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BIODIVERSITY RESEARCH

Assessing changes in habitat quality due to land use changes in the spur-thighed tortoise *Testudo graeca* using hierarchical predictive habitat models

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ABSTRACT

In this study we propose a model-building approach based on the hierarchical integration of the main environmental factors (climate, topography/lithology, and land uses) determining the distribution of the spur-thighed tortoise in south-east Spain. Data on the presence/absence of the species were primarily based on information derived from interviews to shepherds. The hierarchical modelling exercise consisted of three steps. First, we constructed a model for the entire region using climate variables, thus obtaining a potential climatical model. Second, we introduced variables referring to topography and lithology that fall within the climatic distribution range (*potential* model). Third, by using this second model as a starting point, we included land use variables to obtain the *actual* distribution model.

We analysed the changes in the values of probability of the presence of this species for a given cell between the *potential* and the *actual* model, assessing areas where habitat quality has decreased, been maintained or increased. The spatial representation of these changes was highly coherent. A discriminant analysis linked areas where habitat quality has dropped with agriculture landscapes, whereas those areas where habitat quality has been maintained or increased were located mainly in shrublands. Twenty-five per cent (479 km^2) of the *potential* distribution of the species became suboptimal when land use was included, which emphasizes the importance of land use changes in both the range dynamics and the conservation of the spur-thighed tortoise in south-east Spain.

Keywords

Species distribution models, *Testudo graeca*, hierarchy, habitat quality, landscape.

INTRODUCTION

Habitat fragmentation and loss due to human activities are currently considered to be the main threats of biodiversity. Habitat loss is actually just one extreme of a continuous gradient comprising an array of changes in habitat quality, ranging from positive (habitat enhancement) to negative alterations (habitat degradation). The study of changes in habitat quality has received enormous attention in ecological and conservation literature (e.g. Brawn *et al*., 2001; Fahring, 2003; Hanski, 2005). Most studies focus on the effect that target habitat changes have on either target taxa or biodiversity indexes. However, they seldom tackle the spatial extent of such processes. This second step is of great practical relevance for conservation aims since it actually appraises the absolute importance of such changes.

Predictive habitat modelling may offer an appropriate tool for this purpose. Specifically, what we hereby propose is that the hierarchical integration of different environmental factors into habitat modelling constitutes an adequate theoretical framework to explore how human-related changes modify the habitat quality imposed by natural factors and produce maps showing the spatial expression of these changes. A hierarchical perspective in the understanding of ecological systems was proposed more than 20 years ago (Allen & Star, 1982; Salthe, 1985; O'Neill *et al*., 1987; Urban *et al*., 1987). The development of habitat modelling and predictive distribution maps is coetaneous (see Guisan & Thuiller, 2005 for a recent revision). However, the integration of an explicitly hierarchical perspective in habitat modelling has been rarely and only recently employed (Mackey & Lindenmayer, 2001; Cushman & McGarigal, 2004; Pearson *et al*., 2004; Anadón *et al*., 2006a; Latimer *et al*., 2006).

The spur-thighed tortoise *Testudo graeca* is a Mediterranean terrestrial tortoise, whose populations in south-east Spain are endangered mainly by habitat fragmentation and loss, and by the fact that it is collected as a pet (Giménez *et al*., 2004; Pérez *et al*.,

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2004). Despite its threatened status, their current and past distributions together with the effects of human land-use changes on the habitat quality of the species are poorly known. Habitat modelling and radiotracking data suggest that the species is favoured by traditional human activities (Anadón *et al*., 2006a,b). This pattern coincides with those found in other studies that associate terrestrial tortoises with intermediate perturbation levels (Auffenberg & Franz, 1982; Stubbs & Swingland, 1984; Kazmaier *et al*., 2001; Anadón *et al*., 2006b). On the other hand, the species is negatively affected by agriculture-dominated landscapes where fragmentation processes are likely to occur (Anadón *et al*., 2006a). *Testudo graeca* appears to be an appropriate case-study to explore the effect of changes in habitat quality: positive shifts are expected at intermediate perturbation levels, such as those in traditional landscapes, whereas negative shifts are likely to be found in the two extremes of the human perturbation gradient.

