



Original article

Assessing the distribution of the Argentine ant using physiological data

Sílvia Abril^{a,*}, Núria Roura-Pascual^{a,b}, Jordi Oliveras^a, Crisanto Gómez^a^a Department of Environmental Sciences, University of Girona, Montilivi Campus s/n, 17071 Girona, Spain^b Center for Invasion Biology, Department of Botany and Zoology, University of Stellenbosch, Private Bag X1, Matieland 7206, South Africa

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ABSTRACT

To address the lack of physiological approaches in current models assessing the potential distribution of the Argentine ant, we used data on brood development from distinct sources to evaluate a series of degree-day models for Catalonia (NE Iberian Peninsula), and data on the brood survival and oviposition rates to develop a worker production model. The degree-day model generated using data from Newell and Barber (1913) and Benois (1973) indicated that the number of degree-days required for the complete development from egg to adult worker was 445.4 degree-days above a threshold of 15.9 °C, while the model calibrated using data from Abril et al. (2008, in press) suggested 599.5 degree-days above 18.4 °C. Comparisons between the degree-day model predictions and the currently known distribution of the Argentine ant suggested that the one generated using data from Newell and Barber (1913) and Benois (1973) overestimated the presence of the species, while the one calibrated using data from Abril et al. (2008; in press) underestimated it. On the other hand, the predicted daily net production of Argentine ant workers generated by the worker production model predicted more accurately the distribution of the Argentine ant than the degree-day models. Our results show the utility of incorporating physiological data in models to assess the distribution limits of the Argentine ant, which up to date have taken little account of the physiological needs of the species in terms of its establishment and dispersion in its introduced ranges.

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1. Introduction

The Argentine ant (*Linepithema humile* Mayr) is a well-known invasive species (Lowe et al., 2000). Native to northern Argentina, southern Brazil, Uruguay and Paraguay (Wild, 2004), it has spread worldwide in areas with Mediterranean-type climates usually associated with disturbed habitats as a result of human activities (Suarez et al., 2001). However, its ability to occupy natural habitats has also been reported (Holway, 1998a; Gómez et al., 2003). In its introduced range, the Argentine ant has impacted native ant faunas leading to changes in arthropod communities (Human and Gordon, 1997; Holway, 1998b), ant–vertebrate interactions (Suarez et al., 2000) and ant–plant relationships (Bond and Slingsby, 1984; Gómez and Oliveras, 2003). Its presence has also had negative effects on crops and plantations due to its mutualistic interactions with hemipterans, which reduce plant growth and production (Buckley, 1987; Ness and Bronstein, 2004).

Predicting areas suitable for the establishment of Argentine ants, as well as the rate of spread of the invasion once they have been introduced, are essential steps towards managing the invasion in affected areas. Several studies have already assessed the

potential distribution of the Argentine ant using correlative modelling approaches that relate occurrence data with environmental variables thought to influence its distribution (Hartley et al., 2006; Roura-Pascual et al., 2004, 2006; Menke et al., 2009). However, the establishment of an invasive species in a new area is a complex phenomenon that includes other elements responsible for the restriction or enhancement of its geographic range, such as the physiological requirements of the species for colony growth and survival (Jumbam et al., 2008). Few studies have assessed the distributional range of Argentine ants at local scales while taking into consideration the physiological basis of its establishment. Based on the assumption that temperature is the main factor influencing the developmental rate of insects, Hartley and Lester (2003) and Krushelnycky et al. (2005) used a degree-day model to predict the most suitable areas for the species' development and, therefore, its survival and subsequent establishment. However, recent data on the effect of temperature on Argentine ant's brood survival (Abril et al., in press) and oviposition rates (Abril et al., 2008) allows the generation of modelling approaches based on other physiological traits. One of these approaches is the development of a worker production model. The production of new Argentine ant workers is closely linked to temperature (Newell and Barber, 1913; Abril et al., 2008, in press), and we can use this relationship to estimate the distribution of the species under a new approach: the colony's temperature requirements for

* Corresponding author. Tel.: +34 972418268; fax: +34 972418150.

E-mail address: silvia.abril@udg.edu (S. Abril).

producing new individuals and, therefore, maintaining its presence in an area.

Estimating a species potential range in an introduced area on a physiological basis should be taken into consideration in combination with predictions of the species distribution via ecological niche models (Helmuth et al., 2005). The present study attempts to gauge the usefulness of new models in determining the potential distribution of the Argentine ant in Catalonia (NE Iberian Peninsula, Fig. 1a and Appendix) using recent data on brood development and survival (Abril et al., in press), and on the oviposition rates of queens (Abril et al., 2008), to address the lack of physiological data in predictive models.

2. Materials and methods

To predict the potential distribution of the Argentine ant, while including data on the development and survival of the species, we adopted two different modelling approaches: (1) a degree-day model, based on the fact that an insect's growth is closely linked to temperature; and (2) a worker production model, which relates the daily net production of workers per queen to the mean temperature of the most productive months.

