

Predicting potential distributions of invasive species: the exotic Barbary ground squirrel in the Canarian archipelago and the west Mediterranean region

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Abstract This contribution aimed to predict the invasive Barbary ground squirrel (*Atlantoxerus getulus*) potentiality for invading the Canary Islands and western Mediterranean region, by determining firstly the climatic suitable areas in its native range and secondly, using presence data in the invaded range. Nineteen environmental variables submitted to a Principal Components Analysis selected those variables with higher factor loadings, which represent the main environmental conditions of the Northern African region (temperature in the coldest

quarter, seasonal temperature, precipitation in the coldest quarter, temperature in the wettest quarter). After selecting hundred times more pseudo-absence points than presence observations ($n = 6600$ at a 0.083° resolution), Generalized Additive Models and Single-hidden-layer Neural Networks fitted in R were used to calibrate the model. Model results were extrapolated for the Canary Islands and the western Mediterranean region. In order to select between the two techniques, we calculated three accuracy measures (specificity, sensitivity and AUC) after using a Jack-knifing procedure and models were repeated ten times. The GAM model was less accurate than the NN model. Suitable areas did not have mean temperatures in the coldest quarter lower than -5°C and precipitation in the coldest quarter higher than 300 mm, respectively. We predicted favorable climatic areas across almost all the Maghreb, the European western Mediterranean region and in all the Canary Islands. Nevertheless, the seven islands differed significantly in the mean favorability scores, with El Hierro, Lanzarote and Gran Canaria being the most suitable. Same methodological analysis was applied to predict *A. getulus* distribution in other Canarian islands based on presence data from the invaded Fuerteventura. In this case, only Lanzarote and Gran Canaria appeared to be climatically suitable for the species. Our predictive model is an applicable tool to establish the invasive potential of *A. getulus* and to prioritize management strategies, within and outside the

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Canarian archipelago, to impede the expansion of this invasive squirrel out of Fuerteventura Island.

Keywords *Atlantoxerus getulus* · Canary Islands · Generalized additive models (GAM) · Invaders' distribution · Predictive models · Range expansion · Single-hidden-layer neural networks (NN)

Introduction

Many recent publications support the assumption that biological invasions are a major cause of global biodiversity change and pose a great hazard to ecosystems (Williamson 1996). Intentional or unintentional introductions of species represent a core component of human-induced global change (Vitousek et al. 1996; Mack et al. 2000). As a result of this concern, many advances have been made in understanding the mechanisms underlying the ecology of invasions (e.g. Shigesada and Kawasaki 1997; Elton and Simberloff 2000; Mooney and Hobbs 2000; Van Driesche and Van Driesche 2004), helping to design conservation practices to fight against invaders (Coblentz 1990; Donlan et al. 2003; Hulme 2003). Undoubtedly, improving the knowledge of species distributions is crucial to managing biodiversity (Noss 1983). Thus, predicting invasions is probably one of the most highly recommended and cheapest ways to fight this battle (Leung et al. 2002).

Some authors reviewed progresses in predicting invasions based on biological characteristics of the species (Kolar and Lodge 2001), which are useful techniques for understanding the ecology of invasion, but are too complex to be applied in the management of each invader in each region. Alternately, some theorized about the role of geographical variables in explaining invasion success (Blackburn and Durcan 2001), while predicting potential species' invasions through modeling their distribution has been suggested as a very applicable and encouraging tool (Peterson and Vieglais 2001; Peterson 2003; Soberón and Peterson 2005; Thuiller et al. 2005; Peterson 2006). Predictive species distribution modeling, carried out through a wide variety of methods, has become increasingly used as a tool to address species-environment relationships and to tackle diverse ecological disciplines (Guisan and Zimmermann

2000; Thomas et al. 2004; Thuiller 2004; Guisan and Thuiller 2005; Araujo and Rahbek 2006). In the case of invasive species, these modeling approaches are based on the estimation of species' distributions in environmental space, which can be subsequently used to derivate a geographical distribution hypothesis able to represent the invasive environmental favorable areas for the species (potential distribution) based on native-range environmental characteristics (Soberón and Peterson 2005; Peterson 2006). Many studies have predicted the potential distribution of invasive species using this theoretical and methodological framework (see Peterson 2006 and references therein), whose prediction success is related to the maintenance on environmental adaptations between the individuals of the same species and species belonging of the same lineage group (the so called niche conservatism; see e.g., Peterson et al. 1999; Peterson and Vieglais 2001; Martínez-Meyer et al. 2004 or Parmesan et al. 2005). Although niche modeling constitutes a key tool in predicting invasibility and in assessing species invasion and proliferation (Peterson and Vieglais 2001), there are few examples that apply these methods as a management tool (Beerling et al. 1995; Peterson and Vieglais 2001; Welk et al. 2002; Peterson 2003; Peterson and Robins 2003; Robertson et al. 2004; Welk 2004; Cassinello et al. 2006; Muñoz and Real 2006).