In the present work, we have attempted to assess the distribution of *T. graeca* in south-east Spain as well as to analyse the changes in the species' habitat quality owing to human land-use changes. For these purposes, we developed predictive distribution models where different environmental variables were integrated following the hierarchical scheme of factors that rule the species' distribution in south-east Spain. Climate is the main factor to shape the distribution of *T. graeca* and to determine the presence of this species within its range, followed by topography and lithology, and lastly by land uses (Anadón *et al*., 2006a). First, we attempted to model the species' potential climatic distribution. Second, this model was modified by lithology and topography variables within the resulting climatic distribution area, yielding a finer *potential* distribution model. This model can be understood as a historical predictive distribution model. Third, we modified this second model by including land-use variables, thus obtaining the *actual* distribution model. Finally, we explored the changes in the probability of the presence of this species between the *potential* and the *actual* model. This modelling rationality will be further detailed in the methodology section.

METHODOLOGY

Study area

We modelled the distribution of *T. graeca* in the Region of Murcia. The Region of Murcia is located in the south-east of the Iberian Peninsula and covers an area of 11,317 km^2. Its climate is semiarid mediterranean with an annual rainfall ranging from 200 mm to 500 mm (Sánchez-Zapata & Calvo, 1999). Previous descriptions of the potential distribution range of this species have indicated an area of *c*. 3000 km^2 located in the south-east corner of the province, the equivalent of around 60% of the species' total range in south-east Spain. The remaining contiguous 40% is located in the neighbouring province of Almería (Giménez *et al*., 2004).

Tortoise survey and environmental characterization

Obtaining data on the presence/absence of terrestrial tortoises over large areas is a difficult task due to their low detectability (Averill-Murray & Averill-Murray, 2005). In the present work, the majority of the presence/absence data was collected by interviewing shepherds. Over many years shepherds cross the same area daily and are therefore a valuable source of information for assessing the absence or presence of the species. Only with *sampling* intensities as great as those provided by shepherds it is possible to detect the species at low densities or assess reliable absences (Beshkov, 1993; Anadón *et al*., in prep.). We interviewed 132 shepherds in the southern Region of Murcia, in an area that largely contains the species' range. Information derived from interviews was incorporated into a Geographic Information System (GRASS GIS 5.0; http://grass.itc.it/) using a grid cell of 1 × 1 km. Interviews yielded 363 cells with information regarding the presence or absence of the species in the 1980s or 1990s. For modelling purposes, we also included data from northern Murcia, where the species is known to be absent; here we randomly selected 456 cells that were automatically treated as absences. Similarly, we treated those cells where the species is known to be present as presences, given the data derived from the authors or naturalists. In total, we obtained information for 867 cells of 1 × 1 km, including 235 presences and 632 absences.

The Region of Murcia was characterized according to variables describing climate, topography, lithology, and land uses (Table 1). Environmental information sources are detailed in Anadón *et al*. (2006a). For continuous variables (climate, altitude, and slope), the value of each variable for the 1 × 1 km cell was taken as the mean value. For categorical variables (lithology, land use, and aspect), the value of each 1 × 1 km cell was the dominant type ('1 × 1 variables'). Anadón *et al*. (2006a) has recently suggested that the species' presence is largely dependent on characteristics of the neighbouring habitat. For this reason, we also constructed another set of variables related to the landscape composition around the cell based on relief, lithology, and land-use variables. In these variables ('3 × 3 variables'), the value for each 1 × 1 km cell varied between 0 (a variable neither present in the cell nor in the eight neighbouring cells) and 9 (a dominant variable in the cell and in the eight neighbouring cells).

