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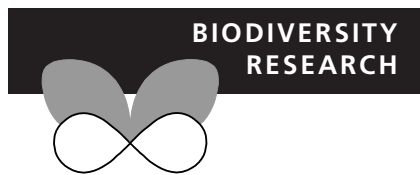
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Predicted range expansion of the invasive fire ant, *Solenopsis invicta*, in the eastern United States based on the VEMAP global warming scenario

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ABSTRACT

The red imported fire ant, *Solenopsis invicta* Buren, is an invasive pest from South America that currently occupies much of the south-eastern USA. Global warming is likely to allow range expansion of many invasive species, including *S. invicta*. We used a dynamic, ecophysiological model of fire ant colony growth coupled with models simulating climate change to predict the potential range expansion of *S. invicta* in the eastern USA over the next century. The climate change scenario predicted by the Vegetation–Ecosystem Modelling and Analysis Project (VEMAP) was used in our analyses. Our predictions indicate that the habitable area for *S. invicta* may increase by c. 5% over the next 40–50 years (a northward expansion of 33 ± 35 km). As the pace of global warming is expected to quicken in the latter half of the century, however, the habitable area for *S. invicta* in 2100 is predicted to be > 21% greater than it currently is (a northward expansion of 133 ± 68 km). Because the black imported fire ant, *Solenopsis richteri* Forel, occupies higher latitudes than *S. invicta*, the overall area of the eastern USA infested with invasive *Solenopsis* species could be greater than that estimated here.

Keywords

Biological invasions, climate change, Formicidae, global warming, *Solenopsis invicta*, VEMAP.

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INTRODUCTION

Average global temperature has increased over the past 100 years and is predicted to continue to rise (Houghton *et al.*, 2001). Although the Earth's climate is constantly in flux, recent changes have occurred at an accelerated rate. The effects of global warming are becoming evident for a great diversity of organisms (Penuelas & Filella, 2001; Schneider & Root, 2002; Walther *et al.*, 2002; Hughes *et al.*, 2003; Parmesan & Yohe, 2003; Root *et al.*, 2003). In addition to impacts on native species, global warming may allow range expansion in many exotic species. For example, many invasive species in the United States have tropical or subtropical origins, and their current northward distribution is limited by cold. Yet range expansion due to climate change has been modelled for only a handful of invasive species (e.g. Beerling *et al.*, 1995; Kremer *et al.*, 1996; Zavaleta & Royval, 2002; Kriticos *et al.*, 2003).

A prime example of such a species is the red imported fire ant, *Solenopsis invicta* Buren. Accidentally introduced to the United States from South America in the 1930s, this ant has since spread to > 128 million ha in 13 states and Puerto Rico (Callcott, 2002). *S. invicta* is one of the worst invasive ant pests (see reviews in

Adams, 1986; Lofgren, 1986; Davidson & Stone, 1989; Allen *et al.*, 1994; Vinson, 1997; Taber, 2000; Holway *et al.*, 2002). Although *S. invicta* is still expanding its range in the USA, its northern distribution is limited by cold temperatures and winterkill (Morrill *et al.*, 1978; Francke *et al.*, 1986; Porter, 1988; Callcott *et al.*, 2000).

The potential range expansion for this species, based on current temperature and rainfall patterns, has been modelled for the continental USA (Korzukhin *et al.*, 2001) and worldwide (Morrison *et al.*, 2004). Global warming, however, is likely to increase the habitable area for *S. invicta*. We adapted the model of Korzukhin *et al.* (2001) to estimate the increase in habitable area for *S. invicta* in the eastern USA over the next century, based on the VEMAP climate change scenario.

METHODS

Model description

We used the dynamic, ecophysiological model of *S. invicta* colony growth and alate production developed in Korzukhin *et al.* (2001). A number of other models have been used to predict

S. invicta range limits in the continental United States (Pimm & Bartell, 1980; Stoker *et al.*, 1994; Killion & Grant, 1995). We used the model of Korzukhin *et al.* (2001) because it contains certain advantages relative to the other approaches (discussed in Korzukhin *et al.*, 2001).

A full description of the model may be found in Korzukhin *et al.* (2001). In brief, the model assumes soil temperature is the key ecological factor regulating *S. invicta* colony growth and reproduction. Winter kill caused by extended cold periods is the principal factor limiting colony survival. Colonies are described by two dynamic variables: colony size (as described by territory area) and daily alate production. Variation in colony size is governed by changes in soil temperature. The model estimates colony growth with two time steps per day, based on minimum and maximum daily temperatures. The colony is allowed to grow and lifetime female alate production (i.e. total number of alates produced by a colony during its lifetime) is calculated.

