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Article

Predicting the spread speed of red imported fire ants under different temperature conditions in China

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SUMMARY

Red imported fire ants (RIFA, Solenopsis Invicta Buren), are invasive species that have strong negative impacts on ecosystems and human society. Since the invasion of Chinese Mainland in 2004, the average annual spread rate of RIFA in southern China has exceeded 26.5 km, showing a rapid expansion trend. Given that this species has two spread pathways - natural expansion (nuptial flight and nest migration) and human-mediated transmission (horticultural plant transfers, etc.), we hypothesized that natural mechanisms alone cannot account for the observed spread rate, and human activity induced transmission should be the dominant factor in its high spread rate. To test this hypothesis, we developed a mathematical model based on nuptial flight to simulate the natural spread process. We inputted historical temperature data from seven representative Chinese cities into this model. Simulations revealed a natural spread rate of merely 1.4-7.0 km/year, lower than the observed actual speed (26.5-48.1 km/year). This simulation result indicates that human-mediated transmission may be the main reason for the rapid spread in southern China.

INTRODUCTION

Red imported fire ants (RIFA), *Solenopsis Invicta* Buren, native to South America, are listed among "100 of the World's Worst Invasive Alien Species". They have invaded many regions of the world, causing strong negative impacts on the ecosystems, public health, and economic development (1-3). In China, the invasion of RIFA has caused substantial agricultural damage. For instance, in Fujian Province, direct and indirect economic losses attributed to RIFA amount to 744.70 CNY/ha and 2,756.48 CNY/ha, respectively (4). RIFA also pose a threat to human health. Surveys in four southern Chinese provinces reveal that over 30% of residents have been stung by RIFA and experienced itching, redness, and pustules to life-threatening anaphylaxis (4). In addition, RIFA reduce the diversity and richness of local arthropod species through resource competition and nest expansion (4). Thus, investigating the spread rate of RIFA in China is critical in predicting when those impacts happen and enabling local governments to deal with those impacts at an earlier stage.

When invading a new region, RIFA spread in two main ways: human-mediated transmission and natural expansion (5). Human-mediated transmission is caused by human activities, such as transporting flowers, trees, soil or garbage (5). Natural expansion refers to the spread achieved through natural mechanisms, including nuptial flight and nest migration, with the former being the main method of long-distance expansion (5). Nuptial flight (or mating flight) refers to aerial mating between alate females and males from nearby colonies (5). The alate females that complete mating will then fly to establish new colonies. Nuptial flight is not limited by seasons and can occur on any day in a year with appropriate temperature and humidity for RIFA (5).

Regarding the expansion of RIFA in China, existing research have mapped the potential invasion range and habitats of RIFA, predicted their changes due to climate change, and studied spread rate in the last 20 years in China (6-8). However, none of these studies focused on understanding the transmission dynamics of RIFA over time, which may be a critical piece of information for predicting and preventing the spread of RIFA. In terms of spread rate, RIFA invasion was first found in Chinese Mainland in 2004. As of 2020, RIFA had spread and invaded 448 regions in 12 provinces of southern China over a period of 16 years, with an average speed of 26.5-48.1 km/year (9). However, we hypothesized that the spread rate of RIFA through natural mechanisms such as nuptial flight should be much lower than this rate.

To compare the natural and observed spread rate of RIFA, we developed a mathematical model to quantify the natural spread rate without human activity and implemented this model in Python. In our model, we divided the expansion process into two phases: colony establishment and active dispersal. During the establishment phrase, our program simulates the process of a queen ant landing, constructing a nest and gradually reproducing into a mature ant colony. Upon reaching maturity, this colony will enter a dispersal phase, during which it will produce new alate female and release them to undertake the nuptial flight. The mated queens fly a certain distance, land in an area, and initiate subsequent cycles of colony establishment and dispersal. To calculate the spread rate, we set a running time in the model, such as 10 years, and then iteratively execute the establishment-dispersal cycle. The final output can provide the farthest spread distance and maximum spread rate (10).