The equilibrium state of a species with their environment (all suitable locations are inhabited) has been claimed as a requisite in developing correlative species distribution models (Franklin 1995). However, depending on the considered extent, the majority of the species is more likely to be in a non-equilibrium state. This lack of environmental equilibrium in the distribution of species is one of the most important obstacles to obtaining reliable distribution maps when one wants to model the realized distribution of a species (see Lobo 2007). However, if the aim is to obtain a geographical representation of all possible areas with some probability of being colonized and affected by the invader in the future (the potential distribution), we need to elaborate distributional simulations able to estimate the probable distribution of the species in absence of biotic interactions or dispersal limitations. Predictive distribution models performed for invasive species constitute simulations that must be considered as maps of

risk; i.e., geographical representations of the areas that host environmental conditions similar to those present in the native region. This potential distribution can subsequently be used to approximate the future distribution of an invader, assuming that the species is not able to disperse into environments not found in their native range and that limiting factors are similar among native and introduced areas. The fulfilment of these assumptions is essential to interpret the obtained potential distributions. Some recent evidences show that the climatic conditions in the successfully invaded localities can differ from the observed in the native range (Mau-Crimmins et al. 2006; Broennimann et al. 2007; Fitzpatrick et al. 2007). Thus, although the species generally retain their climatic tolerances (Wiens and Graham 2005) biotic or dispersal limitation forces can also play a role in the native distribution range. In this case, the existence of suitable but uninhabited localities in the native region will inevitably cause that the derived potential distributions underestimate the invasion risk in non-native territories.

In this contribution, we applied predictive models to simulate the extent and location of climatic suitable areas for an invader species, already successfully established in the Canary archipelago: the Barbary ground squirrel (*Atlantoxerus getulus* Linnaeus, 1758). The species was deliberately introduced from Morocco onto Fuerteventura Island in 1965 (Machado and Domínguez 1982), and has since been translocated to other Canary Islands and to mainland Spain. Using a set of non-correlated climatic variables and the available distributional data of *A. getulus* in its native distribution range (North-western Africa), and also in its invasive area, we build predictive distribution models to estimate the potential geographical range of this species across the whole western Mediterranean region, and especially to delimit the favorable regions in the invaded Canary archipelago. The general aim of this study is to provide information on how risky would be the introduction of *A. getulus* in other Canary Islands, through exploring the environmental capacity of the remaining uninvaded islands to withstand future introductions. Knowing whether the rest of the islands would be environmentally suitable for being invaded is essential for prioritizing on conservation guidelines to prevent the species establishment in the rest of the archipelago.

Methods

The species

Atlantoxerus getulus, the current unique species of the *Atlantoxerus* monospecific genus, is native to Northern Africa and is widely distributed through Morocco and some parts of Algeria (Aulagnier and Thrévenot 1986; Kingdon 1997). In 1965, a pair was introduced as a pet into Fuerteventura Island (Canarian archipelago) from some Sahara territories (Sidi Ifni, former Spanish Sahara; Machado 1979; Machado and Domínguez 1982). After around half a year in captivity, one of them escaped and the other was subsequently released. A few months later, the spread was facilitated by other deliberate translocations inside the island (Machado and Domínguez 1982; personal data). *Atlantoxerus getulus* has shown a great capacity to establish and spread, and its colonization has been extremely successful in Fuerteventura (López-Darias and Lobo unpublished). Since 1996, it has been introduced on several occasions from Fuerteventura into Gran Canaria (Calabuig 1999) and in 2006, into Lanzarote (López-Darias 2006). The scale of its impacts is remarkable; it disrupts the dispersal mechanisms of native and introduced plant species (Nogales et al. 2005; López-Darias and Nogales unpublished), alters predator populations (Gangoso and López-Darias 2004), introduces parasites and diseases (i.e., Lorenzo-Morales et al. 2007), predated upon breeding birds and endemic terrestrial snails that are in danger of extinction, and causes great losses in agriculture.

Study area

The predictive distribution model was carried on the North-western African region (-14° to 12° longitude, and 27° to 38° latitude; $2,002,155 \text{ km}^2$) at a resolution of 0.083° (around 100 km^2). This area comprises diverse vegetation types including localities from sea level to $3,237 \text{ m}$ in altitude. Model results were extrapolated at the same resolution to the western Mediterranean region (from -19° to 12° longitude, and 27° to 46° latitude). Lastly, the obtained predictive function was extrapolated to the Canary Islands at a lower resolution (1 km^2) (Fig. 1). The so obtained downscaled distribution for the Canary

Islands was compared to another obtained after using the presence data of an exhaustive sampling effort carried on the invaded Fuerteventura (López-Darias and Lobo unpublished). Fuerteventura Island is the second largest (approximately 1,660 km²), the second lowest in altitude (807 m a.s.l) and the closest to Africa (around 115 km; Fig. 1) of the Canarian archipelago. Island climate is arid, and habitats are semi-desertic, with mean annual temperatures around 20°C (Dorta 2005) and annual precipitation below 100 mm/m². The island flora has been altered by the exploitation of wood resources, intensive livestock grazing and the introduction of exotic herbivores (Rodríguez 2005; Gangoso et al. 2006). Fuerteventura Island is currently dominated by substitution vegetation, and small patches of native vegetation relegated to inaccessible or unfavorable areas (Rodríguez 2005).

