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Environmental factors affecting the distribution of three armadillo species (*Xenarthra*, *Dasypodidae*) in Argentina

DOI 10.1515/mammalia-2015-0084

Received May 19, 2015; accepted March 31, 2016

Abstract: Environmental temperature, rainfall, vegetation structure, soil composition and land use were recognized as relevant factors limiting the distribution of armadillos. The aim of this study was to identify environmental and spatial factors influencing the geographical distribution of the most widespread armadillos occurring in Argentina (*Chaetophractus vellerosus*, *Chaetophractus villosus* and *Zaedyus pichiy*), through the most simple and accurate explanatory modeling. General linear models (GLMs), partitioning analyses of variance and hierarchical partitioning analyses were applied to estimate the species-environment relationships. Climatic variables were recognized as the most relevant factors influencing the three species distribution, consistent with that expected from the hierarchical structure theory in ecological systems. Optimal conditions were mainly arranged in a longitudinal geographic gradient for *Chaetophractus* species and in a latitudinal-longitudinal gradient for *Z. pichiy*. The optimal habitat identified for *C. vellerosus*, larger than previously documented, was characterized by warm, rainy summers and moderately cold, dry winters. The distribution of *C. villosus* was mainly influenced by temperate conditions of temperature and isothermality, scarcity of rainfall with high seasonality and low aridity conditions, and prevalence of sandy soils. Optimal habitat of *Z. pichiy* was affected by low temperatures with high seasonality, scarcity of rainfall with aridity conditions and sandy soils.

Keywords: Dasypodidae; distributional predictive models; explanatory environmental factors; general linear models; partitioning analyses of variance.

Introduction

Environmental conditions have been recognized as relevant factors limiting the distribution of living armadillo species (e.g. Poljak et al. 2010, Abba et al. 2014, 2015a Taulman and Robbins 2014). Armadillos (*Xenarthra*, *Dasypodidae*) are Neotropical mammals, inhabiting different environments from the United States to Argentina (Wetzel 1985). Of the 21 species, only two occur outside of South America and one of them (*Dasypus novemcinctus* Linnaeus 1758) has recently dispersed into the United States probably limited by climatic factors (Taulman and Robbins 1996, 2014). Among environmental conditions, ambient temperatures strongly affect the behavior (McDonough and Loughry 2008) and physiology (McNab 1985) of these fossorial mammals. Geographical distribution of armadillos could be secondary related to rainfall through its effect on ecosystem primary productivity (e.g. Taulman and Robbins 2014). Some species seems to be associated with arid conditions (Gregeor 1985, Wetzel 1985, Vizcaíno et al. 1995), whereas rainfall that resulted in flooding could preclude the burrowing activity of other species (Abba et al. 2015a). The effect of soil composition on ease of burrow construction would also influence the distribution of armadillos (e.g. Gregeor 1985, Carlini and Vizcaíno 1987, Abba and Cassini 2008, Superina 2008, Abba et al. 2011, 2015a). The open structure of vegetation would also account for the geographic distribution of some species (Wetzel 1985). In contrast, knowledge of ecological requirements and environmental factors with biogeographical implications is insufficient for other species of armadillos with South American distribution (see Superina et al. 2014 for a review). Argentina offers an excellent opportunity to explore factors affecting the distribution of South American armadillo species, due to 13 species (70% of South American armadillos) occurring within its

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borders and the wide latitudinal environmental gradient across the country (McNab 1980).

Species distribution models based on ecological niche theory (Guisan and Zimmermann 2000, Guisan and Thuiller 2005) are useful methodologies to assess the influence of environmental factors on species distribution and to analyze species-environment relationships. Most environmental variables are spatially structured, resulting in patched structures or gradients, and potentially induce a similar organization of living beings and of biological processes (Legendre and Fortin 1989). Models previously applied to armadillo species in Argentina were based on a maximum entropy algorithm (MaxEnt, Phillips et al. 2006) and allowed detecting priority areas for conservation of armadillos (Tognelli et al. 2011), as well as species richness patterns and ecosystems of interest to 13 species (Abba et al. 2012). Both studies highlighted the importance of potential distributions, particularly in armadillo species whose optimal habitats are little known on a broad geographic scale.

Three of the most widespread armadillos in Argentina (*ChaetophRACTUS vellerosus* Gray 1865, *ChaetophRACTUS villosus* Desmarest 1908 and *Zaedyus pichiy* Desmarest 1908) showed no strong association with any particular environmental variable (Abba et al. 2012). These three species belong to the subfamily Euphractinae Winge 1923 (Wetzel et al. 2005) and have generalist feeding habits with carnivorous-omnivorous tendencies (Redford 1985). Precipitation seasonality and precipitation of the warmest quarter of the year had a relative importance in the MaxEnt distribution model of *C. vellerosus* (16% and 15%, respectively, Abba et al. 2012). The diet of this species differs among populations and among seasons, associated to the food availability and precipitation (Greegor 1985, Soibelzon et al. 2007, Cuéllar 2008, Abba et al. 2011). Water conservation by concentrating urine in the kidneys is another adaptation of this species to xeric environments (Greegor 1985). Land elevation and precipitation of the coldest quarter were of relative importance in maximum entropy distribution models for *C. villosus* (18% and 14%, Abba et al. 2012). This generalist species occupies a wide variety of environments and has an omnivorous diet (Abba and Cassini 2008, Cuéllar 2008). Mean temperature of the coldest quarter and precipitation of the warmest quarter had a relative importance in the MaxEnt models of *Z. pichiy* (18% and 14%, Abba et al. 2012). *Zaedyus pichiy* presents physiological adaptations for inhabiting the cold south-eastern region of the South American continent. Indeed, *Z. pichiy* has the lowest thermal conductance among all armadillo species (McNab 1985), little body temperature regulation (McNab 1980), and capability to enter in deep

hibernation and daily torpor (Superina and Boily 2007). Omnivory was proposed as an enabler for extending its distribution to seasonal habitats as Patagonia (Superina et al. 2009).