During the model's establishment phrase, we developed a dynamic process from a single queen to a mature colony based on Korzukhin's algorithm (10). The model simulates the growth process in different environments by constructing a functional relationship between temperature and colony growth rate. Two critical temperature thresholds (21°C and 32°C) are defined in the model: when the temperature falls below 21°C, the colony enters a negative growth state; above

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21°C, the growth rate shows a positive temperature related increase; at 3°C, growth rate reaches its maximum: above 32°C, the colony sustains the maximum rate.

During the model's dispersal phrase, the system simulates spatial spread in the coordinate system of the program. We referred to Ryti's model and designed a circular spread model to simulate the nuptial flight process (11). The model defines an area centered on the original mother nest and with the maximum nuptial flight distance as the radius for generating new ant colonies. Then, model randomly generates flight angles and distances for each queen ant, and records the landing point coordinates of these queens in the system as the position of the new ant colony, and uses them as the starting point for the next spread cycle.

RESULTS

We selected seven representative Chinese cities in terms of geographical location and climate, namely Beijing in the north, Zhengzhou and Wuhan in the middle, Chongqing in the west, Nanjing and Fuzhou in the east, and Guangzhou in the south. We imported the monthly historical temperatures data of these seven cities into our model respectively. Through program execution, we obtained simulated spread rate of RIFA in these seven cities. Due to the stochasticity in the program simulation settings, we conducted multiple simulation runs for each city to improve result accuracy. Based on multiple running results, we calculated the average spread rate and standard deviation (**Table 1**).

In Beijing and Nanjing, our results show that RIFA cannot survive and spread, so we marked the spread rate of these two cities as 0 (**Table 1**). In the real world, no RIFA invasions have been detected in these cities, which match our simulation outcomes (4). The reason for this result in the simulation program is as follows: Beijing is the northernmost city among these seven cities in terms of geographical location, and also the city with the lowest average temperature. There are nine months in Beijing with a monthly average temperature below 21°C, and even two months below 0°C, long term low temperature causes the ant colony to shrink and disappear in the model. Nanjing has slightly higher temperatures than Beijing, but there are still eight months every year when the temperature is below 21°C, and in the simulation program, ant colonies cannot survive either (**Figure 1**).

Zhengzhou and Wuhan are two inland Chinese cities. Though Zhengzhou is located further north, the monthly average temperatures of the two cities are similar: seven months below 21°C and five months above 21°C annually (**Figures 2 and 3**). The results of the program simulation show that RIFA could survive and expand, but the spread rate is relatively slow. The expansion distances in ten years are 14.7km and 14.9km respectively (**Table 1**). In the real world, RIFA invasions have been detected near Wuhan, but no invasions have been observed in Zhengzhou to date (4).

Chongqing, Fuzhou and Guangzhou have relatively high monthly average temperatures, ranked from low to high as Chongqing, Fuzhou, and Guangzhou. The corresponding simulated 10-year expansion distances are 29 km, 43 km, and 70 km respectively (**Figures 4 - 6**). Among them, Guangzhou is one of the southernmost cities in China and also one of the regions with the highest temperatures. From the simulation results, it is also the area where RIFA expand the fastest and is most suitable for RIFA survival. In the real world, all three cities have already been invaded by RIFA, which are consistent with our simulation results (4).

In summary, China has a vast territory with a north-south span of about 5500 kilometers, resulting in significant differences in average temperatures among cities. Simply put, cities in the south have higher temperatures, while cities in the north have lower temperatures. According to our simulation results of different cities, the basic rule is that cities in the south are more suitable for RIFA to survive, with a faster spread rate. As the temperature decreases towards the north, the speed gradually decreases until they cannot survive.

DISCUSSION

The simulation results for the seven cities mentioned above are all based on the natural expansion mode of nuptial flight. Our results on the expansion potential of RIFA in Zhengzhou have an inconsistency with the reality. Our results shows that RIFA can expand in Zhengzhou, but currently there's no invasion there (4). We speculate that this inconsistency between the actual situation and the simulation results may be due to two reasons. First, RIFA's invasion in China is gradually advancing from south to north and has not yet spread to this area. Second, there may be other factors that hinder the expansion of RIFA, but these factors were not included in our simulation program.