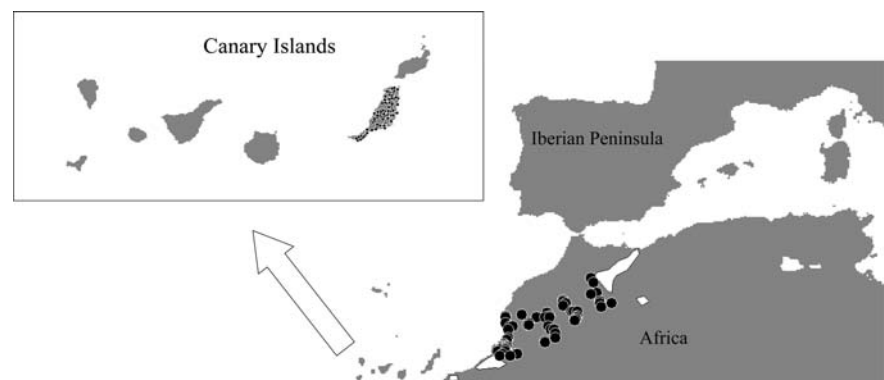
Distribution and climatic data

Atlantoxerus getulus presence data in its native range come from Gouat and Yahyaoui (2001; $n = 59$), and other unpublished presence data ($n = 101$) were also incorporated. Only presence information with precise locations was considered (66 0.083° squares), and distributional data from atlas without precise localities (Aulagnier and Thévenot 1986) and points less than 10 km distant were excluded in order to work at a resolution of 100 km² squares.

Eighteen climatic variables were extracted from the Worldclim interpolated map database (Hijmans et al. 2005) at the same resolution: mean temperature

of the coldest quarter, mean temperature of the driest quarter, mean temperature of the warmest quarter, mean temperature of the wettest quarter, annual mean temperature, annual temperature range, seasonality of temperature, temperature of the coldest month, temperature of the warmest month, annual precipitation, precipitation of the coldest quarter, precipitation of the driest quarter, precipitation of the warmest quarter, precipitation of the wettest quarter, precipitation of the driest month, precipitation of the wettest month, seasonality of precipitation and isothermality (mean diurnal range/temperature annual range). Additionally, we used the mean altitude of each cell extracted from a global DEM with a 1-km spatial resolution (Clark Labs 2000). All environmental variables were standardized to eliminate measurement-scale effects (a mean of 0 and a standard deviation of 1). Then, they were submitted to a Principal Component Analysis (PCA), and three non-correlated factors with eigenvalues ≥ 1 were obtained (11.26, 4.82 and 1.77). These three PCA factors explained 89.29% of the climatic variation across the region (56.31%, 24.11% and 8.85%, respectively). For each one of these PCA factors, the variable with the highest factor loadings (which measure the correlations between the original variables and the factor axes) was selected; these were temperature of the coldest quarter, temperature seasonality and precipitation of the coldest quarter. Temperature of the wettest quarter was also included as an explanatory variable because it was the only one that was not significantly correlated with any of the three formerly mentioned PCA factors. These four variables are only slightly correlated between them and

Fig. 1 The current native and invasive distribution range of *A. getulus*. Presence-data in Northern Africa region are represented as black points, while the grey area shows places outside the sampling area where the species has been reported. Points in Fuerteventura Island (Canary Islands) show localities in the invaded range where the species has been reported



have been considered as the most representative of the climate in this Northern African region. All geographic analyses were done with IDRISI Kili-manjaro software (Clark Labs 2003).

Atlantoxerus getulus presence data in Fuerteventura come from an exhaustive field campaign accomplished between July and October 2005 on 229 100 × 100 m UTM squares proportionally distributed across the island in order to cover all the vegetation types and environmental conditions (López-Darias and Lobo unpublished). After joining the presence data coming from the same 1 km² UTM cells ($n = 133$) the formerly mentioned climatic variables were used both to downscale the model obtained in the native region and to derive a new potential distribution model for the whole archipelago based on the environmental characteristics of the invaded island.

Distribution models

The key objective when invasive species are implied is to obtain a distribution map which reliably represents the potential distribution of the species. We define potential distribution as the area with a priori favorable climatic conditions for the existence of the species, being these conditions estimated from the climate in the observed presence localities. As real absence information should not be used to obtain a potential distribution because a species can be absent from a locality due to dispersal limitations, human induced factors or biotic interactions, the best option is to first delimit pseudo-absences within the environmental domain outside from the areas *a priori* environmentally favorable for the species (Engler et al. 2004; Lobo et al. 2006). This pseudo-absence selection implies the use of a profile technique (i.e., environmental envelope) that, considering only presence data, allows us to calculate a first habitat suitability map for the species. With this map, pseudo-absence points are selected outside the environmental space obtained from the observed presence points of the species. Then, both presence data and pseudo-absence data are included as a binomial dependent variable in one of the available group discrimination methods that use environmental predictors to model the distribution (see Guisan and Zimmermann

2000). In this study we use a simple bioclimatic envelope model (BIOCLIM; Nix 1986) which involves intersecting the ranges inhabited by the species along each environmental variable to define the range outside which pseudo-absences were selected (see Lobo et al. 2006).