2.1. Degree-day model

The development rate of insects is mainly linked to temperature: to develop from one point in their life cycle to another, insects require a certain degree of heat (Chiang, 1985). The measurement of this degree of heat is called "physiological time", which is expressed in units called "degree-days" ($^{\circ}\text{D}$). A degree-day is the heat experienced in 24 h by an insect when the temperature is one degree above its lowest development threshold. A degree-day model predicts the number of degree-days on the basis that the development rate is a linear function of temperature (Hartley and Lester, 2003), and it is expressed as follows:

$$DT = k + t_0D$$

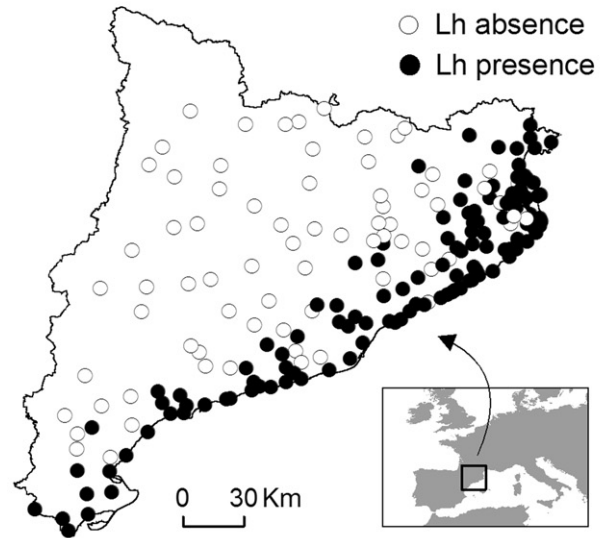
where D = duration of development in days, T = temperature, t_0 = a baseline temperature of theoretically zero development, and k = a thermal constant for development measured in units of degree-days.

To generate a degree-day model, data on the species' developmental rates at different temperatures are needed. Previous studies used the only development data available at that period from Newell and Barber (1913) and Benoist (1973). Although these data contain enough observations to develop a degree-day model, they have certain limitations. For example, the accurate calibration of a degree-day model requires a considerable amount of data at constant temperatures (Blank et al., 2000). However, data from Newell and Barber (1913) and Benoist (1973) have missing replicates at each measured temperature, and daily averages were used instead of fixed temperatures to measure brood developmental times. Recent data on brood development and survival of Argentine ants at different temperatures is an improvement on previous data: there are more replicates at each measured temperature and the brood is incubated at fixed temperatures (Abril et al., in press).

To search for differences between models calibrated using these different development datasets, we applied the degree-day model developed by Hartley and Lester (2003) using data on development rates from Newell and Barber (1913) and Benoist (1973) to predict the potential distribution of the Argentine ant in Catalonia. We then compared this prediction with one obtained using data from Abril et al. (in press). We estimated the " t_0 " and " k " values necessary for developing the degree-day model from the slope and intercept respectively of a linear regression of DT vs. D , as Hartley and Lester

a OCCURRENCE DATA

Source: Roura-Pascual et al. (2004)



b NICHE MODEL

Source: Roura-Pascual et al. (2006)

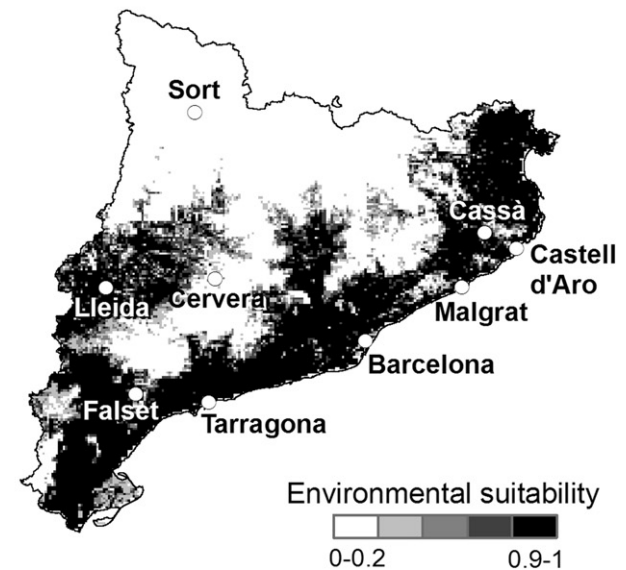


Fig. 1. Localization of the study area (Catalonia, NE Iberian Peninsula), indicating: (a) the current observed distribution of the Argentine ant (Roura-Pascual et al., 2004), and (b) its predicted potential distribution by means of a correlative modelling approach calibrated using data from invaded ranges in the Iberian Peninsula (see Roura-Pascual et al., 2006). The darker the shades of the bottom map, the higher the suitability of the environment for the species.

(2003) did in their study. The standard errors of " t_0 " and " k " were calculated from the standard errors of the slope and intercept.

The potential distribution of the Argentine ant was then assessed by projecting these degree-day models onto various locations across Catalonia. We calculated the average annual accumulation of degree-days above t_0 from 136 meteorological stations, based on mean daily air temperature values from 2000 to 2005 provided by the Meteorological Service of Catalonia (<http://www.meteocat.com>). Missing values were omitted, and we only used time series with a minimum of 1500 days' measurements. The

performance of models at the developmental thresholds identified by both degree-days models to predict the distribution of the Argentine ant was measured using the kappa index (Cohen, 1960), where $k \leq 0$ indicates no agreement and $k = 1$ almost perfect agreement, and various additional measures of model performance (sensitivity, specificity, and percent of correctly classified presences and absences) (Fielding and Bell, 1997). Because presence/absence data for each meteorological station were not available, we considered the value of the closest known locality within a radius of 3 km (Fig. 1a; Roura-Pascual et al., 2004).

2.2. Worker production model

To evaluate the utility of data on daily net production of workers per queen for assessing the distribution limits of the Argentine ant, we developed a worker production model using data on oviposition rates and brood survival from egg to adult worker at different temperatures (Abril et al., 2008, in press). Data on the oviposition rates of the species have been reported under different monogynous and polygynous experimental conditions (Abril et al., 2008). As the oviposition rate can vary depending on the number of queens in a colony (Keller and Cherix, 1985; Keller, 1988; Abril et al., 2008) and it is widely recognised that there is a high level of polygyny in the natural nests of this species (Passera, 1994; Keller, 1995; Ingram, 2002), we used data on oviposition rates from the highest level of polygyny studied (eight queens per nest) to calculate the net production of workers per queen.

