Disentangling the Effect of Climate and Human Influence on Distribution Patterns of the Darkling Beetle *Scotobius pilularius* Germar, 1823 (Coleoptera: Tenebrionidae)

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DISENTANGLING THE EFFECT OF CLIMATE AND HUMAN INFLUENCE ON DISTRIBUTION PATTERNS OF THE DARKLING BEETLE *SCOTOBIUS PILULARIUS* GERMAR, 1823 (COLEOPTERA: TENEBRIONIDAE)

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Abstract.— *Scotobius pilularius* Germar 1823 (Tenebrioninae: Scotobiini) is mainly distributed in natural temperate and mesic grasslands of the Pampean biogeographic province. However, it is also found in climatically extreme environments such as cold and dry grasslands within the Patagonian biogeographic province. In these extreme environments, *S. pilularius* is found outside of natural habitats, in areas associated with human settlements. In the present paper, the role of climatic conditions and human settlements as determinants of the observed spatial distribution of *S. pilularius* in its natural distribution and outside that area is assessed. Three following hypotheses are tested: species occurrence is determined by i) climate; or ii) human settlements; or iii) both climate and human settlements. The results suggest that, while the climate and human settlements hypothesis is consistent with the data acquired within the *S. pilularius* natural distribution area, only the human influence hypothesis significantly explains its distribution outside of its natural area. This outcome suggests that *S. pilularius* moved from living in a complete disassociation to human settlements or asynanthropy before human settlements in its natural area, to living in close association with human settlements or synanthropy outside of its natural area.

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Key words.— Distribution models, species occurrence, climatic variables, human activities, asynanthropy, eusynanthropy

INTRODUCTION

The darkling beetle *Scotobius pilularius* Germar, 1823 (Tenebrionidae: Tenebrioninae: Scotobiini) is a flightless species distributed in southern South America (Kulzer 1955). It was formerly known from museum collections and publications as *Scotobius miliaris* (Billberg, 1815) because of an incorrect synonymy (Silvestro and Flores 2016, this volume). A complete redescription, taxonomic history, and adult

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habitus can be found in Aballay *et al.* (2016, this volume) and Silvestro and Flores (2016, this volume). Throughout its distribution, *S. pilularius* occurs as a free-living organism in natural temperate and mesic grassland environments (Silvestro and Flores personal observation; Fig. 1) in the Pampean biogeographic province (Morrone 2006). Climatic conditions in these grassland environments are characterized by mean annual temperatures of 16°C, and mean annual precipitations ranging from 600 to 1200 mm (Fernández *et al.* 2012). Despite of the above mentioned affinity to natural habitats, during several collecting trips we have found this species in more extreme climatic conditions in anthropogenic environments. For example, we noticed that *S. pilularius* occurs in cold and dry grassland environments in the Patagonian biogeographic province (Morrone 2006; Fig. 2) which are characterized by mean annual temperatures of 8°C and mean annual precipitations of 200 mm (Paruelo *et al.* 1998). Notably, in these habitats specimens of *S. pilularius* were found only in isolated areas associated with human settlements. We consider that the factors that determine its spatial distribution probably are different in the temperate and humid grasslands, in which this species was found as free-living organism, of those in cold and dry grasslands, in which this species was found associated to human settlements. Specifically, we were interested in examining the relative role of climatic conditions and human settlements as determinant of the observed spatial distribution of *S. pilularius* in its natural distribution area and recognizing to what extent those factors are responsible of its distribution outside of this area.

Figure 2. Geographic distribution of *Scotobius pilularius* (black stars) in Patagonian biogeographic province (grey area) before museum collections revisions.