For the potential model derived from Africa data a hundred times more pseudo-absences than presences ($n = 6600$) was randomly selected within unfavorable climatic areas in order to include a large part of the environmental conditions in which the species do not occur (see Thuiller et al. 2004; Jiménez-Valverde and Lobo 2006). Presence and pseudo-absence data ($n = 6666$) were subsequently used to calibrate the model using two standard techniques, which are usually considered to be among the most efficient (Thuiller 2003; Segurado and Araújo 2004): (i) generalized additive models (GAM) with cubic-smooth splines; and (ii) single-hidden-layer neural networks (NN). GAMs are non-parametric regressions that capture complex response curves, while a NN is a machine learning method used extensively in modeling species distributions to contend with non-linear responses to environmental variables. GAM and NN models were fitted in *R* (<http://www.r-project.org>) using the *mgcv* and *nnet* packages. In the case of the potential distribution derived from data of Fuerteventura Island only 44 sites of 1 km² have climatic conditions outside the range defined by known presences. Thus, both GAM and NN models have been built using a total of 177 points (133 presences and 44 pseudo-absences).

As probability values derived from predictive functions are unavoidably biased toward the highest number of absence data used (Cramer 1999; Hosmer and Lemeshow 2000), we re-scaled favorability scores by applying a function whose results are not affected by the uneven proportion of presences and absences, thus allowing favorability values that vary in a 0 to 1 scale to be obtained (Real et al. 2006). Favorability scores are also converted into a binary variable (presence-absence) selecting the cut-off value that minimize the difference between sensitivity and specificity, which generate most accurate predictions (Jiménez-Valverde and Lobo 2007).

Model predictions derived from African native data were subsequently projected at the same resolution for the whole Western Mediterranean region

(100 km² squares), and for the Canary Islands (1 km² squares) considering the same predictive functions but using climatic data at a lower resolution (1 km² squares). By their own nature, potential distributions cannot be validated using real distributional data. However, as our model was carried out using African data, we expect that the obtained distribution will be able to correctly predict those Canary areas recently colonized by the species, as well as other North African areas without precise distributional information (Fig. 1). Estimating the regions where the model correctly predicts the invaded range is the usual approach in this kind of study (see Peterson 2003). On the other hand, model predictions derived from the invaded island (Fuerteventura) were projected for the whole Canary archipelago at the same resolution (1 km² squares).

In order to select between the two different modeling techniques and to evaluate the performance of accomplished models with the used data, predicted favorability scores were compared against observed presences and selected pseudo-absences. Three main accuracy measures were calculated from this confusion matrix (see Fielding and Bell 1997): (i) specificity (the proportion of correctly predicted absence cells relative to the total number of pseudo-absences), (ii) sensitivity (the proportion of correctly predicted presences), and (iii) the total area that falls under the receiver operating characteristic (ROC) curve (AUC). Specificity and sensitivity were estimated after converting favorability scores in a binary variable. To calculate AUC, sensitivity is plotted against 1-specificity over a number of thresholds (100 in this case), and the area under the curve (AUC) calculated as a threshold-independent accuracy measure (Zweig and Campbell 1993; Fielding and Bell 1997). These three accuracy measures (AUC, sensitivity and specificity) were also computed using as predicted favorability scores those derived of a jack-knifing procedure (see Olden et al. 2002; Engler et al. 2004). With a dataset of n observations, the model was recalculated n times, leaving out one observation in turn. Each one of the regression models based on the $n-1$ observations was then applied to the excluded observation, and these new model-derived predictions retained to calculate new sensitivity, specificity and AUC jack-knife-derived scores. Comparisons of the three used accuracy measures derived from complete and jack-knife predictions allow us to estimate the stability of the

models regarding to use data. All models were carried out ten times changing the randomly selected pseudo-absences, in order to obtain a variability measure of model performance. An ANOVA univariate test was applied to check for significant differences in mean suitability scores of the seven islands. Tukey HSD post-hoc test were used to analyze mean favorability scores among all pair-wise island comparisons.