We used generalised linear models (GLM) with Poisson error distribution and a log-link function to evaluate net worker production as a function of temperature. Because the relationship between workers' daily net production and temperature was curvilinear, we generated a quadratic function of our response variable. We measured the goodness-of-fit of the model generated by the change in deviance, as calculated by the χ^2 test, with a 5% significance level. We also calculated the percentage of explained deviance (Dobson, 1999).

It has been reported that Argentine ant queens have a period of physiological rest during the winter months (December–March) in which egg production stops (Benois, 1973). Having obtained the model summarising the relationship between net worker production and temperature, we therefore estimated the potential net production of Argentine ant workers across Catalonia considering only the months from March to November when queens lay eggs. We calculated the mean value of monthly air temperatures for March–November (measured over the past 15 years) from the Digital Climatic Atlas of Catalonia (raster format at 180×180 m resolution available at <http://magno.uab.es/atles-climatic/>; Pons, 1996; Ninyerola et al., 2000). Months were selected according to the Argentine ant queen's oviposition period (Benois, 1973). The performance of the models was measured as previously using the kappa index and various measures of performance. We extracted the value predicted by the production model in each occurrence locality (Fig. 1a; Roura-Pascual et al., 2004), and then used the first quartile of predicted values for the presence localities as the threshold at which to evaluate the performance of the model. This threshold was calculated using only presence localities because absences could correspond to false absences (i.e. localities with appropriate conditions that the species has not had time to invade). All the analyses were performed using ESRI ArcGIS 9.0 and S-Plus (version 6.1) softwares.

3. Results

3.1. Degree-day model

As noted in the previous section, the degree-day model is based on the assumption that development rate is a linear function of

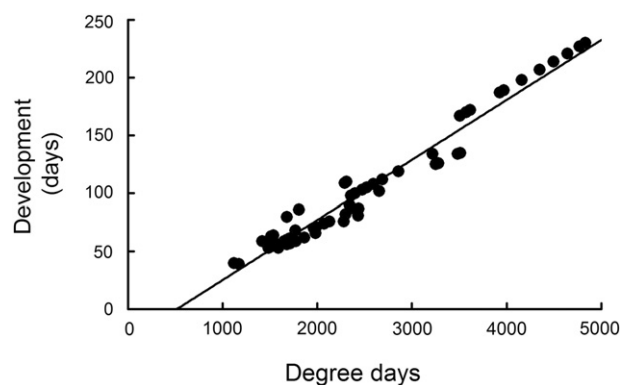


Fig. 2. Relationship between duration of development in days and degree-days from egg to adult worker in the Argentine ant.

temperature (Hartley and Lester, 2003). Therefore, the data relating development rates to temperature used to generate the model should present a linear relationship. The relationship between duration of development (D) and duration of development multiplied by temperature (DT) appeared fairly linear in data on development time from egg to adult worker from Abril et al. (in press) (Fig. 2).

The degree-day model generated with data from Newell and Barber (1913) and Benois (1973) estimated that a total of 445.4 (± 18.9 SE) degree-days above a developmental threshold of 15.9 (± 0.8 SE) $^{\circ}\text{C}$ would be required for total development from egg to adult worker (Hartley and Lester, 2003). However, the degree-day model using new data on brood development from Abril et al. (in press) suggested that a higher annual accumulation of degree-days above a higher developmental threshold would be necessary to complete development, specifically 599.5 (± 58.5 SE) degree-days above a developmental threshold of 18.4 (± 0.5 SE) $^{\circ}\text{C}$ (Table 1).

Fig. 3 illustrates the estimated degree-days calculated at various locations within Catalonia based on the minimum temperature threshold for development determined from Newell and Barber (1913) and Benois (1973) (Fig. 3a), and Abril et al., (in press) (Fig. 3b). The two predictions are different: Fig. 3a indicates that a total of 92.6% of the locations studied are suitable for the survival and establishment of the Argentine ant, in contrast to only 39.7% shown in Fig. 3b. Comparing these two degree-day models with the current known distribution of the species (Fig. 1a; Roura-Pascual et al., 2004), we can see that the model based on data from Newell and Barber (1913) and Benois (1973) predicts the survival and establishment of the species in locations where the species is not present (e.g. Cervera, Falset, Lleida or Sort). On the other hand, the degree-day model generated with data from Abril et al. (in press) predicts that many locations where the Argentine ant is currently present are not suitable in terms of the temperature the species needs for its survival and establishment (e.g. Castell d'Aro, Barcelona, Cassà de la Selva or Malgrat de Mar).

In terms of model performance, our results indicate that the degree-day model calibrated using data from Newell and Barber

Table 1

Estimated parameter values for two degree-day models developed using different data on brood development and survival of Argentine ant at different temperatures. n is the sample size for development.

