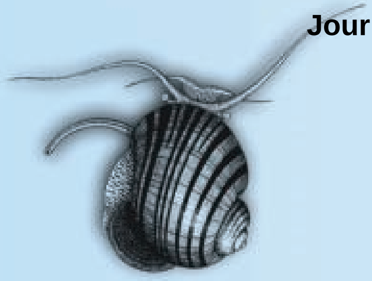
Journal of Molluscan Studies Advance Access published 1 June 2015



Journal of
Molluscan Studies

The Malacological Society of London

Journal of Molluscan Studies (2015) 1–8. doi:10.1093/mollus/eyv018

Habitat suitability modelling of four terrestrial slug species in the Iberian Peninsula (Arionidae: *Geomalacus* species)

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(Received 1 October 2013; accepted 7 April 2015)

ABSTRACT

Ecological niche modelling (ENM) determines habitat suitability of species by relating records of occurrence to environmental variables. Here, we investigated habitat suitability of four terrestrial slugs of the genus *Geomalacus* from the Iberian Peninsula using ENM. The potential distribution of these species was estimated using maximum entropy modelling. For this we used published presence records, together with observations from our fieldwork, and 10 layers of environmental variables in a crossvalidation design using 'minimum predicted area' as a measure of success. For each species, the models predicted distributions with high accuracy, while restricting predictions to minimum areas. Precipitation, and to a lesser extent temperature, were the most important variables to predict the distributions of the four species. We then compared the predicted distributions with the currently known distributions. For *G. anguiformis* and *G. maculosus* the predicted distributions included the known distributions, but also nearby mountain areas where these species have not previously been found. For *G. malagensis* and *G. oliveirae* the models predicted much wider distributions. Subsequent dedicated fieldwork could not confirm the presence of *G. oliveirae* in the newly predicted areas. Conversely, *G. malagensis* was found at five new and distant localities, including areas in Portugal where the species has not previously been recorded.

INTRODUCTION

Most of the information on the geographical distribution of species stems from fieldwork data accumulated for centuries. However, the advent of habitat suitability modelling or ecological niche modelling (ENM) has allowed the inference of hypothetical geographical distributions of species by relating the presence (or presence and absence) of a species to environmental variables (Franklin, 2010). This method predicts the environmental conditions that are suitable for a species by classifying grid cells according to the degree to which they are suitable/unsuitable for a species, resulting in a predictive model describing the suitability of any site for that species (Guisan & Thuiller, 2005). Based on these predictions, new putative areas can then be surveyed for the presence of the species. Common applications of ENM include exploring the response of geographical species distributions to climate change (Fouquet *et al*., 2010; Peterson *et al*., 2011), predicting range expansions of invasive species (Benedict *et al*., 2007), supporting conservation planning (Wilson, Roberts & Reid, 2011), identifying areas of endemism (Raxworthy *et al*., 2007) and facilitating field surveys of species with poorly known geographical distributions (Raxworthy *et al*., 2003; Guisan & Thuiller, 2005; Rebelo & Jones, 2010). Here, we use the term ENM *sensu lato* (for a discussion on the use of the terminology 'ENM' see Warren, 2012, and references therein).

Terrestrial slugs of the genus *Geomalacus* Allman, 1843 (Arionidae) comprise four species: *G. anguiformis* (Morelet, 1845), *G. oliveirae* Simroth, 1891 and *G. malagensis* Wiktor & Norris, 1991, all endemic to the Iberian Peninsula, and *G. maculosus* Allman, 1843, which is also present in southwestern Ireland. The geographical ranges of these species vary from being restricted to Gibraltar and adjacent areas in southern Spain for *G. malagensis* (Castillejo, 1998) to a wider area comprising central and northern Portugal and northern Spain (Fig. 1). *Geomalacus maculosus* is legally protected under the Habitats Directive 92/43/CEE and Bern Convention Appendix II, while all *Geomalacus* species are listed as 'vulnerable' in Red Lists of Spain (Castillejo & Iglesias-Pineiro, 2008; Verdú, Numa & Galante, 2011).

In the last few decades, the habitat of *Geomalacus* species has suffered severe fragmentation and deterioration due to an