Results

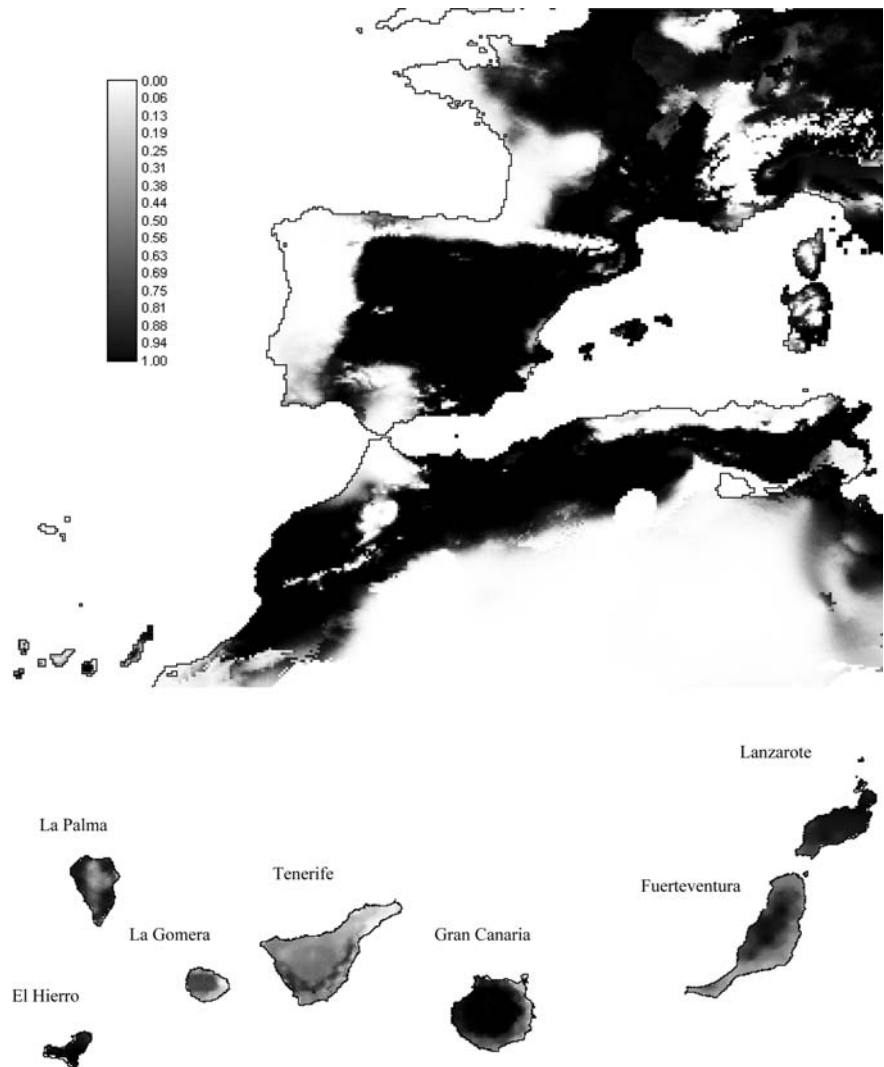
Potential distributions based on native data

The GAM model resulted in an AUC score of 0.956 ± 0.002 (mean \pm SD), while the NN model seemed to offer more accurate results (AUC = 0.998 ± 0.001). Once the sensitivity-specificity minimizer threshold was applied, the GAM model correctly predicted $89.3\% \pm 0.2$ of presences and $89.2\% \pm 0.1$ of pseudo-absences. However, the NN model correctly predicted $97.1\% \pm 0.1$ of presences and $96.9\% \pm 0.1$ of pseudo-absences. Jack-knife accuracy derived scores were also higher in the case of the NN (AUC = 0.964 ± 0.002 , sensitivity = 0.962 ± 0.002 , specificity = 0.929 ± 0.001) than for the GAM (AUC = 0.936 ± 0.002 , sensitivity = 0.827 ± 0.002 , specificity = 0.821 ± 0.001). The differences in accuracy measures when complete and jack-knife predicted scores are used show that NN models are also more stable with the change in the data of training.

The potential distribution of *A. getulus* (Fig. 2) generated high suitability scores in the African regions for which we do not have precise locations (Aulagnier and Thévenot 1986; Fig. 1). There were favorable climatic areas for this species across a wide area of North Africa, but also in a high part of the west Mediterranean region of Europe. This result demonstrates that the real distribution of this species should be conditioned by factors other than climatic variables (Fig. 2). Suitable areas did not have a mean temperature during the coldest quarter that was lower than -5°C and precipitation scores during the coldest quarter that were higher than 300 mm (Fig. 3), and the scores of these two climatic variables was significantly different among suitable and unsuitable west Mediterranean areas (t -test with probabilities lower than 0.00001).

Downscaling the predicted scores for the Canary Islands showed that there are climatic favorable areas

Fig. 2 Map of predicted suitability for *A. getulus* in Northern Africa, western Mediterranean Europe and the Canary archipelago, according to the neural network model built using the data of the African native territory. Mean favorability scores (ten repetitions) ranges between 0 and 1



in all the islands (Fig. 2); 90.4% of the Canary territory appeared as climatically suitable for this species (7.030 km²). However, there were statistically significant differences in the mean suitability scores of the seven islands ($F_{(6,7765)} = 1226.5$; $P < 0.00001$). Tukey HSD post-hoc test demonstrate that mean favorability scores significantly differed among all pair-wise island comparisons (Fig. 4).