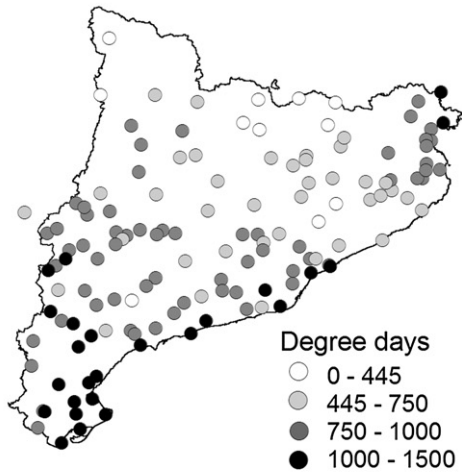
Complete development egg \rightarrow adult worker	Threshold temperature, $t_0 \pm$ s.e. ($^{\circ}\text{C}$)	Cumulative degree-days, $k \pm$ s.e. ($^{\circ}\text{C days}$)	Temperature range of linear relationship ($^{\circ}\text{C}$)	n
Degree-day ^a	15.9 \pm 0.8	445.4 \pm 18.9	17–30	52
Degree-day ^b	18.4 \pm 0.5	599.5 \pm 58.5	18–32	63

^a Degree-day model using data from Newell and Barber (1913) and Benois (1973).

^b Degree-day model using data from Abril et al. (2008, in press).

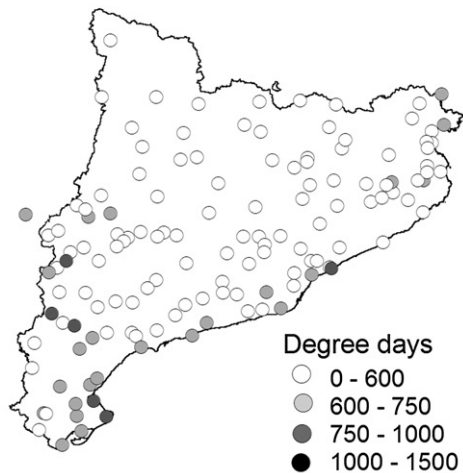
a DEGREE-DAY MODEL

Data: Newell & Barber (1913), Benois (1973)



b DEGREE-DAY MODEL

Data: Abril et al. (2009)



c WORKER PRODUCTION MODEL

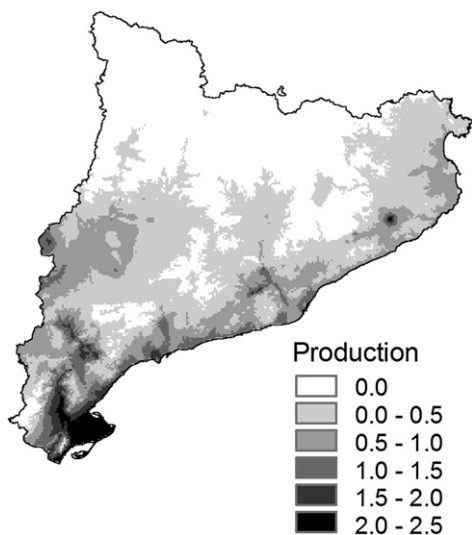


Table 2

Performance of three physiological models assessing the distribution range of the Argentine ant. n is the sample size of independent occurrences, and pcc corresponds to the percent of correctly classified presences and absences.

Model	n	Threshold	Sensitivity	Specificity	pcc	Kappa
Degree-day ^a	40	445.4	1	0.08	0.63	0.10
Degree-day ^b	40	599.5	0.22	0.92	0.50	0.12
Worker productivity	136	0.512	0.75	0.66	0.71	0.41

^a Degree-day model using data from Newell and Barber (1913) and Benois (1973).

^b Degree-day model using data from Abril et al. (2008, in press).

(1913) presents a low specificity (i.e. proportion of absences correctly predicted) and tends to overestimate the presence of the Argentine ant (Table 2). On the other hand, the degree-day model generated with data from Abril et al., (in press) has a low sensitivity (i.e. proportion of presences correctly predicted), which indicates that the model underestimates the presence of the Argentine ant (Table 2). As a result, the kappa index for both degree-day models created is relatively low, indicating a slight agreement between their predictions and the current distribution of *L. humile* in Catalonia (Table 2).

3.2. Worker production model

The final model was:

$$y = -0.0367x^2 + 1.9331x - 23.388$$

where y is the predicted number of workers produced per queen and per day, and x is the temperature. The GLM model showed a change in deviance of 46.745, which differed significantly from the Null Deviance of the model (Null Deviance: 129.0197, df: 189; χ^2 test ($P|\text{Chi}| < 0.001$). This model explained 36.23% of the total deviance.

The predicted net production of Argentine ant workers for Catalonia generated by the model (Fig. 3c) fits fairly well with the current distribution of the species (Fig. 1a; Roura-Pascual et al., 2004), showing a marked peripheral distribution range over the whole coastal area. The kappa index for this model is higher than the ones obtained for the two degree-day models, indicating that the worker production model predicts the distribution of the Argentine ant more accurately (Table 2). Furthermore, localities where the species is known to be present have significantly higher predicted values of worker production than those localities where the species is absent (Kruskal–Wallis test: $k = 41.68$; $df = 1$; $P < 0.001$; Fig. 4), showing a fairly clear relation between the current presence of the species and the worker production predictions of the model.

4. Discussion

The degree-day model generated using data from Newell and Barber (1913) and Benois (1973) predicted the establishment and survival of the species in many locations in Catalonia where it has

Fig. 3. Predicted potential distribution of the Argentine ant in Catalonia according to: (a) degree-day model based on brood development data from Newell and Barber (1913) and Benois (1973); (b) degree-day model based on brood development data from Abril et al. (2008, in press); and (c) worker production model based on oviposition rates and brood survival data from Abril et al. (2008, in press). Each point in (a) and (b) corresponds to a meteorological station. White circles indicate unsuitable conditions for the establishment and survival of the species according to the model predictions, while grey and black circles indicate higher suitable conditions for the development of the species. Prediction (c) refers to the predicted daily net worker production per queen according to temperature. White areas indicate unsuitable places for the production and survivor of workers, while grey and black areas indicate higher suitable conditions for their production and survivor according to temperature. Production units: daily net production of workers per day per queen.