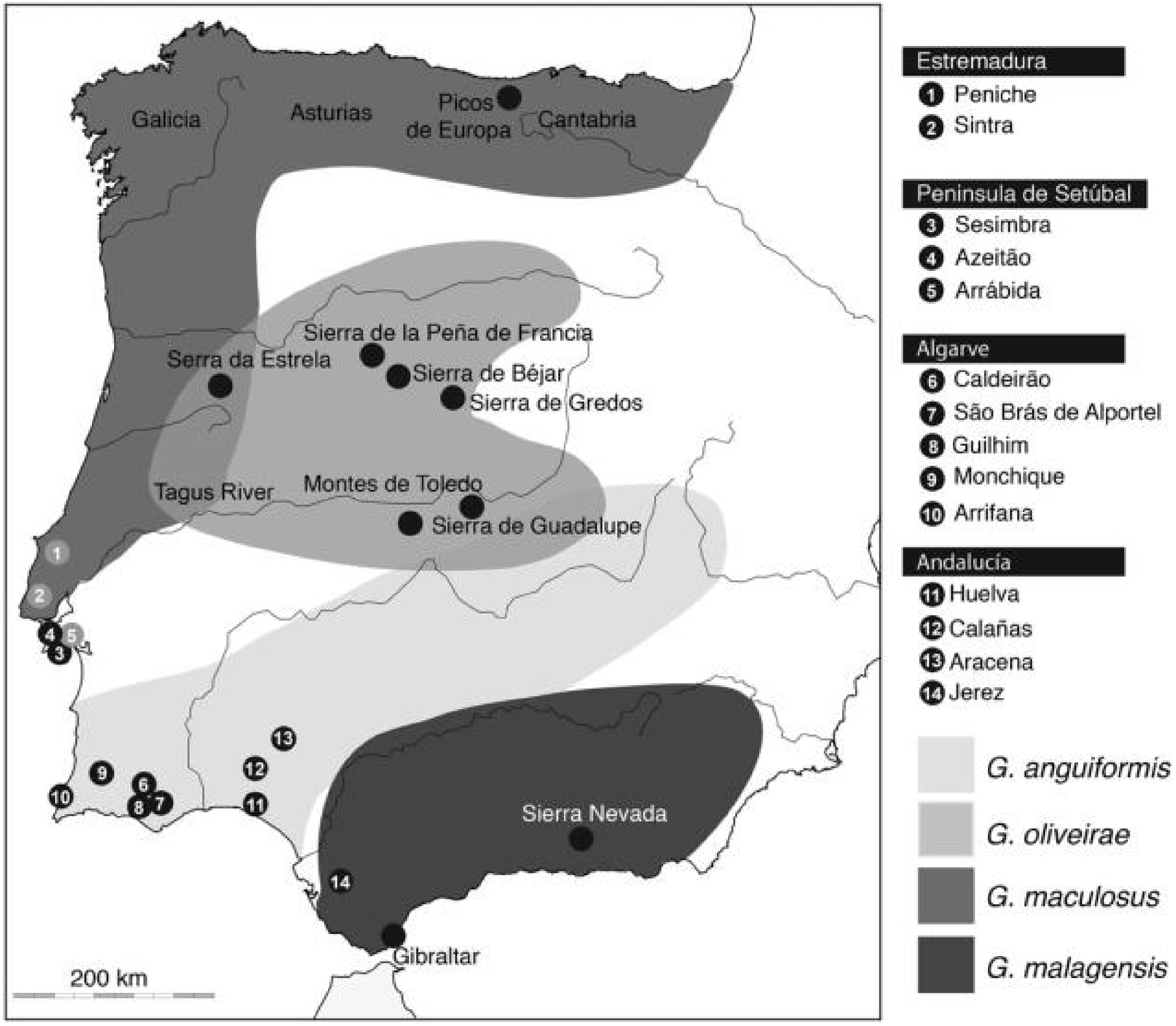

Figure 1. Geographic distribution of all *Geomalacus* species based on Castillejo *et al*. (1994) (shadowed areas). Presence of *G. malagensis* was confirmed in locations marked with numbered circles and grey circles represent locations where no specimens were found.

expansion of urban development (Castillejo & Iglesias-Pineiro, 2008; Verdú *et al*., 2011). Habitat loss has negative impacts on organisms by narrowing their geographical distribution, decreasing their abundance and reducing connectivity among patches. However, it is presently unknown if the geographical distributions of *Geomalacus* species have shrunk as a result of such putatively damaging pressures.

With the exception of *G. maculosus*, *Geomalacus* species are usually hard to find, due to their relative small size and poor knowledge of their ecology and behaviour. Furthermore, *G. anguiformis* and *G. oliveirae* are morphologically similar and can be confused with each other (for a discussion of morphology of *Geomalacus* see Rodriguez *et al*., 1993). Here, we apply ENM to explore the distributions of the four *Geomalacus* species in the Iberian Peninsula, using presence-only data with maximum entropy (MaxEnt; Phillips, Dudík & Schapire, 2004; Phillips, Anderson & Schapire, 2006), with the objective to predict the potential distributions of these species for future monitoring programmes. As such, our aims were (1) to explore which environmental variables shape these species' distributions, (2) to produce models of the potential geographical distributions of the four species and (3) to assess how well the predicted ENM distributions fit the current distribution records, particularly in rare species such as *G. malagensis*.

