Research Article

Assessing the Conservation Status of an Iberian Moth Using Pseudo-Absences

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ABSTRACT Knowing the distribution of endangered species is of substantial importance for conservation. We considered a useful approach for modeling species distribution when managing information from atlases and museums but when absence data is not available. By modeling the distribution for *Graellsia isabelae*, a threatened moth species, we assessed its current conservation status and identified its most relevant distribution explanatory variables using Geographic Information System and Generalized Linear Models. The distribution model was built from 136 occurrence records and 25 digitized explanatory variables at a 10×10 km resolution. Model predictions from logistic-regressed pseudo-absences, obtained from a presence-only method (Ecological-Niche Factor Analysis), explained 96.23% of the total deviance. We found that the best predictor variables were summer precipitation, aridity, and mean elevation. With respect to host plants, the presence of *G. isabelae* associated mainly with Scots pine (*Pinus sylvestris*) and Austrian pine (*P. nigra*). The finding of 8 areas, exclusively in the eastern Iberian territory, and a larger unoccupied habitat in the western Iberian Peninsula indicates that this species is probably not in equilibrium with its environment by historical factors. Sites of Community Importance under protection do not seem sufficient to maintain current populations, necessitating the protection of suitable neighboring habitats. Our methodology is useful to manage the conservation status of species for which reliable absence data is not available. It is possible to determine those variables that most affect the distribution of species as well as the potential suitable areas with the purpose of evaluating protected areas, connectivity among populations, and possible reintroductions. (JOURNAL OF WILDLIFE MANAGEMENT 71(8):2507–2516; 2007)

The prediction of species' distributions is relevant to diverse applications in evolution, ecology, and conservation science. Producing accurate predictions with available data is challenging due to the lack of information regarding the great majority of species. In order to solve the limitations in data, several statistical techniques and computer tools for data management have been combined for the purpose of obtaining information about the conservation status, geographic distribution, and habitat requirements of endangered species.

The conservation of biodiversity is a priority that has lead to the elaboration of multiple Red Lists in an effort to document the status of endangered species. Analyses of habitat requirements, distribution, and habitat suitability of threatened and endangered species can help to compensate for the lack of information on ecology, a major obstacle to conservation, especially of invertebrates. Computer tools such as Geographic Information System (GIS) and statistical modeling techniques applied to information from atlases and museums can be used to draw up predictive maps of the requirements and conservation status of such species (Dennis and Hardy 1999, Reutter et al. 2003, Chefaoui et al. 2005). Because sampling and identification are laborious tasks, predictions for regions not yet exhaustively surveyed can be based on pseudo-absences (Zaniewski et al. 2002, Engler et al. 2004, Lobo et al. 2006). Good absence data is fundamental to consistent models (see Anderson et al. 2003 or Loiselle et al. 2003). Unfortunately, our maps were not drawn up from reliable absence data. Thus, probable absence

localities far from the environmental domain defined by presences may be selected for the modeling of species distribution to avoid false absences that can decrease model reliability. With the goal of obtaining a predictive model based on generalized linear models (GLM) without reliable absence data, we procured the pseudo-absences with a presence-only method. This strategy allows researchers to use presence data alone to obtain distribution models able to delimit the potential range of species (Svenning and Skov 2004).

Graellsia isabelae (Lepidoptera: Saturniidae; Graëlls 1849) is a host-limited species protected by the Habitats Directive (the European Community initiative for an ecological network of special protected areas, known as Natura 2000), Bern Convention, Red Book of Lepidoptera, and other regional catalogues. Over the last 30 years, the decline of European butterflies (Warren et al. 2001, Wenzel et al. 2006) has occurred mostly in specialist and sedentary species (Steffan-Dewenter and Tscharntke 2000, Thomas 2000), highlighting the need to protect species with characteristics similar to those of *G. isabelae.*

Graellsia isabelae has a sedentary and nongregarious caterpillar, develops in 5 stages, and dwells in pine forests. Larvae feed from June to August before pupating. It is a univoltine species that flies at dusk, from March to July (only 1 brood/yr; Masó and Ylla 1989). Because *G. isabelae* is an emblematic and conspicuous species (the beautiful adults are markedly sexually dimorphic), occurrence records can be considered reliable (Ylla 1997).

There is controversy about larval food plants as various authors (Agenjo 1943, Gómez-Bustillo and Fernández-

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Rubio 1974, Vuattoux 1984, Masó and Ylla 1989, Ylla 1997) have cited different pine species: Scots pine, Austrian pine, dwarf mountain pine (*P. uncinata*), aleppo pine (*P. halepensis*), maritime pine (*P. pinaster*), and stone pine (*P. pinea*) as possible host plants based on captivity experiments.