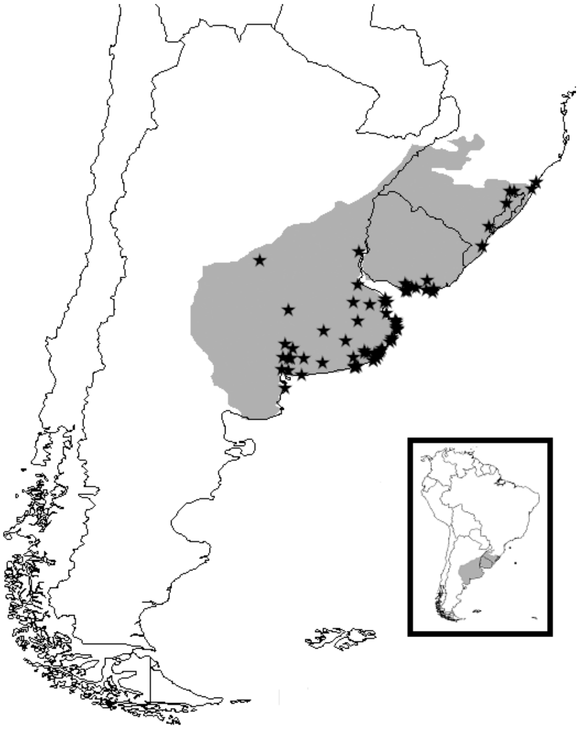

Figure 1. Geographic distribution of *Scotobius pilularius* (black stars) in Pampean biogeographic province (grey area) before museum collections revisions.

At least three hypotheses can be postulated to explain the observed distributional pattern of *S. pilularius*. First, climatic conditions that allow the subsistence of this species in its natural area are the same that allow its subsistence in more extreme climatic environments. This hypothesis assumes that climatic niche is the main factor responsible for the observed *S. pilularius* distribution pattern. Therefore, we predict that climatic conditions explain *S. piluarius* distribution in both temperate and mesic grassland environments in the Pampean region (natural area) and also in different and more extreme climatic conditions outside of this area. Second, conditions found in human settlements that allow the subsistence of this species in its natural area are the same that allow its subsistence in more extreme climatic environments. This hypothesis assumes that *S. pilularius* has developed a strong dependence on human settlements because this generates the suitable conditions for its subsistence, independently of the climatic conditions. Therefore, we predict that human activities explain *S. piluarius* distribution in its natural area and also outside of this area. Third, that the interplay between climatic conditions and human settlements allow its subsistence in natural and extreme environments. This hypothesis assumes that within its climatic niche, *S. pilularius* has found more suitable conditions for living in humans settlements (e.g., lack of competition, better micro-environmental conditions, etc.). Therefore, we predict that climatic variables and human settlements explain *S. piluarius* distribution in its natural area and also outside of this area.

The objectives of this work are: (1) to build the geographic distribution of *S. pilularius* based on data obtained from an exhaustive survey on museum collections and collecting trips, (2) to identify the best model that explains the distribution patterns of *S. pilularius* within its natural area using both information on climatic conditions and human settlements, and (3) from the models fitted above, to evaluate which model better explains the distribution patterns of *S. pilularius* outside its natural area.

MATERIALS AND METHODS

Data source

We obtained our data by studying the material from several collecting trips and museum collections. Argentina: Instituto Argentino de Investigaciones de las Zonas Áridas (IADIZA, Sergio Roig-Juñent), Mendoza; Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires (Arturo Roig Alsina); Museo de La Plata, La Plata (Nora Cabrera); Fundación e Instituto Miguel Lillo, San Miguel de Tucumán (Emilia Pérez); Museo Municipal Lorenzo Scaglia, Mar del Plata (Juan Farina); Instituto Patagónico de Ciencias Naturales, San Martín de los Andes, Neuquén (now deposited at IADIZA), Instituto Patagónico para el Estudio de los Ecosistemas Continentales (CENPAT, Germán Cheli), Universidad Nacional de San Luis, Cátedra de Zoología, San Luis (Ana Medina); Chile: Museo Nacional de Historia Natural, Santiago (Mario Elgueta D.); Brazil: Museu de Ciências Naturais, Porto Alegre, RS (Luciano Moura); Germany: Museum fur Naturkunde der Humboldt Universität, Berlin (Manfred Uhlig and Bernd Jaeger).

The specimens were identified according to their collection information and their geographical location of the collection site (latitude and longitude). It should be noted that any specimen that was found more than once with the same collection information and georeference was considered a duplicate data point. These combined data points were entered into the database as a single record. Specimens with incomplete information about its spatial location were discarded of this analysis.