Our results indicate the simulated natural spread rate of RIFA in China ranges from 1.4 to 7.0 km/year, which is far less than the observed spread rates of 26.5 and 48.1 km/year (8). This difference may result from another spread pathway – human mediated transmission, such as horticultural plant transfers. Therefore, it is necessary to take action to suppress the non-natural expansion caused by human activities. Suggested actions include: goods and transport vehicles from affected areas must undergo a thorough inspection and RIFA eradication pre-treatment; High risk materials such as garbage and food residues in affected areas should be immediately disinfected and treated. For areas with little human activity or intervention, the natural spread rate we provided can serve as a warning value for ant prevention.

	Average (km)	Standard Deviation (km)	Minimum (km)	Maximum (km)
Zhengzhou	14.70	0.24	13.79	15.00
Wuhan	14.87	0.11	14.46	15.00
Chongqing	29.35	0.28	28.50	29.90
Fuzhou	43.28	0.59	41.87	44.61
Guangzhou	70.03	0.47	69.12	71.47
Beijing	0	0	0	0
Nanjing	0	0	0	0

Table 1. Predicted spread distance of red imported fire ants. Predicted spread in seven Chinese cities in 10 years (2024-2034).

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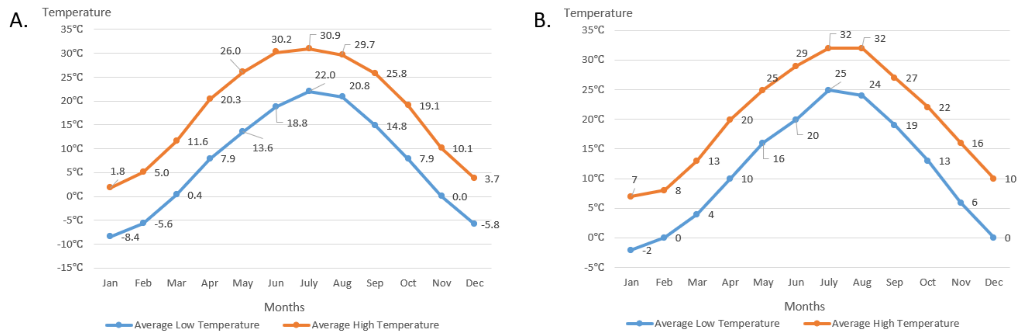

Figure 1. Temperature conditions in cities red imported fire ants cannot spread. Average temperature condition of **A)** Beijing and **B)** Nanjing from 1994 to 2023. The temperature data are from the website Weather Atlas (18).

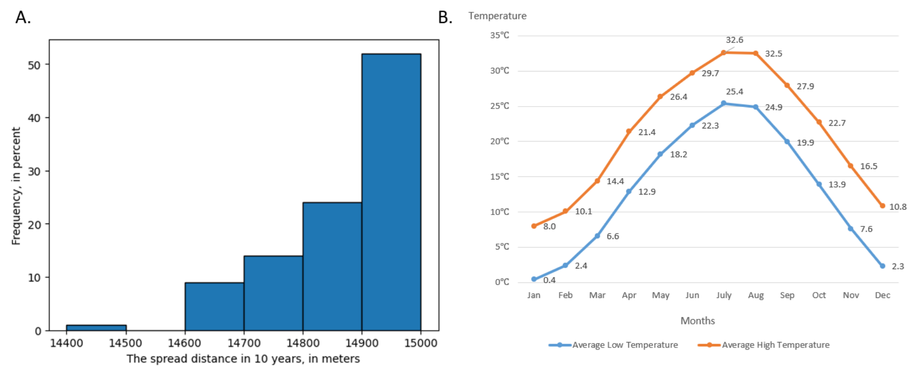

Figure 2. Expansion of red imported fire ants under temperature condition of Wuhan, China. A) The distribution of the maximum distance red imported fire ants can spread in 10 years (n=100), derived by simulating with T(i) using the temperature condition of Wuhan. **B)** The average temperature condition of Wuhan from 1994 to 2023. The temperature data is from the website Weather Atlas (18).