There are 9 described subspecies of *G. isabelae* (Vives 1994), but the real variability among populations is not clear. Among them, the autochthonous origin of *G. isabelae galliaegloria* (Oberthür 1923), present in the Jura and Alps mountains of France and Switzerland, is controversial (Fernández-Vidal 1992, Ylla 1997). With the exception of these populations, the distribution of the insect is eastern Iberian.

We aimed to estimate the potential distribution of *G. isabelae* on the Iberian Peninsula and also to identify the explanatory variables most relevant to its occurrence. In an effort to identify the current conservation status of *G. isabelae*, we examined suitable regions for fragmentation, degree of connection, and the area currently under protection.

STUDY AREA

As *G. isabelae* had an eastern Iberian distribution, the study area was the Iberian Peninsula (excluding the Portuguese territory but including the Balearic Islands), which included the whole known range of the species. In total, the area comprised 498,150 km^2 divided into 5,270 cells of 10 × 10 km, for which corresponding biological and environmental data were described. We chose this resolution because the majority of biological data were originally referred to by that pixel size and the relation between grid size and study area was appropriate.

METHODS

Biological Data

We obtained species presence data mainly from a distribution atlas (Galante and Verdú 2000), additional unpublished data from the Valencia region (J. Baixeras, University of Valencia, personal communication), and other bibliographic references (Viejo 1992, García-Barros and Herranz 2001, López-Sebastián et al. 2002). As species data came from diverse sources and some references were old, we checked all references by comparing species locations with pine woods distributions to eliminate possible outliers. We discarded 6 presence data points with probably erroneous Universal Transverse Mercator (UTM) coordinates. Finally, we considered 136 presence points at a UTM spatial resolution of 100 km^2.

Predictor Variables

We used IDRISI Kilimanjaro GIS software to set up the explanatory variables we introduced in the preparation of distribution models (Table 1) from different sources. We extracted topographic variables (elevation and slope) from a global digital elevation model with 1-km spatial resolution (Clark Labs 2000), and we calculated aspect diversity using the Shannon index. Temperature and precipitation data at 1-km resolution were provided by the Spanish Instituto

Nacional de Meteorología. We calculated aridity as $Ia = 1/(P/T + 10) \times 10^2$, where P is the mean annual precipitation and T the mean annual temperature (see Verdú and Galante 2002). We extracted from a forest map woods containing the host plants species cited above (Ruíz 2002). We included in the analysis as a predictor variable the area of each forest patch present in each cell with respect to the different kinds of pine woods. In addition, we digitized 4 lithology variables from a lithology map (Instituto Geográfico Nacional 1995) to calculate the area of calcareous deposits, siliceous sediments, stony acidic, and calcareous soils for each cell. Spatial variables were the central latitude (Lat) and longitude (Lon) of each UTM cell and we derived their polynomial transformations from Trend Surface Analyses. The inclusion of these variables can help to determine unaccounted-for variable influence on species distribution (see Legendre and Legendre 1998). All continuous explanatory variables referred to the same 10 × 10 km UTM grid cells as those of species data using IDRISI Kilimanjaro's Resample and Contract modules. We standardized the predictor environment variables to zero for means and one standard deviation to eliminate the effect of varying measurement scales. We also standardized latitude and longitude in the same way as environment variables.

Predictive Distribution Models

Because accurate absence data were not available, we used a presence-only modeling technique (Ecological-Niche Factor Analysis [ENFA]) to map habitat suitability, from which we selected pseudo-absences to be used with presence data in a logistic regression procedure (GLM; see Engler et al. 2004).

We applied ENFA to presence data ($n = 136$) and the 28 predictor variables (Table 1) by means of BIOMAPPER 3.1 software, which was designed to build habitat suitability models and maps for any species. The principle of ENFA is to compare the distributions of the predictor variables between the species distribution and the whole area. This modeling technique (similar to Principal Component Analysis in that it generates orthogonal axes) computes a group of uncorrelated factors with ecological meaning, summarizing the main environmental gradients in the region considered. These factors are 1) the marginality factor, which describes how far the species optimum is from the mean habitat in the study area, and 2) the specialization factors that describe how specialized the species is. We used the selected factors to estimate the degree of ecogeographic similarity of each grid cell to the environmental preferences of the species, that is, the probability of a given cell belonging to the environmental domain of the presence observations. From this, we drew up a habitat suitability (HS) map with values that varied from zero (min. HS) to 100 (max.). We normalized predictor variables through a box-cox transformation (Sokal and Rohlf 1981), and we chose a geometric-mean distance algorithm, which provides a good generalization of the niche (Hirzel and Arlettaz 2003), to perform the analyses.

Unsuitable habitats determined by this profile technique help to identify reliable pseudo-absences for presence–

Table 1. Individual logistic regression of presence–absence of *Graellsia isabelae* against each one of the selected explanatory variables, indicating relationships as linear, quadratic (f^2), or cubic (f^3). Biological data were collected from Spain (since 1849). The sign column indicates the sign for each selected term of each function. We chose spatial variables after backward-stepwise elimination of nonsignificant terms from a third-degree polynomial of latitude and longitude.