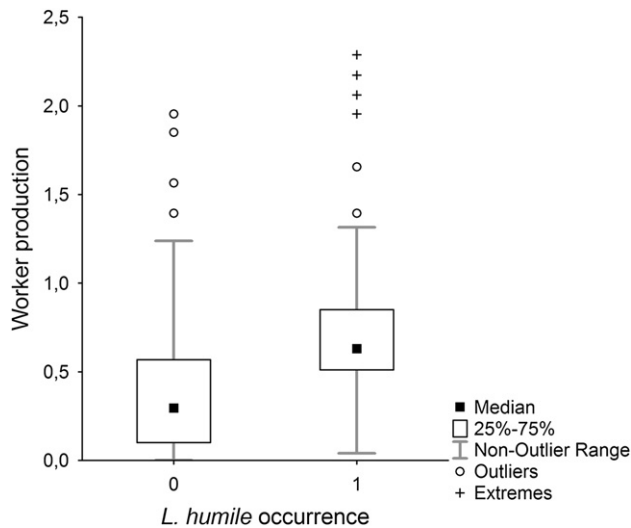


Fig. 4. Box plot representing the divergences on predicted values of worker production between known presences (1) and absences (0) of the Argentine ant in Catalonia (Fig. 1).

never been detected. This could be due to the fact that the species may not yet have had the opportunity to invade these areas, since there have been reports that it is still expanding its distribution range in certain areas (Casellas, 2004). Another possible explanation, however, is that these places are unsuitable for its establishment and survival because of ecological conditions that hamper its expansion (e.g. low temperatures or insufficient relative humidity; Espadaler and Gómez, 2003), and that the model overestimates the potential distribution of the Argentine ant.

In comparison with the degree-day model created with data from Newell and Barber (1913) and Benoist (1973), the model created using data on brood developmental rates from Abril et al., (in press) could have been calibrated more accurately because it predicts a theoretical development threshold closer to the real threshold observed, which seems to be around 18 °C (Abril et al., in press). However, this model predicts that the species would not be able to survive in locations such as Castell d'Aro or Barcelona, where the invasion is serious and quite extensive. A possible explanation for these mismatches between the model output and the species' present distribution is that there are other processes involved in determining growth and survival of a colony, e.g. foraging activity or the fecundity of queens, which can, together with brood development, be determinants of the places where the species could survive.

On the other hand, there are some important limitations that may reduce the reliability of both degree-day models' predictions for Catalonia. Firstly, the environmental temperature inside the nests may well be different from the outside temperature, thereby making the use of data on soil temperatures essential for predicting potential range. Such data are unfortunately not available in Catalonia, where the meteorological stations of the Meteorological Service of Catalonia (SMC) only report air temperatures. Secondly, it only takes into account the effect of temperature on rates of development, when there may be other temperature-dependent processes that could be affecting the growth and survival of the colony such as the oviposition rates of queens (Abril et al., 2008). Thirdly, the use of mean daily air temperatures in predicting distributions from the degree-day models may not provide an accurate estimate of accumulated heat above the minimum threshold, and therefore may underestimate or overestimate the annual amount of degree-days predicted by the models. In that sense, the use of hourly temperatures would provide better predictions of degree-days. Additionally, we think

that the most significant limitation of a degree-day model when it comes to predicting the potential distribution of the Argentine ant on a physiological basis is that it does not take into account the importance of soil moisture in the survival of the species. The Argentine ant is heavily influenced by humidity. It has been reported that it has significantly higher rates of water loss and cuticular permeability than some native ant species adapted to seasonally dry and hot Mediterranean environments (Shilman et al., 2007). This is probably the reason why low humidity environments negatively affect its foraging activity under the influence of high air temperatures (Human et al., 1998; Holway et al., 2002; Abril et al., 2007), and why low soil moisture limits its expansion (Holway et al., 2002; Menke and Holway, 2006; Menke et al., 2007). It has been reported, as well, that an excess of high rainfall can also negatively affect the species, probably through its influence on ground cover and, therefore, soil temperature (Krushelnicky et al., 2005). Thus, the low tolerance of the Argentine ant to both dry and excessively damp environments can restrict its distribution at regional scales (Menke et al., 2007). As the degree-day model does not take into account soil moisture as a factor in predicting the most suitable areas for the species' establishment and survival, the models generated in the present study predict the potential presence of the species in western Catalonia, where warm, dry summers may not allow the survival of the species in non-anthropogenic environments. This is the most likely explanation for the differences observed between the degree-day models' predictions and the present known distribution of the species in the western part of Catalonia.

In view of the new data available on the brood survival and oviposition rates of queens in relation to temperature, we generated a model predicting the daily net production of workers per queen in relation to temperature, to estimate the potential distribution range of the Argentine ant under a novel approach. To predict the species' potential using data on oviposition rates and brood survival, we made three main assumptions. Firstly, we assumed that all the nests of this species contain eight queens, since our data on net worker production are based on the oviposition rates of queens in polygynous colonies containing eight queens (Abril et al., 2008). However, if we take into consideration that the oviposition rate of a queen varies according to the number of queens in the colony (Keller and Cherix, 1985; Keller, 1988; Abril et al., 2008), and that the Argentine ant is a highly polygynous species (Passera, 1994; Keller, 1995; Ingram, 2002), the fecundity and thus the predicted production of workers per queen could be substantially different from the data presented. Secondly, we assumed that the air temperature was equal to the temperature inside the nest. Obviously, nest temperature is probably different from air temperature but, as was the case with the degree-day models generated, meteorological stations in Catalonia do not report soil temperatures. We were therefore forced to use air temperatures rather than soil temperatures to generate the worker production model. Finally, we worked on the basis that the percentage of brood survival obtained under experimental conditions (Abril et al., in press), which we used to calculate net worker production, was the same as the percentage of brood survival in the field, although brood survival might be different in natural nests, e.g. it would be higher due to the thermal gradient present in the nest and the fact that the environmental temperature is not constant but changes throughout the day, or be lower because of predation or environmental fluctuations.