Predictor variables

A total of 4 bioclimatic variables (mean annual temperate, mean annual precipitation, temperature seasonality and precipitation seasonality), each at a resolution of 30 seconds (approximately 1 × 1 km at the equator), were obtained from the WorldClim database (Hijmans *et al.* 2005). We choose these variables because they are cited as main factors influencing insect life cycles (Gullan and Cranston 2005) and because they have relatively low collinearity among them ($r < 0.7$). To represent human settlements on space, we used the Human Influence Index (HII) at the same resolution of bioclimatic variables. The HII is a continuous variable created from nine global data layers covering human population pressure (population density), human land use and infrastructure (built-up areas, nighttime lights, land use/land cover), and human access (coastlines, roads, railroads, navigable rivers) (WCS, 2005). These environmental layers were obtained for *S. pilularius* natural area and for the areas where this species is distributed outside of its natural area.

Hypotheses testing

To examine the factors that influence the distribution patterns of *S. pilularius* in the Pampean biogeographic province (natural area), we evaluated the fit of three models based on presence data of this species: first with only the climatic variables, second exclusively with HII, and third with both these variables. This test was performed by using species distribution modeling. Although this is a method often used to generalize across species distributions (e.g. Kamiński 2015), assess the potential effects of global change and identify areas with potential to be invaded, it is also used to test alternative hypotheses that incorporate different potential causal factors (Anderson *et al.* 2009). Specifically, we used the software MaxEnt (version 3.3.3e; Phillips *et al.* 2006) because it has been recommended in previous comparative studies (Elith *et al.* 2006). This software seems to be least affected by location errors in presence data (Graham *et al.* 2008), and can work with relatively small sample sizes (Hernandez *et al.* 2006, 2008, Wisz *et al.,* 2008). The three nested models were run 100 times, leaving a 70% of data to training and 30% to testing the model and leaving the other parameters by default (Phillips *et al.* 2006). To select the best fitting model, we assessed for significant differences among models considering results on Area

Under the receiver operating characteristics Curve (AUC) by applying Wilcoxon median-test (Blatch-Overgaard *et al.* 2010). This analysis was performed with the package *stats* in the software R (R Core Team 2013). The AUC provides a measure of the accuracy of species distribution models ranging between 0 and 1, where models with AUC values higher than 0.7 are considered good. It should be noted that although AUC is criticized as a measure to assess only presence model fitting, this can be applied safely to evaluate model performance within species (Lobo *et al.* 2008, Blatch-Overgaard *et al.* 2010).

To recognize which model best explains the distribution patterns of *S. pilularius* outside of its natural area, we projected each of the above models (i.e., the 100 runs by hypothesis) to a wider geographical area where the species was found (using "projection" feature, as in Kumar *et al.* 2014). To give more robustness to this analysis we validated each model projection using independent data on species presence and absence. The presences considered were those obtained from the exhaustive compilation of museum collections while absences were obtained indirectly by considering studies including tenebrionid diversity in natural areas with a sampling effort of at least two years (Lagos 2004, Flores *et al.* 2004, Sackman and Flores 2009, Cheli 2009, Cheli *et al.* 2010, Cheli unpublished data, Griotti 2013). As in Kumar *et al.* 2014, we used different measures of accuracy to validate the models (AUC, sensitivity and specificity) from the independent dataset, where sensitivity represents the proportion of presences correctly predicted and specificity represents the proportion of absences correctly predicted. Measures of accuracy were calculated at a 0% training omission rate (commonly known as the Lowest Predicted Threshold, LPT), and a 10% training omission rate (10% Predicted Threshold, 10% PT). Zero percent omission rates indicate that 100% of training location falls inside the suitable areas, and 10% training omission rates means that 10% of training location falls inside the suitable areas (for more details see Liu *et al.* 2013). This analysis was performed with the package *SDMTools* in the software R (VanderWal *et al.* 2011).

Results

Data compilation (a total of 106 valid records, see Appendix) showed that *S. pilularius* was collected within the borders of four countries: Argentina, Brazil, Chile, and Uruguay and six biogeographic provinces: four in the Netropical region: Pampean, Chacoan, Monte, Prepuna and two in the Andean region: Maule and Patagonian (Fig. 3). This implies that the range of climatic variables under which *S. pilularius* can survive is in areas with mean annual temperatures ranging from 8° to 22° C and mean annual precipitations from 144 to 1580 mm. These climatic extremes suggest a great ecological tolerance of the investigated species.

