

Environmental and geographical factors affecting the Iberian distribution of flightless *Jekelius* species (Coleoptera: Geotrupidae)

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ABSTRACT

The degree of influence of environment, location and geography on the distribution of closely-related *Jekelius nitidus* and *Jekelius hernandezi*, coleopteran species endemic to the Iberian Peninsula, was examined. Niche envelope model predictions of probable absence points were based on available presence information. Presence–absence information for each of the two species was logistic-regressed against climate, altitude, lithology, spatial and river basin variables from each of 100 km² UTM Iberian Peninsula squares. Models predict that environmental conditions are suitable for both species in an area larger than that in which they have been found. The best-fitting environment model for *J. nitidus*, based on summer precipitation, area underlain by siliceous rocks, area with siliceous sediments and aridity index, explains more than 81% of total deviance. The final model, which includes spatial and river basin variables, accounts for nearly 89% of total deviance. The best-fitting environment model for *J. hernandezi*, based on the area underlain by calcareous rocks, summer precipitation, aridity index, altitude and minimum annual temperature, explains 63% of total deviance. The final model based on both spatial and river basin variables accounts for nearly 70% of total deviance.

Our results suggest that climate influences the distribution of both species similarly and that the acidic or basic nature of the substrate is the environment variable that most influences the occurrence of both species. The major degree of influence of river basin variables, together with lithologic variables, on the current distribution of both species may be due to the limited mobility of these flightless species.

Keywords

Dispersion, distributional predictive models, flightless, Iberian endemics, *Thorectes*.

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INTRODUCTION

The identification of environment factors limiting species distribution is complicated by the colinearity of explanatory variables and lack of knowledge of the physiological mechanisms directly related with the spatial response of species to environmental conditions (Hengeveld, 1990; Brown & Lomolino, 1998). However, variance partitioning (Borcard *et al.*, 1992; Legendre & Legendre, 1998) or hierarchical partitioning analysis (MacNally, 2000, 2002) of the relationships between explanatory and species presence–absence data can help identify the variables most likely to influence species distribution. Both the spatial autocorrelation of species data and the spatial variability patterns (Legendre & Legendre, 1998; Diniz-Filho *et al.*, 2003) not explained by environmental factors may be due to other factors previously ignored (e.g. biotic or historical).

Many different variables can influence current species distribution (Heglund, 2002; Huston, 2002), especially in the case of rare and endemic species (Gaston, 1994), depending on the biogeographical region studied and the scale considered. On local and regional scales, habitat type (Davis *et al.*, 2001a; McGeoch *et al.*, 2002), degree of habitat fragmentation (Klein, 1989; Estrada & Coates-Estrada, 2002), general landscape morphology (Roslin, 2001) or cultural impact (Verdú *et al.*, 2000; Hutton & Giller, 2003) seem to be factors of major importance in the case of dung beetles. Other relevant factors can be dung type and quantity (Martín-Piera & Lobo, 1996), or the changes over time due to livestock grazing (Lumaret *et al.*, 1992; Kadiri *et al.*, 1997; Lobo *et al.*, 1998). Lithology and soils (Brussaard & Slager, 1986; Osberg *et al.*, 1994; Sowig, 1995; Vessby & Wiktelius, 2003; Davis & Scholtz, 2004) have also been studied as abiotic factors influencing the presence and abundance of some dung beetle

species. On a local scale, species distribution may be the result of the interplay of environment variables and species energy requirements (Krell *et al.*, 2003). However, historical factors should be studied more thoroughly (Palmer & Cambefort, 2000; Davis & Scholtz, 2001), as they have conditioned dung beetle geographical distribution over longer periods of time.