Presence-absence models, such as generalized linear models (GLM: McCullagh and Nelder 1989), can predict the distribution of focal species with higher accuracy than presence/pseudo-absence models (Brotons et al. 2004) such as MaxEnt. GLMs are maximum likelihood mathematical models that do not force data into unnatural scales and, thereby, allow for non-linearity and non-constant variance structures in the data (Hastie and Tibshirani 1990). GLM can help in the development of explanatory models that better represent the underlying data (Guisan et al. 2002) and can increase our understanding of the ecosystems armadillos inhabit. The goal of this study is to identify the relative importance of climatic variables and habitat features on the geographical distribution of the most widespread armadillos in Argentina: *ChaetophRACTUS vellerosus*, *ChaetophRACTUS villosus* and *Zaedyus pichiy*, and to recognize a possible spatial arrangement in environmental variables that could have influence in their distribution. Following the hierarchical structure theory in ecological systems (Pearson and Dawson 2003), we predict that climate conditions account for the distribution of these armadillo species at the broad scale studied. However, soil composition, vegetation structure and land use are predicted to become more relevant variables to account for armadillo's distributions at more local scales. According to the available knowledge about these species, we expect that: a) a tolerance to aridity conditions in warm climates, associated with loose soils, will influence the optimal habitat of *C. vellerosus*, b) a wide tolerance to environmental variables will affect the distribution of *C. villosus*, and c) a tolerance to cold climate conditions and an association with sandy soils will account for the optimal habitat of *Z. pichiy*.

Materials and methods

Study species and presence-data sources

Three armadillo species of small to medium size and similar ecological requirements were selected, taking into account that body mass and diet are related to physiological constraints (McNab 1985). *ChaetophRACTUS vellerosus* (with mean body weight of 850 g) ranges from the south-east of Bolivia and northwest of Paraguay to the center of Argentina (Figure 1, Wetzel 1985, Abba and Cassini 2008,

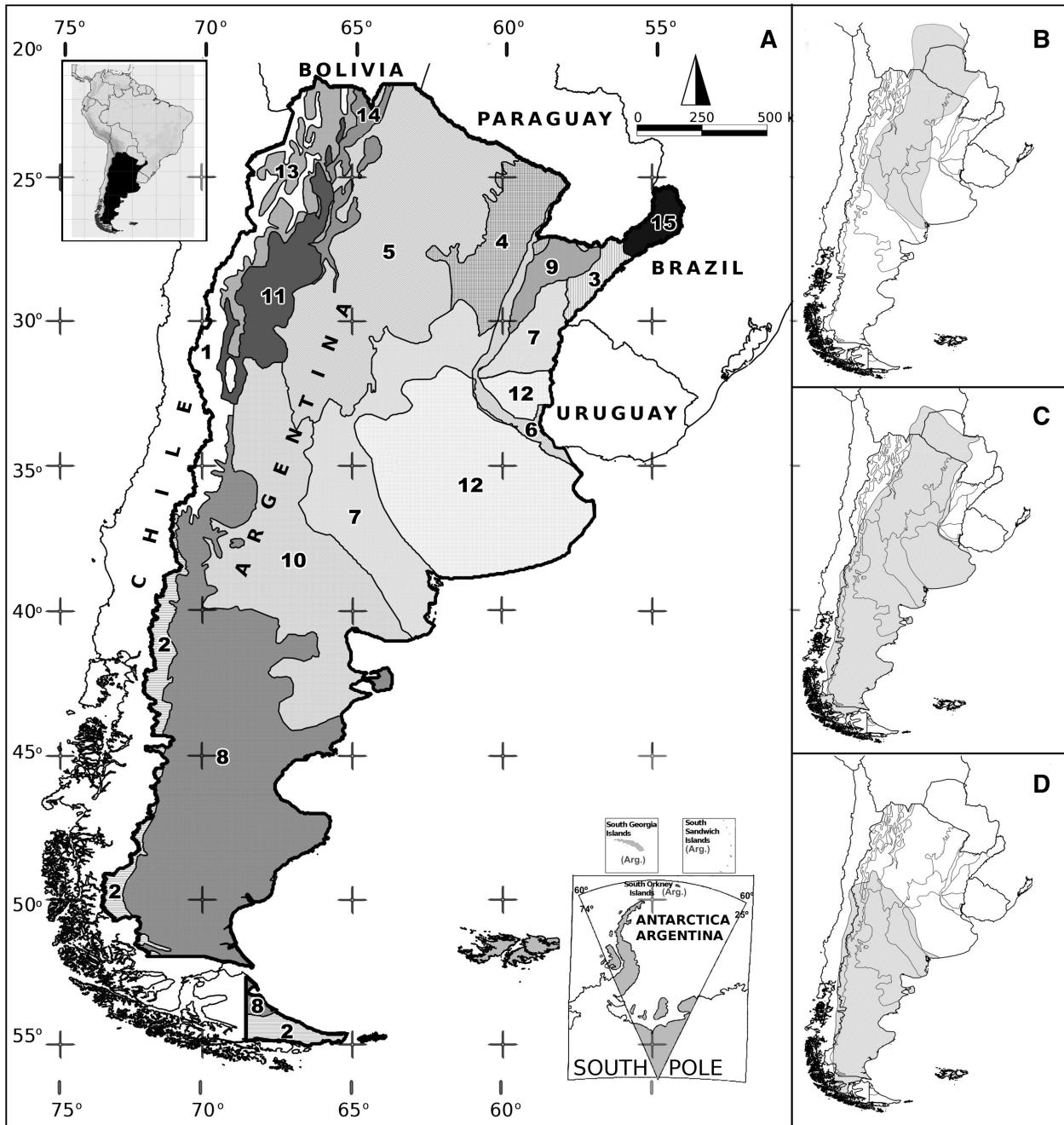


Figure 1: Map of continental ecoregions in Argentina (A) in WGS84 projection (adapted from Burkart et al. 1999) and current distributions of *ChaetophRACTUS vellerosus* (B), *ChaetophRACTUS villosus* (C) and *Zaedyus pichiy* (D) (modified from IUCN 2014). Ecoregions: High Andes (1), Patagonian forest (2), Mesopotamian savanna (3), Humid Chaco (4), Arid Chaco (5), Paraná flooded savanna (6), Espinal (7), Patagonian steppe (8), Iberá marshes (9), Low Monte (10), High Monte (11), Pampas grassland (12), Central Andean Puna (13), Yunga forest (14), Paranaense forest (15).