Modelling rationale

The modelling rationale employed in this work is based on a hierarchical integration of the different environmental factors. This approach explicitly recognizes the spatial hierarchy of factors that determine the tortoise distribution (Anadón *et al*., 2006a). First, we constructed a predictive habitat model for the Region of Murcia using only climatic variables. This model yielded a climatic predictive distribution model (*climatic* model), in which the value for each 1 × 1 km cell was the probability of the presence of the tortoise, depending on its climatic characteristics. The next step was to model the distribution of this species within the distribution area defined by the climatic model, using variables related to topography and lithology, and which included the variables of the climatic model as covariables (variables forced to be included). Climatic variables were also included in this model at a finer scale since climate is determinant in both, as it shapes the species' range and determines the species' presence inside the

Table 1 Environmental variables employed for the model-building. Climate variables referred to a 1 × 1 km grid square cell. Relief, lithology, and land uses variables were extracted for local (1 × 1 km) and landscape scale (3 × 3 km). See Anadón *et al.* (2006a) for further details.

Climate	
R_{AN}, R_{SP}, R_{SU}, R_{AU}, R_{WI}	Annual, spring, summer, autumn, and winter rainfall
T_{AN}, T_{SP}, T_{SU}, T_{AU}, T_{WI}	Annual, spring, summer, autumn, and winter mean temperature
DEF_{AN}, DEF_{SP}, DEF_{SU}, DEF_{AU}, DEF_{WI}	Annual, spring, summer, autumn, and winter mean water deficit values
ETP_{AN}, ETP_{SP}, ETP_{SU}, ETP_{AU}, ETP_{WI}	Annual, spring, summer, autumn, and winter mean evapotranspiration values
TMIN	Mean of the minimum temperatures of the coldest month
FROST	Annual number of days that freezes
MINAVE	Annual mean of the daily minimum temperatures
Relief and lithology	
ALT	Altitude
SLO	Slope
SUN	Sunny aspect
SHD	Shady aspect
FLAT	Flat relief
CALC	Calcareous materials
SIL	Silicious materials
FSED	Fine texture sediments (loams, clays, and sands)
CSED	Coarse texture sediments (conglomerate materials)
QUAT	Quaternary materials
VOLC	Volcanic materials
Land uses	
WOOD	Woodlands
SHRUB	Shrubland
DRYTREE	Dry tree crops
DRYHER	Dry herbaceous crops
IRTREE	Irrigated tree crops
IRHER	Irrigated herbaceous crops
IMP	Unproductive land uses (urban, industrial)

distribution area (Anadón *et al.*, 2006a). For each cell, this second model (called the *potential* model) represents the probability of the presence of the tortoise based on the response to climatic, lithology, and topography variables. Since our goal in these two steps was to obtain predictive habitat distribution models that depend only on natural environmental characteristics and are not influenced by human activities, we only used those presence/absence data on cells with 'natural' land uses (wood and shrublands) for modelling purposes. The last step was to construct a model (*actual* model) using land-use variables, which included the variables of the *potential* model as covariables. For this model, we employed data on both 'natural' (woods and shrublands) and human land uses (agricultural and unproductive).

Models were constructed using multivariate Generalized Linear Models (GLMs; McCullagh & Nelder, 1989). The inclusion of variables in the models was made step-by-step using Akaike's information criterion (AIC; Burnham & Anderson, 2002) as the selection criterion. Variables were added if they resulted in a > 1% increase of the explained deviance. We used the probability value that maximized the sum of sensitivity and specificity (Liu *et al.*, 2005) as the threshold value of occurrence for the models. Model values were transformed from quantitative values (probability of presence from 0 to 1) to a qualitative range of habitat quality. We constructed four probability categories: the first included all values ranging from 0 to the threshold value, which thus represented the suboptimal habitat where the species is not expected to be present. The remaining range, from the threshold value to 1, was divided into three classes that represented low, medium, and high habitat quality for the species, respectively. We employed the threshold-independent Receiver Operating Characteristic (ROC) approach to finally assess the predictive ability of the models by calculating the area under the ROC curve (AUC; Fielding & Bell, 1997). All modelling procedures were carried out using the statistical software R (< http://www.r-project.org/>).