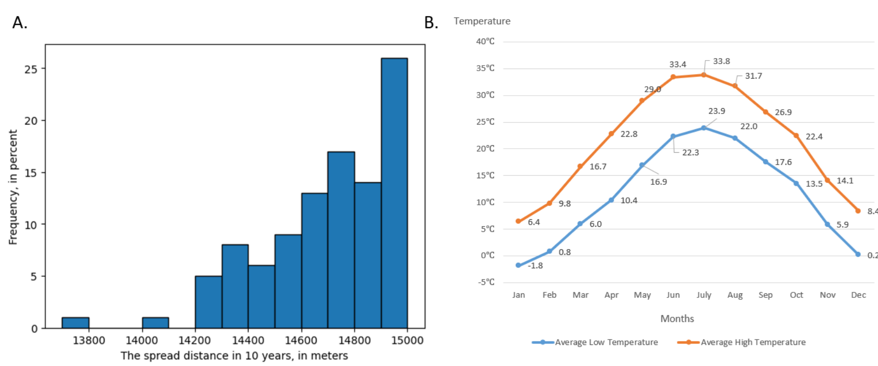

Figure 3. Expansion of red imported fire ants under temperature condition of Zhengzhou, China. A) The distribution of the maximum distance red imported fire ants can spread in 10 years (n=100), derived by simulating with T(i) using the temperature condition of Zhengzhou. **B)** The average temperature condition of Zhengzhou from 1994 to 2023. The temperature data is from the website Weather Atlas (18).

For example, once RIFA are found in a certain area, the surrounding areas that ants can naturally spread to are high-risk areas, and key prevention measures need to be taken.

Additionally, we used historical temperature data to simulate ant expansion. However, the world is impacted by climate change, with some regions experiencing hotter, longer summers and shorter winters. In China, due to the impact of urbanization, the temperature rise rate is higher than the global level. Data indicate that since the 1950s, the national average temperature has risen by 0.25°C per decade (12). This change may be more conducive to RIFA expansion and more areas could be threatened by RIFA invasion. Further studies will be needed to quantify the scope and speed of RIFA expansion caused by climate change, which can provide more references for the prevention and control of RIFA.

There are various factors that could affect the accuracy of the simulation process. The local temperature is a critical factor determining the survival and expansion of RIFA. In our simulation process we employed monthly average temperature data. Although the accuracy of results could theoretically be enhanced by using daily temperatures, it is not very practical for two reasons. First, daily average temperature data of a city

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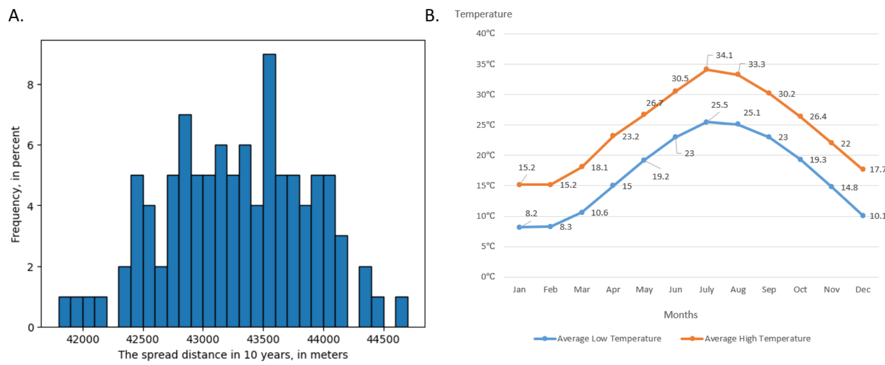

Figure 4. Expansion of red imported fire ants under temperature condition of Fuzhou, China. A) The distribution of the maximum distance red imported fire anta can spread in 10 years (n=100), derived by simulating with T(i) using the temperature condition of Fuzhou. **B)** The average temperature condition of Fuzhou from 1994 to 2023. The temperature data is from the website Weather Atlas (18).