Abba et al. 2011). Within Argentina, it is widely distributed in Chaco ecoregion, occupying xeric environments with loose and sandy soils. Other small isolated population occurs in the humid, temperate Pampas ecoregion, associated to sandy calcareous soils (Wetzel et al. 2005, Abba and Vizcaíno 2011), including agricultural areas

(Greegor 1985, Abba and Cassini 2008, Abba and Superina 2010). *ChaetophRACTUS villosus* (2500–3000 g) ranges from the Chaco region of Bolivia, Paraguay, and Argentina as far south as Santa Cruz, Argentina and Magallanes, Chile (Figure 1, Wetzel et al. 2005, Abba and Superina 2010). Also it was introduced in the southernmost insular region of

Argentina and Chile (Poljak et al. 2007). Within Argentina, it is found in almost all ecoregions, from humid to arid grasslands, savannas and forests, including cultivated landscapes (Abba and Cassini 2008, Abba and Superina 2010). *Zaedyus pichiy* (1000 g) ranges from central Argentina and eastern Chile south to the Magellan Strait (Figure 1, Abba and Superina 2010). This species showed a southward expansion as a response to the recent climate change, triggered during the last century for anthropogenic causes (Abba et al. 2015b). Within Argentina, it occurs in arid and semiarid habitats with firm sandy soils, grasslands and open scrublands of the Patagonia ecoregion, dry forests of southern Chaco, grasslands and scrublands of Espinal, Monte, and Pampa ecoregions (Superina 2008, Abba and Vizcaíno 2011), including farmland areas (Abba and Superina 2010, Superina and Abba 2014).

Georeferenced locations of individuals from each species were compiled from the public collections of IADIZA (five locations for *Zaedyus pichiy*) and of the Mendoza Department of Renewable Natural Resources (21 locations for *Chaetophractus Villosus* and 15 locations for *Z. pichiy*), published data (Tognelli et al. 2011: 123 locations for *Chaetophractus vellerosus*, 240 locations for *C. villosus*, and 107 locations for *Z. pichiy*), and the private collections of Foriasepi (four locations for *Z. pichiy*), Superina (123 locations for *Z. pichiy*), Corbalán (17 locations for *Z. pichiy*) and Seitz (18 locations for *C. vellerosus*, 21 locations for *C. villosus* and 89 locations for *Z. pichiy*). All these data were placed on a grid of 5×5 km cells. Because in some cases more than one location fell within the same cell, *C. vellerosus* was present in 123 cells, *C. villosus* in 227 cells, and *Z. pichiy* in 215 cells.

Study area and explanatory variables

The study area corresponded to Argentina's continental land area (2,780,400 km²), bounded by the Atlantic Ocean on the east and the Andes Cordillera on the west (Figure 1). Temperature decreases from north to south whereas rainfall decreases from east to west, with humid zones (16% of the area), xeric zones (56%) and deserts (28%) (Brown et al. 2006). Differences in these gradients of temperature and precipitation define a great diversity of ecoregions, including subtropical forests, dry woodlands, grasslands with variable precipitation, and deserts (Burkart et al. 1999). Agricultural activities occupy 15% of the suitable land area (Brown et al. 2006).

Based on the knowledge of the ecology of armadillos, 11 potential explanatory variables were chosen representing climate, sedimentology, plant physiognomy and

land use. Climate variables were selected from the overall WorldClim dataset (<http://www.worldclim.org>), using a correlation matrix to compare all 23 available descriptors with each other and to select those loosely related ($r < 0.75$, $p < 0.05$). The selected climate descriptors were: average annual temperature, average annual precipitation, isothermality ($P3 = P2/P7$, where P3: temperature variability index, P2: mean diurnal temperature range, P7: annual temperature range), temperature and precipitation seasonality (i.e. annual coefficient of variation in monthly averages, Hijmans et al. 2005). Aridity index was included ($A_i = 1/[P/Ev]$, where P: average annual precipitation, Ev: average annual potential evapotranspiration, UNEP 1991). Sedimentological descriptors, percentages of loam, clay and sand sediments, were calculated from 11 soil textural categories of the National Edaphic Atlas (Moscatelli et al. 1990). Independent variables represented plant physiognomy (percentages of land area with open and closed vegetation) and land use categories (percentages of land area with natural and cultivated areas) were extracted from the respective categories in available maps (INTA 2009).

Environmental data were analyzed on spatial grids of 147,898 cells, managed in raster format (*.ascii, *.grd) where each cell was 5×5 km, georeferenced in datum WGS84. All locations, variables and results were assembled in a geographical information system, using open source software (gvSIG Association 2012). A spatial variable was included in GLMs, in order to consider the influence of unaccounted-for spatially structured factors such as historical, biotic or environmental variables which were not otherwise considered (Legendre and Legendre 1998). The third-degree polynomial of location (y) was calculated for each grid cell using its central latitude (Lat) and longitude (Lon): $y = b_1 * Lat + b_2 * Lat^2 + b_3 * Lat^3 + b_4 * Lon + b_5 * Lon^2 + b_6 * Lon^3 + b_7 * Lat * Lon + b_8 * Lat^2 * Lon + b_9 * Lat * Lon^2$. All independent variables were standardized to 0 mean and 1 standard deviation, in order to eliminate measurement-scale differences.