Changes in habitat quality

We assessed how the probability of the presence of the tortoise had altered due to changes in land uses by comparing the probability class of the *potential* and *actual* models. Similar approaches that take advantage of the algebraical properties of habitat models can be found in Mace *et al.* (1999) and Rhodes *et al.* (2006). To gain a better understanding of the changes occurring between these two models, we constructed a transition matrix among probability classes.

Table 2 Hierarchical habitat models for the spur-thighed tortoise in the Region of Murcia. R^2 = % of explained deviance. CLIM = array of variables included in the climatic model. POT = array of variables included in the *potential* model.

Model	Variables included	R^2	Modelling extent Data set employed
Climatic	$\mathrm{RAU}^2 + \mathrm{TSU} + \mathrm{RSP}^2 + \mathrm{RSU} + \mathrm{ETPAU}^2$	68.03%	Region of Murcia Only cases in 'natural' land uses
Potential	$\mathrm{CLIM} + \mathrm{ALT} + \mathrm{VOL3} \times 3^2 + \mathrm{ALT3} \times 3^2$	55.86%	Climatic distribution model Only cases in 'natural' land uses
Actual	$\mathrm{POT} + \mathrm{SHURB} + \mathrm{IRTREE3} \times 3 + \mathrm{WOOD3} \times 3^2$	48.85%	Climatic distribution model Cases in all land uses

Two methodological limitations should be pointed out. First, only relatively large changes in habitat quality are expected to be detected since we compare coarse quantitative probability classes. Second, such changes can be due to the direct effect of the land-use variables integrated into the model, and may also be due to the change in the data set employed for modelling. The *potential* model is built only with cells on 'natural' land uses, whereas the *actual* model is employed for modelling cells on all land uses. Since this analysis does not distinguish between both effects, we performed a discriminant analysis to characterize the cells where the probability of presence has increased, decreased, or was maintained as a whole. Variables employed in the analysis were those which referred to land uses, and they were selected step-by-step following a forward procedure (SPSS, version 10, SPPS Institute, Cary, NC, USA).

Table 3 Transition matrix describing the changes among habitat quality classes due to changes in land uses. For a description of the classes see Methodology section. Data in km^2. Cells that do not change of habitat quality class are set in bold.

	Potential				
Actual	Suboptimal	Low	Medium	High	Total
Suboptimal	**1396**	92	99	288	1875
Low	53	**8**	20	100	181
Medium	52	20	**42**	204	318
High	41	16	29	**965**	1051
Total	1542	136	190	1557	3425

RESULTS

Distribution models

The *climatic* distribution model at the regional scale, built with 460 cells on 'natural' land uses in the Region of Murcia, included autumn rainfall followed by summer temperature, spring and summer rainfall, and autumn evapotranspiration (Table 2). The threshold value for this model was 0.27. The *potential* distribution model, constructed with 194 cells on 'natural' land uses within the climatic range, included variables related to altitude and volcanic lithology. In this model, the five climatic variables, considered as covariables, accounted for 28.56% of the variance alone. The threshold value for the *potential* model was 0.72. The data set for the *actual* model comprised 338 cells on all land uses within the climatic range. Most of the variance accounted for by the models was due to the climatic, relief, and lithology covariables which represented 42.64% of the variance alone. The land use variables that were integrated into the model were those referring to shrublands, irrigated tree crops, and woodlands at a landscape scale. The threshold value for the final model was 0.75.