Variables	df	Deviance	% explained deviance	Sign
Environmental variables				
f^2 summer precipitation	1,493	222.03	75.63	− +
f^2 max. annual temp	1,493	400.89	56.01	+ +
f^3 aridity	1,492	420.19	53.89	+ + −
f^2 min. annual temp	1,493	533.82	41.43	+ +
f^3 $\bar{x}$ elevation	1,492	552.77	39.35	− − +
f^2 annual precipitation	1,493	577.93	36.59	− +
f^3 slope	1,492	698.18	23.39	− + −
f^3 aspect diversity	1,492	857.84	5.88	+ + +
Vegetation				
f^2 *P. sylvestris*	1,493	568.27	37.65	− +
f^3 total area with any *Pinus* sp.	1,492	594.63	34.76	− + −
f^3 *P. sylvestris* and *P. nigra*	1,492	621.43	31.82	− + −
P. nigra	1,494	798.67	12.37	−
f^2 *P. nigra* and others	1,493	837.18	8.15	− +
P. sylvestris and *P. uncinata*	1,494	852.62	6.45	−
P. sylvestris and others	1,495	867.75	4.79	−
Groves of *P. sylvestris* and *P. nigra*	1,494	879.87	3.46	−
P. halepensis, *P. pinaster*, and *P. pinea*	1,494	889.62	2.39	+
P. uncinata	1,494	906.74	0.51	−
Mixture of pines	1,494	910.96	0.05	
Lithology variables				
Calcareous stony soils	1,494	635.97	30.22	−
Acidic sediments	1,494	723.15	20.66	+
Acidic stony soils	1,494	902.12	1.02	+
Calcareous sediments	1,494	906.59	0.53	−
Spatial variables				
Longitude^2 × latitude	1,494	647.43	28.96	−
f^3 latitude	1,492	658.39	27.76	− + −
Longitude	1,494	671.94	26.27	−
Longitude × latitude^2	1,494	750.5	17.65	−
Longitude × latitude	1,494	859.85	5.66	−

absence modeling. To avoid bias due to the inclusion of a comparatively higher number of absences (King and Zeng 2000), we randomly selected 10 times more absences (1,360) than presences from the model. We chose pseudo-absences from unsuitable habitats with HS < 10, a threshold value that has been shown to produce good validation results (Chefaoui and Lobo, in press). We regressed the 136 presence data points and the 1,360 pseudo-absences selected from the presence-only model using logistic regressions in GLM. Generalized Linear Models are an extension of the classical linear regression models that allow for nonlinearity in the data as well as a range of independent variable distributions other than the normal (McCullagh and Nelder 1989). The relationship between the dependent and the explanatory variables (the link function) was logistic, and we assumed a binomial error distribution of the dependent variable.

To perform a statistical analysis of the variables, we first related the presence–absence data of the species for the 10 × 10 km UTM cells under consideration separately to each predictor variable. First, to consider possible curvilinear relationships, we selected for inclusion the linear, quadratic, or cubic function of the variable that accounts for the most important change in deviance with significant terms (Austin

1980). With this procedure, we identified the most relevant explanatory variables. Next, we built 4 models from each of the variable sets to estimate the relative relevance of each group of explanatory variables: an environmental model (E), a vegetation model (V), a lithology model (L), and a spatial model (S). Subsequently, we accomplished different models considering all possible combinations among the 4 types of variables (E, V, L, and S). We used Akaike's Information Criterion (AIC), the measures associated with it (ΔAIC, Akaike wt, and Model likelihood; Hastie et al. 2001, Burnham and Anderson 2002), and the percentage of explained deviance values to choose between competing models. We used the STATISTICA 6.0 package (StatSoft Inc., Tulsa, OK) for all statistical computations.

We used the Receiver Operating Characteristic curve (ROC; Zweig and Campbell 1993, Schröder 2004) to estimate model accuracy. A ROC curve is a plot of sensitivity (the ratio of correctly predicted presences to the total no. of presences) versus 1-specificity (false positive rate) as the threshold changes, and the calculation of the area under this curve (AUC) provides a single number performance measure across all possible ranges of thresholds (Fielding 2002). However, when a cut-off point was needed to transform continuous probabilities obtained in GLM

models to binary ones (presence–absence), we used the sensitivity–specificity difference minimizer (Liu et al. 2005, Jiménez-Valverde and Lobo 2006) to select this threshold, due to its generally good performance. Because the small sample size did not allow for the performance of ROC analysis with independent data, we obtained model validation scores by means of a jackknifing procedure (see Olden et al. 2002, Engler et al. 2004) developed with R v.2.2.0 (R Development Core Team, Vienna, Austria) just in those models with better results in AIC-derived measures and deviance scores. In the jackknife procedure, with a data set of n observations, the model was recalculated n times, leaving out one observation each turn. We then applied each of the regression models based on the $n - 1$ observations to the excluded observation, obtaining a probability value for each of the observations. We subsequently used these jackknifing probabilities, together with the binary dependent scores, to calculate AUC, sensitivity, and specificity.