Methods for modeling species distributions

The maximum entropy probability distribution was estimated for each species using the maximum entropy algorithm (MaxEnt version 3.2.19, Phillips et al. 2006). The appraisal was done from a set of occurrence records (individual locations) within the study area and included environmental variables in cells with confirmed presence of each species (Hernández et al. 2006, Phillips et al. 2006). The distribution was modeled 100 times, using 75%

of the randomly selected data points, to generate training models evaluated with the remaining 25%, with the parameters assumed by default (Phillips et al. 2006). The accuracy of the model was estimated by the area under the curve (AUC) in the receiver operating characteristics (ROC) analysis. An AUC=0.5 detected a non-significant difference with a random assignment of presence-absence, whereas an AUC=1.0 achieved a perfect prediction. To ensure that all training locations were included (Phillips et al. 2006), minimum training values were used as a threshold to partition continuous probabilistic values into suitable and unsuitable areas.

Absence locations were randomly selected inside the unsuitable areas and monitored to estimate the linear combination between the average of presence-absence of each species and the cell-centroid values for every explanatory variable. In order to avoid biases due to the inclusion of rare events, the number of absence locations included was 10 times higher than the number of presence locations (Kink and Zeng 2001). As the response variable belonged to a binomial probability distribution family, the applied parameters of the GLMs were logistic-regression and binomial link function. The performance of the model was measured by the Akaike information criterion (AIC) index, in order to remove the likelihood functions so that simpler models (i.e. the model with the smallest value) are preferred (Olsson 2002). The probability distribution being binomial, dispersion was fixed as one and the number of parameters was the number of coefficients. Binomial data were related to a linear, quadratic or cubic function of each variable, in order to consider possible curvilinear relationships. Environmental variables were forward stepwise incorporated into the model and tested for significance (Austin 2002). The procedure was iteratively repeated until no explanatory variables with statistical significance ($p < 0.05$) remained outside the model. The previously selected terms were tested with backward-stepwise method, in order to eliminate terms that had become non-significant. The spatial polynomial was included in the model (trend surface analysis, Legendre 1993) and a backward-stepwise regression allowed only significant terms ($p < 0.05$) to be included in the final model. The significance of spatial heterogeneity to the presence of each species was evaluated with partitioning analyses of variance (Borcard et al. 1992). The R package (R Core Team 2013) was used for all statistical computations. The final value of continuous probabilities was converted into a suitable and an unsuitable area, using a maximum sensitivity and specificity threshold to ensure modeling performance (Liu et al. 2005).

Results

Statistical models of species distribution

Maximum entropy distribution models were constructed with 11 environmental variables and 123 locations to *Chaetophractus vellerosus*, 227 locations to *Chaetophractus villosus* and 215 locations to *Zaedyus pichiy*. All models showed high statistical significance (AUC=0.92, 0.87 and 0.93, respectively, $p < 0.005$, Figures 2A, 3A, and 4A).

Presence locations, together with calculated absence location data, were used to map the explanatory GLM (Figures 2B, 3B, and 4B). These maps were transformed to the final presence-absence distributions (Figures 2C, 3C, and 4C) by using a maximum sensitivity and specificity threshold (*C. vellerosus*: 0.04 and 0.80 true positive rates; *C. villosus*: 0.26 and 0.75 true positive rates; *Z. pichiy*: 0.01 and 0.90 true positive rates). The binary areas detected by MaxEnt were 39%, 61% and 17% greater than those affected by binary GLMs; these last generated acceptable geographical distributions of high statistical significance (*C. vellerosus*: 1,274,715 km², AUC=0.84; *C. villosus*: 1,477,980 km², AUC=0.87; *Z. pichiy*: 1,268,090 km², AUC=0.95).

Environmental variables of relevance to species distribution

Based on a random selection of absence data from regions with unfavourable environmental conditions, precipitation seasonality (cubic function) was the variable with the most influence on the distribution of *Chaetophractus vellerosus* and accounted for the highest percentage of deviance (Table 1). Annual mean temperature and precipitation (cubic functions) affect its distribution pattern. Stepwise analyses (Table 2) selected annual precipitation (with a negative effect), isothermality, precipitation seasonality and average annual temperature (these three variables with positive effects). This environmental model accounted for 84% of total deviance. The spatial variable, considered alone, explained slightly less of total deviance (76%). With the addition of the spatial variable to the final model (mainly longitude terms with positive effects, Table 2) explained deviance increased to 92% (Table 1). The environmental variables that were not spatially structured accounted for 16% of variation in the distribution of *C. vellerosus*, and 68% of the variation could be equally attributed to environmental or spatial