Low-vagility, flightless insects are potentially good indicators of the role played by historical factors (Davis *et al.*, 2001b), because their loss of flight (brachypterism, micropterism and apterism) decreases their dispersal response to habitat perturbations. Southwood (1962) predicted that, within a taxon, temporary-habitat species should be more prone to migrate than species occupying more permanent habitats, where habitat stability, homogeneity and isolation (e.g. Roff, 1990) can be key to the presence of flightless species. One of the most remarkable taxonomic groups that contributes most to the endemism of local Iberian Peninsula dung beetle assemblages (Verdú & Galante, 2002) are the flightless (formerly genus *Thorectes*; see López-Colón, 1989, 2000) genera *Jekelius* and *Thorectes*. Most of the 40 species currently attributed to these two related genera are distributed in the western Mediterranean region, with some others in Central Asia and Nepal. In the Iberian Peninsula, 14 of the 16 recognized species are endemic (Baraud, 1992; Verdú & Galante, 2000). Many flightless dung beetles have been found in arid conditions (*Circellium bacchus* F. and many *Pachysoma* M'Leay, *Neopachysoma* Ferreira, *Mnematium* M'Leay and *Neomnematium* Janssens species; see Doube, 1991; Ferreira, 1968, 1969), as well as in stable, and/or such specialized habitats as ant and termite nests (Paulian, 1988); young leaves in ravines (Popovici-Bazosanu, 1932; Nikolaiev, 1966); fallen leaves in the forest (Montieth & Storey, 1981); rodent nests; or bat excrements in caves (Zunino & Halffter, 1988). As in other regions (Chown *et al.*, 1998; Harrison *et al.*, 2003), most Iberian Peninsula *Thorectes* and *Jekelius* species, generally adapted to aridity, are also associated with stable and persistent microhabitats, such as rabbit latrines (Verdú & Galante, 2004).

Palmer and Cambefort (1997) deduced from a morphological phylogeny hypothesis that vicariance and dispersal seem to have played complementary roles in the current distribution of Iberian *Thorectes* (*sensu lato*) species (see also Palmer & Cambefort, 2000). On the basis of this phylogeny, *J. nitidus* (Jekel, 1866) and *J. hernandezi* (López-Colón, 1988) are the southern Iberian representatives of a monophyletic clade, probably with a northern Iberian ancestor (Palmer & Cambefort, 2000). The other Iberian species of this clade (*Jekelius intermedius* (Costa, 1827)), determined from a review of all available material, are found in Balearic Islands (Menorca), south of France, Corsica, Sardinia, Sicily in Italy and North Africa (Baraud, 1992; López-Colón, 1995). To determine the influence of environment and ecology on the distribution of these two closely related, endemic, flightless *Jekelius* species, the following questions must be answered:

- 1 Which environment factors (altitude, climate or lithology) best explain the distribution of each one of these species?
- 2 Given the a priori low vagility of *Jekelius*, and the geographical barriers to flightless migration, can location or geography explain the presence of these species, independently of the influence of environment?

Table 1 Sources of distribution information for both species

<i>Jekelius nitidus</i>	<i>Jekelius hernandezi</i>
Galante & Rodríguez-Romo (1988)	Carrión (1961)
Galante (1981)	Galante & Cartagena (1999)
Galante (1983)	López-Colón (1988)
López-Colón (1995)	López-Colón (1990)
López-Colón (1996)	López-Colón (1992)
López-Colón <i>et al.</i> (1997)	López-Colón (1995)
CEUA	López-Colón (1996)
JLENCINA	Ruano Marco <i>et al.</i> (1988)
MNCN	Sánchez-Piñero & Avila (1991)
JPLAZA	CEUA
	JLENCINA
	MNCN

CEUA: University of Alicante collection; JLENCINA: private collection of Jose Luis Lencina; MNCN: National Museum of Natural Sciences; JPLAZA: private collection of Jesús Plaza.

MATERIALS AND METHODS

Data sources

The database used herein, compiled from all available bibliographical distribution data for these two species (Table 1), and from some unpublished data, contains 113 *J. nitidus* and 78 *J. hernandezi* records. A critical review led to the deletion of 1 unreliable *J. nitidus* and 8 *J. hernandezi* records. All the distribution data were georeferenced to a resolution of 10 × 10 km UTM squares. As some localities fall in the same UTM square, *J. nitidus* is present in 59 squares, and *J. hernandezi* in 46.

Each ($n = 6063$) of the 100-km² Iberian Peninsula UTM squares is characterized by mean altitude and five climate variables; total annual precipitation, rainfall during the summer months (July, August and September), yearly mean temperature (°C), minimum annual temperature and an aridity index, all of which seem to explain Iberian dung beetle endemism well (Verdú & Galante, 2002). The aridity index is expressed as: $Ia = 1/(P/T + 10) \times 10^2$, where P is the mean annual precipitation and T the mean annual temperature. All climate variables are courtesy of the Spanish Instituto Nacional de Meteorología and the Portuguese Instituto de Meteorología. Mean altitude of all 1-km pixels included in each 100 km² UTM square was obtained from a Digital Elevation Model (Clark Labs, 2000). Four lithology variables, digitized from atlas (ITGE, 1988) categories, were reclassified by calculating the area with stony acidic or siliceous soils, calcareous soils, siliceous sediments or deposits, and calcareous sediments. The area of each of these four categories was calculated for each UTM square using the IDRISI Kilimanjaro version (Clark Labs, 2003). All independent variables were standardized to 0 mean and 1 standard deviation to eliminate the effect of measurement-scale differences.

