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Distributional patterns and conservation planning for a snake assemblage from temperate South America

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A R T I C L E I N F O

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A B S T R A C T

We analyzed the spatial distribution of a snake assemblage from the Sierras de Ventania mountain range, a rich endemism area in east-central Argentina. We used field-collected and museum specimens combined with high-resolution environmental variables to identify common distributional patterns, estimate the suitable habitat for each species, and develop a conservation proposal related to the Protected Natural Areas (PNAs) system. Distributional models diverged into two opposite patterns: suitable habitats for most species at relatively high altitude in the hills, and suitable habitats for *Bothrops ammodytoides* and *Lygophis anomalus* at relatively low altitude in the surrounding hill plain. We assessed two proposals based on different conservation algorithms: the additive benefit function (ABF), which favours hilly environments, prioritizing areas with high specific richness, and the core-area zonation (CAZ), which prioritizes the distribution of all species, further indicating areas with low richness in the surrounding plain. Regardless of the algorithm used, our results indicated that the existing PNAs are not effective in protecting the snake assemblage. Protecting at least 5% of the highest species richness areas (ABF) or 5% of the distribution core areas of all species (CAZ), the existing PNAs only represented 2.2% of these priority areas. Our findings are largely consistent with previous work, highlighting that a widespread area needs to be assigned for conservation purposes. Thus, protection of the snake assemblage should take place both inside and outside the PNAs.

1. Introduction

Detailed knowledge about the geographic distribution of species is fundamental for conservation planning as well as for understanding the ecological and evolutionary constraints involved in diversity patterns (Elith et al., 2006; Ferrier & Guisan, 2006). Pioneer distribution areas were plotted by drawing polygons, grids or circles around the location points. Thus, maps indicating the presence or absence of the species under consideration were created by means of free hand, minimum convex polygon, cartographic and areographic methods (Mota-Vargas & Rojas-Soto, 2012; Rapoport, 1975). Over the last years, the generalization of geographical information systems (GIS) and the development of robust statistical techniques have generated distribution models to better understand the spatial distribution patterns of species (Elith & Leathwick, 2009).

The current rate of biodiversity extinction due to human activities is more than a thousand times higher than the average rates of extinction of the entire history of life on earth (Pimm, Russell, Gittleman, & Brooks, 1995). The Strategic Plan for Biodiversity 2010–2020 was adopted by the parties of the Convention on Biological Diversity (CBD, 2010). It contains 20 key targets, known as the Aichi Biodiversity Targets to halt biodiversity loss. The identification of priority areas for conservation and the evaluation of the effectiveness of the current Protected Natural Areas (PNAs) are among these key targets. To

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accomplish them, both detailed knowledge about biodiversity distribution and spatial mapping at high-resolution scale are required (Ferrier & Guisan, 2006; Vale et al., 2016).

Snakes have been used as study objects for distribution and habitat modelling (Jenkins, Peterson, & Kingsbury, 2009). In particular, the maximum entropy algorithm (Maxent) was extensively tested in modelling the geographic distribution of several neotropical snakes (González-Maya, Castañeda, González, Pacheco, & Ceballos, 2014; Mesquita, Pinheiro-Mesquita, & Pietczak, 2013; Nori, Carrasco, & Leynaud, 2013; Paredes-García, Ramírez-Bautista, & Martínez-Morales, 2011; Rivera, Di Cola, Martínez, Gardenal, & Chiaraviglio, 2011; Urbina-Cardona & Flores-Villela, 2010). Despite the global range of these snakes is relatively well known, there is a knowledge gap about local distribution, suitable habitats and the contribution of environmental variables derived from distribution models. In this sense, the use of high-resolution data for the development of local distribution models is crucial to improve future conservation planning (Brito et al., 2011; Vale et al., 2016). In addition, distribution and habitat models are important tools for assessing the conservation status of snakes, considering that habitat loss and fragmentation are the main causes of their worldwide decline (Gibbons et al., 2000; Jenkins et al., 2009; Reading et al., 2010).