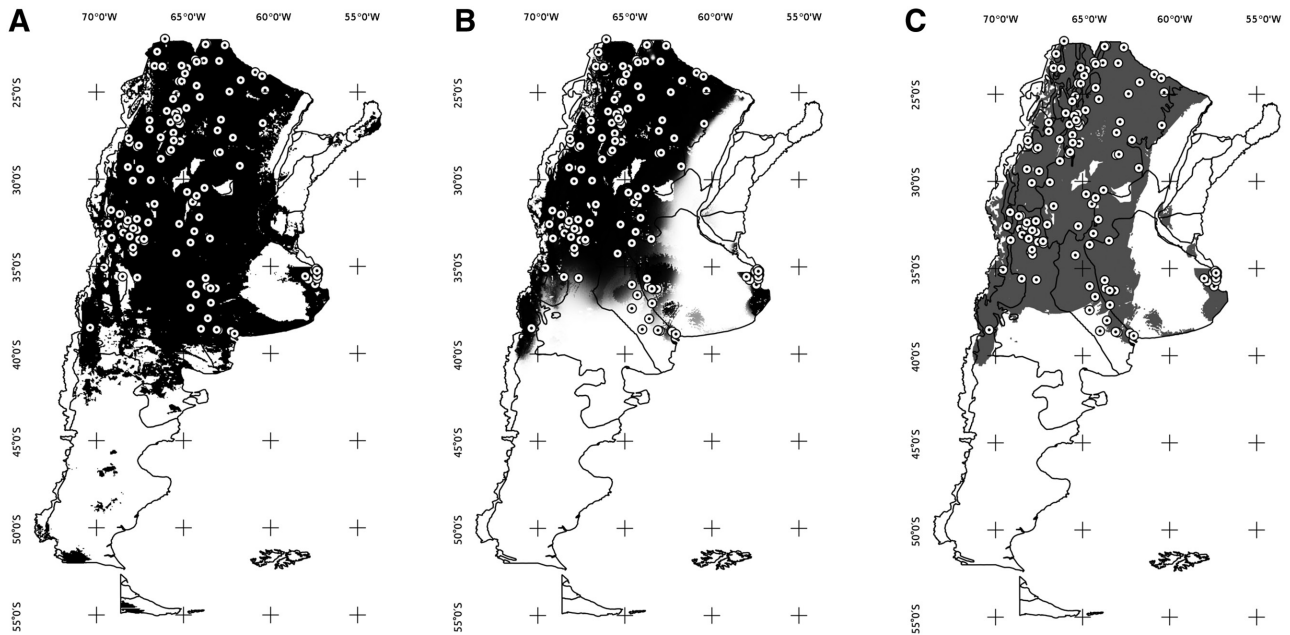


Figure 2: Models for the predictive distribution of *Chaetophractus vellerosus*. White points represent individual locations of presence for this species. (A) Map of maximum entropy distribution. (B) Map of final explanatory model using logistic regression analysis, in which absence points were randomly selected from the area outside the expanded enveloping model (higher probabilities in dark gray, lower in light gray). (C) Map of presence-absence generated from the logistic continuous regression probabilities, where the selected threshold maximized the sum of sensitivity and specificity.

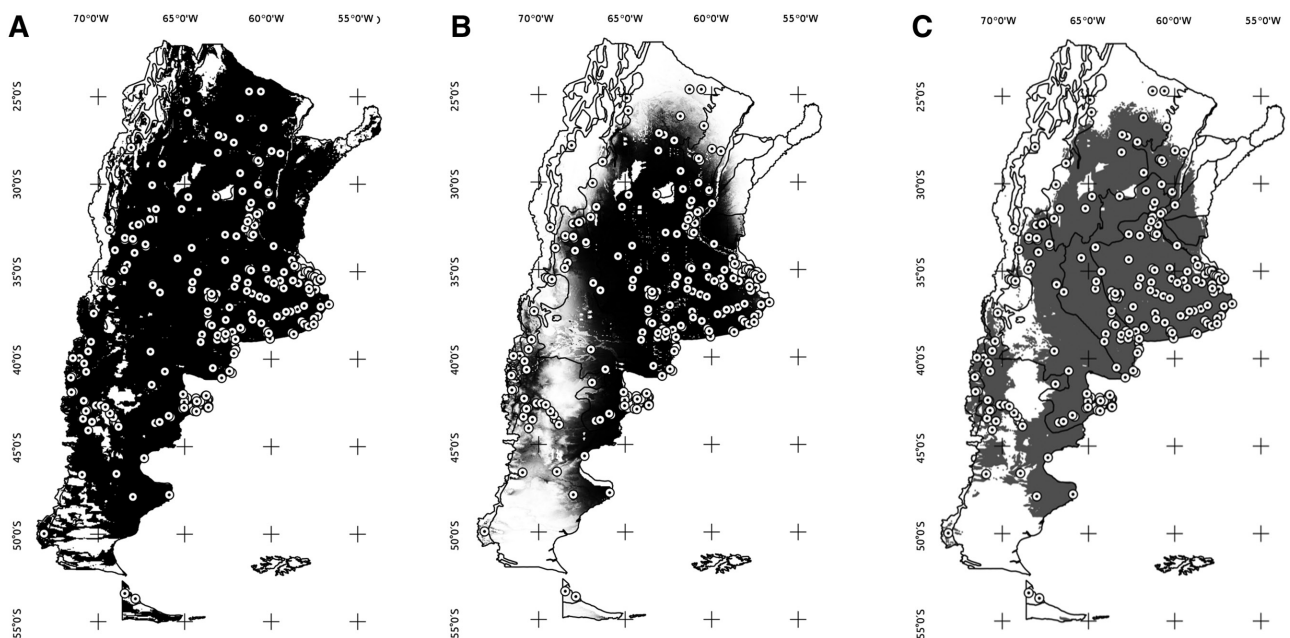


Figure 3: Models for the predictive distribution of *Chaetophractus villosus*. (A) Map of maximum entropy distribution. (B) Map of final explanatory model using logistic regression analysis. (C) Map of presence-absence generated from the logistic continuous regression probabilities. Methodological details of the models are mentioned in Figure 2.

variables because the fractions of variation were additive. Just 8% of the variability in its presence was attributed to spatial structure only, and the same percentage of variability was residual.

Descriptors of temperature (cubic functions of annual average, seasonality and isothermality, Table 1) were the variables most relevant to the distribution of *Chaetophractus villosus*, followed by precipitation (quadratic