The third-degree polynomial of the central latitude (Lat) and longitude (Lon) of each UTM square was also calculated ($b_1\text{Lat} + b_2\text{Lat}^2 + b_3\text{Lat}^3 + b_4\text{Lon} + b_5\text{Lon}^2 + b_6\text{Lon}^3 + b_7\text{Lat} \times \text{Lon} + b_8\text{Lat}^2 \times \text{Lon} + b_9\text{Lat} \times \text{Lon}^2$). These spatial variables can help



Figure 1 Iberian map (30N UTM projection) of the 11 main river basins and the main rivers (broken lines). 1: Miño; 2: Cantabrica; 3: Duero; 4: Ebro; 5: Catalana; 6: Tajo; 7: South-western; 8: Guadiana; 9: Turia; 10: Guadalquivir; 11: Segura.

in the determination of the influence of unaccounted-for spatially structured factors (see Legendre & Legendre, 1998). Lastly, the Iberian river basin (i.e. the entire geographical area drained by a river and its tributaries, see Fig. 1) in which each grid square falls was included in the subsequent model building as a dummy variable. The order of inclusion of independent variables (first, environment variables, subsequently spatial, and lastly, river basin variables) clarifies the percentage of variability, not explained by climate and altitude variables, which can be explained by spatial and river basin variables. This highlights the power of prediction of the latter variables independently of the environmental conditions of the territory (see Legendre & Legendre, 1998).

Modelling distributions

A variety of methods are currently available to model species distributions (see Guisan & Zimmermann, 2000; Scott *et al.*, 2002). These techniques either consider only presence data (niche enveloping models) or also consider absence data (group discrimination techniques). Group discrimination methods seem to predict more accurately (Hirzel *et al.*, 2001; Brotons *et al.*, 2004; Segurado & Araújo, 2004) when reliable species absence data are used. Lack of data reliability in localities with suitable environmental conditions, but unoccupied at the time of sampling, or in cases where the species eluded detection, perhaps as a result of insufficient sampling effort, can be overcome by using random pseudo-absences (Zaniewski *et al.*, 2002; Schadt *et al.*, 2002), or by distinguishing the most probable absence localities through niche-based modelling of presences alone (Engler *et al.*, 2004). An estimate of the distribution of these two Iberian *Jekelius* species was obtained by first tabulating each of the 10 environment variable maximums and minimums for the observed distribution localities, and by calculating the multidimensional

envelope defined by the scores of the locations in which the species was recorded. This niche-based envelope model (see, for example, Busby, 1986) incorporates the generally appropriate environmental conditions for the species found according to the observed presence points. The maximum and minimum scores for each environment variable were augmented by 10% to guarantee that selected absence localities were environmentally distant from presence localities. Probable absence points were selected at random from the area falling outside this augmented envelope. To avoid bias due to the inclusion of a comparatively higher number of absences (Kink & Zeng, 2001), a number of absences 10 times higher than the number of presences were selected. Observed presence points (59 for *J. nitidus* and 46 for *J. hernandezii*) and presumed absence points ($n = 590$ and 460, respectively) were then logistic-regressed, using generalized linear models (GLMs) (Crawley, 1993), to analyse the relationship between the presence/absence dependent variable and the continuous and dummy explanatory variables (see Guisan *et al.*, 2002; Lehmann *et al.*, 2002). GLMs are an extension of linear models that allow for nonlinearity in the data and also a range of independent variable distributions other than the normal. In our case the assumed relationship between the presence/absence of each species and the explanatory variables is binomial (presence/absence, the link function), while a logistic error distribution was assumed.