MATERIAL AND METHODS

Occurrence records

Occurrence records for *Geomalacus* species from the Iberian Peninsula were obtained from the literature and from field surveys conducted across the known geographical ranges during 2007–2010 (Supplementary material, Table S1). The sites were recorded by GPS positioning (GARMIN MAP) and subsequently visited at different periods (dawn, morning, evening and night). Specimens were searched in undisturbed areas (*G. maculosus*, *G. oliveirae* and *G. malagensis*), in abandoned rural areas (*G. anguiformis*) or synanthropic areas (*G. maculosus*, *G. malagensis*) according to the known habitats of the species. Since specimens were also found outside their known habitats, and to reduce sampling bias, other environments were also searched. Although *Geomalacus* is supposed to inhabit mainly mountain areas, we did our field surveys at a range of elevations from sea level up to Picos de Europa. Slugs were identified using the key of Castillejo, Garrido & Iglesias (1994).

Imprecise locations reported in the literature were replaced, whenever possible, by precise georeferenced location data from our field trips. Multiple references to the same location were entered only once in the models, thereby reducing the effects of spatial autocorrelation (e.g. Neiva *et al.*, 2014). We were cautious in our acceptance of literature records. Thus, we did not consider three single-occurrence records (*G. anguiformis* from Lisbon and *G. oliveirae* from Alvega and Monchique) in Hidalgo (1916) that were recorded a century ago and not subsequently confirmed. *Geomalacus oliveirae* and *G. anguiformis* were reported to cooccur in Aracena (Spain) by Castillejo & Iglesias-Pineiro (2011a, b). However, these authors did not mention that they found the species together in the same habitat and location, as could have been expected because the species do not cooccur elsewhere. We have therefore also discarded these records.

For *G. malagensis*, new fieldwork was conducted after running a first set of models and predicting its suitable habitat, to sample in the predicted areas (predicted suitability >0.40; Jackson & Robertson, 2011). Locations were visited at least three times, at different times of day/night. Several habitat types were searched: undisturbed areas, abandoned rural areas and synanthropic areas, at a wide range of elevations (0–1,600 m), even though *G. malagensis* is supposed to inhabit undisturbed mountain areas (Castillejo *et al.*, 1994).

Environmental data

Overparametrization can be a problem with rare species, because the number of presences in the data can be smaller than the number of parameters in the model, leading to low predictive accuracies (Madon, Warton & Araújo, 2013). To avoid this, we used only a subset of current climate and ecological data obtained from the European Soil Database (Center, 2006), WorldClim (Hijmans *et al.*, 2005) and the European Environment Agency (EEA, 2004) using a 1-km spatial resolution (Table 1).

Niche modelling

Niche modelling of *Geomalacus* species throughout the Iberian Peninsula was performed following Assis *et al.* (2014) and Neiva *et al.* (2014). We chose maximum entropy modelling (MaxEnt v. 3.3.3) (Phillips *et al.*, 2004, 2006), a machine-learning method known for its high predictive performance (e.g. Elith *et al.*, 2006), even when only a few occurrence records are available (Wisz *et al.*, 2008). This is a presence-only method that needs occurrence records, background information (i.e. a sample of nonoccurrences chosen throughout the study region) and environmental data to produce a logistic output of environmental suitability values, ranging from 0 (unsuitable environment) to 1 (optimal environment) (Phillips & Dudik, 2008). We used presence-only data, since not finding a species in a particular location does not prove that it is absent or that the niche is not available.

To infer the model with the highest ability to predict distributions outside our sampling regions (transferability), a crossvalidation framework was implemented by randomly dividing the occurrence records of each species into calibration (70 %) and evaluation (30 %) datasets. Multiple models were explored with the calibration records and all possible combinations of noncorrelated environmental variables (Spearman's $\rho \leq |0.85|$). Even though crossvalidation is known to protect models against overfitting and to produce more parsimonious models (Ashcroft, French & Chisholm, 2011), we did not allow models to fit more than five variables, because of the small number of *Geomalacus* records.

Each model ran with default parameters, since these are known to produce consistently accurate results (Bedia, Busque & Gutierrez, 2011; Neiva *et al.*, 2014). To account for the sampling design and to reduce estimation biases introduced by disparities in sampling effort between locations and spatial bias in sampling, background information was chosen with the same underlying weight as our sampling effort (i.e. target group background; Phillips *et al.*, 2009). For this, 10,000 points were randomly selected from a kernel density estimation surface that considered the total number of occurrence records (for all species) within each cell of our study region (e.g. Elith, Kearney & Phillips, 2010; Fitzpatrick, Gotelli & Ellison, 2013).

The accuracy in crossvalidation of each subset of predictors, and therefore their potential for transferability, focused on the information of presence records only (see Lobo, Jimenez-Valverde & Real, 2008, for a review). To that end, we used the minimum predicted area (MPA; Franklin, 2010), a criterion that measures the anticipated proportion of the study area with presences when applying a threshold that retrieves at least 0.9 of the sensitivity (the ability to detect true presences; see Results). This was done by comparing the evaluation records with a predicted map produced for each subset of predictors, when using an MPA threshold converting the habitat suitability scores to binomial responses. In this exercise, MPA ranged between 0 and 1 (lower values identifying more accurate predictions), producing smaller presence areas while retaining high sensitivities.

