432.21*
2.06–2.4	*90*	*83,464*	*46.15*	*2.49*	*1754.85*
2.4–2.71	7	24,768	3.59	0.74	386.15
2.7–3.53	0	21,888	0	0.65	− 100.00

Table 5 Association between variable conditions and termite infestations (1 = favorable habitat; 0 = unfavorable habitat)

Case	Variable conditions		Favorable habitat	% of infested grid cells
	Urban density > 10 m^2	Annual minimum temperature > 1.7 °C		
1	1	1	1	87.1
2	1	0	1	6.1
3	0	1	1	6.3
4	0	0	0	0.5

Termite spread

Temporal model

Given the parameter values of Tables 1 and 2 and assumptions, we found that each life stage/caste displayed different temporal dynamics as a function of colony age (Chouvenc and Su 2014). Figure 4 shows the model output for a colony for a 20-year period starting with colony foundation. After 20 years, we consider that alates production remains stable.

Termites' density increases exponentially. The time delay between the different life stages is due to the slow development of a new colony, with nymphs starting to produce in average neotenics after 3 years and alates after 4 years. The number of reproductives is limited by the number of individuals in the colony, more the colony grows, more the reproductive potential increases.

Spatial spread of termites

Figure 5 represents the occurrence of termite infestations between 1985 and 2013 in the French administrative department of Indre and Loire.

In 1985, three cities were known to be infested: Fondettes, Chouzé and Richelieu. Between 1985 and 2013 termites have colonized new territories around the three cities already infested in 1985. We observe that the new points of infestation are in the favorable area. This favorable area is concentrated in the center of the department.

Figure 6a depicts mean model output for the termite's distribution in 2013.

Predicted infestations points are close to the real infestations.

To validate our model, we compared model output with the termite's observed distribution in 2013. The areas infested in the model and in real life corresponded well, although the model slightly overestimated how far the termite had spread. In both the model and the observed data, the mean distance among colonies in 2013 was 1.5 km over a total spatial scale of around 100 km × 100 km.

We also used the model to predict the termite's spread from 2013 to 2030. Figure 6b represents the mean output for the termite's distribution in 2030.

Colonies of termites have dispersed around the three sources. The north of the favorable area is completely invaded whereas there is a part of the south which is still free from termites. Termites have propagated more around Richelieu and Fondettes than around Chouzé. This is because Chouzé is not enough favorable (see Fig. 5).

Impact of climate warming

First, we compared favorable termite habitat under normal conditions versus climate warming in the department of Indre et Loire. The favorable termite habitat expanded into the north of the department when temperatures increased (see Fig. 3). And secondly, we modeled changes in the termite's distribution through 2030 under normal conditions and given a temperature increase of 1 °C (Fig. 7).

As the favorable termites' habitat extends to the north when temperature increases of 1 °C, termites propagate to the north.

Discussion

Our results show the potential regional spread of *R. flavipes*, an invasive termite, in the coming years. The spatiotemporal model developed in this study, which includes detailed information on termite dispersal and