The dependent variable (presence/absence) for the 10×10 UTM squares considered was first related separately to either a linear, a quadratic or a cubic function of each environment variable in order to take possible curvilinear relationships into account (Austin, 1980). Subsequently, variables were forward-stepwise incorporated in the model (see Nicholls, 1989; Austin *et al.*, 1996): that is, first the linear, quadratic or cubic function of the variable that accounts for the most important change in deviance was selected for inclusion. Next, all the remaining variables were tested for significance, adding them sequentially, according to their estimated importance. The procedure was iteratively repeated until no more statistically significant explanatory variables remained ($P < 0.05$). After each inclusion, the significance of the terms previously selected was also tested, to backward-select (eliminate) terms that had become non-significant. Subsequently, the third-degree polynomial of the central latitude and longitude of each square was included in the model (Trend Surface Analysis; see Legendre, 1993) to take into account spatial structures, or the effect of historical, biotic or environment variables not otherwise taken directly into consideration (Legendre & Legendre, 1998). Latitude and longitude were standardized as were environment variables. Backward stepwise regression with the nine terms of the equation as predictor variables removed non-significant spatial terms, while significant terms ($P < 0.05$) were retained and included in the model. Lastly, dummy river basin variables were added to the model to check this geography variable's effect. The STATISTICA package 6.0. (StatSoft Inc., 2001) was used for all statistical computations.

The receiver operating characteristic (ROC; Zweig & Campbell, 1993), from a plot of sensitivity (ratio of correctly predicted positives to the total number of positive cases) vs. 1-specificity (ratio

of correctly predicted negative cases to the total number of negative cases), was used to measure the performance of models. To compare observed and predicted maps, the continuous probability variable generated by logistic regression should be converted to a binary one (presence/absence), selecting a threshold cut-off point for the decimal fraction. The area under the ROC function (AUC), independent of the presence/absence threshold (Fielding, 2002), is taken to be the best measure of model prediction accuracy. An AUC value of 0.5, from a possible range of 0–1, indicates that prediction of presence/absence does not differ from that of a random assignment, while an AUC score of 1 indicates perfect presence/absence prediction.

RESULTS

For both *J. nitidus* and *J. hernandezi*, niche envelope model areas with a priori favourable environmental conditions are much larger than those predicted by GLM (Figs 2a & 3a). The area of the 10%-augmented enveloping models is 442,100 km² and 248,700 km², respectively, two and eight times greater than the area predicted by the corresponding final GLM distribution models (210,800 km² and 30,600 km²; see Figs 2 & 3).

Based on a random selection of absence data from regions with unfavourable environmental conditions, the quadratic function of summer precipitation seems to be the most important environment variable negatively related to the distribution of *J. nitidus* (Table 2). It accounts for 35% of total deviance. The cubic function of annual minimum temperature and the quadratic function of the area underlain by siliceous rocks are also relevant to explain the distribution pattern of this species. Stepwise selection of all environment variables produced a final environment model in which the quadratic function of summer precipitation, the area underlain by siliceous rocks, the aridity index and the area with siliceous sediments explain more than 81% of total deviance (Table 2).

Spatial variables alone produce slightly less accurate model predictions (75% of total deviance), while the dummy river basin variables alone accounted for 55% of total deviance in *J. nitidus* distribution. However, the inclusion of spatial or river basin variables in the final environment model increased explained deviance by only an additional 5% and 1%, respectively (Table 2). The alone spatial term added to the model built from environment variables is the interaction of latitude \times longitude². The incorporation of river basin dummy variables, including the Tajo and the Guadiana basins, increased the explained deviance by less than 2%, but eliminated the aridity index (Table 2). Thus, most of the variability explained by spatial and river basin variables seems to be accounted for by the environment variables used. With non-significant variables eliminated, the final model with spatial and river basin variables added, accounts for almost 89% of total deviance (Table 3).

In the case of *J. hernandezi*, the quadratic function of the area underlain by calcareous rocks is the most important environment variable, followed in importance by the quadratic function of summer precipitation, the total annual precipitation and the aridity index (Table 4). The explanatory variables in the final