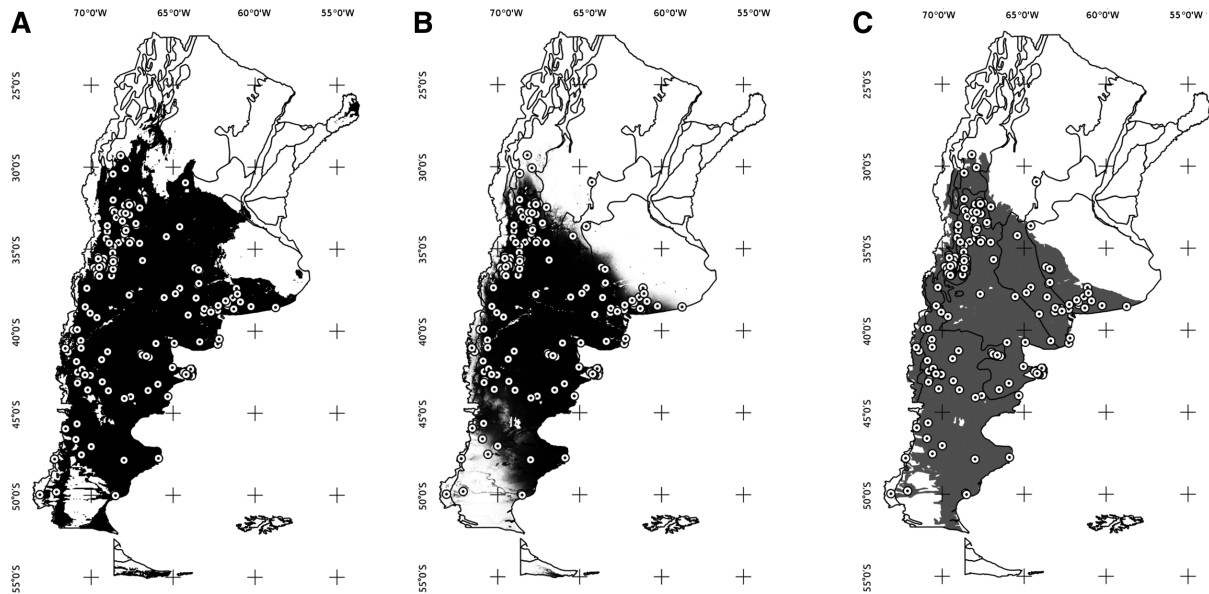


Figure 4: Models for the predictive distribution of *Zaedyus pichiy*. (A) Map of maximum entropy distribution. (B) Map of final explanatory model using logistic regression analysis. (C) Map of presence-absence generated from the logistic continuous regression probabilities. Methodological details of the models are mentioned in Figure 2.

Table 1: Environmental variables that accounted for significant changes of deviance in the basin, final and composite models of distribution for each armadillo species in Argentina (from left to right: $n=123$, $n=227$ and $n=215$).

	<i>Chaetophractus vellerosus</i>			<i>Chaetophractus villosus</i>			<i>Zaedyus pichiy</i>					
	d.f.	Deviance (%)	AIC	d.f.	Deviance (%)	AIC	d.f.	Deviance (%)	AIC			
Basin model	f	1357	848 (0)	850	f	2501	1545 (0)	1547	f	2501	2033 (0)	2035
Annual mean temperature	f^3	1354	704 (17)	712	f^3	2498	950 (39)	958	f^2	2499	1462 (28)	1470
Annual precipitation	f^3	1354	696 (18)	704	f^2	2499	1254 (19)	1260	f^3	2498	1275 (37)	1283
Aridity index	f^2	1355	830 (2)	836	f^3	2498	1435 (7)	1443	f^2	2499	1661 (18)	1667
Clayey sediments	f	1356	830 (2)	834	f^3	2498	1477 (4)	1485	f^2	2499	1974 (3)	1980
Isothermality	f^3	1354	781 (8)	789	f^3	2498	1257 (19)	1265	f^3	2498	1914 (6)	1922
Land use	f	1356	834 (2)	838	f	2500	1337 (14)	1341	f	2500	1971 (3)	1975
Loamy sediments	f	1356	830 (2)	834	f^3	2498	1477 (4)	1485	f^2	2499	1974 (3)	1980
Plant physiognomy	f	1356	836 (1)	840	f	2500	1493 (3)	1497	f	2500	1885 (7)	1889
Precipitation seasonality	f^3	1354	499 (41)	507	f^3	2498	1367 (12)	1375	f^3	2498	1882 (7)	1890
Sandy sediments	f^3	1355	802 (5)	810	f^3	2498	1366 (12)	1374	f^2	2499	1714 (16)	1720
Temperature seasonality	f^3	1354	678 (20)	678	f^3	2498	1162 (25)	1170	f^3	2498	923 (55)	931
Final environmental model	–	1344	136 (84)	164	–	2486	361 (77)	393	–	2487	182 (91)	212
Final spatial model	–	1348	646 (76)	222	–	2495	493 (68)	513	–	2492	233 (89)	253
Adding significant spatial variables	–	1350	203 (76)	219	–	2492	493 (68)	513	–	2493	233 (89)	251
Adding environmental and spatial variables	–	1342	67 (92)	99	–	2483	281 (82)	319	–	2483	129 (94)	167

Variables were expressed as linear functions (f), quadratic functions (f^2) or cubic functions (f^3). Significant changes ($p < 0.05$, d.f.: degrees of freedom) were expressed as percentage of deviance between brackets. The Akaike information criterion (AIC) measures the fitness of each model.

function of annual average, cubic function of seasonality, and aridity index). Land use and sandy sediments (linear functions) less affected its distribution. Stepwise

analyses (Table 2) selected seasonality of precipitation and temperature, average annual temperature and rainfall, isothermality, aridity and sandy sediments (positive

Table 2: Model selection statistics and performance measures for models using logistic regression to explain geographical distribution of each armadillo species in Argentina.