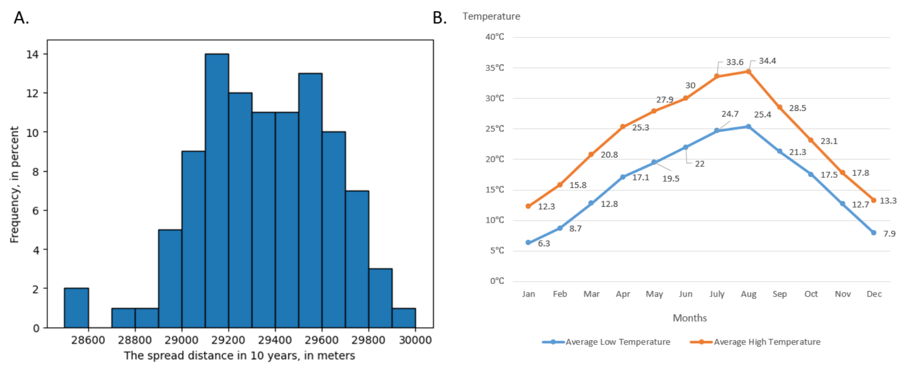

Figure 5. Expansion of red imported fire ants under temperature condition of Chongqing, China. A) The distribution of the maximum distance red imported fire ants can spread in 10 years (n=100), derived by simulating with T(i) using the temperature condition of Chongqing. **B)** The average temperature condition of Chongqing from 1994 to 2023. The temperature data is from the website Weather Atlas (18).

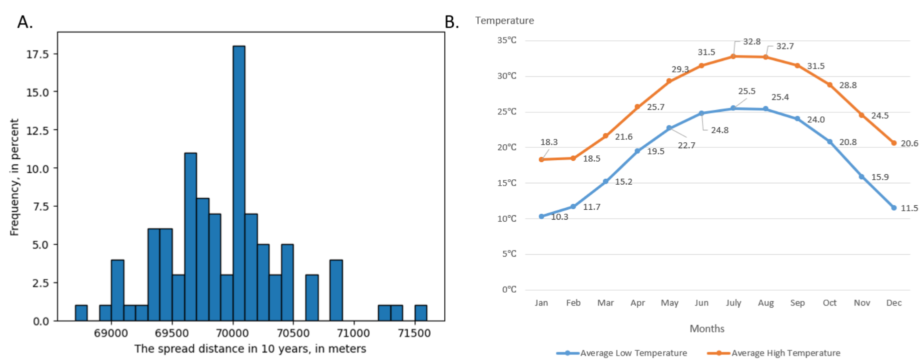

Figure 6. Expansion of red imported fire ants under temperature condition of Guangzhou, China. A) The distribution of the maximum distance red imported fire ants can spread in 10 years (n=100), derived by simulating with T(i) using the temperature condition of Guangzhou. **B)** The average temperature condition of Guangzhou from 1994 to 2023. The temperature data is from the website Weather Atlas (18).

is either not well documented or difficult to obtain. Secondly, if calculated based on daily temperature, simulation on a multi-year timescale would require high software computing power and hardware resources. Therefore, Modeling based on monthly temperature is a trade-off between accuracy and feasibility.

Another factor that could affect the accuracy of the simulation process is the distance of each RIFA nuptial flight. Previous studies concluded variations in nuptial flight ranges, including 0.1–1.6 km, 5 km, and 12–15 km (13). To quantify these variations' impact on model outcomes, we used data from Fuzhou to test the effects of the above three data on the final simulation results. While keeping other parameters constant, we ran the program with three different flight distances, and saw that the minimum spread rate is 0.42 km/year and the maximum is 4.3 km/year (**Figure 7**). As the purpose of our simulation is to study the possible maximum spread rate in natural conditions, we selected 12-15 km for

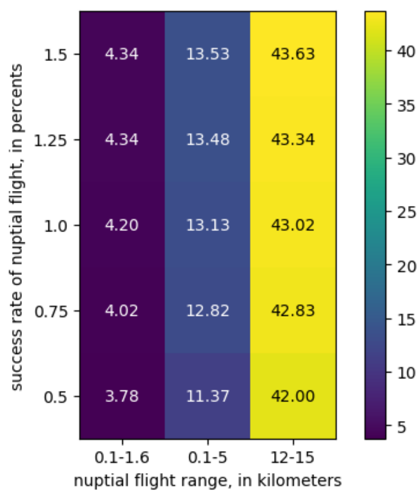

Figure 7. Impact of nuptial flight range and nuptial flight success rate on red imported fire ant's expansion distance (km) in Fuzhou in 10 years. The heatmap shows the average maximum spread distance of red imported fire ants in 10 years in Fuzhou under different nuptial flight ranges and success rates of nuptial flight (n=10). Figure created through simulating red imported fire ant expansion under each condition of nuptial flight range and success rate using the temperature condition in Fuzhou.

final nuptial flight distance. As this parameter can enhance the accuracy of the results, we could investigate it in future studies.