Despite the aforementioned constraints, our results suggest that the production of Argentine ant workers, and the consequent species' distribution, may well be limited by temperature. In this sense, the model predicts a coastal distribution similar to that observed in other parts of the world as a reflection of the species' need for a temperate climate and high humidity (Majer, 1994; De Kock and Giliomee, 1989; Suarez et al., 2001; Espadaler and Gómez, 2003).

However, as with the degree-day model, its most important limitation is that it does not take into account the importance of humidity for the Argentine ant's survival and, therefore, its invasive potential. This may explain the main differences between the present known distribution of the species and the predictions of the worker production model in western Catalonia, where the low humidity present in the area probably makes it unsuitable for the establishment of this pest species.

Comparing the results of these two physiological modelling approaches (i.e. degree-day and worker production model, Fig. 3) with the predictions derived from a correlative modelling approach using data from the invaded range to estimate the distribution of the species in the Iberian Peninsula (Fig. 1b, Roura-Pascual et al., 2006), we identified the similarities/divergences between both approaches. The correlative model was developed using the Genetic Algorithm for Rule-set Prediction software (Stockwell and Peters, 1999), that uses a genetic algorithm to search for non-random associations between occurrence of the species (in this case 341 presences from the Iberian Peninsula, including the ones for Catalonia) and various relevant environmental variables (topographic and remotely-sensed indices) to identify the areas suitable for the species (Roura-Pascual et al., 2006). The area predicted as suitable by this correlative model presents a similar pattern to the one predicted by the worker production model, but differs in many ways with the predictions derived from the two degree-day models that tend to over- and under-predict the known distribution of the species. Both physiological and correlative modelling approaches, however, coincide in suggesting that areas most favourable for the Argentine ant are found at low altitudes along the coast and following the main rivers. It is important to note that all models suggest localities along the Ebre River, where the species is not known to occur presently, as suitable for the species. Overall, areas predicted as suitable by most models can be considered as appropriate for the establishment of the Argentine ant. However, to delimit the definitive limits of the invasion in Catalonia we should pay accurate attention to those areas where model predictions are in disagreement.

5. Conclusions

Predicting the potential distribution of an invasive insect is a complex undertaking, but the information that it can give us is valuable for controlling the invasion in areas where it has been introduced. This study is an example of the great possibilities that physiological data offer in the creation of new prediction models combining both climatic and physiological factors to determine the potential distribution range of the Argentine ant. But it also reveals the need for data on the effect of soil moisture on the physiology of the species (i.e. the effect of soil moisture on the oviposition rate of queens, and on the development and survival of the brood), if confidence in future predictions is to be improved.

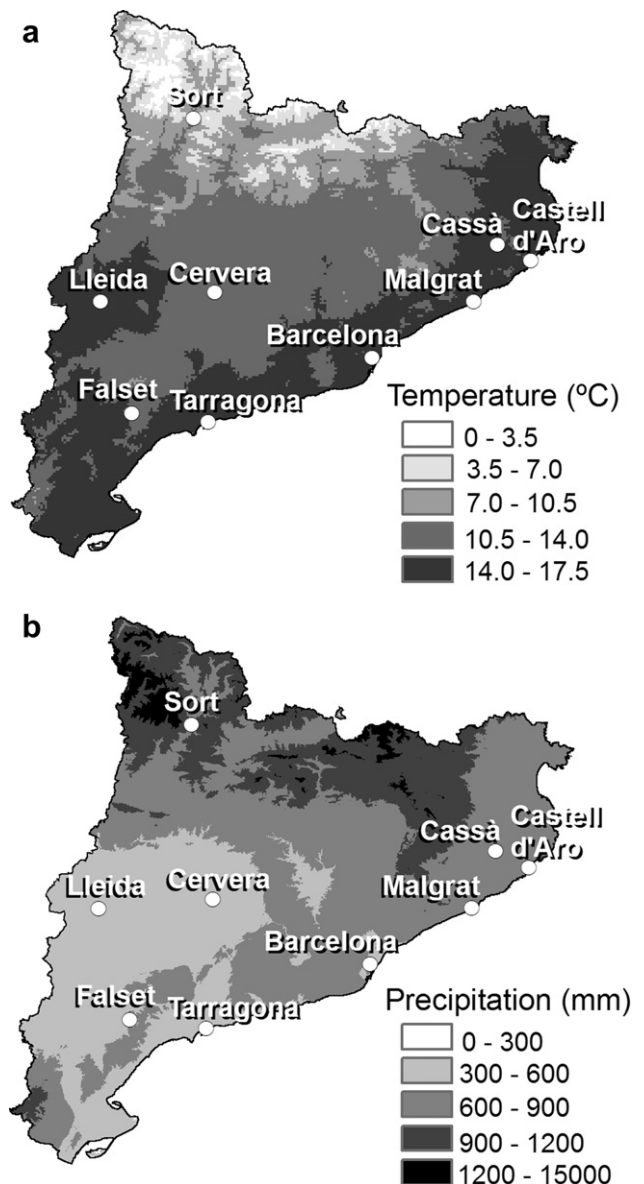
Overall, the information derived from these models refers to areas at high risk of invasion (if they have not been invaded already) by the Argentine ant in response to the species' thermal requirements. Therefore, it is only applicable to non-altered habitats where humans cannot facilitate the survivorship of the species in non-optimal environments. Disturbed habitats, such as crops or urban centers, usually offer ideal conditions for the establishment and reproduction of the species (Hölldobler and Wilson, 1990; Suarez et al., 2001). The real importance of our results is that it provides new insights into future model predictions of the species potential distribution. This opens the door to improvements in these valuable tools, which can be of use for the management of the Argentine ant invasion.