Based on estimated alate production, the model predicts geographical range limits. *S. invicta* is predicted to survive in areas where queens are able to produce some critical number of alates, but not in areas where cold temperatures cause lower reproductive rates and winter kill. The critical threshold is the point at which each mature queen reproduces herself, in which case the number of colonies is neither expanding nor contracting.

Because the exact number of alates required is unknown, the model was calibrated based on empirical data obtained from the northern range of *S. invicta* in the central and eastern United States (Oklahoma, Arkansas, and Tennessee). Northward expansion in this region has occurred very slowly over the past decade, indicating the northern range limit is being approached. A critical threshold of 3900 alates was determined to indicate certain colony proliferation success, based on the coldest areas where *S. invicta* is known to survive across the landscape. This is a conservative estimate because it is based on current northward range limits; further expansion (in the absence of climate change) would necessitate revising this threshold. A full description of the calibration procedure may be found in Korzukhin *et al.* (2001).

Data sources

Historical weather data were obtained from National Oceanic and Atmospheric Association CD-ROMs (NOAA, 1994). Minimum and maximum daily soil temperatures (when available) and air temperatures were extracted for 2615 meteorological stations within the area of interest, from 1982 to 1993. Soil temperature (10 cm deep) data were not available for all stations, and regression algorithms were used to estimate soil temperatures from air temperatures. Minimum and maximum daily soil temperatures were entered into the model of colony growth and reproduction for each station selected (see Korzukhin *et al.*, 2001 for a full description of these procedures).

We restricted our area of interest to the continental USA below 39° N latitude and east of 103° W longitude because much of the northern USA is too cold, and much of the western USA too dry, to support *S. invicta*. States included were Alabama, Arkansas, Delaware, Florida, Georgia, Kansas (below 39° N latitude),

Kentucky, Louisiana, Maryland, Missouri (below 39° N latitude), Mississippi, North Carolina, Oklahoma, South Carolina, Tennessee, Texas, and Virginia.

To predict the future potential distribution of *S. invicta* due to global warming, we used the climate change scenario predicted by the Vegetation–Ecosystem Modelling and Analysis Project (VEMAP; Kittel *et al.*, 1995; 1997; VEMAP Members, 1995; <http://www.cgd.ucar.edu/vemap/>). VEMAP includes a high-resolution topographically adjusted climate history of the USA from 1895 to 1993 on a 0.5° grid, with soils and vegetation cover. Ecosystem models based on 1895–1993 data simulate current ecosystem biogeochemistry. To simulate future continental USA climate for the period 1994–2100, these models have been integrated forward using coupled atmospheric–ocean global climate model experiments with transient greenhouse gas and sulphate aerosol forcing, by the Canadian Centre for Climate Modelling and Analysis and the Hadley Centre for Climate Prediction and Research.

Range expansion

The area of interest in the south-eastern USA contained 943 0.5° × 0.5° cells, each having 106-year long (1994–2099) minimum and maximum temperature trajectories as determined by VEMAP predictions. We selected three time intervals for our analyses: 1994–99, 2040–49, and 2080–89.

We first compared VEMAP predictions for the period 1994–99 with historical data from 1982 to 1993 derived from meteorological stations included in the NOAA database. All NOAA stations were sorted by 0.5° × 0.5° cells and average temperatures were calculated for each cell. The VEMAP predictions matched the NOAA historical data for most cells fairly closely (Fig. 1). Twenty-three cells contained no NOAA weather stations with usable data; these cells were not included in the VEMAP–NOAA comparisons.

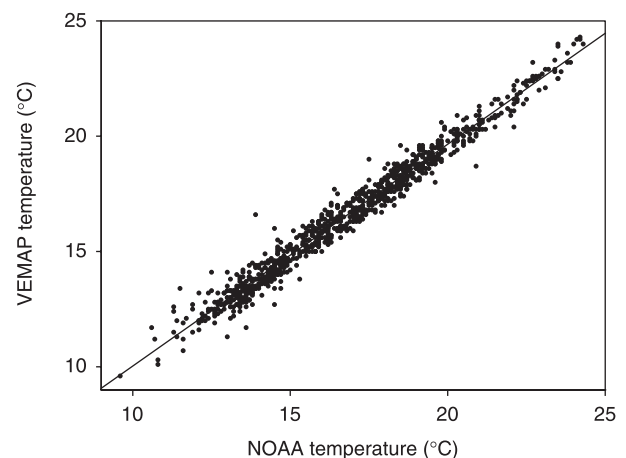


Figure 1 Correlation of air temperature data obtained from NOAA historical archives for 1982–93, and VEMAP predictions for 1994–99, by cell. ($y = 0.962x + 0.412$; $r^2 = 0.973$, $n = 920$, $F = 32603.54$, $P = 0.0001$, d.f. = 1).

