

ORIGINAL CONTRIBUTION

Estimation of climatic favourable areas for locust outbreaks in Spain: integrating species' presence records and spatial information on outbreaks

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Abstract

For millennia, locust swarms have recurrently devastated crop productivity across continents. In much of Europe, locust outbreaks have been considerably reduced by human pressure in recent decades, but important *foci* of outbreaks still exist in Spain. Distribution models are often used to derive spatial hypotheses and risk maps. Because insufficient information is available to include the extreme plasticity of the solitary and gregarious phases of locusts in large-scale spatial models, we modelled the distribution either of Acrididae species or of outbreaks *per se*. Confirmed occurrences of *Docostaurus*, *Calliptamus* and *Chorthippus* species were obtained from a field survey complemented by museum collection data and the published literature. The locations of confirmed or potential outbreaks covering two time periods of 20 years each were obtained from the literature and from Spanish autonomous community reports. Models were built with one topographic and eleven climatic predictors. We evaluated the ability of different models to predict outbreak recurrence and found that models based on Moroccan locust data or outbreak occurrence data performed the best. We generated a predictive map of the climatic favourability for locust outbreaks in Spain and found that the major *foci* of locust swarms were encompassed by those areas categorized by the models as areas of highest risk. Predictive maps of outbreak favourability can facilitate the more sustainable use of insecticides and more efficient integrated pest management.

Introduction

References to locust outbreaks are as ancient as the Bible. Historically, several locust species have recurrently devastated crop productivity across continents. Today, locusts remain among the most costly insect pests in some countries, and a number of studies have aimed to prevent or minimize the adverse impact of locust swarms (e.g. Stige et al. 2007). In much of Europe, decades of human pressure have reduced the impact of locusts to the point that the genetic diversity of species such as the Moroccan locust might be threa-

tened (Latchininsky 1998). However, a similar reduction in economic impact has not occurred in Spain, where several areas still harbour favourable conditions for locust outbreaks (Latchininsky 1998).

Over the past decade, predictive models of the potential distribution of organisms have received significant attention. These correlative techniques, which are based on the association between environmental factors and the spatial arrangement of species, aim to identify the environmental conditions in which populations of a given species can persist. The suitable conditions identified by such a model are

projected into geographical space to derive spatial hypotheses about the distribution of a species. In the case of pervasive species representing important threats, such as pests or invasive species, the derived hypothesis is used to generate maps that indicate areas of different degrees of risk. These predictive maps are considered complementary tools for preventing or reducing the pervasive impact of the target species (Peterson 2003; Aragón and Lobo 2011; Jiménez-Valverde et al. 2011).

An important benefit of species distribution models designed to mitigate the impact of locust swarms is that they can help reduce the overuse of chemical insecticides. As has been true around the world, the use of chemical insecticides has thus far been the most widespread action against locust outbreaks in Spain, with a concomitant negative effect on ecosystem service and function (Del Moral et al. 2004). Generating maps that express the relative risks of outbreak events might facilitate more reasonable, effective and environmentally sustainable use of chemical insecticides, controls and integrated pest management (e.g. *sensu* Klass et al. 2007a).

At the same time, several limitations inherent to the use of these modelling techniques require researchers to interpret the output of such models with caution. First, it is difficult to assess the potential distribution from the realized distribution reflected in occurrence data (Jiménez-Valverde et al. 2008, 2011; Soberón and Nakamura 2009). Second, it is impossible to encompass all of the complexity of biotic interactions (Guisan and Thuiller 2005; Botkin et al. 2007; Dorman 2007; Buckley et al. 2010). Finally, insufficient information is available to incorporate adaptation or niche evolution and, as is especially relevant in this study, phenotypic plasticity (in its broad sense) across time and space into the models (Dorman 2007; Buckley et al. 2010). An extreme example of phenotypic plasticity is the change from the solitary phase to the gregarious phase that occurs in several locust species. This phase change is accompanied by profound changes in the morphology, physiology and behaviour of locusts (Moreno-Márquez 1942; Barranco and Pascual 1995; Collet et al. 1998; Stige et al. 2007). Complete knowledge about the spatio-temporal drivers of this phase change would facilitate the prediction of when and where locust outbreaks will occur. Unfortunately, current knowledge is not sufficient for the incorporation of this information in distribution models. Assuming that outbreak data reflect a higher occurrence of the gregarious phase, an alternative approach to generating and evaluating risk maps of potential outbreaks is to integrate and compare

models of the entire locust distribution and models of the distribution of outbreak events in particular.

A number of studies have documented the influence of climatic factors, at various spatial and temporal scales, on various aspects of locust biology. For example, both temperature and water-related factors have been shown to affect population dynamics (e.g. Stige et al. 2007; Feng et al. 2012).

In Spain, two locust species are known to be responsible for pervasive impact on crop production: *Calliptamus italicus* (Linnaeus, 1758) (the Italian locust) and *Dociostaurus maroccanus* (Thunberg, 1815) (the Moroccan or Mediterranean locust). Both *C. italicus* and *D. maroccanus* present two phenotypically distinct solitary/gregarious phases (Latchinsky 1998; Sergeev and Van'kova 2008). Currently, the species *Calliptamus wattenwylanus* (Pantel, 1896) is also being monitored in Spain because it has been found to be more abundant than *C. italicus* in several localities. For all three of these species, climatic factors have been shown to influence embryonic development, outbreak occurrence and biotic interactions (Latchinsky 1998; Nechols et al. 1998; Stolyarov 2000; Klass et al. 2007a). Other orthopteran species that occur in Spain are known to be pests in other countries (*Calliptamus barbarus* (Costa, 1836); COPR 1982) or have been found to be relatively abundant (*C. barbarus*, *Chorthippus apicalis* (Herrich-Schäffer, 1840), *Dociostaurus genei* (Ocskay, 1833) and *Dociostaurus jagoi* Soltani, 1978) or spatially associated with pest species such as *D. maroccanus* (*D. genei* and *D. jagoi*; M. Coca-Abia, unpublished data). Thus, it is worth comparing the capacity of distribution models to predict outbreaks of these latter species with their capacity to predict outbreaks of focus potential pest species (*C. italicus*, *D. maroccanus* and *C. wattenwylanus*). Similarly, distribution models of endemic species that are not expected to become pests, such as the Spanish endemism *Dociostaurus hispanicus* (Bolivar, 1898), can be useful as reference controls.