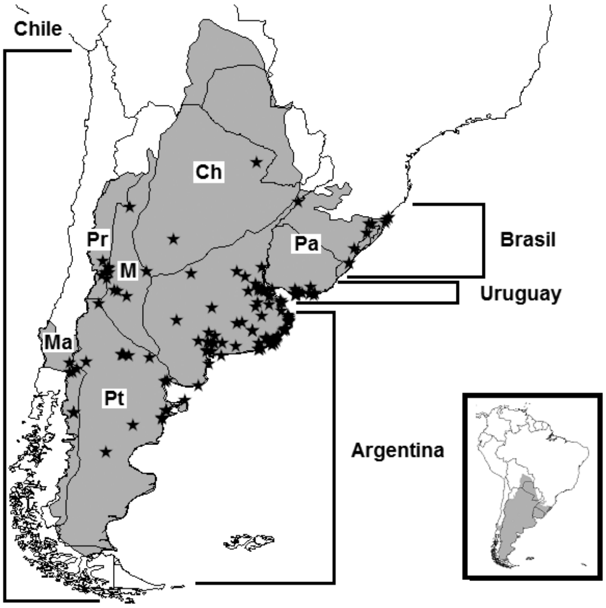

Figure 3. Geographic distribution of *Scotobius pilularius* (black stars) after museum collection revisions across countries and biogeographic regions in South America: Pa = Pampean, Ch = Chacoan, M = Monte, Pr = Prepuna, Ma = Maule and Pt = Patagonian.

Hypotheses tests demonstrated that the model which incorporates climatic conditions and HII showed the best fit to *S. pilularius* distribution data in natural areas [median AUC over 100 runs = 0.99], followed closely by the climatic conditions [median AUC over 100 runs = 0.98] , and more distantly by the HII [median AUC over 100 runs = 0.93] (Fig. 4). These results suggest that climatic conditions and human settlements generate the conditions to the subsistence of this species. However, contrary to our expectations, the model that best explained presences and absences of *S. pilularius* (Fig. 5a, b) outside of its natural area was the HII, followed by climatic conditions and HII and finally by the climatic condition model (Table 1). When we observed model projections on Argentina and Chile, it is possible to recognize a climatic unsuitable area in the center, southeastern and northwestern of Argentina and north and southwestern of Chile (Fig. 5c, e). These projections cannot explain much of observed distribution of *S. pilularius* in Argentina. Thus, this species is negatively influenced by climatic conditions outside the Pampean province, and the probable explanation to its subsistence is closely related to the conditions that are generated in human

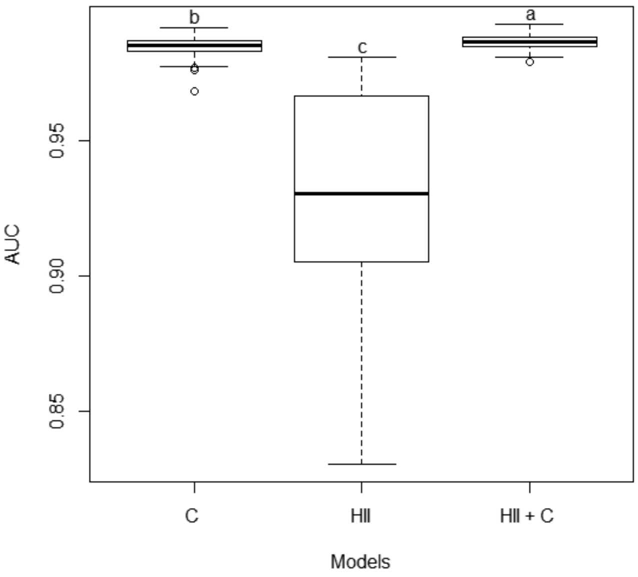

Figure 4. Box plots displaying the median, interquantile range, and maximum and minimum values of area under the receiver operating characteristics curve (AUC) for each competing hypothesis assessed within *S. pilularius* natural area. Lowercase letters indicate significant differences among models at $p < 0.001$, Wilcoxon median-test; and, capital letters different models: C, climatic conditions, HII, human influence index and HII + C, human influence index plus climatic conditions.

settlements (Fig. 5d). An important finding that should be considered is that along the central to southern political limit between Argentina and Chile, there are unexpected climatic conditions suitable for *S. pilularius* subsistence. Therefore, if this species reaches these areas it could probably exist as free-living organism such as in Pampean biogeographic province.