The global network of PNAs has been growing steadily since 1992, increasing by an average of 2.5% per year (Butchart et al., 2010). Although PNAs currently cover almost 17 million km^2 worldwide (about 19% of the land area), only about 5.8% is strictly designated to protect biodiversity (Jenkins & Joppa, 2009). In recent years, snakes have been considered a good biodiversity surrogate species, so much so that they were chosen as the new model organism in ecological and conservation research (Mullin & Seigel, 2009; Shine & Bonnet, 2000). In addition, PNAs play a fundamental role in preserving them, since snakes are often killed due to exacerbated cultural fear and the assumption that all snakes are dangerous (Arzamendia & Giraudo, 2004, 2012; Dodd, 1993; Giraudo, 2001). Numerous studies have focused on facilitating the optimal selection of reserves using quantitative criteria for delimitation and definition according to habitat quality for species (Corbalán, Tognelli, Scolaro, & Roig-Juñent, 2011; Nori, Lescano et al., 2013; Tognelli, Abba, Bender, & Seitz, 2011; Urbina-Cardona & Flores-Villela, 2010). These reports pinpointed that more land area was needed to achieve the conservation goals proposed. Based on these works, we speculated that the current PNAs turned out ineffective in protecting the studied snake assemblage.

The present work analysed the spatial distribution of a snake assemblage from the Sierras de Ventania mountain range, a rich endemism area in east-central Argentina. High-resolution environmental variables were combined with precise presence data from most species of the snake assemblage to respond the following questions: 1) Can common geographical distribution patterns be recognized? 2) Which environmental variables better explain species distributions? 3) Where are located the suitable habitats for each species? 4) Which are the priority conservation areas? Finally, the information gathered was integrated to develop a conservation proposal related to the current PNAs system.

2. Material and methods

2.1. Study area

The Sierras de Ventania is an isolated orographic system of subparallel low mountain ranges located in the southwest of Buenos Aires province, Argentina (Fig. 1; Sellés-Martínez, 2001). This system covers an area of 7100 km^2 from NW to SE (Vargas Gil & Scoppa, 1973). The four main mountain ranges are Sierra de Cura Malal, Sierra de la Ventana, Sierra de las Tunas and Sierra de Pillahuincó, with maximum altitudes of 1015, 1243, 650 and 550 masl, respectively. The area has been defined as an orographic island since it is biologically rich and home to several endemic species (Cranwell, 1942; Crisci, Freire, Sancho, & Katinas, 2001; Kristensen & Frangi, 1995). Current PNAs in the region are (http://www.opds.gba.gov.ar/): the Cerro Ventana Natural Monument (Law 11750/1995; 680 ha) within the Ernesto Tornquist Provincial Park (ETPP; Law 18818/2001; 6147 ha), and the Sierras Grandes Private Natural Reserve (SGPNR; Decree 526/2013; 2742 ha).

The climate of the region is temperate (14 °C mean annual temperature) and humid-subhumid (800 mm mean annual precipitation; Burgos, 1968), with altitudinal temperature gradients decreasing by 6.9 °C/1000 m (Kristensen & Frangi, 1995) and precipitation varying from 745 mm at the base to 828 mm at the top of Sierra de la Ventana (Pérez & Frangi, 2000). Marked climatic seasonality is characterised by warm rainy summers and cold dry winters with occasional snowfall (Kristensen & Frangi, 1995). The area shows both high grass and bush diversity. Native vegetation corresponds to the Austral Pampean District (Cabrera, 1976), with more than 400 plant species, many of which are endemic (De la Sota, 1967; Frangi & Barrera, 1996; Frangi & Bottino, 1995). Although many patches have been forested with exotic forest trees, such as *Pinus* sp., *Cedrus* sp., *Acacia* sp., *Eucalyptus* sp. and *Ulmus* sp., the area still has great conservation value for its natural grasslands (Bilenca & Miñarro, 2004).