The third factor that affects the simulation results is the establishment success rate of RIFA colonies by newly mated queens. Queen ants are vulnerable to predators during nuptial flight and subsequent ground excavation process. Previous studies suggested that the success rate could be less than 1%, thus we adopted 1% as the success rate in our simulation to obtain the maximum spread rate (14). In theory, there is a positive correlation between success rate and expansion distance. To assess parameter sensitivity, we examined the impact of different success rates on the final expansion results. We used data from Fuzhou for testing, and while keeping other parameters constant, when the success rate increased from 0.5% to 1.5%, the final spread rate only increased from 4.2 km/year to 4.36 km/year (**Figure 7**). From the results, small changes in success rate have little impact on the final outcome.

In addition, there are some natural factors that can affect the expansion of RIFA. The amount of rainfall and soil humidity may influence the growth rate of a RIFA colony (15). Air humidity may influence the selection of nuptial flight dates (16). Additionally, there are two forms of ant colonies, monogyne (single-queen) and polygyne (multiple-queen). For polygyne, some new queens will return to their original colonies to form "super colonies." These massive colonies have greater environmental problems than monogyne (17). We did not incorporate these factors into our model. In further research, considering more factors in our model will improve the accuracy of the simulation results.

MATERIALS AND METHODS

In our model, we divide the expansion process into two phases: colony establishment and active dispersal. For the colony establishment phase, we simulated the development process from a new queen ant to a mature ant colony. The main factor influencing the development speed of an ant colony is temperature. We use *T*, in degrees Celsius, to represent temperature and *r* to represent colony growth speed. We referred to the equation in Korzukhin et al. **(Eqn 1)** (10).

$$S(T,t+1) = S(T,t) + r(T)S(T,t)[1 - \frac{S(T,t)}{S^{max}}] \qquad \text{(Eqn 1)}$$

Where *S(T,t)* is the colony size as described by territory area on the *t*-th day with an average temperature of *T*. S^{max} is the maximum size of a RIFA colony. *r(T)* is the growth rate of RIFA colony under an average temperature of *T* (13). For the value of *r(T)*, measured in days, we also referred to Korzukhin et al. **(Eqn 2)** (10).

$$r(T) = \begin{cases} 0.03286, \ T \geq 32 \\ 0.002987 * T - 0.06273, \ 21 \leq T < 32 \end{cases} \qquad \text{(Eqn 2)}$$

However, in our simulation program, the simulation duration is 10 years. If we use days as the simulation time unit, it will generate plenty of calculations. Therefore, we converted the above formula to use months as the fundamental simulation unit. We introduced *D(i)* to represent the monthly growth rate of the colonies. For *T* ≥ *32°C*, by estimating the time required for a colony to grow from *S0*, the initial area, to *Smax*, we obtained a *D(i)* of 0.0833. For *21°C* ≤ *T* < *32°C*, we use a monthly linear function to approximate the model in Korzukhin (10). For *T* < *21°C*, We also referred to the formula in Korzukhin et al. In this condition, RIFA colonies enter negative growth, and the rate of negative growth is *D(i)* = - *1* / *L(T)*, where *L(T)* is the average longevity of RIFA workers under average temperature of *T* (10). Our final monthly growth rate formula is a function on *T(i)* (**Eqn 3**).

$$D(i) = \begin{cases} 0.08333, \ T(i) \geq 32 \\ 0.0227 * T(i) - 0.4772, \ 21 \leq T(i) < 32 \\ -0.0649, \ T(i) < 21 \end{cases} \qquad \text{(Eqn 3)}$$

T(i), in degrees Celsius, is the average temperature in *i*-th month (**Eqn 4**).

$$T(i) = \frac{T_h(i) + T_l(i)}{2} \qquad \text{(Eqn 4)}$$

Th(i) is the average high temperature in *i*-th month. *Tl(i)* is the average low temperature in *i*-th month. We derived the temperature data *Tl(i)*, *Th(i)* from the website Weather Atlas (18). The length of the colony establishment phase, *G*, in months, is determined by *D(i)* (**Eqn 5**).