The evaluation of the models showed AUC values above 0.9 (0.97, 0.95, and 0.93 for the *climatic*, *potential*, and *actual* models, respectively). The resulting predictive distribution maps are shown in Fig. 1. The *climatic* distribution map shows a potential distribution range of 3425 km^2. The addition of lithology and topography variables notably reduces the species range to an area of 1883 km^2 (Table 3), where the abrupt fall in probability in the range borders stands out. Finally, the *actual* distribution map covers an area of 1550 km^2, which is considerably fragmented in some areas.

Changes in habitat quality

Habitat quality values increased due to land-use changes in 211 km^2, decreased in 803 km^2, and were maintained in 2411 km^2 (Table 3 and Fig. 2). As a result, the potential distribution area of the species (above the threshold value) decreased in 333 km^2 (from 1883 to 1550 km^2). Of the 14 land-use variables, four variables were selected to construct the discriminant functions, all of which describe the land uses at the landscape scale (Table 4). All pairwise comparisons showed significant differences among the three groups ($P < 0.0001$ in all cases). The first function accounted for 94.5% of the variance and mainly discriminated between those cells whose quality decreased and those whose probability values either increased or were maintained (Fig. 3). This function was correlated directly with agricultural land uses (both irrigated and dry crops) and correlated inversely with the proportion of shrubs. The discriminant function correctly classified 59.7% and 80% of the cells whose quality had either decreased or been maintained, respectively. Despite the significant differences among groups, however, this function failed to correctly classify cells with increased quality, which were all classified as without change of quality (0% of success).