From the first herpetological list compiled for the region (Koslowsky, 1895) to subsequent records (Couturier & Grisolia, 1989; Di Pietro, Alcalde, Williams, & Cabrera, 2012; Di Pietro, 2016; Gallardo, 1968; Viñas, Daneri, & Gnida, 1989), 25 species of reptiles have been reported (one turtle, two amphisbaenids, seven lizards and 15 snakes). Of these, two are microendemic, the snake *Lygophis elegantissimus* (Koslowsky) and the lizard *Pristidactylus casuhatiensis* (Gallardo).

2.2. Occurrence data

We used specimens collected over 15-week-long study periods between February 2010 and March 2014. To enhance field records, we examined museum specimens previously collected within the study area and housed at the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (MACN, Buenos Aires), Museo de La Plata (MLP.JW and MLP.R, Buenos Aires) and Fundación Miguel Lillo (FML, Tucumán). These specimens were collected between 1895 and 2003; 88.6% were collected after 1950, matching the temporal range of the environmental data (see below). Localities of the specimens collected before 1950 were entirely coincident with localities after 1950. The field-collected and museum specimens used in this study are listed in Appendix A. Field records were georeferenced using GPS Garmin eTrex Vista. The coordinates of museum specimens in some cases were approximated by the Google Earth Pro software. Three types of distribution were considered: restricted (falling in the first quartile of frequencies), intermediate (between the first and the last quartile), and extended (in the last quartile; Langhammer et al., 2007).

2.3. Selection of predictive variables

Environmental variables were taken from the WorldClim Project site (http://www.worldclim.org/) using the highest possible resolution (30 Arc seconds, ~1 km^2 per cell). The project data bank consists of an altitude variable and 19 bioclimatic variables which represent annual and seasonal trends and extreme climatic values (see references in Table 1). These values are derived from monthly temperature and precipitation measurements obtained by meteorological stations in the period 1950–2000 and interpolated with the Anuclim software (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). In addition to the WorldClim variables, we used the annual potential evapotranspiration and the Thornthwaite aridity index (Title & Bemmels, 2018), both taken from the ENVIREM dataset (http://envirem.github.io/). All variables were processed and dimensioned according to the study area (latitude,