We used hierarchical partitioning to measure the relative importance of each type of explanatory variable (Birks 1996; MacNally 2000, 2002). First, we calculated the percentage of explained deviance for each type of variable, as well as the variability explained by all possible variable combinations. Subsequently, we calculated the average effect of inclusion of each type of variable in all models for which this type of variable was relevant. We took such averages as estimations of the independent contribution of each type of explanatory variable.

Conservation

Because *G. isabelae* is a host-limited moth, we used pine species significantly related with the distribution of this insect species to filter potential predictive model habitats as a means of identifying currently suitable regions. After assigning a buffer area of 10 km around each suitable UTM cell, we identified groups of connected cells (habitat patches) that maintain a priori separate populations. We selected the buffer size in accordance with dispersal distance data cited by other authors (Montoya and Hernández 1975, Baixeras 2001).

Because habitat area has been shown to greatly influence the conservation of European specialist butterflies (Steffan-Dewenter and Tscharntke 2000, Wahlberg et al. 2002, Krauss et al. 2003), we calculated the area, perimeter, and a compactness ratio (Clark Labs 2003) for each habitat patch. The compactness ratio compares the patch area:perimeter ratio with that of a circle of the same perimeter. We characterized isolation of populations or patches by the maximum, minimum, and mean distance to the nearest occupied patch or region, computed as the distance to the closest edge of nearby patches.

To examine the possible distribution expansion through reforested pine woods, reflected in the reforestation relationship with species occurrence, we used a contingency table with Cramer's V coefficient, a measure of the strength of variable association (Ott et al. 1983, Clark Labs 2003). We made Gap Analysis of habitat patches and Natura 2000 protected Sites of Community Importance (SCIs) to evaluate the current conservation status of *G. isabelae*.

RESULTS

Relevant Explanatory Variables

Regression of each variable separately showed that environmental variables, mainly those related to precipitation and temperature, were most relevant to the prediction of *G. isabelae* distribution (Table 1). Vegetation variables also explained the occurrence of *G. isabelae*, although they were less relevant. Mean value of percentage of explained deviance for environmental variables was 31.18% larger than for vegetation variables. The presence of Scots pine and Austrian pine woods seemed to be the most important vegetation variable, along with the highly correlated total area of *Pinus* species. With regard to lithology variables, species presence correlated negatively (sign −) with calcareous stony soils but positively (sign +) with acidic sediments; both variables explained >45% of the total variability in species presence (see lithology model; Table 2). Lastly, spatial variables also explained the occurrence of *G. isabelae*, confirming that the Iberian distribution of this species forms a spatially structured pattern.

The complete environmental model accounted for >95% of total variability, an astonishing percentage of variability that none of the other types of predictor variables could explain (Table 2). The addition of vegetation, lithology, and spatial variables slightly increased (<1%) the explanatory capacity of the environmental variables. The mean percentage of variation accounted for by vegetation, lithology, and spatial variables was 22.25%, 12.34%, and 11.09%, respectively.

Predictive Models

The analysis for model selection suggested that the model carried out with environmental, lithological, and spatial variables (E + L + S) and the model encompassing only the environmental and lithological variables (E + L) were those that had higher percentages of explained deviances, lower AIC values, and the best model likelihood (Table 2). However, jackknifing validation indicated that the E + L + S model had higher accuracy scores; its AUC, sensitivity, and specificity scores were 0.9841, 0.9705, and 0.9977, respectively, whereas the results for the E + L model were 0.9834, 0.9705, and 0.9963, respectively.

This E + L + S model explained >96% of the total variability when we considered all significant explanatory variables together in order of importance (Table 2). Variables retained in the final model were summer precipitation, aridity, mean elevation, slope, calcareous stony soils, calcareous sediments, and latitude (Table 3). After selecting the appropriate threshold value (0.09) for this final model, we converted the continuous GLM probability map values to binomial (Fig. 1). The total a priori suitable area, found to be about 203,100 km^2, was reduced to a current suitable area of 114,500 km^2 after filtering for the presence of the appropriate pine woods (Scots pine and Austrian pine).

Table 2. Deviance, percentage of explained deviance, Akaike Information Criterion (AIC), ΔAIC, AIC weight, and model likelihood values for each one of the generalized linear model accomplished with each type of explanatory variables and with all possible variable combinations. To perform environmental (E), vegetation (V), lithology (L), and spatial (S) models we used *Graellsia isabelae* data from Spain since 1849. Variables that constitute models E + V + L and E + L are coincident because vegetation variables did not contribute to models when added, so these two models are equivalent (the same with E + V + L + S and E + L + S).