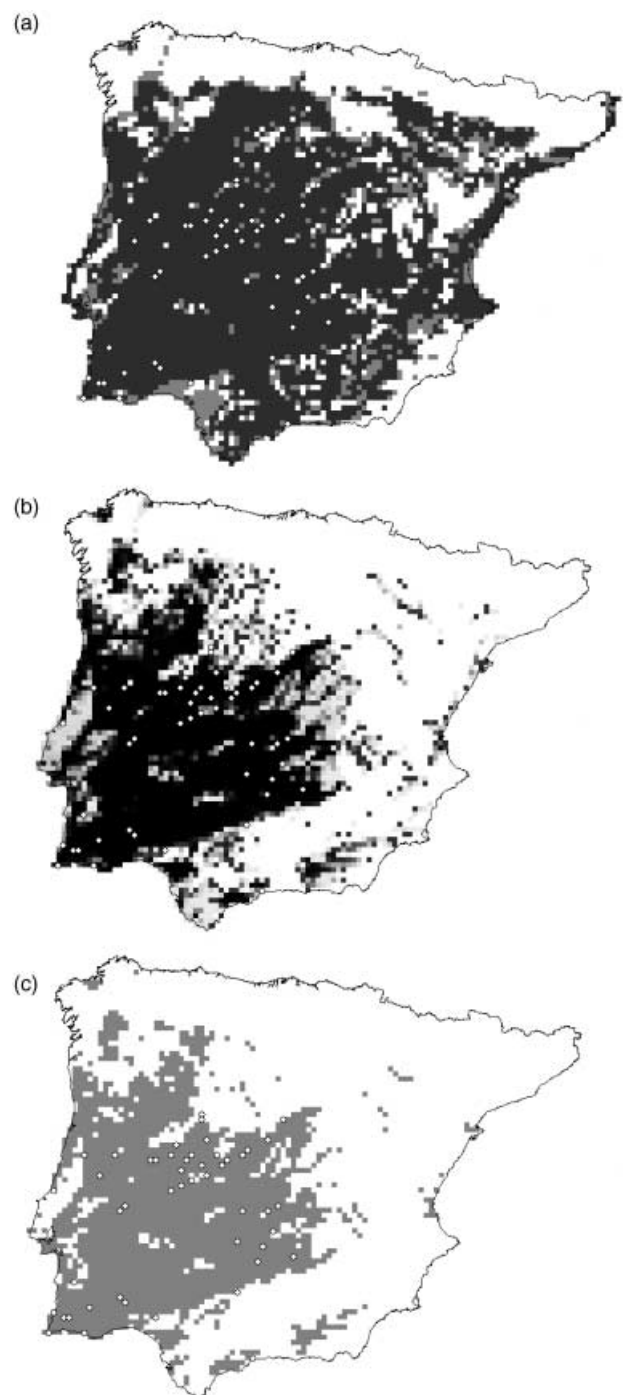


Figure 2 (a) Niche enveloping distribution model for *Jekelius nitidus* based on the six environment variables considered. In grey, the expanded model in which the maximum and minimum scores for each environment variable were extended by 10%. (b) Final predictive model using logistic regression analysis (see Table 2) in which absence points were randomly selected from the area outside this expanded enveloping model. (c) Binomial predictive map generated from the logistic continuous regression probabilities. From out of 100 possible thresholds, the one which maximized the sum of sensitivity and specificity was selected. In all maps, white points represent the observed distribution of species.