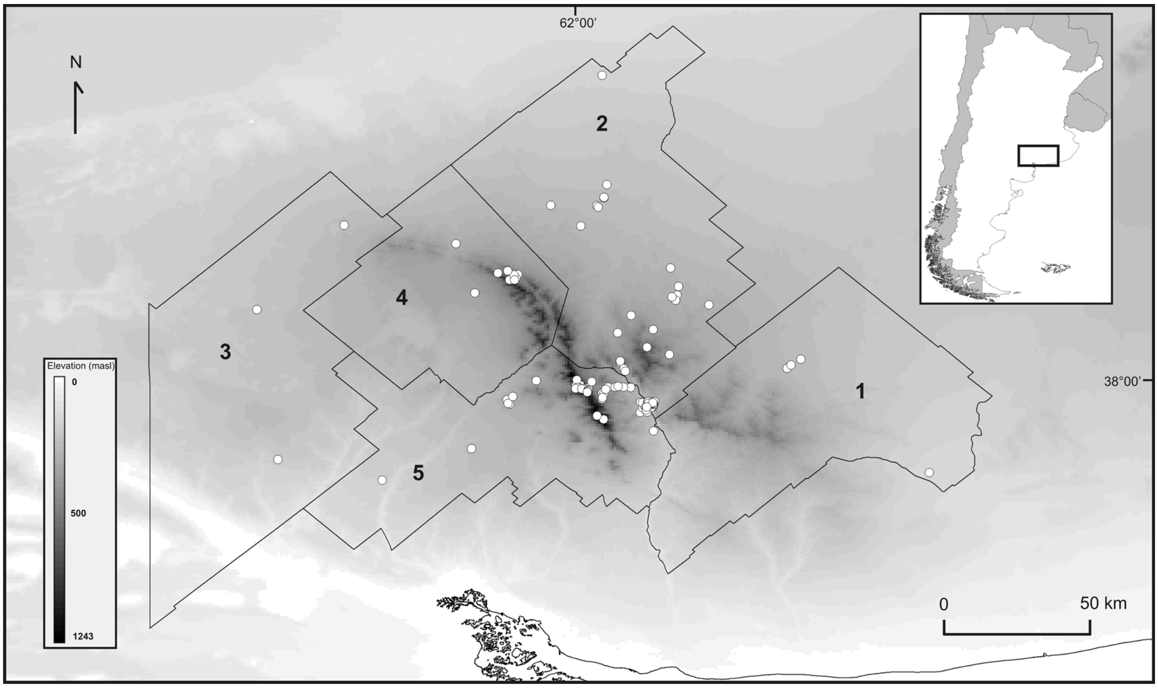

Fig. 1. Study area - Localities of the specimens examined (dots). Detail of the selected area in Buenos Aires province, Argentina, to generate the potential distribution models. References for departments: Coronel Pringles (1), Coronel Suárez (2), Puan (3), Saavedra (4) and Tornquist (5).

-38.8791 to -36.8375; longitude, -63.4541 to -60.5875; Fig. 1) using DIVA-GIS software version 7.5 (Hijmans, Guarino, & Mathur, 2012). Principal Component Analysis (PCA) was used to summarize the environmental variability of the study area (Brito et al., 2011). A set of 1000 random points based on the snake assemblage was used to extract the values of the 22 environmental variables using DIVA-GIS. Subsequently, PCA was performed using PAST software version 3.04 (Hammer, Harper, & Ryan, 2001). Since the first three components of the PCA retained much of the environmental variability of the study area (see Results), environmental variables with high loading scores (> ± 0.10) were employed for modelling purposes (Vale et al., 2016).

2.4. Distribution model and validation

The potential distribution models were generated with the Maxent software version 3.3.3k (Phillips & Dudík, 2008; Phillips, Anderson, & Schapire, 2006), which uses an algorithm based on maximum entropy to predict suitable species habitats in each landscape unit. Compared with other techniques, Maxent has a quantitatively superior performance (Elith & Leathwick, 2009; Elith et al., 2006), requires only presence data, and shows reliable results with a small number of observations (Franklin, 2011).

Modelling was carried out according to the following protocol: (1)

Table 1

Code, variable description, range, percentage of explanation of the first principal components (PC1, PC2 and PC3) and loading scores of the environmental variables derived from the Principal Component Analysis. The variables used to model the distribution (loading scores > ± 0.10) are shown in bold. Temperature units are in ˚C*10, precipitation in mm (millimeter), annual potential evapotranspiration in mm/year and altitude in masl (meters above sea level).