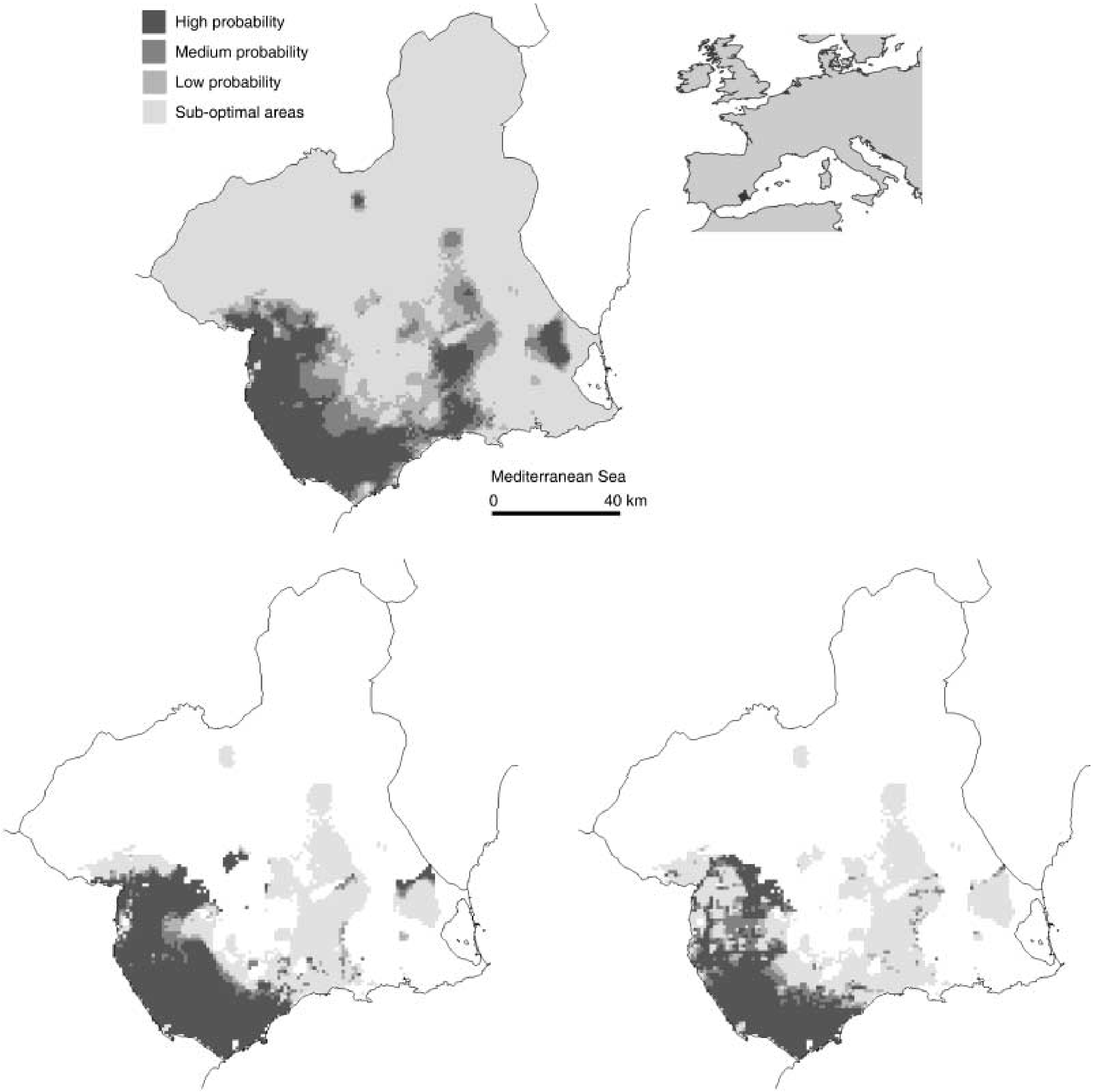

Figure 1 Hierarchical modelling of the spur-thighed tortoise in the Region of Murcia. From top to bottom: *climatic*, *potential*, and *actual* model.

DISCUSSION

Distribution models

Hierarchical modelling successfully integrated climate, lithology/topography, and land uses. The AUC values obtained for the three models indicate a very high prediction success (Manel *et al.*, 2001). The three predictive models (*climatic*, *potential*, and *actual*) constitute an ecological meaningful sequence of how different environmental factors act at different scales to shape the species' range consecutively, following the hierarchy of factors as previously identified in Anadón *et al.* (2006a). As expected, climate shapes the species' range, whereas lithology and topography notably modify the distribution and the probability of the species' presence within the climatic range. When compared to topography and lithology, land use changes the habitat quality for the species to a lesser extent (Guisan & Hofer, 2003; Anadón *et al.*, 2006a). The spur-thighed tortoise showed strong species–habitat relationships, especially with climate as shown by the high values of the explained variance. The limiting ecological processes behind the detected patterns have been discussed in detail in Anadón *et al.* (2006a). In relation to climate, the limiting factors are likely to be different at the two extremes of the environmental gradient. The species may be constrained by the