In this study, we generated predictive maps of area favourability for locust outbreak events in peninsular Spain as a function of abiotic factors. Then, as an example of applicability, we considered biotic factors of potential economic importance by overlapping the resulting map with a map of cultivated and managed areas. For this purpose, we performed three types of models: (i) individual distribution models for eight Acrididae species based on presence records from an exhaustive field survey complemented with information from a museum collection and the bibliography, (ii) models of Acrididae species richness and (iii) distribution models of locust outbreaks based on spatial

information about confirmed or potential outbreak occurrences over two time periods of twenty years each (1920–1940 and 1991–2010). We used all these results to examine whether the occurrence of outbreaks is related to the Acrididae species richness and in which direction. Finally, we evaluated the extent to which the areas identified as most favourable (either for each species or for outbreaks) match the recurrence of outbreaks.

Materials and Methods

General procedure

To derive spatial hypotheses about the risks of locust outbreaks, we first identified those locations where abiotic environmental conditions are favourable for such outbreaks. We used species distribution modelling (SDM) techniques to generate a predictive map of potential locust outbreaks. Specifically, we modelled those locations where locust outbreaks were confirmed, where the locust density was high enough to be considered potential outbreaks by managers and/or where locusts had done significant damage to crops. Then, as an example of applicability for a given time period, the resulting map of environmental favourability was overlapped with a map of Spain representing cultivated and managed areas for the year 2000 (Global Land Cover 2000 Project, GLC 2000; <http://bioval.jrc.ec.europa.eu/products/glc2000/glc2000.php>). GLC 2000 is a harmonized database obtained from the SPOT 4 satellite images, which uses the FAO hierarchical classification system based on regional information.

A previous study in north-eastern Spain showed that the species *D. maroccanus*, *C. wattenwylanus* and *D. jagoi* can occur jointly in the same region (Coca-Abia et al. 2007). In agreement with this, the field data gathered throughout Spain for this study indicate that other Acrididae species were associated with the main locust species (*D. maroccanus* and *C. italicus*). Taking into account all of the data used in this study (from field surveys, bibliographic information and museum collections), the average percentages of coincidence within 1 km² UTM cells for *D. maroccanus* and *C. italicus* with six other species were 49.89% and 52.38%, respectively. Thus, we also considered in our analyses the species or subspecies *C. barbarus barbarus*, *C. wattenwylanus*, *D. genei genei*, *D. jagoi occidentalis*, *D. hispanicus* and *C. apicalis*. Because all of these species, except one, shared genus with the focus species, we can explore, under the assumption of niche conservatism (Peterson et al. 1999; Wiens et al. 2010),

whether several species share ecological requirements reflected in the spatial structure of outbreaks. On the other hand, certain assemblages might induce competition among species, which might counteract an increase in the density of a given species (Ritchie and Tilman 1992; Beckerman 2000; Liu et al. 2007). With these possibilities in mind, we can test the extent to which potential Acrididae species richness can be a predictor of potential outbreaks. To this end, we modelled potential outbreaks as a function of 11 climatic variables, one topographic variable and two estimates of potential species richness.

The modelling procedure consisted of three phases. First, using confirmed species presence records, we built individual species distribution models for each of the eight species separately as a function of abiotic factors. Second, we built species richness models using the same predictors. Finally, we built distribution models of outbreaks as a function of both abiotic factors and the previously estimated potential species richness, using both confirmed and potential locust outbreak records.

If a positive association is found between potential species richness and the probability of outbreak, it remains plausible that other species might also be responsible for outbreaks. To explore this possibility, we performed additional analyses comparing the capacity of each individual species model to predict outbreak recurrence in relation to models of outbreaks themselves.

Species presence records

Confirmed presence of the eight species considered was obtained from field surveys carried out in 2008 and 2009 and completed with data of the entomological collection of the Museo Nacional de Ciencias Naturales and by the published literature (Herrera and Jordana 1977; Herrera 1979; Llorente 1982; Lluçà-Pomares 2002).

Surveys were conducted in seven Spanish autonomous communities (Andalucía, Aragón, Castilla-La Mancha, Castilla y León, Extremadura, Madrid and Murcia), which, together, cover about 73% of peninsular Spain. To maximize the coverage of the spatial-temporal range of the focal species within the study area, sampling was conducted during two periods in 2008: spring (April 15 to May 15) and early summer (July 1 to July 31) and two periods in 2009: late summer (July 15 to August 28) and early autumn (September 2 to October 15).

To maximize the environmental representativeness of the surveys, sampling effort was allocated both in

areas where the species of interest are known to be present and in areas of higher climatic variability. To assess climatic variability, we performed a principal component analysis (with varimax normalized rotation) of nineteen GIS-based bioclimatic variables and obtained two main factors (with eigenvalues >1) that explained 83.4% of the climatic variability. The scores of these factors and the standardized latitude and longitude values of each grid cell (10 × 10 km UTM grid cells) were then included as variables in a *K*-means cluster analysis to identify groups of cells that are spatially contiguous and climatically similar (see Legendre and Legendre 1998). The number of clusters ($n = 85$) was chosen *a priori* to represent a realistic sampling effort. Within each cluster and for each sampling period, a site of 0.5 km² was delimited within natural areas, abandoned crop fields or grazing lands. Each of the 85 sites was divided into plots of 400 m² for sampling. Five and one of these plots were randomly chosen for sampling in 2008 and 2009, respectively. Thus, a total of 204 000 m² were sampled.