We developed a crossvalidation framework that was run 50 times for each species. In each run, the calibration and evaluation datasets were randomized to verify the relative contribution of each variable in the response of models by determining the mean MPA of the models produced with every variable alone (univariate effect) and the increase in MPA when adding

Table 1. Environmental, climatic and soil variables tested for the distribution models of the four *Geomalacus* species.

Code	Description	Type	Source	Range	Mean
Alt	Elevation	CAT	ESDB		
AWC	Topsoil available water capacity	CAT	ESDB		
Bio12	Annual precipitation	CON	WCDB	104–1798 mm	606 mm
Bio13	Precipitation of wettest month	CON	WCDB	13–273 mm	80 mm
Bio17	Precipitation of driest quarter	CON	WCDB	5–373 mm	72 mm
Bio5	Maximum temperature of warmest month	CON	WCDB	9.2–40.7 °C	29.4 °C
Bio6	Minimum temperature of coldest month	CON	WCDB	−12.5–9.4 °C	2.1 °C
OC_top	Topsoil organic carbon content	CAT	ESDB		
Usedo	Code for dominant land use of the STU	CAT	ESDB		
vqi_2008	Vegetation quality index	CAT	EEA		

For continuous variables, range and mean values are provided, calculated across the Iberian Peninsula.

CAT, categorical; CON, continuous; ESDB, European Soil Database; EEA, European Environment Agency; WCDB, WorldClim; STU, soil typological unit.

variables to all other models. For a better interpretation of each relative contribution, the MPA scores were transformed as 1 minus MPA and scaled to sum 100, so that higher values would graphically indicate stronger contributions of the response variable (e.g. Eskildsen *et al.*, 2013). The subset of environmental variables with higher potential for transferability (across iterations) was inferred using a nonparametric Kruskal-Wallis test with the null hypothesis of no differences in the mean MPA. We sorted the combinations of variables according to increasing MPA and added them sequentially to independent Kruskal-Wallis tests until the significance level was reached ($\alpha = 0.05$).

Since more than one subset of variables can be equally transferable (no differences in the mean MPA), the final distribution maps were produced by doing the ensemble of their resulting surfaces with a median function (i.e. ensemble modelling; see Araujo & New, 2007), an approach highly recommended for prediction (Whittingham *et al.*, 2006). The ensembles for *G. maculosus*, *G. anguiformis* and *G. oliveirae* were based on literature records and fieldwork in areas indicated by the literature. Two distinct ensembles were run for *G. malagensis* (the rarest of the four species): the first was based on literature records with added locations as a result of fortuitous, preliminary fieldwork by the authors. The second included the same data plus new records resulting from directed fieldwork in areas ranked as highly suitable by the first analysis. Finally, partial dependence plots were developed to investigate the effect of the most important variables for the distribution of each species. Nevertheless, while these plots provide a useful basis for interpretation, they are not an exact description of the effects of each variable, especially if there are strong interactions between predictors (Friedman & Meulman, 2003).

All analyses were performed using R statistical software (R Development Core Team, 2013) using the packages dismo, doparallel, gbm, raster and sdmtools.

RESULTS

Models for the four species performed with high predictive accuracy (sensitivity ranging from 0.93 ± 0.00 to 1.00 ± 0.00), while restricting the predicted areas to minimum values at most (MPA ranging from 0.11 ± 0.01 to 0.19 ± 0.03). The distributions of all modelled species were largely explained by bioclimatic variables (Fig. 2).

Geomalacus maculosus is a crepuscular and nocturnal slug that was found near houses and gardens, mostly on stone walls or rocks, but was extremely hard to find in non-anthropogenic environments. Only in Galicia, Asturias and Cantabria did we find slugs crawling on oak (*Quercus* sp.) and chestnut (*Castanea* sp.) trees in early dawn, whereas in all other locations the species was found crawling on rocks or stone walls. The predicted distribution of *G. maculosus* was based on 96 locations: 79 from the literature and 17 from our fieldwork (Supplementary material, Table S2). The ensemble of this species' distribution included six variables (Fig. 3A) and yielded a mean sensitivity of 0.93 ± 0.00 and mean MPA of 0.14 ± 0.01. The variables with highest contribution to the models were 'annual precipitation' (Bio12), 'precipitation of wettest month' (Bio13) and 'maximum temperature of the warmest month' (Bio5), with mean percentages of 14.36 ± 0.11, 14.21 ± 0.09 and 13.56 ± 0.71 when modelled alone, and 3.22 ± 1.99, 3.78 ± 1.97 and 1.84 ± 1.72 when modelled with other variables. The partial dependent plots showed higher suitability scores (above 0.4) when Bio12 ranged from 721 to 1,773 mm (maximum 1,721 mm), Bio13 ranged from 96 to 271 mm (maximum 271 mm) and when Bio5 ranged from 17.2 to 29.6 °C (maximum 20.7 °C) (Supplementary material, S3). The Pyrenees had a habitat suitability of 0.50, but *G. maculosus* was not found there. The mean predicted area for this species was 206,169 ± 18,390 km^2.

