



Potential global range expansion of the invasive fire ant, *Solenopsis invicta*

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Abstract

The red imported fire ant, *Solenopsis invicta* Buren, is an invasive pest that has become widespread in the southern United States and Caribbean after introduction from South America in the 1930s. This species, which has diverse detrimental impacts on recipient communities, was recently discovered in Australia and New Zealand and has the potential to colonize numerous other regions. We used a dynamic, ecophysiological model of colony growth to predict the potential global range expansion of this invasive species. Based on minimum and maximum daily temperatures, the model estimates colony alate production and predicts future geographic range limits. Because *S. invicta* populations are limited by arid conditions as well as cold temperatures, we superimposed precipitation data upon temperature-based predictions, to identify regions that do not receive enough rainfall to support this species across the landscape. Many areas around the globe, including large portions of Europe, Asia, Africa, Australia, and numerous island nations, are at risk for *S. invicta* infestation. Quarantine officials should be vigilant for any accidental introductions of this pest in susceptible regions. Costs of eradication increase dramatically as the area of infestation grows, and large infestations may be impossible to eradicate. Other South American *Solenopsis* fire ants (e.g., *S. richteri* Forel) may become invasive if the opportunity arises, and our predictions for *S. invicta* may approximate the potential range limits for these species as well.

Introduction

Exotic ants are among the most problematic invaders. Many ant species, particularly those of tropical and subtropical origins, are easily transported around the globe by human commerce (McGlynn 1999). Some of these species are known to have wide ranging deleterious impacts on the native fauna of invaded regions (e.g., Vander Meer et al. 1990; Williams 1994; Human and Gordon 1997; Jourdan 1997; Holway 1998; Vanderwoude et al. 2000).

One of the most notorious ant invaders is the red imported fire ant, *Solenopsis invicta* Buren. *Solenopsis invicta* detrimentally impacts human health, livestock,

wildlife, crops, machinery, and electrical equipment (see reviews in Adams 1986; Lofgren 1986; Davidson and Stone 1989; Allen et al. 1994; Vinson 1997; Taber 2000). This species may also have dramatic, wide-ranging impacts on the biodiversity of invertebrates in invaded areas (e.g., Porter and Savignano 1990; Morris and Steigman 1993; Gotelli and Arnett 2000; but see Morrison 2002).

Native to sub-Amazonian South America, *S. invicta* was probably introduced into the United States in the 1930s or 1940s (Callcott and Collins 1996). It now occupies >128 million hectares in 13 states and Puerto Rico (Callcott 2002), is established on numerous Caribbean islands (Davis et al. 2001), and was recently

discovered in New Zealand (Harris 2001; Pascoe 2001) and Australia (Natrass and Vanderwoude 2001; Solley et al. 2002).

Although this invader may ultimately impact many regions of the globe, no previous attempt has been made to estimate its potential worldwide distribution. We adapted the model of Korzukhin et al. (2001), which was used in predicting range limits of *S. invicta* in the continental United States, to estimate the potential global range of this invader. Identification of geographical areas that are climatically susceptible to *S. invicta* infestation should facilitate efforts to limit the further expansion of this pest ant.

Materials and methods

Model description

We used a dynamic, ecophysiological model of colony growth and alate production. A full description of the model is given in Korzukhin et al. (2001). In general, the model assumes that 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. 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 future geographic range limits. In general, *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 United States (Korzukhin et al. 2001).

Korzukhin et al. (2001) determined a critical threshold of 3900 alates to be an estimate of 'certain' colony proliferation success, based on the coldest areas where *S. invicta* is known to survive across the landscape. Given the uncertainty associated with this estimate, we also used a more liberal critical threshold of alate

production (1500) to indicate areas of 'possible' future infestation. Locations where predictions of alate production were <1500 were deemed 'unlikely' to support sustainable populations of *S. invicta*.