Potential distributions based on invaded data

The GAM model had a higher AUC score than the NN model (0.996 ± 0.002 and 0.614 ± 0.002), being able to correctly predict 98% of presences and pseudo-absences in the training data (± 0.1). GAM Jack-knife AUC derived scores were slightly smaller

(0.985 ± 0.003) showing the stability of model results with the used data. The predicted scores for the whole archipelago showed that there were only climatic favorable areas in Fuerteventura, Lanzarote and Gran Canaria Islands (Fig. 5). In this case only 31.9% of the Canary territory appeared as climatically suitable for this species (2.480 km²), almost three time less than the potential distribution derived from the native African data.

Discussion

Potential and observed distributions in Africa

Using only climatic variables, our model predicts a wider distribution area than that currently described

Fig. 3 Environmental characteristics of the suitable areas for *A. getulus* according to the mean temperatures and precipitation during the coldest quarter. The circle in the suitable environmental area represents the climatic conditions in Fuerteventura Island (between 15–17°C and 53–95 mm)

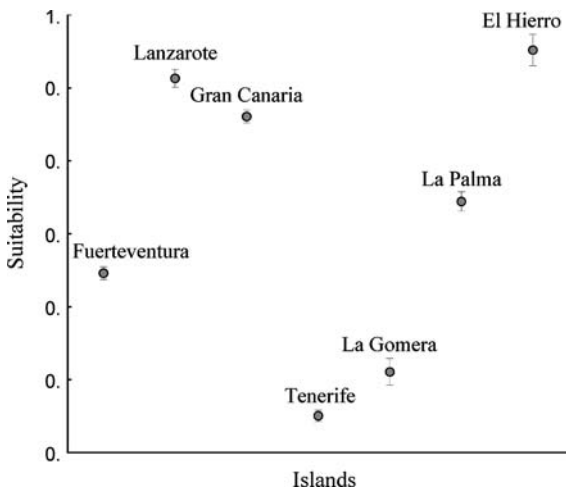
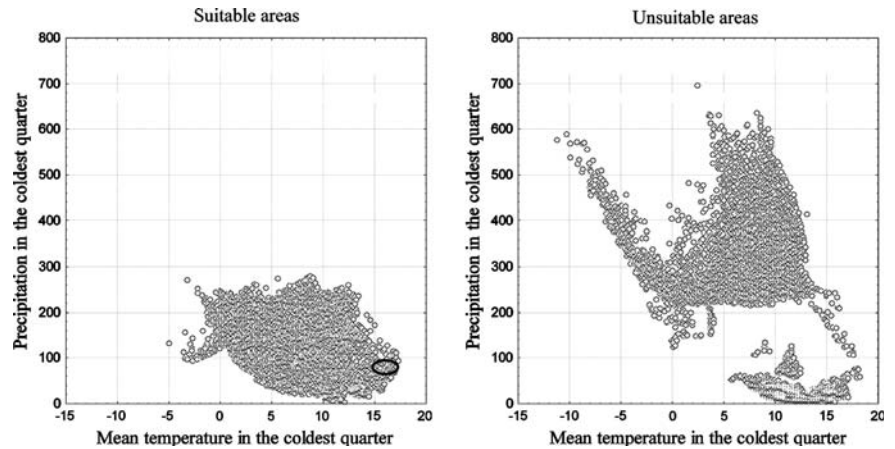
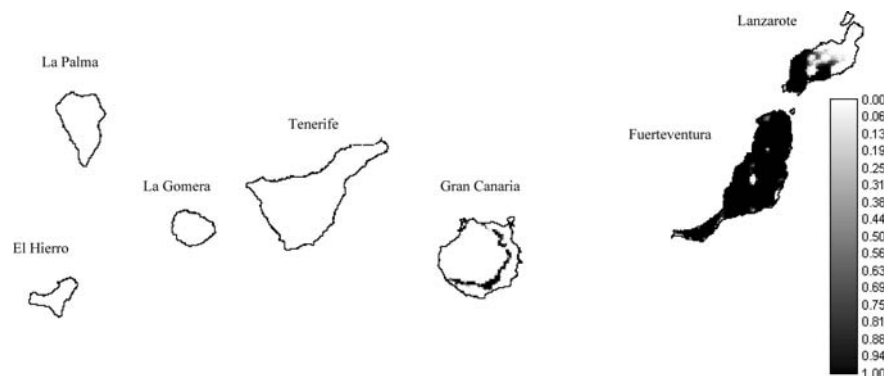


Fig. 4 Mean climatic favorability of *A. getulus* in the 1 km² squares of each Canarian island ($\pm 95\%$ confidence interval) according to the neural network models built using the data of the African native territory. El Hierro, Lanzarote and Gran Canaria Islands were identified as the most suitable islands

in the native range (Aulagnier and Thévenot 1986; Kingdon 1997), showing suitable climatic areas in almost all the Western Maghreb Mediterranean strip, from Morocco to Tunisia, and even Libya. Nevertheless, the species is only reported to inhabit Morocco and small areas of Algeria: all along the Atlas, from Wad Tensift and Wad Sus (Atlantic coast), with southern limits in El Aaiun, to the eastern limits of the Algerian Sahara (Moggar), and Algerian Ksour Mountains (from Aïn Sefra to Beni-Ounif) (Machado and Domínguez 1982; Aulagnier and Thévenot 1986; Kingdon 1997; personal data). The limit of the southern distribution of *A. getulus* on our potential map is highly coincident with the observed limit, probably because the Sahara Desert constitutes a strong climatic barrier (Douady et al. 2003). Within Morocco, the species has not been reported in the Coastal and Central Plateau of the Atlantic coast (Aulagnier and Thévenot 1986), data that fit with our