Geomalacus anguiformis was found on abandoned farms, except in Monchique (Fig. 1), where it was found in pristine habitats, mainly under the bark of oak logs. Although the species is mostly active at night, we also found it active under tree logs during daytime, as long as the air was humid. The predicted geographical distribution of *G. anguiformis* was based on 21 locations: 12 from the literature and 9 from our fieldwork (Supplementary material, Table S2, Fig. 3B). The ensemble included six variables (Fig. 2) and yielded a mean sensitivity of 1.00 ± 0.00 and mean MPA of 0.11 ± 0.01. The variables with highest contribution were 'precipitation of wettest month' (Bio13), 'precipitation of driest quarter' (Bio17) and 'minimum temperature of the coldest month' (Bio6), with mean percentages of 16.76 ± 0.38, 16.31 ± 0.58 and 14.55 ± 1.19 when modelled alone, and 3.50 ± 1.61, 6.17 ± 1.63 and 3.01 ± 1.55 when modelled with other variables. Higher suitability scores were retrieved when Bio13 ranged from 74 to 148 mm (maximum 98 mm), when Bio17 ranged from 15 to 33 mm (maximum 24 mm) and increasing Bio6 (range from 2.3 to 8.8 °C; maximum 5.8 °C) (Supplementary material, S3). Mountains in Malaga province in southern Spain (Fig. 3B), had a habitat suitability between 0.70 and 0.80, but *G. anguiformis* was not found there. The mean predicted area for this species was 155,112 ± 18,504 km^2.

Geomalacus oliveirae was found at night, crawling on stones near streams or under rocks in pinewoods, in areas with little or no human disturbance. The predicted geographic distribution of *G.*

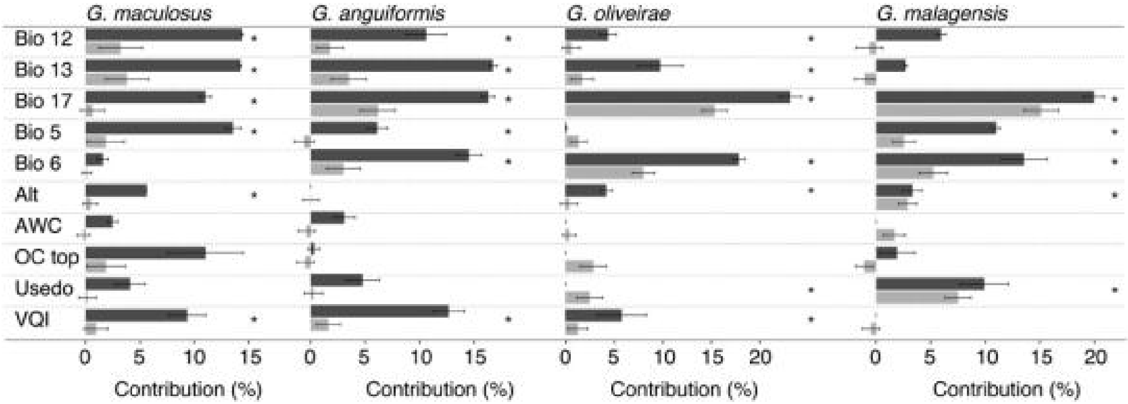

Figure 2. Mean relative importance (percentage) of the environmental variables used in niche modelling of *Geomalacus*. Black bars represent the contribution when a variable is modelled alone while grey bars represent the contribution when a variable is added to a model. Error bars represent one standard deviation from the mean. Asterisks represent the variables included in the ensemble of *Geomalacus* species.