This lower critical value, compared to the 2100 alates employed by Korzukhin et al. (2001) to estimate 'possible' success, was used to better calibrate the range estimates of this paper with that of Korzukhin et al. (2001) for the United States. This was necessary because different data sets were used in the two analyses, encompassing different weather station locations and a different range of years. This lower value was also chosen to reduce the chances of underestimating future range limits and instilling a false sense of security to some regions.

Arid conditions will also reduce the probability of *S. invicta* survival in many locations. Thus we added a second layer of climatic information in the form of mean annual precipitation. We adopted a threshold of 510 mm per year (see rationale in Korzukhin et al. 2001) to identify areas that may be too dry to support *S. invicta* across the landscape.

Data sources

Minimum and maximum daily temperature data from meteorological stations around the globe were extracted from the National Climatic Data Center CD ROM covering the period 1977–1991 (NCDC 1994). We used regression algorithms developed in Korzukhin et al. (2001) 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.

Station selection was based on geographic position and robustness of data. We initially selected stations located between 45° N and 60° S latitude. This included all continental areas in the southern hemisphere except Antarctica. High latitudes in the northern hemisphere were excluded because of the large number of weather stations (which would be uninformative and slow down the model run) and the unlikely potential for *S. invicta* survival in cold climates.

After elimination of stations with incomplete data (see below), an initial run of the model revealed that *S. invicta* may survive near 45° N in some regions. Thus, we included additional stations in the northern hemisphere in regions that were near the predicted northern range limit. These included: (1) the northwestern United States (Washington and Oregon) and

southern British Columbia (between 45° and 51° N latitude and between 117° and 129° W longitude), (2) the British Isles and northwestern France (between 45° and 60° N latitude and between 2° E and 12° W longitude), and (3) a section of Europe and Asia lying north of the Mediterranean, Black and Caspian Seas (between 45° and 49° N latitude and between 2° and 56° E longitude).

A total of 5971 weather stations were located within these regions and were evaluated for inclusion in the model. At least five total years of reliable data had to be available for locations to be included. For latitudes above 22.5° N and below 22.5° S latitude, years with more than nine missing days in winter (December, January, and February in the northern hemisphere; June–August in the southern hemisphere) or more than 54 missing days in all other months were discarded. Only nine missing days were allowed in winter months because these months are critical in determining winter kill. For tropical latitudes (between 22.5° N and 22.5° S) where winter kill is usually not a factor, years were discarded when they contained more than 54 total missing days. Missing values within years were interpolated by regression for three or fewer consecutive missing days and substituted from previous years for missing blocks of more than three days. Missing years were not reconstructed. After elimination of stations that did not meet our criteria, 3421 total locations were included in the final run of the model.

Because weather stations in some regions were densely clustered (e.g., Europe and East Asia) relative to the scale of our maps, we employed an algorithm to reduce the density of symbols of the same infestation probability in the final maps. The algorithm deleted weather station locations in densely clustered areas until all remaining locations (of the same infestation probability) were at least one degree apart. This procedure eliminated dense clusters of symbols relaying redundant information in the final maps.

Precipitation data was derived from the Environmental Systems Research Institute ArcAtlas CD ROM (ESRI 1996). ArcAtlas generates map isohyets of mean annual precipitation based on information published in climatic atlases and maps.

Model validation for the United States is given in Korzukhin et al. (2001). The distribution of *S. invicta* in the United States may be found in Korzukhin et al. (2001) or online (<http://cmave.usda.ufl.edu/ifahi/ifarange.us.html>). An annually updated map of counties under imported fire ant (*S. invicta* and *S. richteri*)

quarantine is available at <http://www.aphis.usda.gov/ppq/maps/>. Unfortunately, the distribution of *S. invicta* (and other *Solenopsis* species) in South America, particularly the critical southern range limit, is not well known.