	<i>Chaetophractus vellerosus</i>			<i>Chaetophractus villosus</i>			<i>Zaedyus pichiy</i>		
	Coef.	SD	Z-value	Coef.	SD	Z-value	Coef.	SD	Z-value
Annual mean temperature	1.4	0.55	2.56 ^a				-4.7	1.78	-2.64 ^b
Annual mean temperature ²				-3.48	0.69	-5.03 ^b	-3.76	0.88	-4.29 ^b
Annual mean temperature ³				-0.95	0.22	-4.23 ^b			
Annual precipitation	-8.76	3.77	-2.32 ^a				-6.32	2.02	-3.13 ^b
Annual precipitation ²	-24.55	7.21	-3.41 ^b	-3.04	1	-3.04 ^b	-4.25	1.43	-2.97 ^b
Annual precipitation ³							5.54	1.54	3.61 ^b
Aridity index				-1.91	0.57	-3.35 ^b	-2.3	0.87	-2.63 ^b
Aridity index ²				0.45	0.16	2.81 ^b	0.46	0.15	3.11 ^b
Isothermality	5.97	2.53	2.36 ^a	-3.32	0.79	-4.19 ^b			
Isothermality ²	9.13	2.26	4.04 ^b				-1.59	0.69	-2.31 ^a
Isothermality ³	-6.04	1.48	-4.07 ^b						
Latitude				-1.93	0.86	-2.24 ^a	-126.6	26.96	-4.7 ^b
Latitude ²	-0.13	0.04	-3.12 ^b				-1.55	0.34	-4.54 ^b
Latitude ³							0	0	3.86 ^b
Longitude	272.1	114.41	2.38 ^a	-230.8	68.74	-3.36 ^b	-166.3	36.21	-4.59 ^b
Longitude ²	5.65	2.35	2.41 ^a	-4.68	1.44	-3.26 ^b			
Longitude ³	0.04	0.02	2.46 ^a	-0.03	0.01	-3.08 ^b			
Longitude×latitude	0.13	0.05	2.85 ^b				-4.65	1	-4.65 ^b
Longitude×latitude ²				0	0	2.15 ^a			
Longitude ² ×latitude							-0.04	0.01	-4.61 ^b
Plant physiognomy							-1.5	0.4	-3.73 ^b
Precipitation seasonality	3.68	1.46	2.53 ^a	4.87	0.69	7.04 ^b			
Precipitation seasonality ²	3.56	1.67	2.13 ^a						
Precipitation seasonality ³				-3.44	0.59	-5.8 ^b			
Sandy sediments				0.81	0.19	4.28 ^b	0.83	0.35	2.37 ^a
Temperature seasonality				-4.06	1	-4.07 ^b			
Temperature seasonality ³							1.48	0.42	3.56 ^b

Coefficients (Coef.) and standard deviations (SD) for parameters included in the final model for each species. Z-value of the regression coefficient with the p-level (^afor $p < 0.01$ and ^bfor $p < 0.001$). ² and ³ denote quadratic and cubic terms of a curvilinear function.

effects of precipitation seasonality and sandy sediments, negative effects of the other variables). The environmental model affected 77% of total deviance. The spatial variable, considered alone, accounted for 68%. With the addition of the spatial variable to the final model (mainly longitude terms, with negative effects, Table 2), the explained deviance increased to 82% (Table 1). Spatially structured environmental variables accounted for 63% of variation in the presence of *C. villosus*, environmental variables without spatial influence accounted for 14%, 5% could correspond to some spatial structure which has not been considered, and 18% could not be explained by this model.

Temperature seasonality (cubic function) was the main variable in the distribution of *Zaedyus pichiy* and accounted for 55% of its variation (Table 1). Annual precipitation (cubic function), average annual temperature and aridity index (quadratic functions) were also relevant

variables, followed by sandy sediments. Stepwise analyses (Table 2) selected annual rainfall and average annual temperature, aridity index, temperature seasonality, isothermality, plant physiognomy and sandy sediments (positive effects of temperature seasonality and sandy sediments, negative effects of the other variables). This environmental model, the most accurate of all three species, accounted for more than 91% of the deviance. The spatial variable, considered alone, slightly less influenced over total deviance (89%). With the addition of the spatial variable to the final model (latitude as well as longitude terms, Table 2), the explained deviance increased to 94% (Table 1). Spatially structured environmental variables accounted for 86% of variation, 5% could be attributed to environmental variables without spatial configuration, <3% was affected by a spatial structure that had not been studied, and 6% was residual variation which had not been resolved by the model.

Spatial location of armadillos: optimal distribution

The final model for the distribution of *ChaetophRACTUS vellerosus* identified two optimal areas for its presence, distant 300 km one from the other (Figure 2C). The main area (1,256,179 km²) was located from 40° to 21° S and between 57° and 71° W. A least optimal area (18,536 km²), together with smaller scattered habitats, was located in Pampas grasslands. Optimal environments for *ChaetophRACTUS villosus* were situated from 25° to 50° S and between 55° and 70° W (Figure 3C). This model showed optimal habitats in the west of Patagonia, represented as several fragments. Appropriate environments were also in the east of the distribution, from 29° to 34° S and between 57° and 61° W, namely the ecoregions Mesopotamia, Pampas, Espinal, Delta and Paraná islands. The optimal habitats for *Zaedyus pichiy* had a continuous northern boundary running diagonally from 29° S in the west to 39° S in the east, occupied all of Patagonia and southern part of Espinal, Monte and Pampas (Figure 4C). In southern Patagonia, the optimal habitat was interrupted by an island of unsuitable habitat that extended from 53° to 48° S.

Discussion and conclusion

Consistent with the hierarchical structure theory in ecological systems (Pearson and Dawson 2003), climate characteristics were identified as major factors influencing the distribution of *ChaetophRACTUS vellerosus*, *ChaetophRACTUS villosus* and *Zaedyus pichiy* in the broad scale studied, the mainland Argentina.

Optimal conditions for both *ChaetophRACTUS* species were mainly arranged in a longitudinal geographic gradient. Scarcity of rainfall, concentrated in summer, and high temperatures were major factors affecting the distribution of *ChaetophRACTUS vellerosus* in Argentina, consistent with the tolerance to dry conditions and the association to warm climates expected from previous knowledge available about this species. In arid environments, precipitation is a climatic factor positively related to aboveground net primary production (Sala et al. 1988). Precipitation seasonality as a key factor for the optimal habitat of *C. vellerosus* could account for the seasonal dietary changes documented in northern populations (Gregor 1985). The distribution of the other *ChaetophRACTUS* species studied, *ChaetophRACTUS villosus*, was mainly associated to mean annual temperatures with low isothermality, followed by scarcity of rainfall with high seasonality and low aridity

conditions. Considering the previous knowledge available about *C. villosus*, the high tolerance of this species to environmental characteristics would justify that its distribution model had the lowest deviance explained of the three species studied.