Predictive models	df	Deviance	% explained deviance	AIC	ΔAIC	AIC wt	Model likelihood
E	1,488	43.67	95.20	59.67	5.99	0.0135	0.0500
V	1,486	187.24	79.45	207.24	153.56	0.0000	0.0000
L	1,491	500.58	45.08	510.57	456.89	0.0000	0.0000
S	1,490	539.85	40.77	551.85	498.17	0.0000	0.0000
E + V	1,487	39.38	95.67	57.38	3.70	0.0424	0.1572
E + L	1,487	35.68	96.08	53.68	0.00	0.2695	1.0000
E + S	1,488	49.26	95.59	65.26	11.58	0.0008	0.0031
V + L	1,483	121.40	86.68	147.36	93.68	0.0000	0.0000
V + S	1,484	229.41	86.89	143.41	89.73	0.0000	0.0000
L + S	1,490	176.40	80.64	188.44	134.76	0.0000	0.0000
E + V + L	1,487	35.68	96.08	53.68	0.00	0.2695	1.0000
E + V + S	1,487	42.09	95.67	60.09	6.41	0.0109	0.0406
E + L + S	1,486	34.31	96.23	54.31	0.63	0.1967	0.7298
V + L + S	1,486	82.92	90.90	102.92	49.24	0.0000	0.0000
E + V + L + S	1,486	34.31	96.23	54.31	0.63	0.1967	0.7298

The regions considered to be suitable exhibit very specific environmental conditions (Table 4), in which precipitation is higher than the average for the entire territory, and temperatures and aridity lower than the Iberian average. Elevation and slope scores were also higher than those observed for the whole territory, showing that the general environmental conditions for this species were those found in medium elevation mountain ranges. This final distribution model also revealed the existence of unoccupied regions, potentially suitable for *G. isabelae,* in the northwestern quadrant of the Iberian Peninsula (Cantabric mountains, Zamora and Galician mountains, the western area of the Iberian Central System, and the Iberian System), and in some southern mountains (Sierra Nevada).

Connectivity and Conservation Status

The presence of *G. isabelae* was observed in 8 unconnected patches, comprising the buffered occurrence cells of the currently suitable area (see Fig. 1). The total area was 41,600 km^2, although the individual patch sizes were quite dissimilar; 67% of this area consisted solely of the 2 largest patches (Table 5). The mean distance to the nearest occupied patch was 47.2 km, with 10 km the minimum distance between patches (pairs 1–2 and 5–6) and 120 km the maximum (between patches 6 and 7). These habitat patches exhibited a slightly differing compactness ratio (patches 1, 2, 3, and 6 with a larger edge effect; Table 5). The patches could be grouped in 4 regions connected by suitable habitat between them (see Fig. 1): 1–2 (Catalan-Pyrenean), 3 (Guadarrama Mountains), 4-5-6 (Iberian

Table 3. Parameter estimates from environmental + lithology (E + L) and environmental + lithology + spatial (E + L + S) final generalized linear models (±SE) performed for Spanish *Graellsia isabelae* data since 1849. Wald statistic scores test the significance of regression coefficients.

| Parameters	Wald	*P* values	Coeff.	SE
E + L				
Summer precipitation	17.83	<0.001	−13.03	3.08
Summer precipitation^2	14.67	<0.001	2.68	0.70
Max. annual temp	8.76	0.003	2.27	0.76
Aridity	13.10	<0.001	6.14	1.69
Min. annual temp	10.65	0.001	−10.12	3.10
$\bar{x}$ elevation	15.20	<0.001	−12.04	3.08
Slope	10.59	0.001	2.10	0.64
Calcareous sediments	6.63	0.010	−1.70	0.66
E + L + S				
Summer precipitation	17.20	<0.001	−10.29	2.48
Summer precipitation^2	18.74	<0.001	2.69	0.62
Aridity	13.80	<0.001	6.17	1.66
$\bar{x}$ elevation	8.85	0.003	−2.39	0.80
Slope	6.00	0.014	1.53	0.62
Calcareous stony soils	11.07	<0.001	−2.62	0.78
Calcareous sediments	5.92	0.010	−1.72	0.70
Latitude	5.49	0.020	4.20	1.79
Latitude^2	7.33	0.007	2.77	1.02
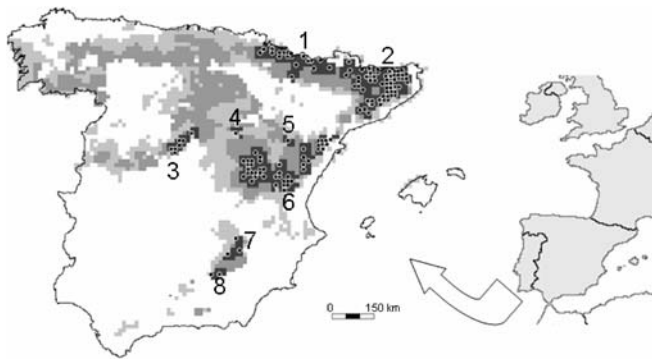
Figure 1. Distribution of occurrence data for *Graellsia isabelae* in Spain since 1849 (black dots), suitable area according to final generalized linear model (light grey), and suitable area with Scots pine and Austrian pine woods (dark grey). Habitat patches (black): 1) Pyrenees, 2) Catalonia, 3) Sierra of Guadarrama, 4) Anguita (Guadalajara), 5) Montalbán (Teruel), 6) Iberian System, 7) Sierras of Segura and Alcaraz, 8) Sierra of Cazorla.