Results

The potential global range expansion of *S. invicta* based on our model is illustrated in Figures 1 and 2. Each symbol represents the location of a weather station that provided sufficient data for inclusion in the model. Red circles indicate sites of certain infestation, yellow triangles indicate areas where infestation may be possible, and white circles indicate areas where infestation is unlikely, based on the effects of temperature.

Continental areas receiving >510 mm of precipitation per year generally would be able to support *S. invicta* throughout the landscape. Continental areas receiving < 510 mm of precipitation per year would probably only support *S. invicta* near sources of permanent water (i.e., lakes, rivers, springs, etc.), or regularly irrigated areas (i.e., fields, lawns, etc.). More detailed maps, containing all weather station locations, can be viewed online (http://cmave.usda.ufl.edu/ifahi/ifarange_global.html).

Unfortunately, the distribution of weather stations providing reliable data was uneven, leaving some relatively large areas of the globe devoid of predictions of *S. invicta* survival based on temperature. The critical regions in the north and south temperate zones where cold temperatures begin to become a limiting factor, however, are relatively well represented by stations. A band of points representing unlikely infestation is present across the entire northern hemisphere, indicating that our final model included enough high north latitude stations at all longitudes. The potential for *S. invicta* survival in most tropical and subtropical regions can be determined primarily from annual rainfall patterns, with the exception of mountainous regions where temperature may become limiting.

Based on temperature data, in the New World large areas of Mexico and Central America are at risk, as are many Caribbean islands that have not yet been invaded. Range expansion for the continental United States is discussed in detail in Korzukhin et al. (2001). Northern South America may also be susceptible. This area is already occupied by other dominant *Solenopsis* species (*S. geminata* [F.] and *S. saevissima* [F. Smith]),