Fig. 5 Map of predicted suitability for *A. getulus* in the Canarian archipelago (mean scores of ten repetitions), according to the GAM models built using the data of the invaded Canarian island (Fuerteventura). Favourability ranges between 0 and 1



model predictions. This area comprises particular vegetation types and climatic conditions (Benabid and Fennane 1994; Knippertz et al. 2003). However, a discrepancy exists between the predicted and observed distribution of this species in the eastern limit of the analyzed North African region (Figs. 1 and 2). This disagreement could be explained through three alternative scenarios: (i) that the current distribution of *A. getulus* in its native area would be highly conditioned by factors other than climatic ones (biogeographical or biological); (ii) that unconsidered climatic variables could have substantial effects on the current distribution of this species; or (iii) that the species is present in most part of its North African potential area but has not been detected by the lack of surveys.

Although the Palaearctic African region is generally considered to be an expansion of the Mediterranean region (Olson et al. 2001; Olson and Dinerstein 2002) in a biogeographical sense (Kier and Barthlott 2001), the Maghreb region is currently divided longitudinally by the Tell Atlas, the territory extending about 1,600 km from eastern Morocco through Algeria to Tunisia. Western Moroccan Atlas and Tell Atlas have had different biogeographic and geological histories which have resulted in different faunas, vegetations types and land cover characteristics (Quezel 1986; De Jong 1998; Blondel and Aronson 1999; Mickus and Jallouli 2000; Mayaux et al. 2003). Recent analyses show that the gene flow between the populations of some species that inhabit these two regions is surprisingly low (Gantenbein 2004), and that Tell-Atlas organisms are often related to those which inhabit the south of the Iberian Peninsula (De Jong 1998; Álvarez et al. 2000; Harris et al. 2002; Sanmartin 2003; Veith et al. 2004; Pinho et al. 2006; Zangari et al. 2006). Even though similar climatic conditions could exist between these two regions, they are separated by large rigid cores (Moroccan Meseta and Algerian High Plateaux; De Lamotte et al. 2000) and the Moulouya River Basin can act as barrier for organisms.

As well, resources and predator pools could differ between these two areas and could affect the presence of *A. getulus*, as could other biological factors. *Atlantoxerus getulus* is highly dependent on rocky shelters, which are crucial to colonizing and expanding into new environments (Gouat and Yahyaoui 2001). More field research will be needed to

determine whether the absence in most of Algeria is due to spatial heterogeneity in rocky refuge abundance.

The only climatic variable that seems to differ between western and eastern North African regions is the seasonal pattern of rainfall variation. A recent analysis of the daily occurrences of surface pressure centers and monthly rainfall data (Littmann 2000) showed that Central and Southern Spain have a rainy seasonal pattern similar to the Atlantic parts of Morocco (a very short rainy season from October to January), while that of the North African Mediterranean Coast and Tell Atlas regions show a pattern similar to the North Western Mediterranean region of Europe (a long rainy season from September until April with some summer precipitation). This regional variation in the seasonality of rainfall is due to differences in the moisture transport from the Atlantic circulation (Knippertz et al. 2003). This could be highly relevant in explaining the current distribution of *A. getulus* since it affects the seasonal variation in trophic resources and its interplay with the biology of the species. In order to understand if rainy seasonality or dispersal limitations are the factors responsible for the apparent absence of *A. getulus* in the eastern North African area, more systematic and reliable survey data are needed, as well as more precise studies on the main ecological factors that affect the demography and dispersal of this species in its native area.

As far as we know, the third hypothesis about the lack of data in the area can be rejected. Gouat and Gouat (1984) have extensively explored the Ksour Mountains region between Ain Sefra and Beni Ounif, where *A. getulus* was found. In fact, the complete Saharan Atlas was explored by Gouat and Gouat (Gouat and Gouat 1982; Gouat and Gouat 1983), while Séguignes (1983) did the same in Tunisia, and no squirrels were reported. Therefore, due to the density of these investigations and to the diurnal activity of *A. getulus*, we might conclude that the species is not present in the region.

Model predictions in foreign areas

The predicted potential distribution accomplished with the native data shows the existence of a priori favorable areas in the European Mediterranean

region, including numerous Mediterranean islands. The Strait of Gibraltar, a biogeographical barrier that separates the Iberian Peninsula from the Maghreb by a gap of 14 km, currently hinders the colonization of Europe by *A. getulus*. Only the active geological history of the Strait (Krijgsman 2002) could explain the past existence of *Atlantoxerus* species in Europe and some Mediterranean islands (see Peláez-Campanones 2001), as well as the phylogeographic relationships between the Maghreb and Iberia (i.e., Beerli et al. 1996; de Jong 1998; Castella et al. 2000; Gantenbein 2004). According to our results caution is necessary to prevent the introduction of this species in the North Mediterranean region because this species can have many favorable climatic places.