Surveys were conducted when the insects were most active and in good weather conditions only (no heavy rain and wind speed lower than 18 km/h). In 2008, surveys were conducted using two main techniques. In the first of these, two workers made parallel sweeps of the vegetation over periods of 10, 15 and 20 min with a pentagonal entomological net 25 cm in diameter. In the second technique, four open pitfall traps were run for 24, 48 and 72 h. These traps were 9 cm wide and 0.5 l in volume and were positioned in each corner of the plot at 20 m apart to avoid interference effects and to maximize efficacy. Traps were filled with water, and a few drops of detergent were added to break the surface tension and thus prevent the insects from escaping. In all, forty persons swept the vegetation for a total of 19 125 min and 1700 pitfall traps were run for a total of 61 200 h. In 2009, only the sampling method that proved most efficient in 2008 was used, and eighteen persons performed parallel sweeps of the vegetation in 20-min segments for a total of 1700 min.

From these surveys, 228 406 adult and juvenile specimens (219 918 sampled in 2008 and 8488 in 2009) were identified to genus or species. The proportion of specimens from the field surveys reliably identified to species were 46.5% for 2008 and 95.7% for 2009. The numbers of specimens of the eight focal species represented in the data obtained from the literature and from the museum collection were 2104 and 2113, respectively.

Because in the field surveys our spatial resolution was higher (0.5 km²) than that of abiotic predictors

(1 km²), the centroid of each locality was used to give a resolution of 1 × 1 km. In the case of the information coming from bibliographic and natural history collections, the spatial resolution of the species' presence records was variable (from cells of 1 × 1 km to cells of 10 × 10 km), and records were homogenized considering as a presence points the 1 × 1 km centroids of the municipal polygonal area. We assume that these differences in resolution are not biased towards any species and can be considered as randomly distributed.

Spatial information on outbreaks

Localities of confirmed or potential outbreaks were obtained from the literature (Navarro 1922; Lapazarán y Beristaín 1925; Cañizo 1939; Benlloch and Cañizo 1941; Cañizo-Gómez 1942; Moreno-Márquez 1943, 1946; Benlloch 1947) and from reports provided by the pest managers of each Spanish autonomous community. The information that was used covered the time periods of 1920–1940 and 1991–2010. The data for the period 1920–1940 represent confirmed locust outbreaks but did not include confirmation of the species involved. The information obtained for the period 1991–2010 included both confirmed and potential outbreaks, and most of these were considered to be associated with *D. maroccanus*. Potential outbreaks were episodes in which damage to crops and/or locust densities were considered high enough by managers to implement outbreak prevention measures. Information on the location of outbreaks was available either as spatial coordinates or as the precise localities. In the latter case, the centroid of the municipal area polygon was used as the spatial coordinates.

Abiotic environmental predictors

Nineteen bioclimatic variables and one topographical variable, each at a resolution of 1 km² UTM cells, were downloaded from the WorldClim data set (Hijmans et al. 2005; www.worldclim.org) for potential use as predictors in the models. Climate layers of this data set were obtained by the interpolation of average monthly climate records generated by climate stations from 1950 to 2000. To reduce redundancy and collinearity, we performed Pearson correlations among variables (after normalization with the Box-Cox transformation) before selecting those explanatory variables to be included in the distribution and richness models. Seven variables were excluded because they were strongly correlated with other variables ($R > 0.90$). Thus, the models incorporated eleven bioclimatic predictors and one topographical

predictor (mean elevation). The bioclimatic predictors included seven temperature variables (annual mean temperature, minimum temperature of the coldest month, maximum temperature of the warmest month, mean temperature of the wettest quarter, mean temperature of the driest quarter, temperature annual range and isothermality) and four precipitation predictors (annual precipitation, precipitation of the warmest quarter, precipitation of the coldest quarter and precipitation seasonality).

Estimation of potential species richness

It has been shown that Orthopteran species richness and assemblages at various scales can be partially driven by climate parameters, including Acrididae (Szövényi 2002; Bieringer and Zulka 2003; Steck and Pautasso 2008). We used species richness as a parsimonious predictor of outbreak distributions in our models because it can integrate either abiotic (climatic drivers of Acrididae's spatial arrangements) or biotic influences (e.g. competition or facilitation). We included two different estimations of species richness in models: (i) a prediction of species richness from a model built with the observed richness of field samplings, bibliography and museum collection specimens and projected over the entire Spanish territory and (ii) overlaps of predicted species distribution, the result of the overlap among the predicted distributions of each of the eight species modelled separately.

A prediction of species richness (the first estimation mentioned above) was obtained by modelling the observed richness as a function of the abiotic variables. We used the software SAM (Spatial Analysis in Macroecology) to select the most parsimonious linear model based on the Akaike information criterion (Rangel et al. 2010), which reduced the number of predictors by half. Additionally, we obtained the Akaike weights (which can be interpreted as the probability that a given model is the best) to assess predictor importance (Aubad et al. 2008, 2010) and averaged across 4095 possible models arising from all combinations of the 12 predictors used (Rangel et al. 2010). We then ran Generalized Linear Models (McCullagh and Nelder 1989) with observed richness as the dependent variable and the six best predictors as the independent variables. Because species richness was in the form of counts, we specified a Poisson distribution and a log-link term (McCullagh and Nelder 1989). Finally, we used this model to geographically project the observed species richness over the entire Spanish territory.