DISCUSSION

Our findings demonstrate a change in the strength of factors that determine *S. pilularius* geographic distribution within and outside of its natural area. While interplay between climatic conditions and human settlements create the conditions for its subsistence in its natural area, only human settlements determine its distribution outside of the natural area. Taking into account that a fossil of *S. pilularius* was found within its natural area and was dated between 12000 and 13400 years before present, it is possible to assume that this darkling beetle occurred in this area before human settlements (Ramirez *et al*. 2016, this volume). Thus, *S. pilularius* moved from living in a complete disassociation to human settlements or asynanthropy to living in close association with human settlements or synanthropy. According with Nuorteva (1963), who established a gradient of synanthropy, it is possible that in its natural area *S. pilularius* is associated to rural areas (hemisynanthropy) or even to urban areas (eusynanthropy). However, outside of this area this species only showed eusynanthropic associations. Under these evidences, we can argue that *S. pilularius* could have been dispersed in human displacements throughout Argentina, but as its climatic niche was not satisfied in these new environments the unique conditions to its subsistence were provided by human settlements.

Contrary to other tenebrionid species that are grain pest and are commonly found in human settlements (e.g., Marcuzzi 1979), *S. pilularius* is not reported as a grain pest. So, what determines that this darkling beetle survive in human settlements? To our knowledge, refuge and alimentation are keys to understand this survival. For example, the places where *S. pilularius* was found outside of its natural area were related to decomposing organic matter (compost), under garbage containers and trunks, in irrigated parks and gardens and even inside houses (Carrara, Cheli, Flores and Silvestro pers. obs.). Commonly, these sites have different climatic conditions at micro-scales where

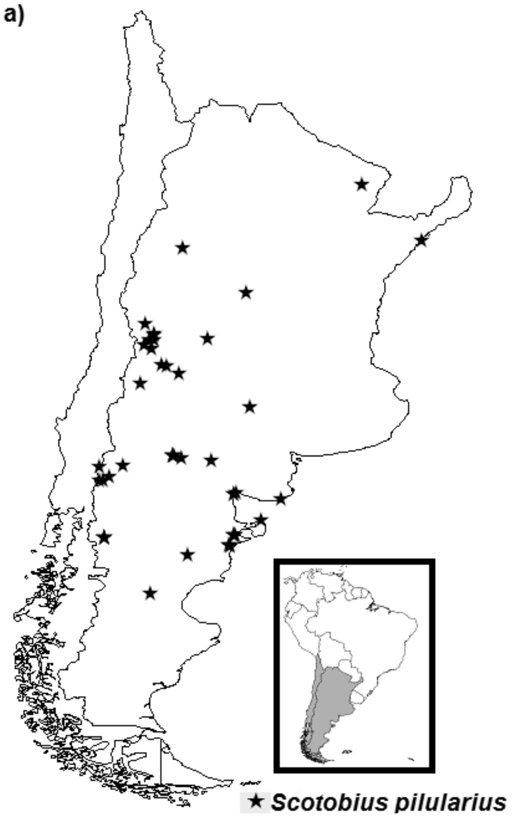

Figure 5 (continued next page). Geographic distribution of *Scotobius pilularius* outside of its natural area: (a) presences.