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Appendix

Spatial visualization of the climatic conditions present in the study area (Catalonia, NE Iberian Peninsula): (a) gradient of annual mean temperature, and (b) annual mean precipitation. Source data: Digital Climatic Atlas of Catalonia <<http://magno.uab.es/atles-climatic/>>; (Pons, 1996; Ninyerola et al., 2000).



References

- Abril, S., Oliveras, J., Gómez, C., 2007. Foraging activity and dietary spectrum of the Argentine ant (Hymenoptera: Formicidae) in invaded natural areas of the northeast Iberian Peninsula. *Environ. Entomol.* 36, 1166–1173.
- Abril, S., Oliveras, J., Gómez, C., 2008. Effect of temperature on the oviposition rate of Argentine ant queens (*Linepithema humile* Mayr) under monogynous and polygynous experimental conditions. *J. Insect Physiol.* 54, 265–272.
- Abril, S., Oliveras, J., Gómez, C. Effect of temperature on the Argentine ant's development and survival – an experimental study. *J. Insect Sci.*, in press.
- Benois, A., 1973. Incidence des facteurs écologiques sur le cycle annuel et l'activité saisonnière de la fourmi d'Argentine, *Iridomyrmex humilis* Mayr (Hymenoptera, Formicidae), dans la région d'Antibes. *Insect Soc.* 20, 267–295.
- Blank, R.H., Gill, G.S.C., Kelly, J.M., 2000. Development and mortality of greedy scale (Homoptera: Diaspididae) at constant temperatures. *Environ. Entomol.* 29, 934–942.
- Bond, W., Slingsby, P., 1984. Collapse of an ant–plant mutualism: the Argentine ant (*Iridomyrmex humilis*) and myrmecochorous Proteaceae. *Ecology* 65, 1031–1037.
- Buckley, R., 1987. Ant–plant–homopteran interactions. *Adv. Ecol. Res.* 16, 53–85.
- Casellas, D., 2004. Tasa de expansión de la hormiga Argentina, *Linepithema humile* (Mayr 1868), (Hymenoptera, Dolichoderine) en un área mediterránea. *Boln. Asoc. Esp. Ent.* 28, 207–216.
- Chiang, H.C., 1985. Insects and their environment. In: Pfadt, R.E. (Ed.), *Fundamentals of Applied Entomology*. Macmillan Publishing Co., New York, pp. 128–162.
- Cohen, J., 1960. A coefficient of agreement for nominal scales. *Educ. Psychol. Meas.* 20, 37–46.
- De Kock, A.E., Giliomee, J.H., 1989. A survey of the Argentine ant, *Iridomyrmex humilis* (Mayr), (Hymenoptera: Formicidae) in South African fynbos. *J. Entomol. Soc. S. Afr.* 52, 157–164.
- Dobson, A.J., 1999. *An Introduction to Generalized Linear Models*. Chapman and Hall/CRC, Boca Raton, Florida.
- Espadaler, X., Gómez, C., 2003. The Argentine ant, *Linepithema humile*, in the Iberian Peninsula. *Sociobiology* 42, 187–192.
- Fielding, A.H., Bell, J.F., 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environ. Conserv.* 24, 38–49.
- Gómez, C., Oliveras, J., 2003. Can the Argentine ant (*Linepithema humile*, Mayr) replace native ants in myrmecochory? *Acta Oecol.* 24, 47–53.
- Gómez, C., Pons, P., Bas, J.M., 2003. Effects of the Argentine ant *Linepithema humile* on seed dispersal and seedling emergence of *Rhamnus alaternus*. *Ecography* 26, 532–538.
- Hartley, S., Harris, R., Lester, P.J., 2006. Quantifying uncertainty in the potential distribution of an invasive species: climate and the Argentine ant. *Ecol. Lett.* 9, 1068–1079.
- Hartley, S., Lester, P.J., 2003. Temperature-dependent development of the Argentine ant, *Linepithema humile* (Mayr) (Hymenoptera: Formicidae): a degree-day model with implications for range limits in New Zealand. *N. Z. Entomol.* 26, 91–100.
- Helmuth, B., Kingsolver, J.G., Carrington, E., 2005. Biophysics, physiological ecology and climate change: does mechanism matter? *Annu. Rev. Physiol.* 67, 177–201.
- Holway, D.A., 1998a. Factors governing rate of invasion. A natural experiment using Argentine ants. *Oecologia* 115, 206–212.
- Holway, D.A., 1998b. Effect of Argentine ant invasions on ground-dwelling arthropods in northern California riparian woodlands. *Oecologia* 116, 252–258.
- Holway, D.A., Suarez, A.V., Case, T.J., 2002. Role of abiotic factors in governing susceptibility to invasion: a test with Argentine ants. *Ecology* 83, 1610–1619.
- Hölldobler, B., Wilson, E.O., 1990. *The Ants*. Belknap Press Harvard, Cambridge, Massachusetts, USA.
- Human, K.G., Gordon, D.M., 1997. Effects of Argentine ants on invertebrate biodiversity in northern California. *Conserv. Biol.* 11, 1242–1248.
- Human, K.G., Weiss, S., Weiss, A., Sandler, B., Gordon, D.M., 1998. Effects of abiotic factors on the distribution and activity of the invasive Argentine ant (Hymenoptera: Formicidae). *Popul. Ecol.* 27, 822–833.