Code	Variable	Range (min-max)	PC1	PC2	PC3
–	% Variance explained	–	67.98	21.55	9.78
BIO1	Annual mean temperature	103-158	0.02	−0.04	0.03
BIO2	Mean diurnal range (Mean of monthly (max temp - min temp))	120-148	0.02	0.01	−0.01
BIO3	Isothermality (BIO2/BIO7) (* 100)	44-48	< -0.01	< -0.01	< -0.01
BIO4	**Temperature seasonality (standard deviation * 100)**	4775-5778	**0.95**	**0.24**	0.02
BIO5	Max temperature of warmest month	263-324	0.04	−0.01	0.04
BIO6	Min temperature of coldest month	−14-35	−0.01	−0.03	0.04
BIO7	Temperature annual range (BIO5-BIO6)	255-314	0.05	0.01	< -0.01
BIO8	Mean temperature of wettest quarter	152-223	0.01	< 0.01	0.03
BIO9	Mean temperature of driest quarter	40-90	0.01	−0.04	0.03
BIO10	Mean temperature of warmest quarter	170-229	0.03	−0.03	0.03
BIO11	Mean temperature of coldest quarter	40-90	0.01	−0.04	0.03
BIO12	**Annual precipitation**	431-882	**−0.17**	**0.58**	**0.63**
BIO13	Precipitation of wettest month	56-121	−0.03	0.07	0.07
BIO14	Precipitation of driest month	14-32	−0.01	0.01	0.01
BIO15	Precipitation seasonality (coefficient of variation)	25-41	0.01	0.01	< 0.01
BIO16	**Precipitation of wettest quarter**	139-298	−0.05	**0.21**	**0.23**
BIO17	Precipitation of driest quarter	53-137	−0.07	0.04	0.08
BIO18	**Precipitation of warmest quarter**	119-279	−0.05	**0.22**	**0.22**
BIO19	Precipitation of coldest quarter	53-137	−0.07	0.04	0.08
ALT	**Altitude**	−39-1000	**−0.13**	**0.70**	**−0.67**
PET	**Annual potential evapotranspiration**	1121.85-1391.33	**0.20**	−0.06	**0.14**
TAI	Thornthwaite aridity index	38.14-67.88	0.01	−0.04	−0.03

duplicate presence points for each cell (1 km^2) were removed (Phillips et al., 2006); (2) then, only species represented in more than five cells (sample size for which Maxent produces reliable models) were considered (Elith et al., 2006; Pearson, Raxworthy, Nakamura, & Peterson, 2007); (3) the predictive capacity of the models was maximized by selecting the options of linear and quadratic adjustment (joints) of the environmental variables, a maximum of 10,000 background points, and a regularization multiplier of 0.5. The regularization multiplier value and feature types were chosen after an initial evaluation of model performance through the area under the curve (AUC) values (see Anderson & Gonzalez, 2011; Shcheglovitova & Anderson, 2013; Vale et al., 2016); (4) the model was cross-validated using the total number of cells occupied by each species as replicate models to evaluate replicate adjustment through the average AUC value for both test (AUCte) and training (AUCtr) data, and to obtain a reliable consensus prediction of the geographic distribution (Dormann, 2007; Elith et al., 2011; Pearson et al., 2007); (5) the area covered by each species was estimated by converting the continuous presence probability maps into binary maps (suitable/unsuitable habitat) using DIVA-GIS (Hijmans et al., 2012). For this purpose, we used the 10 percentile of logistic probability values as the cut-off threshold; thus, cells with presence probability less than 10% of said values (possibly representing extreme habitat conditions or ephemeral populations) were classified as unsuitable habitats (Buckley et al., 2010; Morueta-Holme, Fløjgaard, & Svenning, 2010). Therefore, cell counting (1 km^2) using DIVA-GIS allowed us to estimate the suitable habitat for each species within the study area.

Finally, the relative contribution of each environmental variable to the distribution models was estimated by calculating the percentage increase of gain during the optimization phase of the model through Maxent iterations, and by calculating the gain only with the variable and without the variable, using the Jackknife method (Phillips et al., 2006).