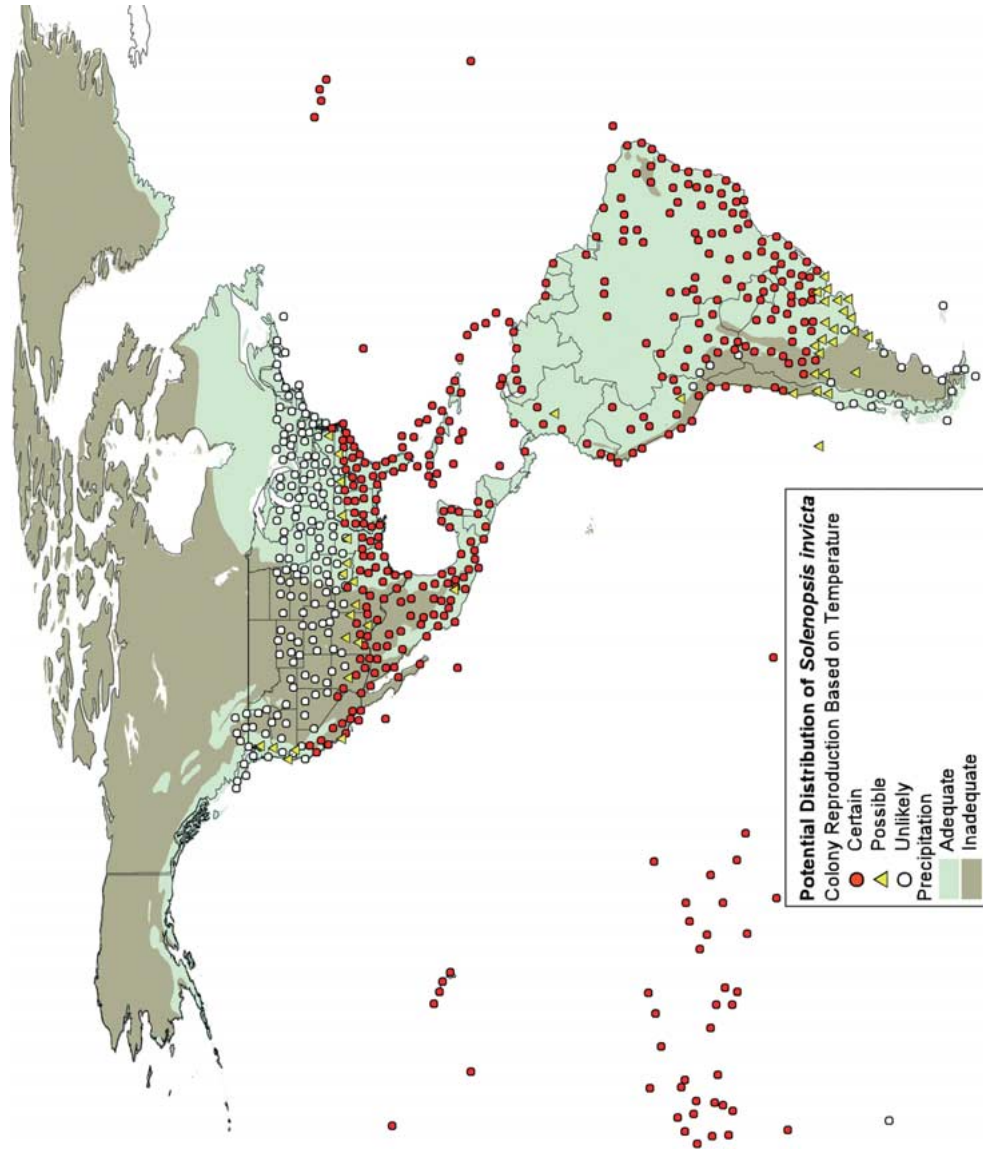


Figure 1. Potential global range of the red imported fire ant, *S. invicta*, in the western hemisphere. Red circles indicate areas of certain reproductive success (> 3900 alates); yellow triangles indicate areas of possible reproductive success (> 1500 but ≤ 3900 alates); white circles indicate areas of unlikely reproductive success (≤ 1500 alates), based on temperature. Green shading indicates regions with sufficient annual precipitation (estimated at > 510 mm) to sustain *Solenopsis invicta* across the landscape; olive green shading indicates arid regions that are likely to have insufficient rain (≤ 510 mm annual precipitation). *Solenopsis invicta* will survive, however, in arid regions that are irrigated or near natural water sources.