System and associated mountains), and 7–8 (Sierras of Cazorla, Segura and associated mountains).

Around 39% of the suitable area is currently protected by the Natura 2000 proposal (SCIs), with protected areas differing greatly from region to region. Included in this reserve proposal are >80% of regions 7 and 8, whereas <20% of regions 2 and 5 would be protected (Table 5). Finally, the presence of *G. isabelae* does not correlate significantly with reforested pine woods (Cramer's V score is 0.02); of the 136 presences, just 8 fell within reforested woods.

DISCUSSION

The Distribution Model

Suitable area identification was highly reliable; 97% of presences and 99% of environmentally derived pseudo-absences were correctly predicted. Pseudo-absence selection by a modeling method that requires only presence data and the inclusion of such absences in presence–absence modeling seems a promising distribution prediction procedure (see also Zaniewski et al. 2002, Engler et al. 2004, Lobo et al. 2006).

Evidently, true distribution absences can never be distinguished with certainty from false ones, due to the lack of information on the species. In our case, the size and

showiness of *G. isabelae* should have led to a reasonably well-known distribution. A nonequilibrium distribution pattern is supposed if a species does not occupy its entire suitable habitat. Because the occupied area is less than the potential derived in our final predictive model, we deduce that the species is not in equilibrium with the current climate. Given the nonequilibrium state, reliable absence information should be sought exclusively in environmentally favorable areas by standardized sampling to confirm species absence there. In addition, the ability of *G. isabelae* to colonize these areas should be examined in the near future. However, the inclusion of reliable absence data from regions with environments similar to those with presences implies a reduction in the goodness-of-fit of models obtained (see Collingham et al. 2000). Predictive distribution modeling assumes that the distribution of species is in an equilibrium or pseudo-equilibrium state (Guisan and Theurillat 2000, Guisan and Zimmermann 2000, Austin 2002, Pearson and Dawson 2003, Guisan and Thuiller 2005). Because non-equilibrium with environmental variables will be common among some groups and in some regions (White et al. 2001, Pearson et al. 2002, Skov and Svenning 2004, Araújo and Pearson 2005), success in forecasting actual species distri-bution could depend on the inclusion of variables represent-ing geographic, demographic, or historical factors that inhibit species distribution across all environmentally favorable locations.

The Most Relevant Variables

We showed that the main explanatory variables accounting for potential distribution may be identified by available species presence information alone. Our results demonstrate that *G. isabelae* does not need environmental conditions marginal to those of the Iberian Peninsula. We found that there are suitable habitats in a wide range of environments, with a preference for midrange mountainous conditions. Keeping in mind that changes in resolution and extent can alter the relevance of explanatory variables, we still found climate variables (summer precipitation, aridity, and $\bar{x}$ elevation) to be the best predictors. The curvilinear relationship between summer precipitation and the pres-ence–absence of *G. isabelae* is especially important (Fig. 2 and Table 1); precipitation from 1,250 mm to 3,250 mm makes species presence highly probable.

Table 4. Environmental conditions of suitable areas for *Graellsia isabelae* in Spanish territory (with data since 1849). The suitable areas were defined by generalized linear model performed with environmental, lithology, and spatial variables (E + L + S model not filtered with pine woods) compared with those of the entire study area.

Environmental variables	Study area		Suitable habitat			
	Min.–max.	$\bar{x}$	Min.	Max.	$\bar{x}$	SD
Summer precipitation (mm)	0–472.4	90.4	22.9	472.4	130.9	61.4
Max. annual temp (° C)	9.1–24.9	19.3	9.6	23.1	17.3	1.9
Aridity	0–1.6	0.4	0.07	0.6	0.3	0.1
Min. annual temp (° C)	−3.5 to 14.3	7.34	−3.5	12.7	5.2	2.2
$\bar{x}$ elevation (m)	0–2,722	665	2	2,632	907	374
Annual precipitation (mm)	0–2,200.6	698.9	365.4	2,165.2	844.9	386.6
Slope (°)	0–46.0	3.4	0	39	4.3	3.4

Table 5. Main characteristics of *Graellsia isabelae* Iberian patches of occurrence data (since 1849). Numbers of each region are those shown in Figure 1. SCIs are Sites of Community Importance protected by the Habitats Directive.