To construct the overlap among predicted species distributions, we first obtained the potential distribution of each of the eight species individually by modelling its observed presence as a function of the abiotic factors. The threshold criterion for transforming the continuous model output into categorical presence/absence maps was the minimum training presence, which represents the environmental range encompassed by all of the presence records. We then constructed a species distribution overlap variable by combining (overlapping) the potential distributions of all eight species.

Distribution models

Distribution models, both for individual species and outbreaks, were built using the three most commonly used only presence modelling techniques: Ecological Niche Factor Analysis (ENFA), a Multidimensional Envelope (ME) procedure and the maximum entropy modelling of species' geographic distributions (MaxEnt). The outbreak models incorporated both the abiotic predictors and the two estimations of species richness. All models were built at the resolution of the environmental predictors (1 km² UTM cells).

ENFA is implemented in the software Biomapper (Hirzel et al. 2002). This approach is analogous to principal component analysis but is grounded in the niche concepts of marginality (the ecological distance between the species' optimum and the mean conditions within the study area) and specialization (the ratio of the ecological variance in mean conditions to that associated with the focal species). Thus, assuming that variables with lower variability associated with the presence locations are playing a key role limiting the species distribution, this procedure provides factors with ecological significance. The original environmental variables are synthesized into a few orthogonal factors, the first of which maximizes the marginality and the others of which maximize the specialization of the focal species. The distribution of the eigenvalues obtained was compared with the MacArthur's broken stick distribution to guide the selection of the subset of factors to be used in generating habitat suitability maps (see Hirzel et al. 2002 for more details).

The ME procedure estimates the environmental range regarding its recorded presence (Busby 1991). This is the simplest procedure for generating a Boolean map of risk areas from the climatic hypervolume encompassed by the minima and maxima of climatic variables within the range of a species (or of outbreak occurrences). The ME procedure gives equal weight

to all predictors included in the models, and therefore, a protocol is needed for identifying the key bioclimatic variables. Following a previously developed procedure (Aragón et al. 2010), we used the ENFA described above to identify the most relevant predictors and included them in the ME procedure. The marginality factor derived by the ENFA explained 72% of the variance, and this was then used to assess the six most relevant predictors for the ME procedure.

The MaxEnt algorithm (Phillips and Dudik 2008) performs a maximum entropy approach that generates outputs of area favourability for a given attribute. This approach also yields a measurement of variable importance in the form of a heuristic estimate of the relative contributions of predictors based on their gain in models. Additionally, we ran the jackknife procedure for predictors, available in MaxEnt, which gives an approximation of the predictors with the most useful information by themselves and those having the most exclusive information.

To increase the predictive power of our maps, we generated favourability maps by combining the predictive maps obtained from the ENFA, ME and MaxEnt procedures. This requires the transformation of the continuous ENFA and MaxEnt output into binary favourability data. To do this, the continuous data from the ENFA and from MaxEnt were reclassified using the first quartile of the continuous output as a threshold for categorizing areas of lower favourability (the lower quartile) and higher favourability (the three upper quartiles). Once these maps were reclassified in this manner, we overlapped the maps from the ENFA, ME and MaxEnt procedures to generate a predictive map with four categories based on the degree of overlap (no favourability, low favourability, medium favourability and high favourability). Finally, an additional map was obtained to represent these categories of risk areas that coincide with land uses of economic importance (cultivated and managed areas from the GLC 2000 database).

Evaluation of models with outbreak recurrence

We aimed to examine the extent to which each distribution model (for each species and for outbreak occurrences) can explain outbreak recurrence. For individual distribution models, an independent evaluation with outbreak data is possible because these models were built using species presence data. However, the evaluation of outbreak distribution models with outbreak data would not be independent. To perform an independent evaluation of the outbreak distribution models, we assigned a new attribute to

the outbreak data that were not used in the building of these models. Outbreak data from reports and other published literature were divided into two categories of recurrence (lower and higher recurrence). Outbreaks that occurred in the same province in different decades (or many even in different centuries) were categorized as higher recurrence outbreaks. Besides the geo-referenced occurrence records included in the distribution models, the scale of province allowed us to add more information of outbreaks whose spatial precision (at the province level) was not accurate enough to be included in models. In other words, using all outbreak occurrence points, each one was then associated with one of these two attributes, so that the outbreak model evaluation is independent because these newly considered attributes were not used to build the outbreak model. Such outbreaks were identified in the provinces of Salamanca, Zaragoza, Cáceres, Badajoz, Ciudad Real and Córdoba. Because the calculation of recurrence values passed through a decrease in resolution at the province level, small resolution differences (between directly given spatial coordinates and those associated with given localities) were absorbed.

To test the degree to which areas of higher recurrence outbreaks matched the areas of highest favourability in our predictive maps (obtained from the combination of models), we used Generalized Linear Models (McCullagh and Nelder 1989). In these analyses, outbreak recurrence was the binomial dependent variable with a logit-link term, and favourability was included as a categorical factor (with the three categories of none/low, medium and high). For these analyses, the categories of 'no favourability' and 'low favourability' were merged because the recorded outbreaks fell within the low, medium and high categories in 95.2% of all cases. P-values of significance were obtained from the chi-square statistic, and we also calculated the percentage of deviance explained for each analysis.

Results

Information from field surveys, museum collection data and the published literature resulted in 86 presence records for *D. maroccanus*, 87 for *C. italicus*, 150 for *C. wattenwylianus* and 83 outbreak localities. Figure 1 shows the distribution of *D. maroccanus*, *C. italicus* and outbreak localities in Spain (for presence records of the other species, see Supporting Information, Appendix S1). Overall, the grid-cell species presence data from the field survey represent an average of 48.5% of the data used for each species.