Table 1 Longitude-dependent temperature corrections to VEMAP data

Longitude range (°W)	100–103	94–100	88–94	82–88	76–82
Temperature correction (°C)	–2.35	–1.53	–1.04	+0.05	+0.20
Accuracy of adjustment*	1	4	5	4	4

*NOAA and VEMAP cell number difference for each longitude range. The indicated temperature corrections were made to the VEMAP data so that the number of cells with *S. invicta* based on the VEMAP data more closely matched that of the historical data.

The *S. invicta* alate production model was run for: (1) historical station data sorted and averaged by cells; and (2) VEMAP predictions for 1994–99. The resulting *S. invicta* range (areas where alate production > 3900) included 577 cells based on historical data and 627 cells based on VEMAP predictions. Because this alate threshold (3900) was determined from empirical data in calibrating the model based on historical data (Korzukhin *et al.*, 2001), we used temperature corrections to adjust the VEMAP predictions. Subtracting 0.82 °C from the VEMAP predictions resulted in alate production > 3900 for 577 cells, matching the cell count for the historical data.

The resulting VEMAP range was skewed, however, with warmer temperatures predicted in the west and cooler temperatures predicted in the east. Thus we made longitude-dependent corrections. The entire 76–103° W longitude range was subdivided into 5 intervals, and separate adjustments were made for each. Each interval contained 12 cells (6°) of longitude except the westernmost, which contained only six (Table 1). After the temperature corrections were incorporated, the *S. invicta* alate production model was run for the VEMAP predictions for each of three time periods: (1) 1994–99; (2) 2040–49; and (3) 2080–89.

This procedure yielded numbers of 0.5° × 0.5° cells suitable for fire ant habitation. We also estimated the total area suitable for *S. invicta* habitation in the three time intervals by calculating the area of each 0.5° × 0.5° cell (which varies with latitude). Along the coastline and border with Mexico, some noticeable gaps among the cells were present, where the land area filled only *c.* 50% of a cell. To correct for this, and make our statewide area estimates equivalent to known areas, we added a total of eight cells with 50% of the average cell area.

RESULTS

Predictions (on a finer scale) for the potential distribution of *S. invicta* in the continental USA derived from the alate production model and based on historical data from NOAA, as well as the current, realized distribution, are presented in Korzukhin *et al.* (2001) or may be found online (http://cmave.usda.ufl.edu/ifahi/ifarange_us.html). The VEMAP predictions for the 1994–99 period were adjusted to match the current potential distribution as closely as possible. It should be noted that these predictions represent the potential maximum distribution of *S. invicta* (in the absence of climate change), rather than the current realized

Table 2 Predicted increase in habitable area for *Solenopsis invicta* in the eastern USA due to global warming

Period	Number of 0.5° cells occupied*	Total area occupied† (× 1000 km ²)	Temperature change‡
1994–99	594	1565	
2040–49	618	1648	< 1 °C
2080–89	722	1901	≥ 3 °C

*Not including 'partial' cells along the coastline.

†Assuming all cells are completely occupied; including 'partial' cells along the coastline.

‡Annual minimum temperature anomaly, based on VEMAP simulations (<http://www.cgd.ucar.edu/vemap/>).

distribution. This species is still gradually expanding its range in the continental USA, and is predicted to move northward by 80–150 km in the eastern USA even in the absence of climate change (Korzukhin *et al.*, 2001).

Based on the VEMAP climate change scenario, our model predicts the area suitable for *S. invicta* habitation will increase from 594 0.5° × 0.5° cells (*c.* 1,565,000 km²) at present to 618 cells (*c.* 1,648,000 km²) in 2040–49, and 722 cells (*c.* 1,901,000 km²) in 2080–89 (Fig. 2, Table 2). Thus the next *c.* 40 years would see a relatively small increment of 24 cells (*c.* 83,000 km²), but the following 40 years would see a much larger increment of 104 additional cells (*c.* 253,000 km²). In most longitudes, the increase in habitable area along the northern boundary would extend 0–1 cells by 2040–49, and an additional 1–3 cells by 2080–89. Each cell is 55.7 km in the north–south dimension, and the northward increase in habitable area for *S. invicta* would be 33 ± 35 (mean ± SD) km by 2040–49, and 133 ± 68 km by 2080–89, assuming cells are entirely habitable.