2.5. Conservation priority areas

The Zonation software version 4 (Moilanen et al., 2014) was used to identify the conservation priority areas for the snake assemblage by integrating information from the potential distribution maps. Landscape connectivity was maintained since this software removes lower value cells from the periphery of the interest area (Moilanen et al., 2014). The value of cells is defined by the number of species present and their relative importance. The value of the remaining cells and the percentage of removed area are re-calculated for each species during successive iterations of the software in order to obtain a landscape management, where regions with more presence of important species receive greater values (Moilanen et al., 2014). Following the current national conservation categorization for snakes which prioritizes endemic and threatened species (Giraudo et al., 2012), we used a logarithmic rating scale (Fiorella, Cameron, Sechrest, Winfree, & Kremen, 2010), giving ten times the weight to microendemic *Lygophis elegantissimus* and five times the weight to partially endemic *Epictia australis* and threatened *Philodryas agassizii* species. Snakes with non-modelled distributions (i.e., present in less than five cells) were included in the analysis as species of special interest (SSI) and their coordinates were managed by the software as equivalent to cells of the potential distribution maps (Moilanen et al., 2014). Two different Zonation cell removal algorithms were employed to choose the best conservation proposal for the area of interest (Moilanen et al., 2014). The core-area zonation (CAZ) algorithm (Moilanen et al., 2005; Moilanen, 2007) removes cells of lowest occurrence values for each species. This means that only the core areas of the geographic distribution of all the species considered are retained. The additive benefit function (ABF) algorithm (Moilanen, 2007) prioritizes areas that maintain specific richness, even if areas of particular species are lost, minimizing the extinction rate through the species-area curve. Because ABF adds all species, the number of species in a cell has a greater significance compared with CAZ.

The correspondence between the priority areas identified here for snake conservation and the existing PNAs in the study area was assessed, resulting in at least 5% of the priority areas with higher conservation values selected for protection (Prendergast, Quinn, Lawton, Eversham, & Gibbons, 1993). Subsequently, the percentage of these priority areas represented within the current system of PNAs was quantified using DIVA-GIS.

3. Results

3.1. Distribution models

The first three PCA components explained 99.32% of the variance of the study area (Table 1). We found six environmental variables with high loading scores (> ± 0.1), four bioclimatic (BIO4, BIO12, BIO16 and BIO18), altitude (ALT) and annual potential evapotranspiration (PET). Thus, these environmental variables were the most informative to generate the potential distribution models (Table 1). The total number of examined specimens of all species (n = 380) allowed us to determine the studied snake assemblage for 159 different sites (Table 2). The comparative analysis of sites and species showed that six species (*Xenodon semicinctus*, *Epictia munoai*, *Paraphimophis rusticus*, *Phalotris bilineatus*, *Philodryas aestiva* and *Philodryas agassizii*) had a restricted distribution (2–4 cells), five (*Xenodon dorbignyi*, *Bothrops ammodytoides*, *Oxyrhopus rhombifer*, *Epictia australis* and *Lygophis anomalus*) had an intermediate distribution (6–13 cells), and four (*Philodryas patagoniensis*, *Bothrops alternatus*, *Erythrolamprus poecilogyrus* and *Lygophis elegantissimus*) had an extended distribution (16–31 cells). Most species with a restricted distribution (*P. bilineatus*, *P. agassizii*, *P. aestiva* and *X. semicinctus*) were recorded in localities very close to each other, while *E. munoai* and *P. rusticus* were recorded relatively distant from each other. Intermediate and extended distribution species matched the requirements to generate potential distribution models, as they were represented in between six and 31 unique sites (mean 15.33; Table 2). Thus, the models obtained for these taxa revealed a high predictive capacity, with AUCte and AUCtr values between 0.82 and 0.95 and 0.84 and 0.96, respectively (Table 2).

The potential distribution of these nine species was obtained by projecting the models into the geographic space of the study area (Fig. 2). The probability of presence of most species was very high in hilly environments and gradually decreased towards the surrounding plain. Although this pattern of distribution was evident in most of the studied snakes, *B. ammodytoides* and *L. anomalus* showed an inverse pattern, with a high probability of occurrence in the surrounding plain and a trend towards low probability in the hilly environment (Fig. 2b, e). Each species of the studied snake assemblage presented relatively similar suitable habitats (Table 2, Fig. 2). *Xenodon dorbignyi* had the lowest occurrence value, followed by *B. alternatus* and *E. poecilogyrus*. Conversely, *E. australis* had the highest occurrence value, followed by *L. anomalus* and *B. ammodytoides*.