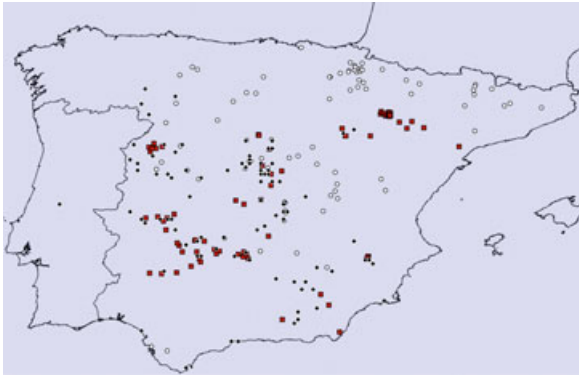


Fig. 1 Confirmed presence records of *Dociostaurus maroccanus* (black circles), *Calliptamus italicus* (white circles) and outbreaks (grey squares) in Spain. Species presence were obtained from field sampling during 2008 and 2009, from the collection of the Museo Nacional de Ciencias Naturales (Madrid) and from the bibliography. Confirmed and potential outbreaks were obtained from the bibliography or provided by managers of administrative communities.

Predictor relevance

We found that the outbreak ENFA and MaxEnt models coincided in their identifications of all but one of the top 50% most relevant predictors (fig. 2a,b). Therefore, the top half of the predictors were used in running the ME models. Among the predictors assessed as most relevant, temperature annual range, precipitation of the coldest quarter and estimated richness appeared to contribute most significantly to the models. Estimated richness appeared in the first and third positions of the relevance rankings in the ENFA and MaxEnt outbreak models, respectively. Temperature annual range was ranked by the MaxEnt jackknife procedure as the predictor with the most useful information by itself, and this predictor was also within the top half in the model of species richness (fig. 2c). Precipitation of the coldest quarter was identified by the MaxEnt jackknife as the factor providing the most information that was not present in the other predictors.

Evaluation of distribution model performance in predicting outbreak recurrence

Generalized linear models of outbreak recurrence as a function of favourability values were significant only when this favourability was obtained from the distribution models of *C. italicus*, *D. maroccanus* and outbreak occurrences (table 1). The capacity of the predicted area favourability to explain outbreak recurrence was highest for *C. italicus*, *D. maroccanus* and outbreak occurrences (table 1).

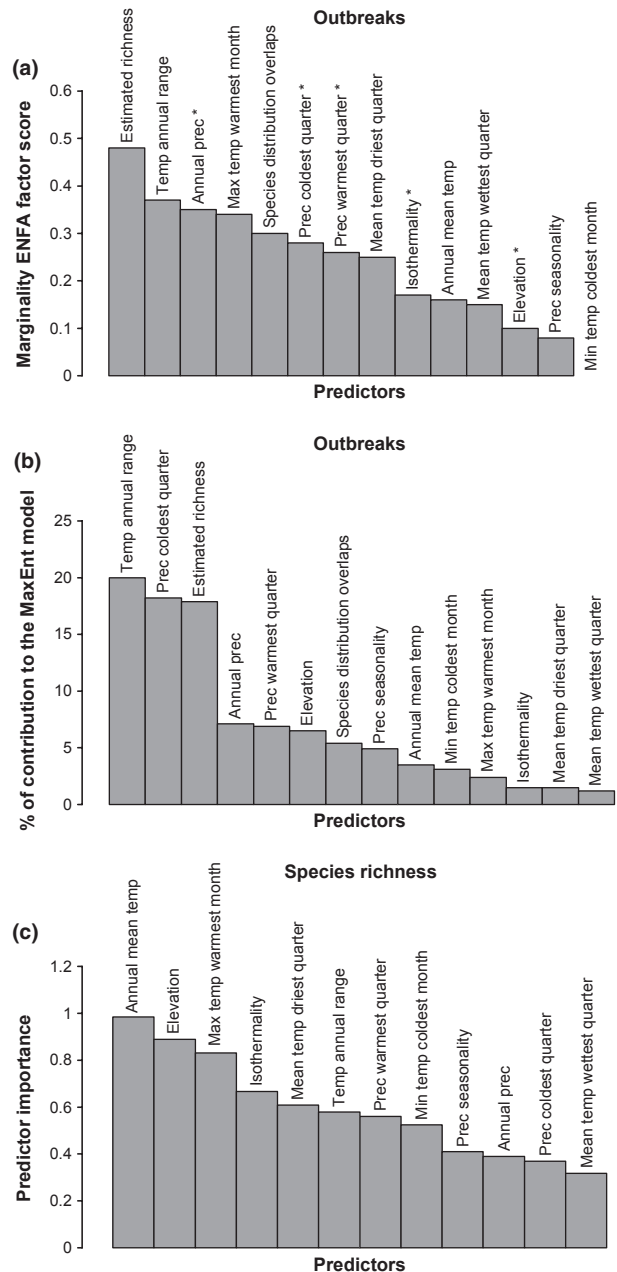


Fig. 2 Relevance of variables to predict area favourability for locust outbreaks assessed by (a) the marginality factor of the ENFA model and (b) the per cent of contribution in the MaxEnt model. (c) Ranking of predictor relevance for OLS orthopteran richness models assessed by averaging parameter estimates across 4095 models, using Akaike weights. Asterisks denote negative association in ENFA factor loadings.