Region	Area (km²)	Perimeter (km)	Compactness ratio	Area included in SCIs (%)	Suitable habitat bordering the region (%)	Oldest reference available (yr)
1 Pyrenees	7,700	660	0.47	35.0	51.5	1943
2 Catalonia	13,800	880	0.47	19.8	36.3	1920
3 Sierra of Guadarrama	2,400	320	0.54	65.7	25.0	1849
4 Anguita (Guadalajara)	500	140	0.56	47.2	35.7	1993
5 Montalbán (Teruel)	600	120	0.72	10.8	50.0	1974
6 Iberian System	14,100	1120	0.37	46.8	60.7	1920
7 Sierras of Segura and Alcaraz	1,600	220	0.64	83.5	40.9	1943
8 Sierra of Cazorla	900	140	0.75	99.3	28.5	1943

Among all possible host plants examined, species presence was shown to be related with Scots pine and Austrian pine, the pine woods most frequently cited in the literature. Other pine species occasionally cited as food in captivity studies (aleppo pine, maritime pine, stone pine, and dwarf mountain pine; see Agenjo 1943, Gómez-Bustillo and Fernández-Rubio 1974, Vuattoux 1984, Masó and Ylla 1989, Ylla 1997) were only marginally related with *G. isabelae* presence.

Because *G. isabelae* feeds only on plants, we did not expect the best model predictions of its distribution to be independent of vegetation variables; although not altogether irrelevant, their inclusion, after environmental variables, did not increase model prediction accuracy. Similar findings presented by Warren et al. (2001) showed that the range limits of 46 British butterflies could be described by 3 bioclimatic variables. Such a result may be due to environmental collinearity between climatic and vegetation variables. The major part (82%) of preferred Scots pine and Austrian pine woods were located within the suitable environmental area, where both types of factors coincided. Because host plant distribution, generally wider than that of most lepidopteran species (Gutiérrez 1997), also depends on environmental factors, it seems reasonable to begin with models based on environmental variables, then filter them

with vegetation variables, rather than incorporate these latter variables at the beginning of the modeling process. Obtaining reliable models including solely vegetation variables would be possible if sufficient information about the studied species' host plant is available. The major difficulties are finding a species whose nutritive requirements are well known a priori along with access to precise vegetation maps.

The possible expansion of *G. isabelae* through reforested areas (Soria et al. 1986, Robredo 1988, López-Sebastián et al. 2002) is not supported by our results. Four records found in reforested pine woods, quite old (1943, 2 records; 1974, 2) have not increased much in number over time (1987, 3; 2001, just one); there was no evidence supporting expansion hypothesis. These more recent records may be due to a greater sampling effort rather than expansion. Historic records and (or) nonreforested pine woods are found in each habitat patch, with the exception of patch 5 (Table 5), which is located in a reforested wood, perhaps the unique recent expansion.

We found lithology and spatial variables to be less relevant to *G. isabelae* distribution prediction. *G. isabelae* was linearly and negatively related with calcareous stony soil area but positively related with acidic sediments. The biological implication of these relationships is obscure, but the inclusion of 2 lithology variables in the final model based on all the variables considered confirmed their slight relevance (Table 1). We suggest that the slight negative influence of calcareous soils may be due to their poorer water retention, as well as their high mineral content. Lastly, the minor relevance of spatial variables showed that, after the inclusion of all aforementioned variables, no other spatially structured factors aided in accounting for potential species distribution.

The Nonequilibrium Distribution

As may be common, *G. isabelae* distribution is not in equilibrium with environmental conditions because models define only potential species distributions in which currently occupied and suitable areas still not colonized, or with extinct populations, are mixed. The suitable area was around 2.7 times larger than the occupied area and, interestingly, favorable areas lacking presence data fall mainly in northwestern Iberia and, to a lesser extent, in some few southernmost Iberian localities. The current nonequilibrium
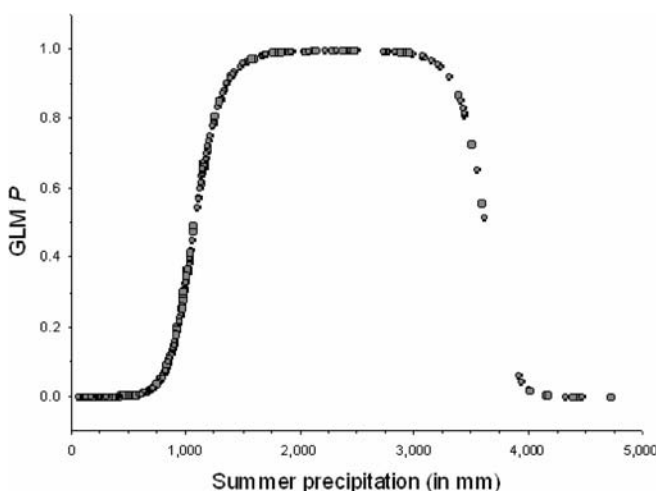
Figure 2. Relationship between summer precipitation and generalized linear model derived probability scores performed for *Graellsia isabelae* with Spanish locations data since 1849.

state of this species suggests that other factors (mainly historical) may help to explain this spatially biased distribution, whereas other contemporary ecological factors (predators, parasites, competitive interactions, or random extinctions) are more unlikely. We suggest that the current *G. isabelae* distribution could be associated with the dynamism of its host plants during glacial periods.