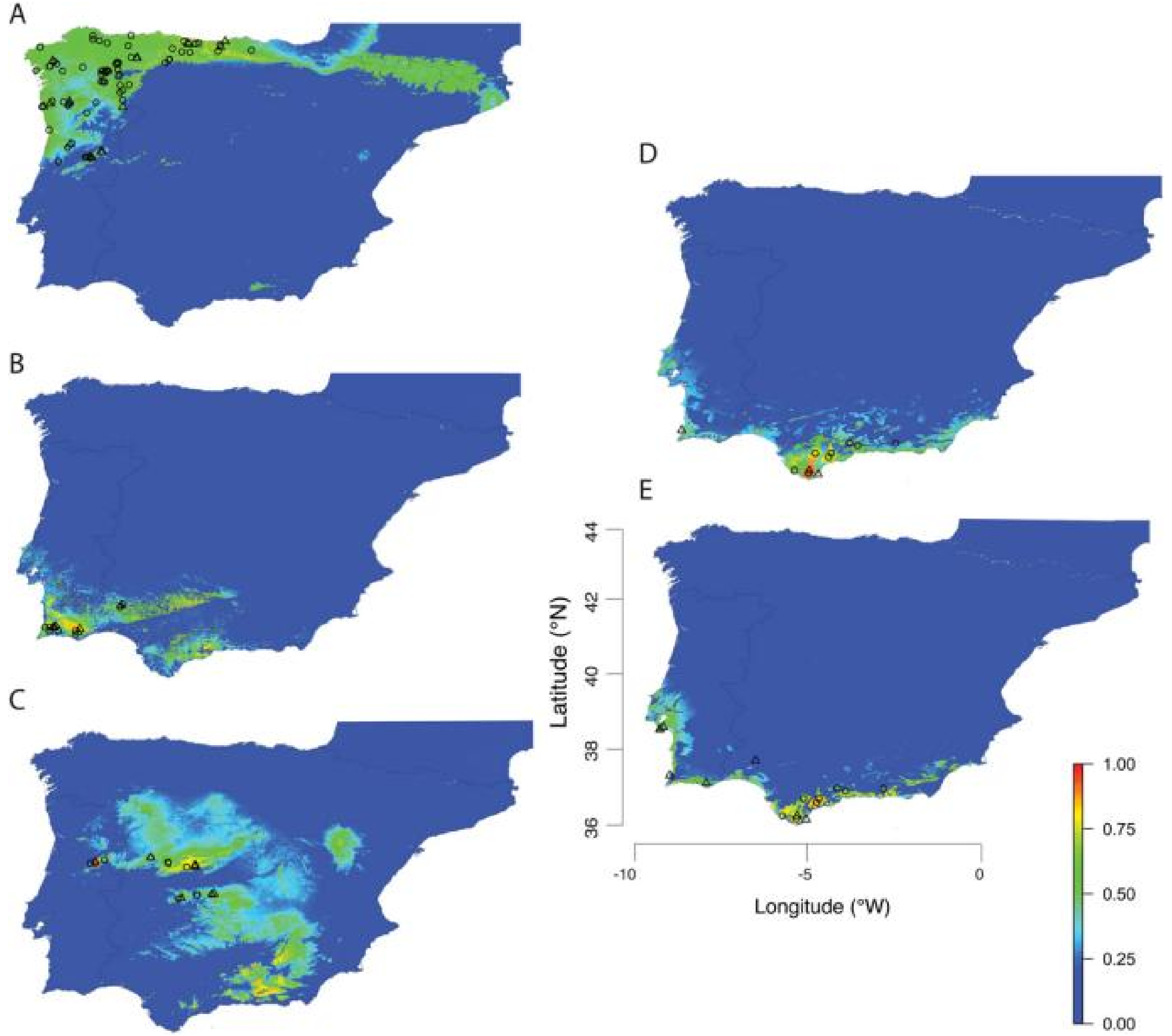

Figure 3. Habitat suitability maps of *Geomalacus* species across the study area predicted from literature records and fieldwork. **A.** *G. maculosus*. **B.** *G. anguiformis*. **C.** *G. oliveirae*. **D.** *G. malagensis* (only locations obtained from the literature and initial fieldwork). **E.** *G. malagensis* (all locations, including new locations). Colour scale represents high levels of predicted habitat suitability in red and low levels in blue. Circles represent data points obtained from the literature and triangles represent specimens sampled during the present work.

oliveirae was based on 23 locations: 14 from the literature and 9 from our fieldwork (Supplementary material, Table S2, Fig. 3C). The ensemble included seven environmental variables (Fig. 2) and its mean sensitivity was 1.00 ± 0.00 and mean MPA 0.19 ± 0.03. The variables with highest percent contribution were 'precipitation of driest quarter' (Bio17) and 'minimum temperature of the coldest month' (Bio6), with average percentages of 23.24 ± 1.15 and 17.92 ± 0.632 when modelled alone, and 15.42 ± 1.316 and 8.05 ± 1.151 when added to other models. The models yielded higher suitability scores when Bio17 ranged from 25 to 121 mm (maximum at 100 mm) and when Bio6 ranged from −5.3 to 2.4 °C (maximum at −0.3 °C) (Supplementary material, S3). Although Sierra Nevada in southern Spain (Figs 1, 3C) had a habitat suitability index of 0.80, *G. oliveirae* was never recorded at this location. The mean predicted area for this species was 279,070 ± 41,038 km^2.