States that would see relatively large increases in habitable area for *S. invicta* include Oklahoma, Arkansas, Tennessee, and Virginia. Expansion into the Texas panhandle may be limited by dry conditions (see Discussion). Further expansion in the eastern North Carolina region is not predicted by the model, probably due to the higher elevations and thus colder temperatures of the Appalachian Mountains. By 2080–89, Delaware and Maryland would be susceptible to invasion, and *S. invicta* may be able to inhabit areas north of 39° latitude along the Atlantic coast.

DISCUSSION

The red imported fire ant, *S. invicta*, was accidentally introduced into Mobile, AL in the 1930s or 1940s (Callcott & Collins, 1996) and has since spread to occupy > 128 million hectares in 13 states and Puerto Rico (Callcott, 2002), despite federal efforts to stop or slow its spread (Lockley & Collins, 1990). This species extended its range by *c.* 8 km per year during the period of maximal expansion in the 1940s and 1950s (Wilson & Brown, 1958). Because it outcompetes most other ant species, and preys upon a great diversity of arthropods (Porter & Savignano, 1990), the factor(s) limiting its spread are likely to be abiotic (*i.e.*

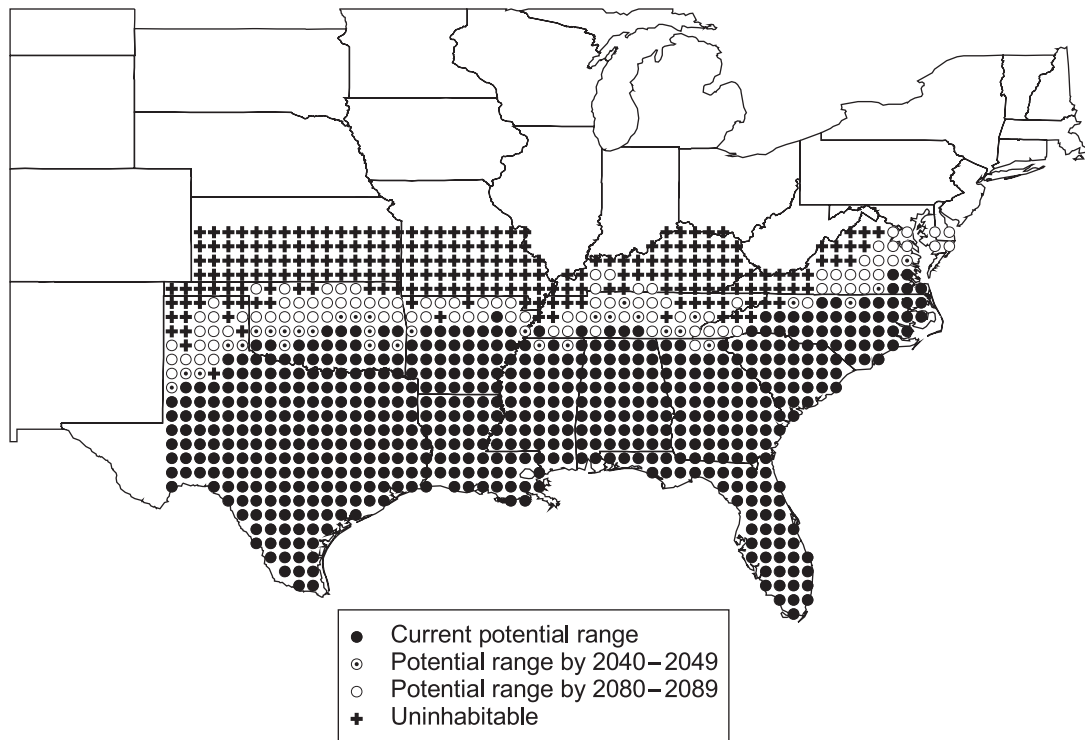


Figure 2 Map showing current and predicted potential range of *Solenopsis invicta* in the south-eastern USA under VEMAP climate change scenario.

climatic) rather than biotic (i.e. interspecific interactions, dispersal ability).