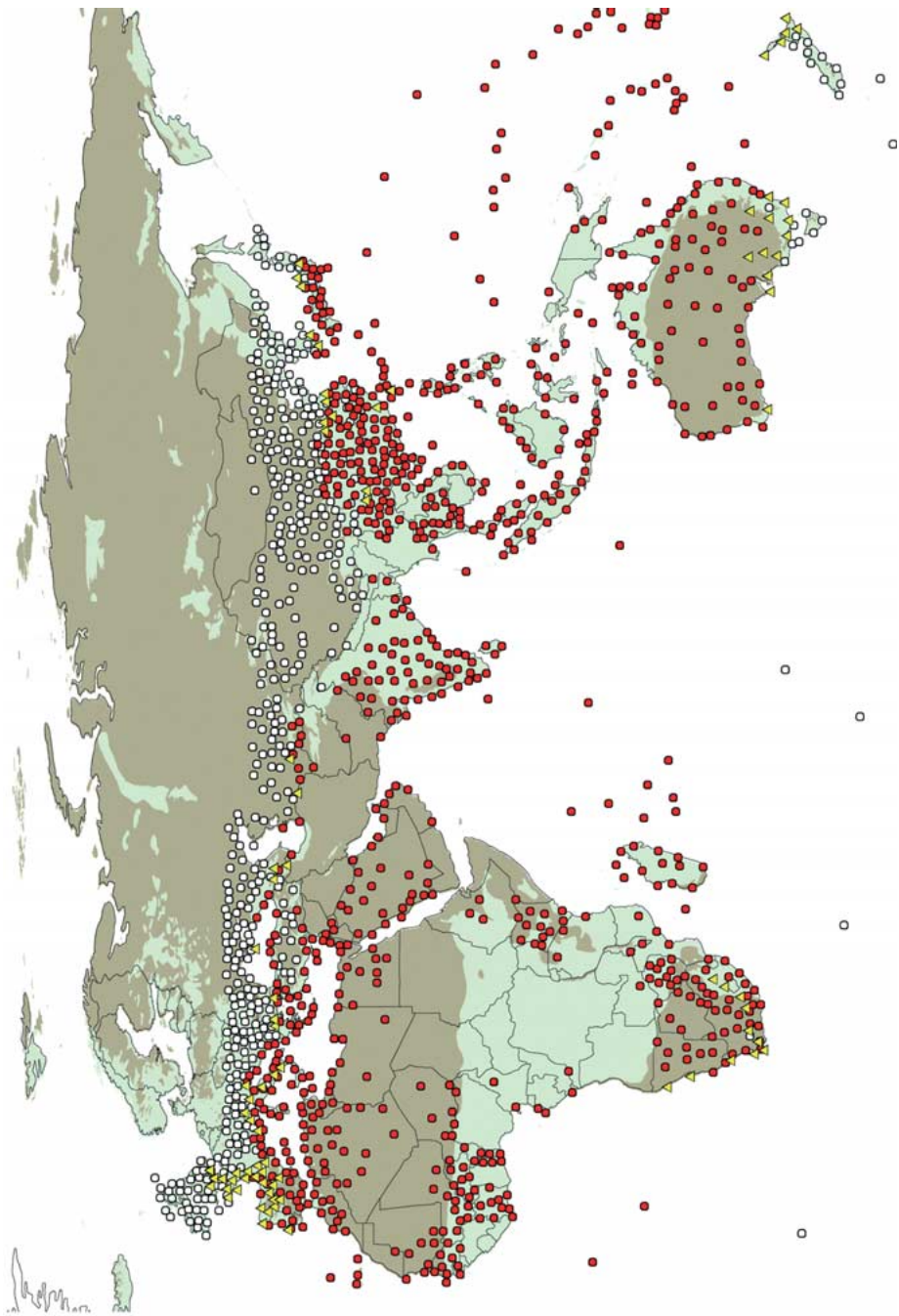


Figure 2. Potential global range of the red imported fire ant, *Solenopsis invicta*, in the eastern hemisphere. See Figure 1 legend for explanation of colors and symbols.

although *S. invicta* is known to displace congeners such as *S. geminata*, *S. xyloni* (McCook) and *S. richteri* Forel (Vinson 1997).

In the Old World, much of the region immediately surrounding the Mediterranean Sea, as well as some areas near the Black and Caspian Seas, are at risk. Based on temperature data, it is possible that *S. invicta* could survive along the southwestern coast of France and even at some sites in south Britain. Further inland, most of Africa and the Middle East are warm enough, although much of Europe and northern Asia are too cold. Most of India, Southeast Asia, and Australia are warm enough. Even southern Japan, southern South Korea, and potentially northern New Zealand are susceptible, based on temperature data.

S. invicta may be able to survive colder climates in the 'possible' or even 'unlikely' infestation zones 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).

Many areas that are warm enough for *S. invicta* survival, however, do not receive enough rainfall to support this species across the landscape. For example, large areas of northern and southern Africa, the Middle East, and Central Australia are too dry. Areas along natural water sources (i.e., rivers or lakes) would be at risk, however, as would any irrigated regions.

Numerous island nations in the Pacific, Atlantic, and Indian Oceans should be vigilant of this invader. Our predictions for islands are based on temperature data alone, and the ultimate suitability for *S. invicta* invasion should be considered on a case by case basis. Some islands may not receive enough precipitation to support this species at all. High islands may be wet enough in the upper elevations yet too dry along the coast (see discussion of the Hawaiian Islands below).