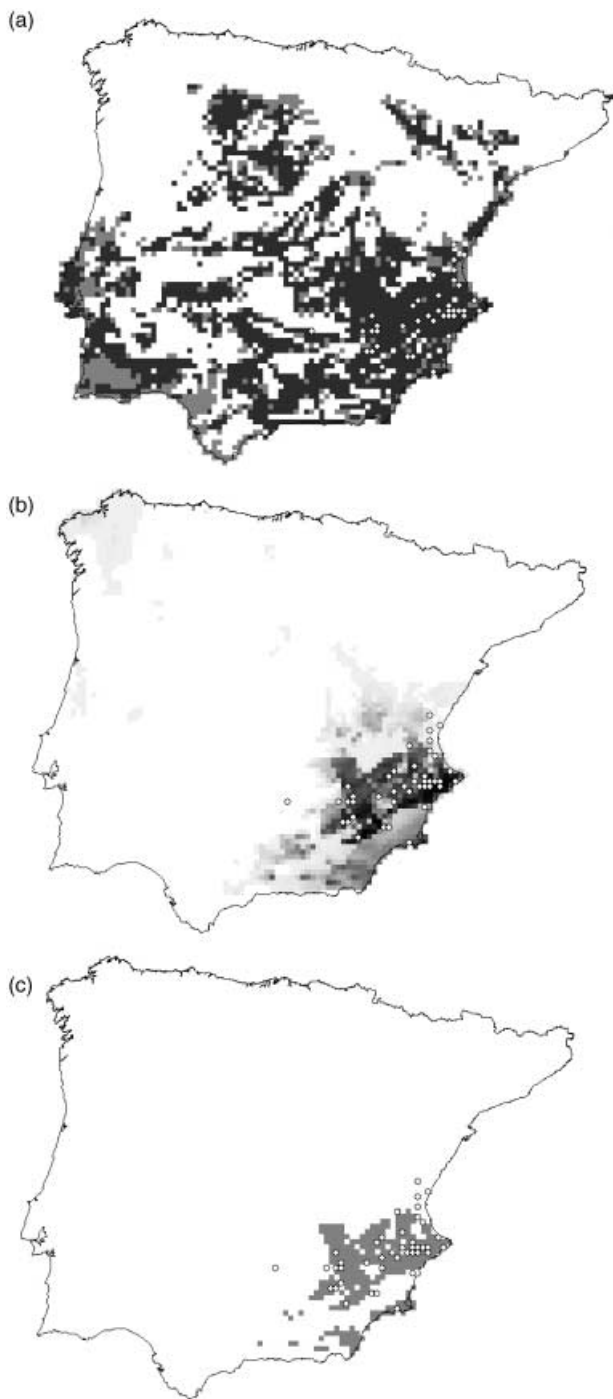


Figure 3 (a) Niche enveloping distribution model for *Jekelius hernandezii* based on the six environment variables considered. In grey, the expanded model in which the maximum and minimum scores for each environment variable were extended by 10%. (b) Final predictive model using logistic regression analysis (see Table 4) in which absence points were randomly selected from the area outside this expanded enveloping model. (c) Binomial predictive map generated from the logistic continuous regression probabilities. From out of 100 possible thresholds, the one which maximized the sum of sensitivity and specificity was selected. In all maps, white points represent the observed distribution of species.

Table 2 Explanation of the distribution of *Jekelius nitidus* and percentage of deviance accounted for by the selected environment variables (% Dev) on a null model in which the number of parameters is equal to the number of observations (Dobson, 1999). Linear, quadratic or cubic functions of each variable that account for a significant change in deviance ($P < 0.05$) were also selected (f^2 and f^3 are the quadratic and cubic functions, respectively). The sign column indicates the sign for each selected term of each function. Spatial variables were chosen after backward-stepwise elimination of non-significant terms from a third-degree polynomial of latitude and longitude

	d.f.	Deviance	% Dev	Sign
f^2 Summer precipitation	646	256.18	35.21	--
f^3 Annual mean temperature	645	324.97	17.82	+--
f^2 Siliceous rocks	646	343.45	13.14	+ -
Calcareous rocks	647	364.19	7.90	-
Annual minimum temperature	647	380.85	3.68	+
Annual precipitation	647	381.83	3.44	-
Calcareous sediments	647	382.14	3.36	-
Altitude	647	390.36	1.28	-
Siliceous sediments	647	392.38	0.77	+
Aridity index	647	394.43	0.25	+
Final environmental model	643	74.73	81.10	
Final river basin model	638	178.31	54.91	
Final spatial model	642	95.61	75.82	
Adding river basin variables	642	70.53	82.16	
Adding significant spatial variables	642	54.81	86.14	
Adding river basin and spatial variables	641	44.06	88.86	

Table 3 Coefficients and standard deviations (SD) for parameters included in the final model for *Jekelius nitidus* and *Jekelius hernandezii*. The Wald statistic, a test of significance of the regression coefficient, and the P level for that statistic are also included. ²denotes quadratic term of a curvilinear function

	Coefficients	SD	Wald	P
<i>Jekelius nitidus</i>				
Summer precipitation	-13.11	3.14	17.42	< 0.0001
Summer precipitation ²	-13.44	3.56	14.21	< 0.001
Siliceous rocks	5.83	1.39	17.50	< 0.0001
Siliceous sediments	3.06	0.85	13.05	< 0.001
Longitude * Latitude ²	-3.30	0.80	17.06	< 0.0001
Tajo basin	2.65	0.91	8.49	< 0.01
Guadiana basin	2.69	1.12	5.74	0.02
<i>Jekelius hernandezii</i>				
Calcareous rocks	6.49	1.40	21.44	< 0.0001
Calcareous rocks ²	-3.07	0.68	20.10	< 0.0001
Summer precipitation	-0.71	0.25	8.04	0.004
Altitude	-3.21	0.94	11.68	< 0.0010
Longitude * Latitude	1.04	0.31	11.25	< 0.001
Segura basin	4.50	1.06	18.11	< 0.0001
Turia basin	0.88	0.38	5.25	0.02