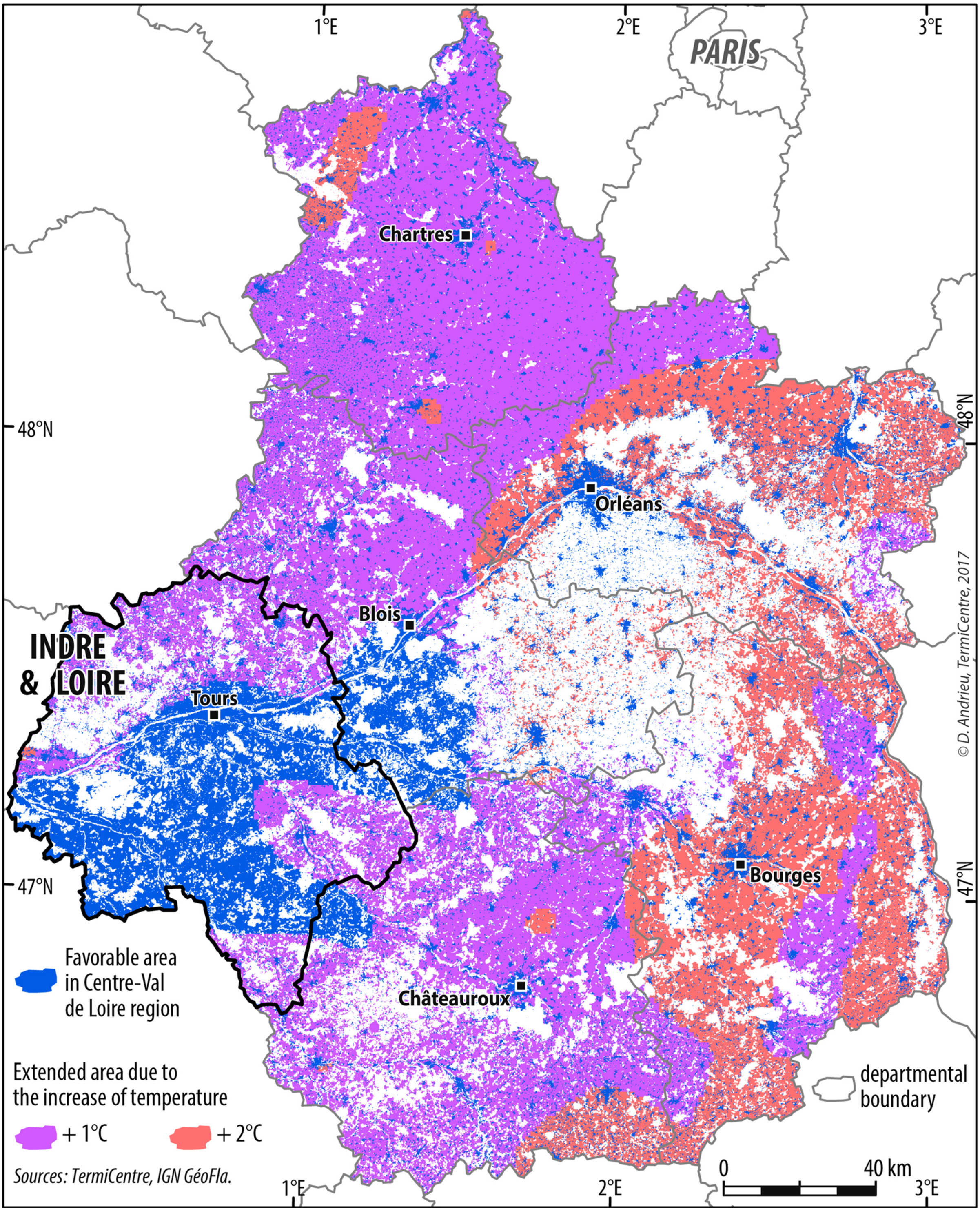
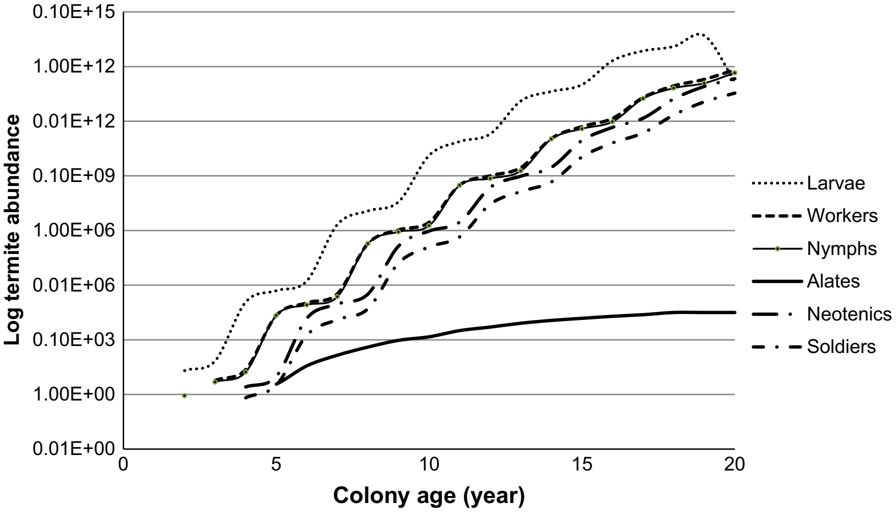