- Ingram, K.K., 2002. Plasticity in queen number and social structure in the invasive Argentine ant (*Linepithema humile*). *Evolution* 56, 2008–2016.
- Jumbam, K.R., Jackson, S., Terblanche, J.S., McGeoch, M.A., Chown, S.L., 2008. Acclimation effects on critical and lethal thermal limits of workers of the Argentine ant, *Linepithema humile*. *J. Insect Physiol.* 54, 1008–1014.
- Keller, L., 1988. Evolutionary implications of polygyny in the Argentine ant, *Iridomyrmex humilis* (Mayr) (Hymenoptera: Formicidae): an experimental study. *Anim. Behav.* 36, 159–165.
- Keller, L., 1995. Social life: the paradox of multiple-queen colonies. *Trends Ecol. Evol.* 10, 355–360.
- Keller, L., Cherix, D., 1985. Approche expérimentale de la polygynie chez la fourmi d'Argentine (Hymenoptera, Formicidae). *Actes Colloq. Insectes Soc.* 2, 263–279.
- Krushelnycky, P.D., Joe, S.M., Medeiros, A.C., Daehler, C.C., Loope, L.L., 2005. The role of abiotic conditions in shaping the long-term patterns of a high-elevation Argentine ant invasion. *Divers. Distrib.* 11, 319–331.
- Lowe, S., Browne, M., Boudjelas, S., De Poorter, M., 2000. 100 of the World's Worst Invasive Alien Species: a Selection from the Global Invasive Species Database. IUCN, New Zealand. <http://www.issg.org/database> Available online.
- Majer, J.D., 1994. Spread of Argentine ants (*Linepithema humile*) with special reference to Western Australia. In: Williams, D.F. (Ed.), *Exotic Ants: Biology, Impact, and Control of Introduced Species*. Westview Press, pp. 163–173.
- Menke, S.B., Holway, D.A., 2006. Abiotic factors control invasion by Argentine ants at the community scale. *J. Anim. Ecol.* 75, 368–376.
- Menke, S.B., Fisher, R.N., Jetz, W., Holway, D.A., 2007. Biotic and abiotic controls of Argentine ant invasion success at local and landscape scales. *Ecology* 88, 3164–3173.
- Menke, S.B., Holway, D.A., Fisher, R.N., Jetz, W., 2009. Characterizing and predicting species distributions across environments and scales: argentine ant occurrences in the eye of the beholder. *Global Ecol. Biogeogr.* 18, 50–63.
- Ness, J.H., Bronstein, J.L., 2004. The effects of invasive ants on prospective ant mutualists. *Biol. Invas.* 6, 445–461.
- Newell, W., Barber, T.C., 1913. The Argentine ant. *U. S. Dep. Agric. Bur. Entomol. Bull.* 122, 1–98.
- Ninyerola, M., Pons, X., Roure, J.M., 2000. A methodological approach of climatological modelling of air temperature and precipitation through GIS techniques. *Int. J. Climatol.* 20, 1823–1841.
- Passera, L., 1994. Characteristics of tramp species. In: Williams, D.F. (Ed.), *Exotic Ants: Biology, Impact, and Control of Introduced Species*. Westview Press, pp. 163–173.
- Pons, X., 1996. Estimación de la Radiación Solar a partir de modelos digitales de elevaciones. Propuesta metodológica. In: Juaristi, J., Moro, I. (Eds.), VII Coloquio de Geografía Cuantitativa, Sistemas de Información Geográfica y Teledetección Vitoria-Gasteiz.
- Roura-Pascual, N., Suarez, A.V., Gómez, C., Pons, P., Touyama, Y., Wild, A.L., Peterson, A.T., 2004. Geographical potential of Argentine ants (*Linepithema humile* Mayr) in the face of global climate change. *Proc. Natl. Acad. Sci. U. S. A.* 101, 2527–2534.
- Roura-Pascual, N., Suarez, A.V., McNyset, K., Gómez, C., Pons, P., Touyama, Y., Wild, A.L., Gascón, F., Peterson, A.T., 2006. Niche differentiation and fine-scale projections for Argentine ants based on remotely sensed data. *Ecol. Appl.* 16, 1832–1841.
- Shilman, P.E., Lighton, J.R.B., Holway, D.A., 2007. Water balance in the Argentine ant (*Linepithema humile*) compared with five common native ant species from southern California. *Physiol. Entomol.* 32, 1–7.
- Stockwell, D.R.B., Peters, D., 1999. The GARP Modeling System: problems and solutions to automated spatial prediction. *Int. J. Geogr. Inf. Sci.* 13, 143–158.
- Suarez, A.V., Holway, D.A., Case, T.J., 2001. Patterns of spread in biological invasions dominated by long-distance jump dispersal: insights from Argentine ants. *Proc. Natl. Acad. Sci. U. S. A.* 98, 1095–1100.
- Suarez, A.V., Richmond, J.Q., Case, T.J., 2000. Prey selection in horned lizards following the invasion of argentine ants in Southern California. *Ecol. Appl.* 10, 711–725.
- Wild, A.L., 2004. Taxonomy and distribution of the argentine ant, *Linepithema humile* (Hymenoptera:Formicidae). *Ann. Entomol. Soc. Am.* 97, 1204–1215.