The highest predictive power was obtained from the combined models of outbreak occurrences. Here, the proportion of outbreaks of high recurrence increased concomitantly with the degree of predicted area favourability (fig. 3a), and the proportion of outbreaks of low recurrence was smaller in the areas of

Table 1 Generalized liner models of outbreak recurrence as a function of area favourability for eight Acrididae species and locust outbreak occurrence. Area favourability in Spain was estimated from distribution models

Species	Explained deviance (%)	Chi-square	P-value
<i>Calliptamus wattenwylanus</i>	2.95	3.04	0.21
<i>Calliptamus italicus</i>	7.46	7.70	0.02
<i>Calliptamus barbarus</i> *	0.17	0.17	0.67
<i>Chorthippus apicalis</i>	2.46	2.54	0.27
<i>Doclostaurus genei</i>	4.25	4.39	0.11
<i>Doclostaurus hispanicus</i>	0.57	0.59	0.74
<i>Doclostaurus jagoi</i>	4.43	4.57	0.10
<i>Doclostaurus maroccanus</i>	8.87	9.16	0.01
Outbreaks	16.01	16.52	<0.001

Percentage of deviance explained, chi-square statistic and the corresponding P-values are shown for each species and for the observed outbreaks. Bold denotes significant P-values. *For the case of *C. barbarus*, the factor had only two levels (medium and high favourability).

highest favourability than in those of medium favourability (fig. 3a). In addition, the proportion of outbreaks in the areas of highest favourability was greater for outbreaks of high recurrence than for those of low recurrence, whereas the opposite was true in the areas of medium favourability (fig. 3a). Similarly, in the case of *D. maroccanus*, the proportion of outbreaks in the areas of highest favourability was greater for outbreaks of high recurrence than for those of low recurrence (fig. 3b). However, in this case, the proportion of outbreaks of high recurrence did not increase concomitantly with the degree of predicted area favourability (fig. 3b). Finally, the results obtained using *C. italicus* data did not clearly match any expected pattern (fig. 3c).

Discussion

In this study, we modelled the distribution of locust outbreaks that occurred in Spain in two time periods (1920–1940 and 1991–2010) and also the distributions of species that have been considered responsible for important damage to crops (such as *C. italicus*, *C. wattenwylanus* and *D. maroccanus*). In addition, we modelled the distribution of other species of Acrididae to test which of the eight species best predict outbreak recurrence and to examine whether species distribution models can predict outbreak recurrence (a temporal parameter) as accurately as outbreak distribution models do. We employed the modelling methods that are most commonly used when only presence data, and not reliable absence data, are available (ME, ENFA and MaxEnt). Model outputs

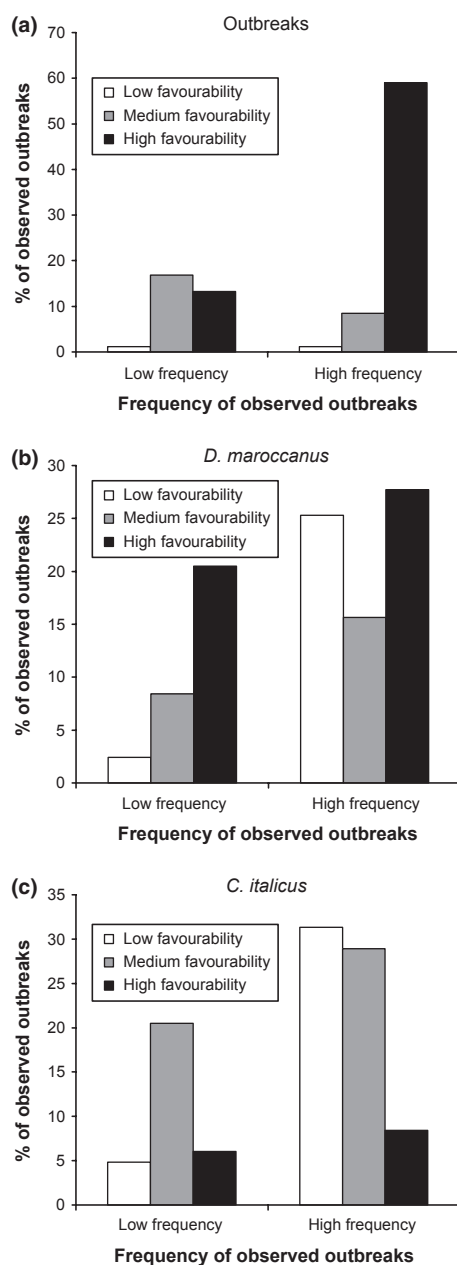


Fig. 3 Percentage of observed outbreaks assigned to high and low recurrence that fallen within areas predicted as low (white), medium (grey) and high favourability (black) by distribution models of (a) outbreak presence, (b) *Doclostaurus maroccanus* and (c) *Calliptamus italicus*. Categories of area favourability were predicted by combining the ME, ENFA and MaxEnt models.

were combined to obtain maps of peninsular Spain indicating areas with different degrees of favourability for each species and for locust outbreak occurrences. Species distributions were modelled as a function of one topographic variable and 11 climatic variables. Outbreak distributions were modelled as a function of

the same abiotic factors along with two estimations of Acrididae species richness. We assessed predictor relevance in models using different types of assessments and found consistency between models.

To put our result in an appropriate framework, it is necessary to consider that our models were not built with data of the entire species ranges but with their distributions in peninsular Spain. A previous study with insects showed that species distribution models that do not incorporate global data misrepresent potential whole distributions yielding smaller predicted potential areas (Sánchez-Fernández et al. 2011). If this applies to the species of this study, we can argue that the risk areas predicted for outbreak climatic favourability would be larger to some extent. On the other hand, it can be also argued that this constraint is more problematic when the aim is to predict the potential distribution of the whole species, regardless of the within-species diversity, such as for evolutionary questions at higher phylogenetic levels. The objective of our study is to apply our models to a regional problem, and thus diversity within species is important because local adaptations of populations far from the area of application might not be relevant or even might override the optimal parameterization to a specific regional case of application. For the case of *D. maroccanus*, genetic and phenotypic differences among separated populations have been suggested (reviewed in Latchininsky 1998). Which subset of populations should be considered to give the best solution in concordance with a specific case of application is challenging, but several reasons allow us to support our data as reasonably informative. First, Spain is part of a glacial refugium where climatic stability has favoured a within-species genetic diversity greater than in northern Europe as found for many species, including Acrididae species (Hewitt 2000). Second, it is expected that because glacial refugia were beyond of strong climatic changes, species distributions in southern Europe are closer to the equilibrium with contemporary climate (e.g. Hawkins and Porter 2003; Svenning and Skov 2007); and the equilibrium assumption for species distribution models is an important requirement that it is not always fulfilled (Guisan and Thuiller 2005; Sinclair et al. 2010). Third, locust outbreaks in other European countries are nearly eradicated and therefore that parts of their current distributions are less representative of climatic favourable conditions and more intensely related to anthropogenic actions (Latchininsky 1998). Finally, peninsular Spain comprises a large environmental heterogeneity regarding Eurasia and Africa, which guarantees a reasonable representativeness to detect