Geomalacus malagensis was found near houses and gardens, sometimes feeding on dog food, on walls or hiding under piles of firewood. The first model for *G. malagensis* was based on 11 records, 8 from the literature and 3 from preliminary fieldwork prior to the ENM analyses: Arrifana, Jerez and Gibraltar (Fig. 1), of which Arrifana is the first record for this species in Portugal (Supplementary material, Table S2, Fig. 3D). The ensemble included seven environmental variables (not shown) and yielded a mean sensitivity of 1.00 ± 0.00, an average MPA of 0.15 ± 0.03 and a mean predicted area of 222,985 ± 39,068 km^2.

Based on the first distribution model, we surveyed areas where the probability of finding *G. malagensis* was over 40 % (Jackson & Robertson, 2011). We visited four main areas (for details see Fig. 1 and Supplementary material, Table S2): (1) Huelva in Andalucía (Spain), (2) Monchique, São Brás de Alportel, Estoi and Caldeirão, in Algarve (Portugal), (3) areas near Sesimbra, Arrábida and Azeitão (Portugal) and (4) Sintra and Peniche in

Estremadura (Portugal). We surveyed 10 localities and recorded the species in 5 of these: Calañas in Spain and Guilhim, Brejos de Azeitão, Fonte de Sesimbra and Cabedal in Portugal (Supplementary material, Table S2). We then improved the first distribution model by adding these five new records to the 11 localities of the first model and reran the crossvalidation design. The new, enhanced ensemble (Fig. 3E) suggested a greatly expanded geographic distribution: northwards up to 39°N and westwards to 9°W. This ensemble model included five variables and yielded a mean sensitivity of 1.00 ± 0.00 and a mean MPA of 0.17 ± 0.03. The variables with highest contribution were 'precipitation of driest quarter' (Bio17), 'minimum temperature of the coldest month' (Bio6) and 'maximum temperature of the warmest month' (Bio5) (Fig. 2), with mean contributions of 20.00 ± 0.94, 13.58 ± 2.11 and 11.01 ± 0.37 when modelled alone, and 15.14 ± 1.62, 5.23 ± 1.30 and 2.56 ± 1.02 when added to other variables. The habitat suitability for this species was higher when Bio17 ranged from 13 to 41 mm (maximum at 25 mm), when Bio6 ranged from −0.6 to 9.1 °C (maximum at 3.3 °C) and when Bio5 ranged from 21.9 to 31.4 °C (maximum at 29.00 °C) (Supplementary material, S3). Although both models predicted a habitat suitability index of over 50 % for *G. malagensis* in Estremadura, north of the river Tagus (Portugal), we were unable to confirm the presence of the species in this area. The mean predicted area for this species using the enhanced dataset was 244,014 ± 44,082 km^2.

DISCUSSION

Distribution models obtained from few presence records should be interpreted as regions with environmental conditions (habitat similarity) similar to those where a species presently occurs (Pearson, 2007), but do not necessarily indicate the presence of a species. Hence, distribution scenarios do not outline the actual distribution range of a species but its putative distribution, meaning that they identify areas of high suitability for a species. Based on predictive species distribution models generated by niche modelling, we were able to significantly extend the known distribution range of *G. malagensis*, discovering five new populations. However, two caveats must be taken into account when ENM methods are employed (Anderson, 2012; Yackulic *et al.*, 2013). First, with only few records available, ENM methods may overestimate the geographical range. Second, ENM methods assume that spatial sampling is such that the relationship between environmental variables and species occurrence accurately represents the suitability of habitats. Below, we discuss the implication of these caveats for the distribution models that we obtained for the four *Geomalacus* species. All distribution models obtained had a high predictive accuracy, with sensitivity scores above 0.93 and MPA below 0.19. Bioclimatic variables, especially precipitation and to a lesser extent temperature, were the most important variables for explaining the distribution of all *Geomalacus* species.

The predictive distribution models for *G. maculosus* and *G. anguiformis* mostly agree with the known geographic ranges of these species (Castillejo *et al.*, 1994), contrasting with the distribution models for *G. oliveirae* and *G. malagensis* that suggested much wider ranges than previously reported. Slugs may exhibit a strong dependence on habitat humidity, but they are nevertheless able to extend their geographical distributional range into semiarid areas such as southern Iberia. This pattern is supported by examples in the literature (Capinha *et al.*, 2014) and is probably related to the plasticity of the slugs' bodies, which enables them to exploit suitable microclimates (Luchtel & Deyrup-Olsen, 2001).

The model for *G. maculosus* encompasses the northwestern coastal area of the Iberian Peninsula, a region with constant humidity and high rainfall, even during the driest months (Altonaga *et al.*, 1994). The third environmental variable that contributed to the explanation of the distribution of *G. maculosus* was the maximum temperature of the warmest month, indicating that in humid conditions the species may endure ambient temperatures up to 29 °C. The species can often be observed on rocky walls in oak or chestnut orchards, in ruins, near houses, churches and cemeteries.