The distribution of *Zaedyus pichiy* in Argentina was influenced by low temperatures with high seasonality and low annual rainfall under aridity conditions, arranged in a latitude-longitude gradient across the broad scale studied. These results were consistent with the tolerance to cold arid climate conditions expected from the previous knowledge available about this species. The strong relationship of the distribution of *Z. pichiy* with seasonality temperature agrees with its physiological adaptability to environmental temperature (Roig 1971, McNab 1985, Superina and Boily 2007). In a cool-temperate region like Patagonia, seasonal changes in temperature usually determine seasonal changes in food resources, and therefore in the diet of residents mammals (e.g. Johnson and Franklin 1991, Puig et al. 1996). Seasonal changes in the diet of *Z. pichiy*, already documented in the Monte ecoregion (Seitz 2013), are also expected in Patagonia populations.

Differing from the previous MaxEnt models (Abba et al. 2012), the present study worked with a higher number of presence-data corresponding to the three species studied and without redundant information between environmental descriptors, which allowed to detect the importance of climatic variables in optimal habitats for species. GLMs highlighted the importance of rainfall seasonality in the distribution of *ChaetophRACTUS vellerosus*, a variable previously detected to have little contribution. Redundant information could also have hidden the main role of temperature behind terrain elevation, identified as relevant variable in the previous model for *ChaetophRACTUS villosus*. GLMs for *Zaedyus pichiy* highlighted the importance of annual descriptors (pronounced temperature seasonality and aridity conditions), which are more parsimonious variables than the seasonal variables previously detected (winter temperatures and summer rainfall).

The distribution range of *ChaetophRACTUS vellerosus* modeled was larger than the previously documented (Abba and Superina 2010), extending optimal habitat to including highland ecoregions such as Puna, Yungas and High Andes to West, and Patagonia steppe to South. Our model agreed with the description of two disjunct populations (Crespo 1974, Carlini and Vizcaíno 1987), but suitable habitat of small isolated population in Pampas ecoregion was broader than current distribution. Our results support a currently retracted distribution of this species, suggested by an historically more extended southern limit for the individual locations documented in museums (Abba

and Vizcaíno 2008), probably due to recent changes in land use (Abba and Cassini 2008, Abba et al. 2011, 2012).

The distribution of *Chaetophractus villosus* optimal habitat was smaller than that previously documented (Wetzel et al. 2005, Abba and Superina 2010). Unsuitable habitat in where this species is documented, as northern Argentina (Wetzel et al. 2005, Aguiar and da Fonseca 2008) or patches of suboptimal habitat in Patagonia, could represent an artifact because of the few locations of presence has been collected. Conversely, the model included suitable environments in northeast Pampas, Espinal and Delta ecoregions, where *C. villosus* was not documented (Wetzel et al. 2005, Abba and Superina 2010). Recent studies proposed that this species would have expanded its distribution range in Patagonia during the last century, in a process led by climate temperature changes (Abba et al. 2014). If *C. villosus* is still expanding its range, identification of the environmental factors responsible for its distribution can lead to biased results (Hirzel et al. 2001). Habitat models using new data obtained by sampling at different spatial scales in Argentina will give a better understanding of the responses of *C. villosus* to spatial heterogeneity and habitat modification.

Compared to the other two species, optimal habitat modeled for *Zaedyus pichiy* was the most similar to the previously documented model (Abba and Superina 2010). However, our model showed unsuitable habitats inside Patagonia where this species has been cited, and showed appropriate habitats in southern Pampas and Espinal where it has not been observed (Abba et al. 2012). The Patagonian unsuitable habitat detected in the southernmost Argentina (~50° S) is located near the 6°C northwest-southeast isotherm (Paruelo et al. 1998) and suggests thermal restrictions to the presence of *Z. pichiy* in this area. Appropriate habitats detected by GLM but without currently documented presence were occupied by *Z. pichiy* in early Holocene (Abba and Vizcaíno 2011). Due to the sensitivity to environmental changes, *Z. pichiy* was proposed as a climate indicator (Vizcaíno et al. 1995, Tonni et al. 2006, Abba and Vizcaíno 2011), and it will be interesting to analyze its presence in this area in relation to dry climatic pulses and future climate changes.

The GLM method applied provided a useful starting point for better understanding the ecological requirements of *Chaetophractus vellerosus*, *Chaetophractus villosus* and *Zaedyus pichiy* on a biogeographic scale. Further analyses of the models obtained will allow assessing whether the main environmental factors found differ in relevance among ecoregions within the distribution range of each species. However, the complementary positive influence of sandy sediments found in three species habitat models,

as well as the influence of land use in the presence of *C. villosus*, show the relevance to consider habitat features in future models. Soil, vegetation and land use have been detected as variables influencing the presence of these species at a landscape scale (Seitz 2013), which agrees with the predicted increasing importance of habitat features further down the hierarchy, if climate conditions are satisfied (Pearson and Dawson 2003). Hierarchical models of environmental factors operating at different spatial scales are expected to provide more precise simulations of the effects of environmental changes on the distribution of these armadillo species.

Acknowledgments: We are grateful for the loan of material to Agustín Abba, Valeria Corbalán, Department of Natural Renewable Resources of Mendoza province (DRNR), Analía Foriasepi, and Mariella Superina. Special thanks to both anonymous reviewers and Agustín Abba for their valuable suggestions. Thanks to Ivana Mellado and Nelly Horak for language corrections. The research was partially supported by a grant of the Consejo Nacional de Investigaciones Científicas y Técnicas, Instituto Argentino de Investigaciones de las Zonas Áridas (IADIZA, CONICET) and Idea Wild.

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