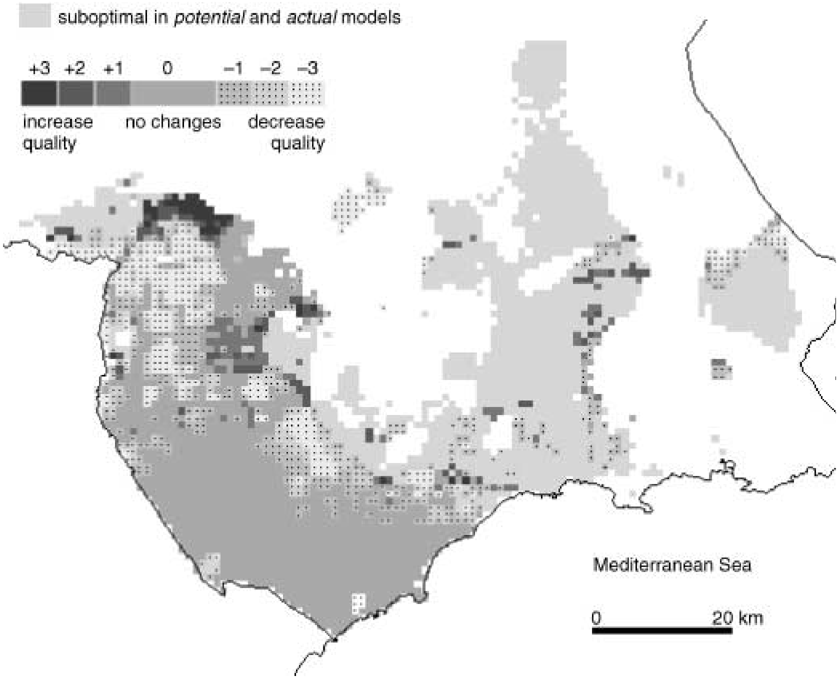

Figure 2 Changes in the probability of presence of *Testudo graeca* between the *potential* and the *actual* model. Changes are given as the difference between the habitat quality class of the *potential* and *actual* model.

Table 4 Correlation coefficients (Pearson's correlation coefficient) for the first canonical discriminant functions and standardized coefficients of the variables that conform the first discriminant function.

	Discriminant function 1	
	Correlation coefficients	Standardized coefficients
SHRUB3 × 3	0.740	0.863
IRTREE3 × 3	−0.583	−0.388
SHRUB	0.522	
DRYHER3 × 3	−0.388	
DRYTREE3 × 3	−0.351	
IRTREE	−0.298	
WOOD3 × 3	−0.267	
DRYHER	−0.220	
WOOD	−0.209	
IMP3 × 3	0.198	0.280
DRYTREE	−0.191	
IRHER3 × 3	0.168	0.475
IRHER	0.073	
IMP	0.057	

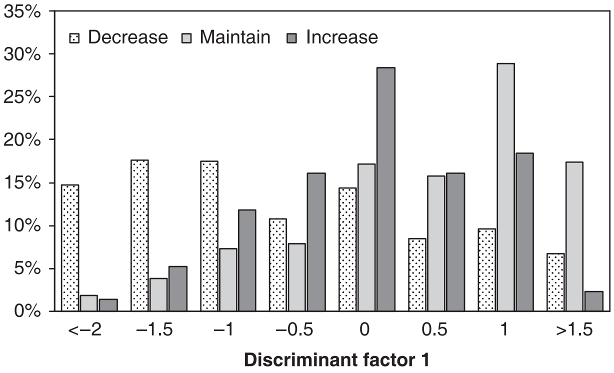

Figure 3 Distribution of the groups (decrease, maintain, and increase in habitat quality when including land uses in the modelling) in relation to the first discriminant factor of the discriminant analysis.

length of the activity periods in the northern areas, whereas the limiting process in the south may be linked to low productivity values, and therefore to a shortage of available energy (Anadón *et al*., 2006a).

As far as we are aware, this work is the first large-scale predictive distribution model of a terrestrial tortoise (but see Baskaran *et al*., 2006 for a lesser scale). Although most species of terrestrial tortoise are severely threatened, their ranges are only vaguely known (McDougal, 2000). The methodologies employed in this work could be very useful in achieving distribution maps. Interviews with local inhabitants, particularly shepherds, whose *sampling* efforts are easy to measure (and may thus be standardized), are a source of information of great value regarding the presence/absence and abundance of species with low detectability, such as tortoises (Beshkov, 1993; authors, in prep.).