The model for *G. anguiformis* includes the southwestern mountains of Monchique, Caldeirão and Aracena. However, the populations are restricted to the most humid parts of these mountains, since rainfall and humidity appear to be limiting factors for the distribution of this species (Castillejo & Iglesias-Pineiro, 2005). Nevertheless, according to the model, *G. anguiformis* can withstand dry (minimum precipitation of 15 mm in the driest quarter) and cold (minimum temperature of 2.3 °C) conditions.

Previously *G. oliveirae* was known to occur in the central mountains of the Iberian Peninsula, namely in Serra da Estrela (Simroth, 1888; Pollonera, 1890; Hidalgo, 1916; Nobre, 1941; Rodriguez *et al.*, 1993), Béjar and Sierra de la Peña de Francia (Hermida, 1992), Sierra de Gredos (Castillejo *et al.*, 1994), Sierra de Guadalupe (Castillejo *et al.*, 1994; Bech Taberner *et al.*, 2005) and Montes de Toledo (Wiktor & Parejo, 1989) (for details see Fig. 1 and Supplementary material, Table S1). However, the MaxEnt model expanded the area to include the southern mountains of the Sierra Nevada. The distribution of this species seems to be restricted to areas with rain during the driest months (minimum 25 mm) and by the temperatures of the coldest months (> −5 °C). However, *G. oliveirae* was never confirmed to occur in the Sierra Nevada. The central mountain ranges where this species is present (Serra da Estrela, Sierras de Guadalupe, Gredos, Béjar and la Peña de Francia) and the Sierra Nevada share similar rain/temperature profiles, which may have influenced the prediction. MaxEnt assumes that spatial sampling is such that the relationship between environmental variables and species occurrence accurately represents the suitability of habitats; it is possible that the habitat is suitable, but the species is absent (Hirzel *et al.*, 2002; Raxworthy *et al.*, 2003; Pearson *et al.*, 2007). The absence of *G. oliveirae* from the Sierra Nevada might be due to methodological flaws such as overestimation of the predictive range or undetected presence. However, we cannot exclude the possibility that the species never reached the Sierra Nevada because of enroute dispersal constraints, related for example to desiccation risks.

The predicted range of *G. malagensis* included Andalucía and the adjacent areas around Huelva, as well as more distant areas in Portugal, where this species has never been reported previously, i.e. Algarve, Setúbal Peninsula and Estremadura. These regions are characterized by more than 13 mm of rain in the driest quarter, a minimum temperature of −1 °C and high temperatures during the warmest months (between 22 and 31 °C). Contrary to reports in the literature (Castillejo *et al.*, 1994), in which *G. malagensis* from outside Gibraltar was described as a nonanthropophilous organism, this species was only found in highly anthropogenic and disturbed habitats, suggesting that the species may survive well when subjected to human impact. We confirmed the occurrence of the species in some of the predicted areas such as Huelva, Algarve and Setúbal Peninsula. However, we were unable to find the species in areas with high suitability of the habitat, namely Arrábida Natural Park and north of the Tagus River in Estremadura (Sintra and Peniche, Portugal). The absence north of the Tagus River might also be explained by an overestimation of the predictive range, due to the few records, resulting in an artificially large predicted area. However, alternative, nonmutually exclusive, explanations are possible, such as competition or dispersal limitations (Guisan & Thuiller, 2005). Obviously, species with poor dispersal abilities as slugs allegedly are, comply with this latter possibility and this may also explain why ranges were overpredicted. The putative absence in Arrábida Natural Park may be explained similarly, but *G. malagensis* is not easily found in undisturbed forests. Because it was not possible to implement grid-sampling throughout the entire predicted range, the absence of *G. malagensis* in the region requires confirmation.

To conclude, a fortuitous out-of-range finding of *G. malagensis* in Portugal prompted the construction of habitat suitability maps, which allowed the authors to conduct directed fieldwork, resulting in a substantial extension of the previously known distribution area of this species. We further identified new and highly suitable regions where *G. anguiformis*, *G. maculosus* and *G. oliveirae* may occur.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Molluscan Studies* online.

ACKNOWLEDGEMENTS

The authors wish to thank K. Erzini, M. C. Ribeiro, P. Cesário, A. Patrão and D. Reis for collecting specimens in the field and T. Rodriguez for assistance with the identification of the specimens. We also acknowledge C. Cox for implementing R on the GYRA cluster. This work was partially funded by Fundação para a Ciência e Tecnologia (Portugal) through C. Patrão PhD grant SFRH/BD/30024/2006, and the project 'Pillars of Hercules—gene flow across the pillars of Hercules: the role of North Africa in the postglacial recolonization of Europe' PTDC/BIA-BDE/74349/2006. T. Backeljau was supported by BELSPO projects MO/36/017 and IUAP-SPEEDY.

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