associations between climatic factors and distributional patterns.

Relevance of abiotic factors and estimated species richness

Although it is always challenging to elucidate the real influence of explanatory variables in correlative models, in this study, different types of assessments consistently revealed temperature annual range, precipitation of the coldest quarter and estimated Acrididae species richness as the predictors with the highest influence in outbreak models. Higher values of temperature annual range were associated with higher outbreak favourability, as reflected by the positive sign of the marginality factor loading in the ENFA (fig. 2) and by the response curve generated by MaxEnt (plot not shown). Thus, it appears that important temperature differences throughout the year are associated with the occurrence of locust outbreaks in Spain. At the same time, lower values of annual precipitation and precipitation of the coldest quarter (in relation to the range of values throughout Spain) were associated with higher outbreak favourability, as reflected by the negative sign of the marginality factor loading in the ENFA (fig. 2) and by the response curve generated by MaxEnt (plot not shown). This is not in contradiction with the minimum requirement of moisture for egg development or food plant growth that has been reported at local scales (e.g. Van der Werf et al. 2005), as our results concern levels of precipitation relative to the entire range of values observed throughout Spain. In fact, it can be argued that excess precipitation can negatively impact locust fitness. In the case of *D. maroccanus*, excess soil humidity can have a pervasive effect on the development of locust eggs by facilitating the action of fungal pathogens (Latchininsky 1998).

Estimated richness of the considered species of Acrididae was positively associated with outbreak favourability obtained from the ENFA (fig. 2) and from MaxEnt (plot not shown). Several non-exclusive mechanisms might explain this result. First, it remains possible that other species in addition to *D. maroccanus* and *C. italicus* were responsible for locust outbreaks. Among the six additional species considered, several (such as *C. barbarus* and *C. wattenwylanus*) have provoked damage to crops, although with lesser impact. However, our independent evaluation of the distribution models regarding outbreak recurrence did not reflect a strong concordance with the output of models for other species (table 1). An alternative explanation is that although other species are not directly

responsible for outbreaks, they might favour outbreaks of the focal species. It is also plausible that other innocuous species coexist with the other more pervasive species but do not provoke outbreaks either directly or indirectly. It has been conjectured that interspecific responses to sibling species might be positive, negative or indifferent (Applebaum and Heifetz 1999). Finally, it is important to note that our predictor of Acrididae species richness was a projection of observed richness as a function of certain abiotic factors. Therefore, we can conclude only that many of the species considered share, at least partially, ecological requirements that coincide with those conditions in which outbreaks occur. Further studies are needed to identify which of the proposed explanations underlie this association between species richness and outbreak probability.

Evaluation of model performance in predicting outbreak recurrence

We found that the models with the highest capacity to predict temporal structure of outbreaks (recurrence) were those built using the spatial structure of *D. maroccanus* or outbreak occurrences. The spatial prediction for *D. maroccanus* was superior in predicting outbreak recurrence in comparison with other species. This does not necessarily imply that other species cannot provoke damage to crops; rather, our results suggest that *D. maroccanus* might be responsible for most of the outbreaks analysed in this study. Indeed, presence records of *C. italicus* were scarce in some zones of south-western Spain (fig. 1), where important foci of locust outbreaks exist.

It remains possible that the distribution of conditions that favour a switch to the gregarious phase is not exactly the same as the entire distribution of a species. That is, outbreaks may occur not in the entire range of a species, but only in a part of it. The combination of model outputs that best predicted outbreak recurrence in this study was that obtained using simple outbreak occurrence, followed to a lesser extent by the outputs for *D. maroccanus*, whereas predictions based on *C. italicus* data did not follow an expected pattern. This is in line with previous studies arguing that species distribution models might be too simplistic because of the difficulty of incorporating phenotypic plasticity (Dorman 2007; Buckley et al. 2010). Locust outbreaks are paradigmatic examples, as many locust species considered to be pests have evolved two extremely differentiated phenotypes (the solitary and gregarious phases; Collet et al. 1998; Stige et al. 2007; Simpson and Sword 2008). Taken together, this suggests that the best way

to predict locust outbreaks that may cause damage to crops should integrate and/or compare models of both outbreak and species occurrences.