Fig. 3 Map of favorable termite habitat in the Centre-Val de Loire region. Blue area depicts the favorable area to termites taking into account the results of Table 5. Also depicted is the expansion in favorable habitat due to temperature increases (+ 1 °C in purple and + 2 °C in red)

Fig. 4 Termite abundance per caste as a function of colony age



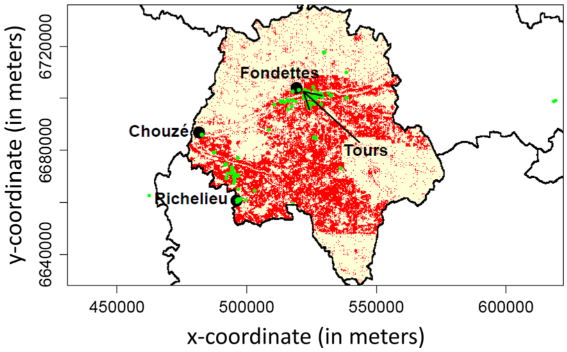


Fig. 5 Termite infestation points in 1985 (black circles) and in 2013 (green dots). Favorable habitat is represented in red

colony organization, may be helpful to urban development managers because its results highlight the geographical areas that should be carefully monitored. However, our findings should be interpreted with caution since there is some uncertainty with regards to the definition of favorable habitat and the accuracy of the spatial model.

Defining habitat favorability: discoveries and uncertainties

Based on our results, it should be possible to generate extrapolated continuous spatial data by integrating a

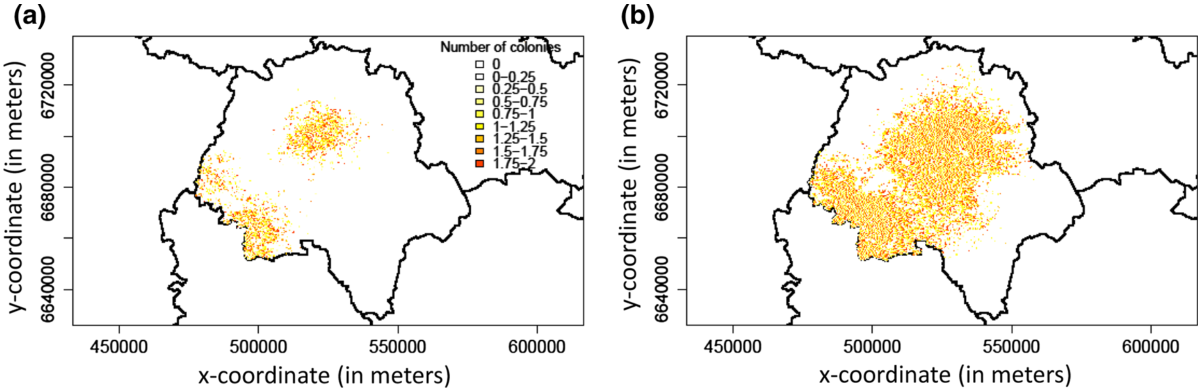


Fig. 6 **a** Termite presence in 2013 based on model output (mean of 25 replicates). **b** Termite presence in 2030 under normal conditions (mean of 16 replicates). Dot color represents colony density (*N*) in each grid cell

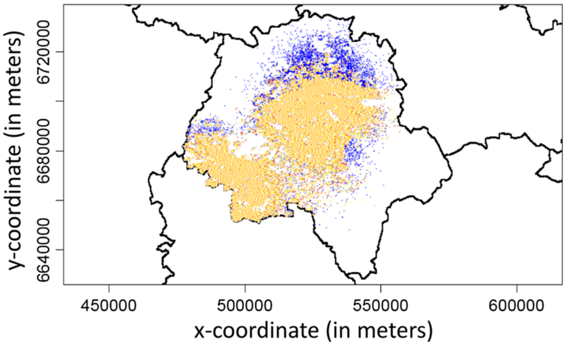


Fig. 7 Termite presence in 2030 under normal versus climate warming conditions (means of 16 versus 5 replicates, respectively). The additional colonies resulting from a 1 °C increase in temperature (blue dots) have been superimposed over the results from Fig. 6b

model parameter that describes the infestation probability (Tonini et al. 2014; Bertelsmeier et al. 2013) or to create a "confidence map," a tool used by archeologists to deal with incomplete data (Nuninger et al. 2011).