$$\sum_{i=1}^{G} D(i) > 1 > \sum_{i=1}^{G-1} D(i) \qquad \text{(Eqn 5)}$$

When an ant colony enters the active dispersal phase, it begins to produce alate ants. The total number of alate ants produced per acre on average is 187,000/year (16). For simplicity, we adopted the 50 colonies/acre from Morrill et al. (16). Reports indicate that the ratio of male to female alate ants is approximately 1:1 (19). Therefore, we estimated that each ant colony releases 3,800 alate ants per year for in nuptial flights, of which approximately 1,900 are female alates participating in the flight. As shown in the discussion section, the success rate of these female ants that can land and build

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a new colony does not exceed 1% (14). Therefore, we use 1% in our simulation system, which means 19 new ant colonies from one mature ant colony during each expansion.

In our program, a RIFA colony is defined as *(x, y, is)*, where *x* is the x-coordinate of the colony on the map, *y* is the y-coordinate of the colony on the map, and *is* is the number of months from the simulation beginning to the queen ant landing and building a nest. The first ant colony is *(0, 0, 0)* (**Figure 8**).

For the nuptial flight process, we assumed that the mated female ant would independently and randomly fly a distance *N* in a uniform distribution, with the value of *N* ranging from 12,000 to 15,000 m. The angle between the new landing point and the previous ant nest is θ. θ is 0 when the direction is due east and π when the direction is due west. Therefore, if the previous ant colony that produced the female ant is identified as *(x, y, is)*, the new ant colony will be $(x + N\cos\theta, y + N\sin\theta, i)$.

After a new queen ant lands, in the model, it means a new ant colony point is generated. The program will check the distance between ant colonies that are close together. We define *d*, in meters, the distance between any two colonies *(X0, Y0, t0)* and *(X1, Y1, t1)* (**Eqn 6**).

$$d = \sqrt{(X_1 - X_0)^2 + (Y_1 - Y_0)^2} \qquad \text{(Eqn 6)}$$

If $d < 1{,}000$, we believe that one colony has some overlap with the other colony. To simplify the calculation, the program would randomly delete one of the two colonies.

The program simulated the above colony establishment and active dispersal phases for each colony. The length of the colony establishment phase is determined by *G*. Every month, the program checks each ant colony to determine whether it meets the nuptial flight conditions. Only when the ant colony *(x, y, j)* at *i*-th month meets the following equation will the program perform a nuptial flight process for that ant colony (**Eqn 7**).

$$\begin{cases} i - j - G \equiv 0 (mod 12) \\ i - j - G > 0 \end{cases} \qquad \text{(Eqn 7)}$$

Where *G* is the length of the colony establishment phase as mentioned above.

We used Python to run the model. The codes are in the address https://github.com/flyinglower/Modeling-spread-speed-of-RIFA.git. Python has rich development libraries that can simplify the development process and improve development efficiency. We utilized the module NumPy for building arrays, the module Matplotlib for plots, and the module Pandas for data preparation. The simulation time is 10 years. We obtained a list of RIFA colonies in the simulation system. By calculating the distance between the farthest colony and the original colony, we could obtain the farthest spread distance. Then we repeated the simulation 100 times and to determine the mean and standard deviation of the maximum spread distance.

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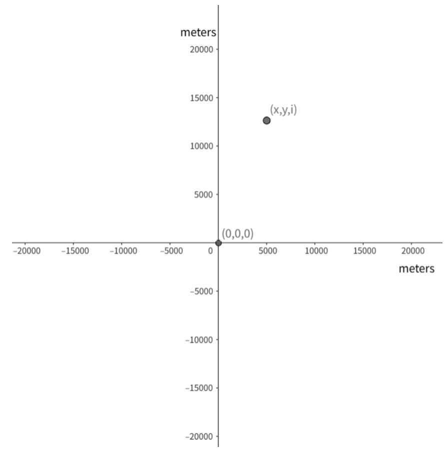

Figure 8. Definition of the first RIFA colony (0, 0, 0) and a RIFA colony (x, y, i) on map. On the map, (0, 0, 0) is the original colony, a colony built in the 0th month at the location (0, 0). (x, y, i) is a colony built in the i-th months at the location (x, y).

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