Changes in habitat quality due to land use changes

The comparison made between the *potential* and the *actual* distribution models detected both positive and negative changes in habitat quality when land-use variables were included in the model. In almost half the area of the *potential* range of the tortoise, habitat quality dropped when land uses were included. The first discriminant function showed that those cells where habitat quality dropped are linked to agricultural landscapes, whereas the habitat quality in 'natural' areas was maintained or even increased. The conversion of shrublands to crops promotes fragmentation processes on tortoise populations and has a considerable negative impact when they are the dominant land use at a landscape scale (Anadón *et al*., 2006a). This process may be mainly responsible for the loss of 479 km^2 of natural habitat, which shifted from optimal to suboptimal habitat quality values when land uses were included. This area is the equivalent of 25% of the *potential* distribution of the species, and highlights the importance of fragmentation due to land use changes in *T. graeca* in south-east Spain. Figure 3 shows that those cells where habitat quality has dropped are distributed throughout the first discriminate function, reflecting an array of landscapes with varying agricultural/shrublands proportions, where the intensity of fragmentation processes may also vary. The most identifiable agricultural landscapes in the species' range, also identifiable in the spatial representation of changes (Fig. 2), are traditional irrigated areas in secular humanized basins, herbaceous and tree dry crops in great basins, and dry crops at the foot of mountain systems. These agricultural landscapes correspond to economic cycles in different ages, and consequently to different historical processes of habitat degradation and loss. It should be pointed out that these cycles can be considered as completed. In this sense, the changes in habitat quality assessed in the present work are historical. Recent and current processes of habitat loss for the species, mainly new irrigated lands, greenhouses, and new tourism development (Martínez *et al*., 2002; Giménez *et al*., 2004), have not emerged in our analysis, and should be the focus of further conservation research efforts.

The discriminant analysis detected differences between those cells with an increased habitat quality and those where habitat quality was maintained. However, it failed to characterize them and linked both groups to shrublands. The spatial representation of the enhanced areas locates them mostly in the upper distribution limit of the species in both latitude and altitude. The upper distribution limit of the species in south-east Spain is coincident with an annual rainfall of approximately 275 mm (Anadón *et al*., 2006a), and climatically coincides with the lower limit of woodlands. Thus, the upper part of the range (in both latitude and altitude) is characterized by open wooded shrublands. We hypothesize that the detected enhancement in habitat quality may be related to a reduction in the proportion of wooded areas at the landscape scale owing to traditional human activities, such as grazing or gathering firewood. The resulting landscape structure would be of greater quality for thermoregulation purposes, thus increasing the probability of the presence of tortoises in these naturally constraining environments. The positive effect of human activities on the terrestrial tortoise, linked to the maintenance of more simplified and immature stages of vegetation, has been previously reported (Auffenberg & Franz, 1982; Stubbs & Swingland, 1984; Kazmaier *et al*., 2001; Anadón *et al*., 2006b). Interestingly in our case, the enhancement in habitat quality is mainly produced in the distribution limit of the species, thus likely to displace the natural upper limit northward. In our case, 146 km^2 of suboptimal habitat in the *potential* model became optimal in the *actual* model, thus conforming the species' range. As analysed in Shine *et al*. (2002), the effect of deforestation on reptiles may be similar, although on a lesser scale, to that produced by global climate change by shifting ranges northwards (Thomas & Lennon, 1999; Hickling *et al*., 2006).

Lastly, around 54% of the *potential* distribution range did not undergo any change of quality class. These areas are shrublands located in mountainous areas and conform to the core of the distribution range of the species. These mountainous systems of the species' range have also been traditionally exploited by extensive grazing, gathering firewood, and small dry crops. All these activities have most likely probability-increased the habitat quality for the species (Anadón *et al*., 2006b). However, this is probably not reflected in the model since they were formerly of a high quality (in relation to climate, topography, and lithology).

Hierarchical modelling

Hierarchical modelling constitutes one way to underpin species distribution modelling on sound theoretical backgrounds, which is an often neglected issue in modelling development (Austin, 2002; Guisan & Thuiller, 2005). Two essential advantages from the hierarchy theory are included in the distribution models: (1) environmental factors are integrated in a biological meaningful order (i.e. a hierarchy of factors), thus increasing the causal sense of the model; and (2) to a great extent, scale issues are solved since the modelling is based on the recognition of a spatial hierarchy. As a result, the hierarchical framework yields models that comprehensively reflect how nature works. Hierarchical modelling has the potential to address the complexity of the natural system and untangle the effects of environmental factors at the same time (Pearson *et al*., 2004). From an applied point of view, this framework can help to separately explore the effects of changes in environmental factors, such as those of climate change or land uses, as the present work reveals.

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