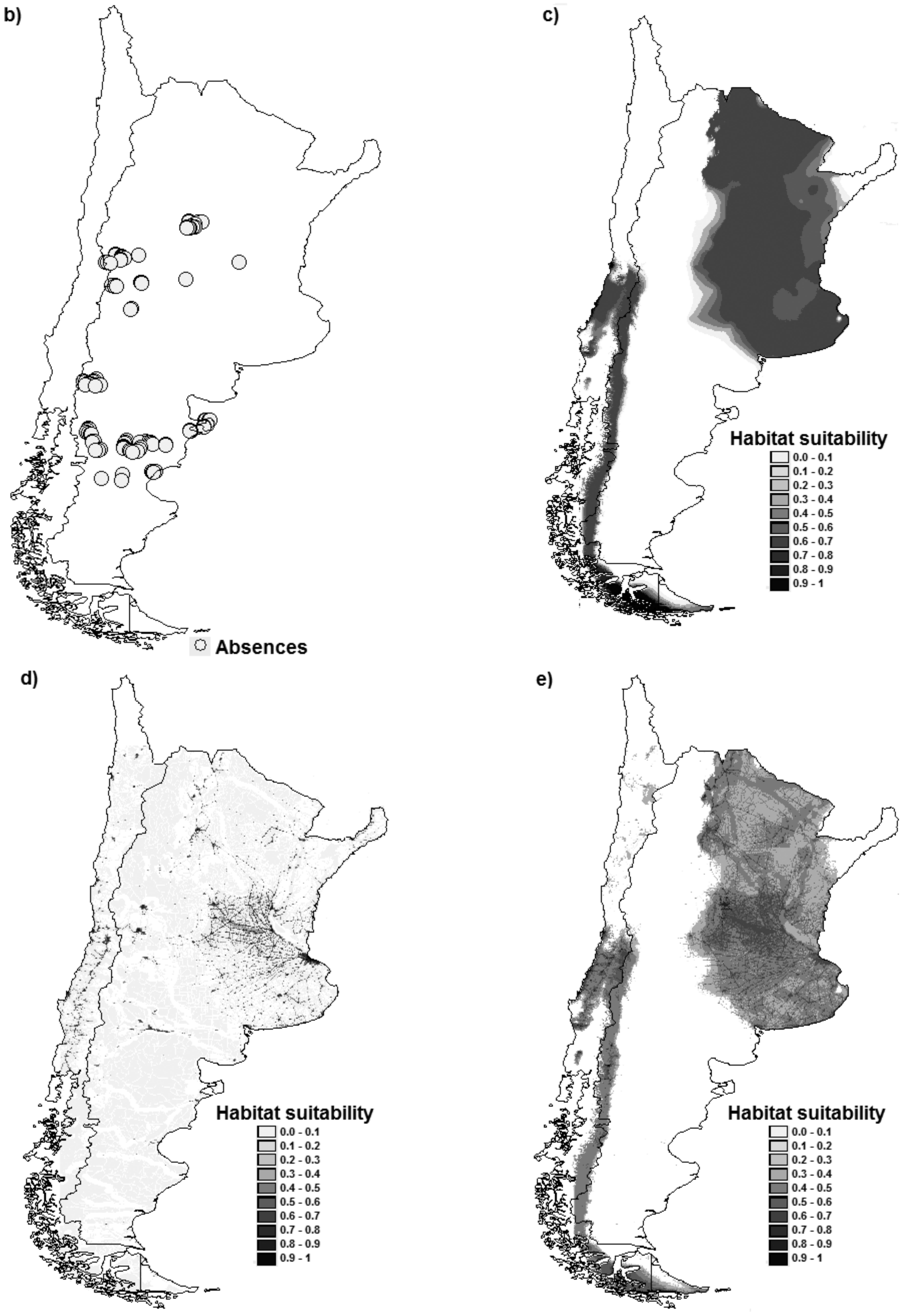

Figure 5 (continued). Geographic distribution of *Scotobius pilularius* outside of its natural area: (b) absences; and model projections in Argentina and Chile: (c) Climatic condition model, (d) Human influence index model, and (e) Human influence index plus climatic conditions model. Each habitat suitability map is represented at lowest predicted threshold. See Appendix.

Table 1. Summary of *Scotobius pilularius* model validations outside of its natural area. AUC, area under the receiver operating characteristics curve; Sensitivity, proportion of presences correctly predicted; Specificity, proportion of absences correctly predicted for two different thresholds: lowest predicted threshold (LPT) and 10% predicted threshold (10% PT). Values represent averages from each of 100 projected runs by hypothesis. Capital letters represent different hypothesis: C, climatic conditions, HII, human influence index and HII + C, human influence index plus climatic conditions.