Our model predicts an increase of *c.* 5% in the habitable area for *S. invicta* in the eastern United States within the next 40–50 years based on the VEMAP climate change scenario. As the pace of global warming is expected to quicken in the latter half of the century, however, the habitable area for *S. invicta* in the eastern United States is predicted to be *c.* 21% greater than it is currently.

Our model considers only temperature as a limiting factor to *S. invicta* survival. Arid conditions will also limit the distribution of this species. Over the area of the south-eastern USA considered, however, only the western edge and parts of south Texas may be too dry for *S. invicta* survival (Korzukhin *et al.*, 2001). Extension of this model to other areas (e.g. the western USA) would require consideration of precipitation data (as in Morrison *et al.*, 2004) to accurately predict occurrence probabilities of *S. invicta*. Mountainous topography, which may be associated with variation in temperature or precipitation over relatively small two-dimensional distances would also complicate such predictions. *Solenopsis invicta* may be able to survive farther north than predicted in urban environments or other areas with artificial heat sources. This species may also be able to temporarily expand its range into colder regions during unusually warm years (Callcott *et al.*, 2000).

Because the last available NOAA temperature data (at the time of the modelling) was for 1993, and the first available VEMAP data was for 1994, there is no temporal overlap in the NOAA-historical-temperature–VEMAP-predicted-temperature comparisons. Some warming may have occurred during this period

(1982–99), and because we adjusted the model without taking this change into account, our predictions could be slightly conservative. However, this is not likely to be a large source of error for two reasons: (1) Our predictions are on a relatively coarse scale ($0.5^\circ \times 0.5^\circ$ cells); and (2) global warming during this period is expected to be relatively minor compared to the latter part of this century.

The accuracy of our estimates is limited by the size of the VEMAP cells, which cover, on average, 2583 km², and decrease in area with increasing latitude. Adding some additional partial cells to compensate for coastline and border irregularities was necessarily subjective. Furthermore, cells along the northern boundary are probably not entirely habitable or uninhabitable at any given time, but some fraction of each cell likely contains habitable and uninhabitable regions. Yet, given that our area of interest contains 943 cells encompassing almost 2.5 million km², the error due to these sources amounts to only a small percentage of the estimated habitable areas. The estimated habitable area in 2080–89 is likely to be a slight underestimate, given that the model predicts *S. invicta* will survive further than 39° N latitude along the Atlantic seaboard.

In the only other published account of the effects of global warming on *S. invicta* distribution, Zavaleta & Royval (2002) simulated the potential spread of this species in the eastern USA. They examined the relationship between January mean minimum temperatures and *S. invicta* occurrence probabilities, and used this relationship to predict future range expansion for temperature increases of 1–4 °C. Their results consisted of predicted increases in the area of infestation (on a county-by-county basis) for each

1 °C increase in temperature. Their predictions, however, were not linked to any specific climate change scenario or timetable.

Zavaleta & Royval (2002) predicted the total area of infestation by *S. invicta* would increase from 1,261,000 km² (currently) to 2,038,000 km² given a 3 °C rise in temperature, and to 2,271,000 km² given a 4 °C rise. Their estimates may not be directly comparable to ours because of a different western limit (i.e. they considered the eastern USA 'east of the Rocky Mountains'). Furthermore, their starting point is the current realized range of *S. invicta*, whereas ours is the current potential range (Korzukhin *et al.*, 2001). Nevertheless, their method does predict a relatively greater increase in habitable area (i.e. potential range) in response to global warming.

The method of Zavaleta & Royval (2002) is likely to overestimate this potential range because they used occurrence probabilities of fire ants predicted by January mean minimum temperatures to predict future infestation. Intermittent periods of cold that could cause winterkill in *S. invicta*, however, may not be reflected in average monthly temperatures, and means would tend to mask the lowest temperatures that would be the most critical for fire ant survival. Our model, by comparison, simulates the growth and survivorship of a fire ant colony over time based on daily minimum and maximum temperatures.

Finally, it should be noted that our model was calibrated based on the biology of the red imported fire ant, *Solenopsis invicta*. The black imported fire ant, *Solenopsis richteri* Forel, which is also an invasive pest, occurs at slightly higher latitudes than *S. invicta* both in the USA and in its South American homeland. This suggests that *S. richteri* may be able to spread somewhat further north than *S. invicta* during global warming, and the overall region of the eastern USA infested with invasive *Solenopsis* species would be greater than that estimated here.

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