Table 4 Explanation of the distribution of *Jekelius hernandezii* and percentage of deviance accounted for by the selected environment variables (% Dev) on a null model in which the number of parameters is equal to the number of observations (Dobson, 1999). The linear, quadratic or cubic functions of each variable that account for a significant change in the deviance ($P < 0.05$) were also selected (f^2 and f^3 are the quadratic and cubic functions, respectively). The sign column indicates the sign for each selected term of each function. Location variables were chosen after backward-stepwise elimination of non-significant terms from a third degree polynomial of latitude and longitude

	d.f.	Deviance	% Dev	Sign
f^2 Calcareous rocks	497	243.33	20.77	+ -
f^2 Summer precipitation	497	270.58	11.90	--
Annual precipitation	498	275.07	10.44	-
Aridity index	498	278.99	9.16	+
Siliceous rocks	498	288.32	6.13	-
Altitude	498	295.93	3.65	+
Calcareous sediments	498	301.34	1.89	-
Annual mean temperature	498	304.79	0.76	+
Annual minimum temperature	498	306.51	0.20	+
Siliceous sediments	498	307.02	0.04	+
Final environmental model	492	114.75	62.64	
Final river basin model	496	164.74	46.36	
Final spatial model	494	107.11	65.13	
Adding river basin variables	491	109.93	64.21	
Adding significant spatial variables	494	102.27	66.70	
Adding river basin and spatial variables	489	93.40	69.59	

environment model are (c. 62% of total deviance) the quadratic function of the area underlain by calcareous rocks, the quadratic function of summer precipitation, the aridity index, altitude and the minimum annual temperature. Adding spatial variables alone produces slightly better model predictions (c. 65%). Dummy river basin variables alone accounted for around 46% of total deviance. Again, location or river basin variable inclusion in the environment model increased the explained deviance by only an additional 4% and 2%, approximately (Table 4). The inclusion of spatial variables in the environment model incorporated the latitude \times longitude interaction eliminating the quadratic term of summer precipitation, the aridity index and the minimum annual temperature. Subsequent incorporation of river basin variables brought in the Segura and the Turia basins, without eliminating any variable. The final model, including spatial and river basin variables, accounts for 69% of total deviance (Table 3).

The final GLM models for both species generate very acceptable geographical distribution hypothesis (Figs 2b & 3b) with impressively high AUC scores (0.9973 for *J. nitidus* and 0.9815 for *J. hernandezii*). Thresholds that maximized sensitivity and specificity (0.457 and 0.440, respectively) were selected, and presence-absence predictions were mapped for both species (Figs 2c & 3c). For *J. nitidus*, the final model suggests the existence of some appropriate but isolated areas in the south of the Iberian Peninsula, along with a northern extension of its current

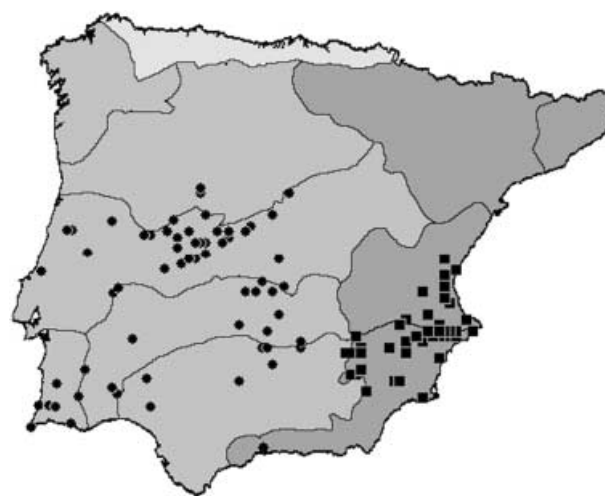


Figure 4 Observed distribution of *Jekelius nitidus* (black circles) and *Jekelius hernandezii* (black squares) and main Iberian river basins. The three different grey tones distinguish basins according to the final destination of their rivers.

distribution. For *J. hernandezii*, the documented distribution range basically coincides with the predicted one.