The spatial autocorrelation among the infestation points could be due to two factors: (1) habitat conditions favorable to termites in the Centre-Val de Loire region, which is of key interest to us, or (2) biased sampling. For example, the importance of the presence of buildings is likely related, in part, to the fact that professionals are specifically called into look for termites in buildings because they may be vulnerable to termite damage.

When data are analyzed using a grid system, they may be sensitive to cell location relative to variables of interest. For instance, there are 12 infested grid cells that are not associated with buildings although neighboring cells are. This challenge is well known to geomaticians and geographers (Langlois and Lajoie 1998). Nonetheless, the grid system remains a useful way of describing space that is free from administrative and political influences, which are of little relevance when studying termites.

It was difficult to assess the influence of urban green spaces on termite infestations for two reasons. The first relates to the social and functional definition of such spaces (Pin et al. 2013), which is too narrow given the range of infestation sites. Private gardens, public parks, and brownfields have all been found to harbor termites. Therefore, restricting analyses to public green spaces can yield unclear results. The second reason relates to the geographic information used to describe such spaces. Although the data for Tours came from a single source, it was very difficult to acquire equivalent data for the rest of the region. OpenStreetMap might have been helpful in this regard, but the information it provides is known to be heterogenous and incomplete (Petit et al. 2012) and would thus yield questionable results.

Termites' distribution is dependant of climatic conditions and more particularly of temperature. But these factors vary in function of the local environment. Based on our findings, it would appear that annual mean minimum temperature is the most important climatic restraint acting on termites—winter temperatures in the Centre-Val de Loire region likely limit termite spread. Although we also looked at temperature maxima, it would appear that there is not enough climatic variation in the region to determine if other climatic variables are also limiting. It would be interesting to carry out the same analysis across France as a whole to get a better picture of temperature-related constraints. An additional problem is that we are uncertain of the actual relationship between external temperatures and temperatures within the nest, given the termite's cryptic lifestyle. It is likely that environmental temperatures do not significantly affect colony conditions, but it could be that climatic factors prevent colonies, at the small scale, and species, at the larger scale, from establishing themselves in certain areas (Vargo et al. 2013). As the analysis of relative humidity shows, it is difficult to gain a clear understanding of this relationship because termites establish colonies in and around buildings, which allows them to avoid exposure to external climatic conditions.

Termite spatiotemporal dynamics: predictions, uncertainties, and limits

Some parts of the spatiotemporal model developed in this study were derived from the model described in Tonini et al. (2013). However, they were modified to reflect the specific behavior and biology of the North American termite, *R. flavipes*. We expanded the model by adding parts, such as the explicit description of growth (via compartments) and human-mediated dispersal.

The reliability of the model essentially depends on the reliability of the parameter estimates. Several parameters were difficult to estimate because data are lacking for our study species. In such cases, we relied on our best judgment (Table 3). Parameters related to reproduction are influenced by climatic and geographic variation (Vargo et al. 2013). Furthermore, as for many invasive species, the precise date on which *R. flavipes* arrived in the study region is unknown. While the first observations date back to the 1980s, termites could have arrived before the eighteenth century on boats carrying ornamental plants and wood.

The model results indicate that the termites spread far and fast from their points of introduction. The model also predicts that there will be a more limited expansion to the northern part of the department by 2030 (Fig. 6b). This pattern results because, theoretically, the termite will have spread throughout all favorable habitat by 2025 and will then be blocked by a thermal boundary. This boundary could shift if temperatures increase, allowing the termite to spread further north. Indeed, when a temperature increase of 1 °C was modeled, the termite spread further than it did under normal conditions and the expansion was particularly pronounced toward the northern end of the department. This result can be explained by the fact that the temperature increase (which is a realistic estimate of what we may experience in the near future) generated additional favorable habitat to the north. Such a scenario would allow termites in the department to move even further north and perhaps all the way to Paris, an area that is already heavily impacted by termite infestations (Clément et al. 2001; Dronnet et al. 2005). Although we do not present the detailed results here, we also looked at the impact of a 2 °C increase. However, no additional favorable habitat was created as compared to with the 1 °C increase (Fig. 3) and thus the termite did not spread further. The 1 °C increase in temperature also increased colony number by 8%, to around 6600 colonies. Here, it is important to recall that thermal constraints play an uncertain role, given that termite nests are often found inside buildings and are thus shielded from external conditions. Finally, it remains unclear why, in spite of increased temperatures, some habitats remain unfavorable to termites, such as forests, which are too humid.