The two models accomplished for the Canary Islands provide very different results. The model built with the African native data correctly predicts the Canary territory that is currently invaded (Fuerteventura Island), but also indicate that all the remaining islands of the archipelago harbor suitable areas from a climatic point of view. On the contrary, the model carried on using only the data from the invaded territory showed that only two additional islands have suitable conditions (Lanzarote and Gran Canaria). Evidently, deriving a potential distribution model from the data of the invaded island unavoidably cannot reflect the whole spectrum of climatic conditions in which this species can survive (Fig. 3). The model carried out only using the data of the Fuerteventura Island can aid to recognize the location of sites with similar climatic conditions to the currently invaded, which are not representative of the whole climatic conditions existent in the native area of distribution (more xeric conditions; Fig. 3). This result highlight the necessity of estimating potential distributions using the environmental niche derived from the native territory of invaders (Soberón and Peterson 2005; Peterson 2006). If we aim to obtain a geographical representation of an invader species as accurate as possible in the invaded region it is necessary to consider the environmental conditions in all the places in which this species occur in its native range. Thus, these suitable regions should be considered areas with risk of suffering the negative inconveniences of the invader species. However, it is necessary to emphasize that this species can also be in a non-equilibrium state with regard to the climatic conditions in its native area. In this case, the potential

distribution of the species could be wider and the risk area higher.

Our large-scale potential distribution model cannot be used to estimate the favorable places at local scale. Although almost all the landscapes of the Fuerteventura Island have been colonized by this species, predicted scores of suitability are not homogeneous along it; some less appropriate predicted areas are known to host abundant squirrel populations. This is due to general climatic variables can control the distribution of a species when it is observed at a large extent and at coarse resolution, however resources, microtopographic variation or habitat fragmentation is more likely to affect the patchy distribution observed over a small area and at a finer resolution (Guisan and Thuiller 2005). A recent study conducted in Fuerteventura supports this assumption; this study showed that the main variables correlated with local rodent abundance are those related with biological species requirements, and that climatic ones are hardly irrelevant. At the Fuerteventura Island scale, species abundance is highly dependent on variables such as refuges (e.g., number of shelters or distance to and presence of stonewalls), the type of landscape or some plant species that are frequently consumed by the species (López-Darias and Lobo unpublished).

Conservation concerns

If deliberate introductions occur, our results suggest that all the Canary Islands could be potentially colonized by *A. getulus*. Fuerteventura, though previously invaded, is not a priori the most suitable island according to the data of the native region. Hence, we argue that its presence on this island is completely fortuitous, as it was human-induced. El Hierro, Lanzarote and Gran Canaria Islands seem to be more appropriate for this rodent than Fuerteventura according to the results derived from native data. The proximity of Fuerteventura and Lanzarote and the frequent flux of tourists between these two islands, suggests that Lanzarote is the most threatened island of the archipelago, especially if recent introductions have already occurred. A similar situation is suggested for Gran Canaria.

The applicability of species distribution models for predicting real or potential invader distributions, and for on-the-ground combating against them (Peterson

and Vieglais 2001) is evident in our example. The globalization and growth in the volume of trade and tourism provide more opportunities than ever before for species to be spread accidentally or deliberately (McNeely 2006) and pets are the cause of many vertebrate introductions (Mack et al. 2000). The Canarian archipelago receives more than 10 million European tourists per year (more than 1 M per year in Fuerteventura; ISTAC 2006), and an unpublished review of invasive squirrels on islands revealed pets to be the major cause of these introductions (López-Darias unpublished). On the other hand, public budgets to fight against invaders are limited and priority actions should be assessed. In our case, previous knowledge about the potentiality of this species to successfully colonize the Canarian archipelago could help authorities to establish conservation priorities. Canary Islands are exceptionally rich and are considered to be part of a biodiversity “hot spot” (Médail and Quézel 1999; Izquierdo et al. 2001), and invasive species (more than 11% of the terrestrial species are introduced; Izquierdo et al. 2001) are a core conservation issue in this archipelago. Legal tools to prevent translocations within the archipelago are nonexistent, insufficient measures exist to control transports occurring with mainland Spain (especially through maritime transportation), and few public educational campaigns are currently undertaken in the area; although all of them are urgently needed. As a consequence, translocations of *A. getulus* from Fuerteventura onto other islands and mainland Spain have already occurred. In Fuerteventura, no control strategies have been carried out since its introduction, in spite of the fact that its eradication on the archipelago has been highly recommended (Group of Experts on Invasive Alien Species 2002). The broad ecological capacity of this species and the presence of favorable climatic areas all over the archipelago, together with all previous considerations, suggest that a management strategy is urgently needed to prevent the expansion of *A. getulus* through the Canary Islands and mainland Spain.

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