Discussion

This paper represents the first attempt to model the potential global range expansion of the red imported fire ant, *S. invicta*. A number of models have been developed to predict *S. invicta* range limits in the continental United States (Pimm and Bartell 1980; Stoker et al. 1994; Killion and Grant 1995; Korzukhin et al. 2001). The model of Korzukhin et al. (2001), however, contains certain advantages relative to the other approaches (discussed in Korzukhin et al. 2001).

Other, more generalized, models may also be useful in predicting the range expansion of *S. invicta* or other invasive ants. For example, CLIMEX (Sutherst et al. 1999) is a dynamic simulation model for predicting the effects of climate on the distribution of a diversity of plants and animals. The potential distribution of *S. invicta* in Australia was recently modeled with CLIMEX (Anon. 2001), and produced qualitatively similar results compared to our model, although it did not differentiate limits due to temperature *versus* those due to precipitation. Comparisons of the predictions of different models over time may facilitate fine-tuning of the models and more accurate predictions.

Scale and resolution of patterns

Our goal was to provide an estimate of the potential range expansion of *S. invicta* on a global scale. A limitation of this approach is that the finer scale patterns of *S. invicta* survival due to microhabitat heterogeneity are not detectable. In regions of relatively flat topography, this is not a problem. In mountainous regions, however, temperature and precipitation may vary dramatically over distances of a few kilometers. Thus, some weather stations located in regions suitable for *S. invicta* survival may lie close to areas (without weather stations) that are not warm or wet enough. The converse of this is also true.

The Hawaiian Islands are a good example. Our data for that chain were derived from six weather stations selected for inclusion from the worldwide data set. All points indicate the potential for 'certain' infestation. However, prediction of the potential infestation of the Hawaiian Islands by *S. invicta* using the same modeling approach and data from a larger set of weather stations revealed that some areas are too cold (i.e., higher elevations) or too dry (i.e., leeward rain shadows) (VanGelder and Korzukhin 2002).

Our model predicts the potential future range expansion of *S. invicta* based on historical temperature and precipitation data. There are other important factors, however, that should be taken into account when assessing invasion possibilities for specific areas. *S. invicta* is well adapted to opportunistic exploitation of disturbed habitats (Tschinkel 1993). It prefers open, sunny areas in which to construct earthen mounds for purposes of brood thermoregulation (Porter and Tschinkel 1993), and is not abundant in densely wooded areas. Some tropical regions that are warm and wet enough to support *S. invicta* are densely forested

and do not represent suitable fire ant habitat. Because of the ability of this species to rapidly colonize disturbed areas (and travel in soil or plant material), however, any deforested areas are potentially at risk.

S. invicta may be unable to invade some regions if the native ant fauna is sufficiently resistant. It is thought that *S. invicta* is more abundant in the United States than in its South American homeland because of numerous natural enemies in South America (Porter et al. 1997). Interspecific competition with other ants is often an important force limiting ant populations in general (Hölldobler and Wilson 1990 and references therein), and it has been proposed that *S. invicta* populations in South America are held in check by a more diverse and aggressive ant fauna compared to that of North America (Buren 1983). It will be of interest to see if tropical regions with diverse ant faunas are naturally more resistant to this invader.

Over the long term, the predictions of the model may need to be modified if *S. invicta* continues to invade further northward in the US, since the model was calibrated along the northern edge of this invasion (Korzukhin et al. 2001). Global climate change would also affect the predictions. Finally, adaptation of populations of *S. invicta* to cooler or drier climates could increase the area of their potential range. In a study of desiccation resistance of *S. invicta* in Texas, for example, populations from the western part of the state were found to be less prone to desiccation than populations from the eastern part of the state, suggesting that *S. invicta* may be able to adapt to more xeric conditions (Phillips et al. 1996). Li and Heinz (1998) found, however, that while genetic variation in desiccation resistance did exist in polygyne *S. invicta*, the low heritability of this trait would likely limit the degree of expansion into arid regions.