From a methodological perspective, some improvements could be made. First, the spatial model is stochastic and, ideally, we should have run it numerous times to obtain a more representative picture of the termite's potential spread. However, the long computation time was a major constraint on the number of replicates we could perform. The spatial model had a fine scale (100 m × 100 m cells; same resolution as in Tonini et al. 2013) and was run over a large area (6000 km^2; only 100 km^2 in Tonini et al. 2013), resulting in a very large number of grid cells (1,070,280). The computation time needed increased exponentially with the number of years and colonies modeled. Consequently, we were able to perform 25 replicates when results were modeled from 1985 to 2013 (28 years and 3 initial colonies) and 16 replicates when the results were modeled from 2013 to 2030 (17 years but 480 initial colonies). We only ran five replicates for the climate warming scenario.

Second, it is important to note that the model overestimates the termite's potential expansion because it does not account for control efforts, which can be highly effective in reducing termite populations. However, the goal of this study was not to evaluate the efficacy of termite treatments but rather to identify the areas that may soon be invaded. They can thus be carefully monitored, and swift action can be taken if and when the termite appears. Indeed, research shows that it is easier to eradicate an invasive species if control measures are implemented early on (i.e., within 4 years of the first observations; Pluess et al. 2012). Generally, once the species is firmly established, it can reproduce. The population can then grow very rapidly, making control efforts difficult or impossible.

Perspectives

To understand and manage invasive insects, it is crucial to characterize their patterns of arrival and spread (Duan et al. 2015). Consequently, future research should examine if there were multiple introduction (and thus dispersal) events in the study region. Molecular ecology is one of the best tools for urban pest management (Vargo 2014) and is also very useful for delving into the origins, invasion dynamics, and life-history traits of the *Reticulitermes* termites we study (Perdereau et al. 2013, 2015).

We examined the potential spread of the invasive termite *R. flavipes* within the French administrative department of Indre and Loire using a spatial model. The next step is to apply this model to other departments in the Centre-Val de Loire region to predict where the termite will spread next and to take action to control it. For instance, the department of Loiret is a logical choice because a termite infestation was found there in 2013, in Fay aux Loges, which is near to the city of Orléans (E. Perdereau personal observations). The model could also be applied to other regions, such as the Paris region, which is highly infested. It could be interesting to explore model dynamics for regions with very different infestation rates (e.g., in highly infested Gironde versus little infested Normandy) or apply the model at the country level, for instance Italy and Spain which harbor large numbers of *Reticulitermes* infestations, at the difference of France where the infestations are more patchy, particularly in areas such as the studied region. However, it will be necessary to improve the model's computational efficiency. For instance, Tonini et al. (2014) derived a lattice-based model to reduce the computation time and obtained results very similar to those of their individual-based model.

Another possible research direction is to use our modeling approach with native European species that are abundant in urban environments in France, such as *R. grassei*. Indeed, France is the European country with the greatest number of *Reticulitermes* species (five of the six species known to occur in Europe; Clément et al. 2001). Furthermore, France is the only European country with termite-related legislation (Law No. 99-471; initially passed on June 8, 1999 but followed up with multiple additional decrees). In 2004, Uva and colleagues reported the presence of an invasive species in France that came from within Europe, and it is possible that non-native subterranean termite species differ in their invasive potentials and behaviors, as has been seen for four species of invasive ants (Bertelsmeier et al. 2015).

To better understand the invasion dynamics of urban pests, it is necessary to consider anthropogenic, sociocultural, and socioeconomic factors; we can thus better help afflicted inhabitants and communities (Haury et al. 2015). For instance, the model developed here could be used by those responsible for pest control efforts because it can help identify areas to which termites are likely to spread in the near future. Systematic monitoring could then be implemented in these areas to detect new infestations as early as possible and thus immediately apply control methods. Such predictive tools are all the more important given that habitat favorable to termites is likely to grow as a result of global warming. As a result, this approach could facilitate the eradication of termites in newly infested locations.

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