	LPT			10% PT		
Models	AUC	Sensitivity	Specificity	AUC	Sensitivity	Specificity
C	0.505	0.289	0.721	0.590	0.289	0.891
HII	0.708	0.947	0.469	0.889	0.868	0.911
C + HII	0.524	0.342	0.707	0.590	0.289	0.891

temperature and humidity increase according with decomposition (in compost), or condense humidity (under containers and trunks), or maintain high levels of moisture (irrigated parks and gardens) or by human wellness (inside houses) (Matuszewski *et al.* 2014). Regarding its diet, it is known that specimens of *S. pilularius* were reared on fruit (banana, apple), vegetables and meat in order to obtain eggs and larvae (Silvestro and Michat 2016, this volume), and were also recorded on pig carcasses (Zanetti *et al.* 2015, as *Scotobius miliaris*). These observations indicate that this species can be omnivorous which sustains that probably one cause of *S. piluarius* dispersion could have been related to human foraging; because ancient people often leave leftover meat and fruits each time they moved through space.

Overall, these results suggest an increasingly high probability of dispersion of *S. pilularius* in environments with human settlements. Thus, far from generating an increase in its extinction risk, human activities promote new niches where this species survives. This has a strong implication under the expected effect of global climate change because probably this species can disappear in natural areas and survive in areas only related to human settlements.

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Appendix. *Scotobius pilularius* distributional data