DISCUSSION

Environment variables account for 81% (*J. nitidus*) and 62% (*J. hernandezii*) of the distribution variability of these species at this resolution. Altitude correlates poorly, but general soil composition correlates well with the distribution of both species (c. 15% and 20% of total variability, respectively). The presence of *J. nitidus* correlates with acid soils, while *J. hernandezii* occurs mainly in calcareous soils. Whereas lithology matters most in the case of *J. hernandezii*, climate seems to be most relevant for *J. nitidus*, present most probably in areas with little precipitation during the summer, and with high mean annual temperatures. Little annual precipitation and high values of aridity seem to favour more the occurrence of *J. hernandezii*. Although *J. hernandezii* tends to occupy an area of extreme xerothermic conditions (SE Iberian Peninsula), and *J. nitidus* less dry areas (SW Iberian Peninsula) (Fig. 4), generally similar Mediterranean areas with high temperatures, little rainfall and considerable aridity seem to favour both *Jekelius* species. Our bio-climate niche-based models also suggest that appropriate environments exist in parts of the Iberian Peninsula not known to be currently inhabited by these species. This seems to be especially the case for eastern species *J. hernandezii*, with a potential geographical range eight times larger than the final predicted distribution, including some western Iberian areas of similar environment. For *J. nitidus* the bioclimate model suggests the existence of a favourable environment in the eastern part of the Iberian Peninsula. Our results suggest that climate restrictions on the distribution of both species could be similar, and that the acidic or basic nature of the substrate is the environment variable that best explains their occurrence.

The distributions of *J. nitidus* and *J. hernandezi* are also influenced by spatial and geographical factors. Although the inclusion of dummy river basin variables hardly improves the explained variability of the models, their importance is highlighted by their explanation of variance when considered alone (55% and 46%, respectively), and by their inclusion in the final stepwise models. Presence of *J. nitidus* seems to be restricted to the Tajo and the Guadiana basins, while the Turia, and mainly, the Segura, basins seem to limit the distribution of *J. hernandezi*. The relevance of river basins to explain the distribution of these two flightless *Jekelius* species could be a consequence of their inability to egress from some Iberian river basins. Thus, the a priori vicariant distribution pattern of both species could also be explained by dispersal limitations. The result of subsequent addition of spatial and river basin variables to the modelled environment indicates that a small fraction of distribution variability (around 1–3%), still spatially structured, has yet to be explained. One of the factors that might explain this spatial structure is dung type. *Jekelius* species' loss of flight does not impede their feeding on generally abundant and persistent trophic resources such as rabbit, sheep and deer pellets (López-Colón, 1985; Verdú & Galante, 2004). In the case of these two *Jekelius* species, there seem to be some trophic differences. *Jekelius hernandezi* would prefer rabbit pellets, feeding occasionally on sheep dung (López-Colón, 2000 and José R. Verdu, unpublished data). However, *J. nitidus* seems to prefer dung of higher hydric content, such as cow dung and fresh sheep and deer dung (López-Colón, 1985 and unpublished data). These trophic preferences have their expression in some anatomic adaptations. Derived characters such as strongly developed denticles in the mandibles, well-developed molar areas, and hairless and sclerotized twisted galea of maxilla, morphological adaptations to the exploitation of rabbit dung, have all been described in mouthparts of *J. hernandezi* (Verdú & Galante, 2004). In the case of *J. nitidus*, a well-developed filtering area in mandibles and typical filtering maxillae (unpublished data) are intermediate between the characteristics of the mouth anatomy of dung-fibre consumers and the usual anatomical adaptations of fresh juice-consuming dung beetles (Cambefort, 1991). As the main herbivorous species in the south-eastern Iberian Peninsula is the rabbit (Malo *et al.*, 1995), the inclusion of dung sources might improve these model predictions.

Finally, our results suggest that the distributions of these two species are not in equilibrium with present-day environmental conditions, since potential distribution ranges are larger than observed ranges. Apterism, with its consequent decrease in dispersal capacity, seems to be the key to an explanation of potential and real distribution differences, and therefore the relevance of spatial and river basin variables. The loss of flight is the unavoidable consequence of the fusion of the elytra, a common adaptation in Coleoptera to reduce the loss of body water in arid conditions (Zachariassen, 1991; Chown *et al.*, 1998). Thus, *Jekelius* flightlessness can be viewed as an adaptation to extremely arid environmental conditions (Verdú & Galante, 2004) that could have favoured the isolation and divergence of populations, and consequently, promoted the current high rate of diversification displayed by these genera in the Iberian Peninsula.

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