Costs of eradication or infestation

Infestations of new areas by *S. invicta*, if not treated immediately, are likely to be expensive or even impossible to eradicate. Eradication of infestations covering several ha may cost thousands of dollars (US), whereas infestations of several hundred ha could cost tens of thousands of dollars to eradicate (Drees et al. 2002).

The first federal quarantine of *S. invicta* in the United States began in 1958, after >25 million ha in 8 states were infested (Callcott and Collins 1996). Eradication of *S. invicta* from the United States by mass

application of pesticides was attempted from the late 1950s to the early 1970s (Williams et al. 2001). Yet over that period *S. invicta* increased its range (Callcott and Collins 1996) and eradication of *S. invicta* in the continental United States is no longer considered a viable option.

It will be of interest to see whether the moderately large *S. invicta* infestations in California (>200 000 ha; Anon. 1999) and Australia (~36 000 ha; Vanderwoude et al. 2002) can be eradicated. California has allocated \$40 million USD over 4 years (California Department of Food and Agriculture 2000), and Australia has allocated over \$120 million AUD (~\$68 million USD) over 5 years (Vanderwoude et al., in press), for *S. invicta* eradication. *S. invicta* has apparently been successfully eradicated from New Zealand, where it was represented by a single colony when discovered (Harris 2001; Pascoe 2001).

Clearly, early detection is critical to any eradication attempt. Although eradication, when possible, may be expensive, it pales in comparison to the economic costs of permanent infestations. The current economic impact of *S. invicta* on humans, agriculture, and wildlife in the United States is estimated to range from one-half billion to several billion dollars annually (Thompson et al. 1995; Thompson and Jones 1996).

In the United States, federal quarantine prohibits the movement of untreated nursery stock, sod, and other regulated articles out of counties infested by *S. invicta* (Code of Federal Regulations 2002). Efforts to quarantine infested counties may have greatly slowed, although not prevented, the spread of *S. invicta* across the southeastern US and into California (Lockley and Collings 1990; Callcott and Collins 1996). Quarantine efforts may have also reduced the accidental importation of *S. invicta* to other countries.

Implications for other Solenopsis species

A second *Solenopsis* fire ant species, the black imported fire ant, *S. richteri*, is also an invasive pest. Because of basic similarities in ecology and physiology, the potential global range expansion of *S. richteri* is likely to be approximated to a large extent by our model.

Native to southern South America, *S. richteri* has also been introduced into the US and occurs at higher latitudes than *S. invicta* both in its native range in South

America and its introduced range in North America (see maps in Taber 2000, pp 27 and 59). The more northerly distribution of *S. richteri* compared to *S. invicta* in the US may be a function of competitive displacement by *S. invicta* (Callcott and Collins 1996), climatic preferences or tolerances, or both. It is interesting to note that the actual southern range limit of *S. invicta* near Rosario, Argentina is near the southern boundary of the predicted 'certain' infestation in Argentina (Figure 1), whereas the actual southern range limit of *S. richteri* is near the southern boundary of the predicted 'possible' infestation (for *S. invicta*).

Solenopsis richteri was reported to be present in the vicinity of Najran, Saudi Arabia, and was implicated as the cause of anaphylaxis in hospital cases (Khan et al. 1999). We have obtained specimens of the ant in question and determined it to be the Samsun ant, *Pachycondyla sennaarensis* (Mayr), which is known to be present in the region (Collingwood 1985) and documented as inducing allergic reactions to its sting (Dib et al. 1995). Thus we regard this record of *S. richteri* from Saudi Arabia to be erroneous.

It is not inconceivable that other *Solenopsis* fire ant species in the *saevissima* subcomplex (Trager 1991) may invade other continents. Variation exists among *Solenopsis* species in physiological tolerances to cold and desiccation (e.g., Braulick et al. 1988; Munroe et al. 1996; Francke et al. 1986; Diffie and Sheppard 1989), however, and thus the ultimate geographical limit to range expansion may differ somewhat for each species.

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