Pleistocene climate oscillations are known to have severely influenced the distribution patterns of most European animal and plant species (Hewitt 2000, Schmitt and Krauss 2004). Among the 3 main European refuges of Scots pine (the Iberian Peninsula, the Alps, and the Balkans; Bennett et al. 1991) existing during the last glacial period, the Iberian one seems to have had populations that may have remained isolated until now, without migration and expansion outside of the glacial refuges (Peñalba 1994, Sinclair et al. 1999, Soranzo et al. 2000, Cheddadi et al. 2006). The current endemicity of *G. isabelae* may be partially due to its association with these Iberian pine populations. Mitochondrial DNA and allozyme variation suggest that Scots pine survived in the Iberian Peninsula during the Pleistocene glaciations in central and eastern Iberian refuges (Sinclair et al. 1999, Soranzo et al. 2000). Pollen fossil evidence and recent potential range simulations indicate that both eastern and northwestern Iberian refuges existed for Scots pine during the last glacial maximum (Blanco et al. 1998, Benito Garzón et al. 2006, Cheddadi et al. 2006). Interestingly, the map of Iberian *P. sylvestris* refuges recently established by Cheddadi and collaborators as well as the predicted distribution obtained by Benito Garzón et al. (2006) basically coincide with the potential range established by us for *G. isabelae*. If both suitable climatic and favorable host plant conditions exist for the presence of *G. isabelae* in the western area of Iberian Central System and the northwestern Cantabric Mountains, why is *G. isabelae* currently absent of these territories? Amid such an arid, cold climate, highland pine woods were one of the most important arboreal elements during the glacial maximum, so the moth distribution should have been wider. However, recent charcoal data (Figueiral and Carcaillet 2005) demonstrate that northwestern Iberian Scots pine populations decreased dramatically from Holocene times as a consequence of climate warming, competition with either angiosperms or other pine species (Blanco et al. 1998), and anthropic factors as fires and grazing, probably causing the extinction of these *Graellsia* populations.

Conservation

Distribution maps drawn up from 10 (Soria et al. 1986) or 6 (Masó and Ylla 1989) different Spanish populations of *G. isabelae* do not show the 8 habitat patches, belonging to 4 main regions, well separated and with historical observational records, identified by our study. The major parts of these patches are surrounded by suitable, possibly connecting, areas for current populations. Probably the most disturbing situation exists in the Iberian Central System, where *G. isabelae* in neighboring suitable areas are scarcest. Although a high proportion, around 66%, of the area of this region is currently protected by Natura 2000 reserve design, <33% of the suitable habitat in all regions is protected. Although all regions would be partially protected by SCIs, just 38.8% of the total area is currently so; even worse, <20% of regions such as 2 and 5 are now protected. In our opinion, the conservation of woods located in protected sites does not seem sufficient to preserve current populations; preservation of surrounding suitable habitats is also necessary.

Some known causes for the decline in *Graellsia* populations are predation by predators such as European robin (*Erithacus rubecula*; Masó and Ylla 1989), parasites, and entrapment in resins or phytosanitaries used to combat pine processionary moth (*Thaumetopoea pityocampa*; Soria et al. 1986). However, habitat loss is the most obvious cause for depletion of lepidopteran populations. Short-term causes of habitat loss in Iberian Peninsula are urbanization (which has increased by 25% from 1990 to 2000; Ministerio de Medio Ambiente 2005), forest fires (2.1 million ha burned from 1991 to 2004; WWF/Adena 2006), and logging. Reintroduction programs in suitable habitats can contribute to the recovery of populations. Successful establishment of the species once reintroduced has already been reported in France (Hautes Alpes) in 1922 and Madrid (Viejo 1992).

MANAGEMENT IMPLICATIONS

Our study proved a direct relation among *G. isabelae* and Scots pine and Austrian pine woods; therefore we emphasize the importance of preserving such forests. Conservation measures must be focused mainly on the preservation of Scots pine and Austrian pine woods. We recommend managing woodlands properly and periodic monitoring of the status of each population. Sites of Community Importance should be wider in habitat patches found in Catalonia and Teruel regions. Similarly, suitable habitats around patches should be preserved as they could connect different *G. isabelae* populations. Because *G. isabelae* is a sedentary and no expansive species, we recommend reintroduction programs in suitable habitats.

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