Species,Latitude,Longitude,Distribution
Scotobius pilularius,-38.984124,-61.309744,Natural area
Scotobius pilularius,-38.716667,-62.266667,Natural area
Scotobius pilularius,-38.694722,-62.252778,Natural area
Scotobius pilularius,-38.7667,-61.9,Natural area
Scotobius pilularius,-38.0103,-62.8164,Natural area
Scotobius pilularius,-38.166975,-61.2,Natural area
Scotobius pilularius,-38.15,-61.8,Natural area
Scotobius pilularius,-38.1,-62.216667,Natural area
Scotobius pilularius,-38.1556,-61.95,Natural area
Scotobius pilularius,-38.366667,-60.266667,Natural area
Scotobius pilularius,-37.6833,-61.7167,Natural area
Scotobius pilularius,-37.4667,-62.1,Natural area
Scotobius pilularius,-33.416667,-63.3,Natural area
Scotobius pilularius,-37.884687,-58.259151,Natural area
Scotobius pilularius,-37.816667,-58.25,Natural area
Scotobius pilularius,-37.898912,-58.104304,Natural area
Scotobius pilularius,-38.568056,-58.706111,Natural area
Scotobius pilularius,-38.57422,-58.691791,Natural area
Scotobius pilularius,-36.8333,-60.2167,Natural area
Scotobius pilularius,-36.7,-56.683333,Natural area
Scotobius pilularius,-35.45,-57.2833,Natural area
Scotobius pilularius,-33.316667,-60.2,Natural area
Scotobius pilularius,-36.783333,-59.85,Natural area
Scotobius pilularius,-36.349153,-58.543496,Natural area
Scotobius pilularius,-36.505109,-56.70953,Natural area
Scotobius pilularius,-34.916509,-56.170081,Natural area
Scotobius pilularius,-36.483333,-56.7,Natural area
Scotobius pilularius,-35.575,-58.008889,Natural area
Scotobius pilularius,-34.933333,-57.95,Natural area
Scotobius pilularius,-35.6833,-58.9639,Natural area
Scotobius pilularius,-34.9953,-58.0481,Natural area
Scotobius pilularius,-34.863889,-56.2025,Natural area
Scotobius pilularius,-35.437137,-58.807864,Natural area
Scotobius pilularius,-34.866944,-56.166667,Natural area
Scotobius pilularius,-34.166667,-58.916667,Natural area
Scotobius pilularius,-33.007778,-58.511111,Natural area
Scotobius pilularius,-34.825194,-56.199167,Natural area
Scotobius pilularius,-34.466667,-58.516667,Natural area
Scotobius pilularius,-34.366667,-58.75,Natural area
Scotobius pilularius,-33.679444,-59.666944,Natural area
Scotobius pilularius,-34.582757,-58.416191,Natural area
Scotobius pilularius,-34.599722,-58.381944,Natural area
Scotobius pilularius,-34.6735,-56.172056,Natural area
Scotobius pilularius,-34.516667,-58.766667,Natural area
Scotobius pilularius,-34.598056,-58.565,Natural area
Scotobius pilularius,-34.854729,-55.285405,Natural area
Scotobius pilularius,-34.533333,-58.716667,Natural area
Scotobius pilularius,-34.770102,-55.76128,Natural area
Scotobius pilularius,-34.8,-54.916667,Natural area
Scotobius pilularius,-34.716667,-55.95833,Natural area
Scotobius pilularius,-34.65,-59.433333,Natural area
Scotobius pilularius,-34.516667,-56.283333,Natural area
Scotobius pilularius,-34.471389,-57.844167,Natural area
Scotobius pilularius,-32.7425,-52.574444,Natural area
Scotobius pilularius,-34.366667,-55.233333,Natural area
Scotobius pilularius,-30.672778,-51.395833,Natural area
Scotobius pilularius,-30.048953,-51.230772,Natural area
Scotobius pilularius,-29.62116,-49.936805,Natural area
Scotobius pilularius,-30.080833,-51.022778,Natural area
Scotobius pilularius,-29.760833,-50.03,Natural area
Scotobius pilularius,-29.975,-50.127778,Natural area
Scotobius pilularius,-45.599576,-69.077673,Outside
Scotobius pilularius,-43.721874,-67.280524,Outside
Scotobius pilularius,-43.300439,-65.274485,Outside
Scotobius pilularius,-43.276247,-65.273185,Outside
Scotobius pilularius,-43.253333,-65.309444,Outside
Scotobius pilularius,-42.905116,-71.315092,Outside
Scotobius pilularius,-42.903735,-71.312809,Outside
Scotobius pilularius,-42.903,-71.302,Outside
Scotobius pilularius,-42.897161,-71.300838,Outside
Scotobius pilularius,-42.786,-65.049,Outside
Scotobius pilularius,-42.785621,-65.049089,Outside
Scotobius pilularius,-42.774944,-65.031028,Outside
Scotobius pilularius,-42.753485,-65.045004,Outside
Scotobius pilularius,-42.079767,-63.759153,Outside
Scotobius pilularius,-41.051213,-62.827931,Outside
Scotobius pilularius,-40.81116,-65.086,Outside
Scotobius pilularius,-40.808333,-65.086667,Outside
Scotobius pilularius,-40.728259,-64.935975,Outside
Scotobius pilularius,-40.153587,-71.350604,Outside
Scotobius pilularius,-40.153193,-71.566356,Outside
Scotobius pilularius,-39.941215,-71.068022,Outside
Scotobius pilularius,-39.427147,-70.418019,Outside
Scotobius pilularius,-39.166667,-66.15,Outside
Scotobius pilularius,-39.024385,-67.576202,Outside
Scotobius pilularius,-38.95832,-68.02889,Outside
Scotobius pilularius,-38.954023,-67.92775,Outside
Scotobius pilularius,-38.933333,-68.016667,Outside
Scotobius pilularius,-38.933333,-68.016667,Outside
Scotobius pilularius,-36.620278,-64.290556,Outside
Scotobius pilularius,-35.474458,-69.585294,Outside
Scotobius pilularius,-34.966667,-67.7,Outside
Scotobius pilularius,-34.6175,-68.335556,Outside
Scotobius pilularius,-34.584764,-68.544785,Outside
Scotobius pilularius,-33.766667,-69.033333,Outside
Scotobius pilularius,-33.603249,-69.384256,Outside
Scotobius pilularius,-33.37812,-69.15881,Outside
Scotobius pilularius,-33.33646,-68.9228,Outside
Scotobius pilularius,-33.277222,-66.3525,Outside
Scotobius pilularius,-33.09054,-68.88623,Outside
Scotobius pilularius,-33.050665,-68.939885,Outside
Scotobius pilularius,-32.58778,-69.34876,Outside
Scotobius pilularius,-31.083333,-64.5,Outside
Scotobius pilularius,-28.916667,-67.516667,Outside
Scotobius pilularius,-28.55,-56.05,Outside
Scotobius pilularius,-25.8636,-58.8858,Outside