Predictive map of the favourability areas for locust outbreaks in Spain

Figure 4(a) shows four categories of favourability for locust outbreaks across Spain obtained from a combination of outbreak occurrence models. The distribution of the high-favourability areas clearly encompasses the zones where locust outbreaks still occur in Spain: Los Monegros in north-eastern Spain (Aragón), Ledesma in the west (Salamanca) and in the south-west, an area encompassing Los Llanos (Cáceres), La Serena (Badajoz), Los Pedroches (Córdoba) and the Alcudia Valley (Ciudad Real). Our example of application restricted to land uses of economic importance for the year 2000 shows that, although areas of higher risk

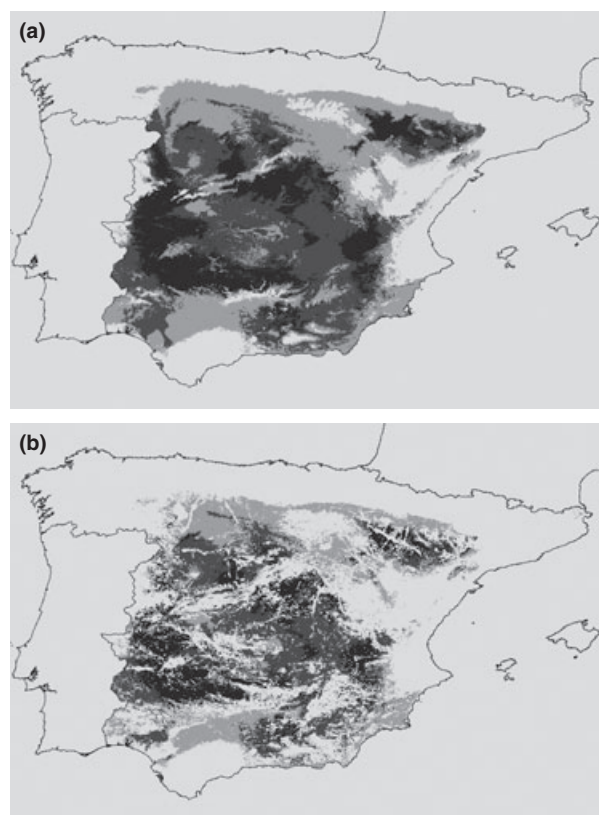


Fig. 4 Predictive maps showing area favourability for locust outbreaks in Spain. Light grey denotes no favourability, and intensity in the grey scale (from deep grey to black) denotes areas from low favourability to high favourability. Categories of area favourability were predicted combining the ME, ENFA and MaxEnt models (see Materials and Methods). (a) Map of predicted area favourability regardless of land use. (b) Map of predicted area favourability only within cultivated and managed areas.

are reduced, they are still represented in important areas of the above-mentioned provinces with a higher area reduction in Salamanca (fig. 4b). This combined map should not be confounded with an influence of a given land use but as suitable conditions of altitude, precipitation and temperature that overlap with cultivated and managed areas, places where the pest may enter in conflict with human interests.

Certainly, it is important to remark that our models were built with climatic parameters, except one (altitude), and that other environmental conditions also affect the locust presence and outbreaks. Favourable climatic conditions are necessary but are insufficient for predicting damage to crops. Another well-known limitation of species distribution models at geographic scales is the difficulty of incorporating biotic interactions (Guisan and Thuiller 2005; Botkin et al. 2007; Dorman 2007; Buckley et al. 2010; Aragón and Sánchez-Fernández 2012). In this vein, weather plays an important role not only directly in locust population dynamics (e.g. by affecting egg development) but also indirectly, by means of its effects on habitat structure (Simpson and Sword 2008). The quality and distribution of food vegetation at local scales might modulate the density-dependent phase polyphenism in locusts (Van der Werf et al. 2005; Simpson et al. 2011). Another example of the importance of biotic interactions is the presence of a fungal entomopathogen associated with natural locust populations in Spain (Jiménez-Medina and Santiago-Alvarez 1999). The efficiency of a *Metarhizium*-based biopesticide against various locust species was recently modelled as a function of climatic parameters, and the spatial variation in its virulence was mapped in Spain (Klass et al. 2007a,b). By integrating our predictive map of favourability for outbreaks (fig. 4) with the map from this previous study (Fig. 1d in Klass et al. 2007b), we can explore where the entomopathogen is expected to be most effective within those areas predicted as being of highest risk. In the area of Salamanca in western Spain, where our models predicted high favourability for outbreaks, the predictive map of pathogen impact showed relatively high effectiveness (Klass et al. 2007b). However, in many other Spanish provinces with higher historical outbreak recurrence, low pathogen impact is predicted (Klass et al. 2007a). Therefore, locust outbreak prevention in Spain should incorporate multiple types of control agents in an integrated pest management approach. Ideally, different prevention techniques should be used based on their spatially structured efficiency. For example, several volatile components identified from egg pods elicit aggregation of gravid females in other locust

species (Torto et al. 1999). Furthermore, it is known that the transmission rate and durability of insect pheromones may depend on temperature and humidity (e.g. McDonough et al. 1989). Previous studies have developed models for integrated pest management using pheromones in atmospheric surface layers, incorporating the effects of wind, temperature and humidity (Bisignanesi and Borgas 2007; Walse et al. 2008). Thus, for locust pest prevention, further research on models of pheromone efficiency as a function of climatic factors and their geographical projections would be informative.

To conclude, we generated a predictive map representing the climatic favourability for locust outbreaks in Spain. A combination of models based on the spatial information of outbreaks (location of occurrences) performed better in predicting a temporal attribute of outbreaks (recurrence) than did individual models based on species presence. Among the species of Acrididae considered in this study, the combination of models based on *D. maroccanus* data performed the best in predicting outbreak recurrence, suggesting that this species caused many of the outbreaks considered. Our results also showed that localities with higher outbreak recurrence were associated with higher values of estimated potential Acrididae species richness. Thus, further studies testing whether certain assemblages can be used as indicators of locust pest risk would be worthwhile.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Figure 1. Confirmed presence records of *Calliptamus barbarus* (a), *Calliptamus watt-enwyllyianus* (b), *Dociostaurus genei* (c), *Dociostaurus jagoi* (d), *Dociostaurus hispanicus* (e) and *Chorthippus apicalis* (f) in Spain. Species presences were obtained from field sampling during 2008 (white dots) and 2009 (gray squares), from the collection of the Madrid Natural History Museum and from the bibliography (black dots).