The relative contribution of each environmental variable to the models revealed that, on average, ALT had the highest contribution, followed by PET and precipitation of warmest quarter (BIO18). The rest of the variables had a lower contribution (≤ 2%; Table 2, Fig. 3a). Within species, ALT had the highest contribution in most cases. However, BIO18 and PET had the highest contribution in *L. anomalus* and *X. dorbignyi*, respectively (Table 2). A similar pattern was obtained using Jackknife (Table 2, Fig. 3b). Although the alternative omission of variables did not substantially affect the results of the models, ALT omission represented the greatest decrease of gain and therefore the greatest amount of information (Table 2, Fig. 3b).

We found different trends between probability of presence and variables identified as the most informative. For example, when considering only the most informative variable (ALT), *E. australis*, *O.*

Table 2
Modelling results obtained with the Maxent algorithm. For each species we present the number of collection sites (N), AUC values for training (AUCtr) and test (AUCte) data, suitable habitats in km^2 (SH), and percentage contribution of the environmental variables (ALT, BIO4, BIO12, BIO16, BIO18 and PET; see references in Table 1). Numbers in brackets indicate the percentage gains in the models with the Jackknife method (without the variable/only with the variable).

Species (N)	AUCtr	AUCte	SH	ALT	BIO4	BIO12	BIO16	BIO18	PET
B. alternatus (18)	0.96	0.95	8841	70.57(89.39/92.66)	1.49(96.51/6.05)	0.04(100/15.09)	0.02(100/13.08)	1.78(100/14.13)	26.10(94.12/64.28)
B. ammodytoides (7)	0.87	0.82	15134	81.17(31.40/56.55)	1.25(99.13/1.79)	0(100/4.97)	17.13(96.58/6.50)	0(100/3.64)	0.45(99.93/2.50)
E. australis (10)	0.90	0.89	39391	74.73(90.85/91.84)	0.13(99.55/7.19)	0(100/4)	0.07(100/3.13)	0.13(99.95/4.95)	24.94(94.67/70.60)
E. munoai (3)	–	–	–	–	–	–	–	–	–
E. poecilogyrus (27)	0.95	0.95	9183	64.60(95.09/89.12)	0.21(99.36/11.06)	0.23(99.69/24.41)	< 0.01(100/22.84)	1(99.64/21.68)	33.95(96.99/77.65)
L. anomalus (13)	0.84	0.83	27794	17.61(90.73/57.51)	0.04(100/12.05)	0.07(99.86/31.65)	0.07(100/31.18)	43.85(89.98/42.95)	38.36(92.05/40.19)
L. elegantissimus (31)	0.94	0.93	11650	59.66(97.34/88.01)	0.10(100/10.58)	1.80(97.92/34.37)	0.10(100/31.91)	4.48(98.41/32.55)	33.86(98.16/68.01)
O. rhombifer (10)	0.96	0.95	10778	77.70(99.79/91.13)	0.69(98.28/4.63)	0.49(99.98/6.69)	0.05(100/6.31)	3.37(98.95/8.61)	17.70(93.67/70.83)
P. rusticus (4)	–	–	–	–	–	–	–	–	–
P. bilineatus (4)	–	–	–	–	–	–	–	–	–
P. aestiva (4)	–	–	–	–	–	–	–	–	–
P. agassizii (4)	–	–	–	–	–	–	–	–	–
P. patagoniensis (16)	0.93	0.92	11258	63.36(91.75/85.82)	1.37(96.64/5.81)	0.78(99.18/10.59)	0.57(100/9.66)	7.84(96.92/13.48)	26.07(91.75/52.96)
X. dorbignyi (6)	0.95	0.95	8438	45.75(99.98/77.60)	1.95(94.85/9.79)	0(100/4.18)	0(100/2.78)	0.88(99.77/4.38)	51.42(83.06/80.68)
X. semicinctus (2)	–	–	–	–	–	–	–	–	–
Average	0.92	0.91	15829.66	61.68(87.37/81.14)	0.80(98.26/7.66)	0.38(99.62/15.11)	2(99.62/14.15)	7.04(98.18/16.26)	28.10(93.82/58.63)

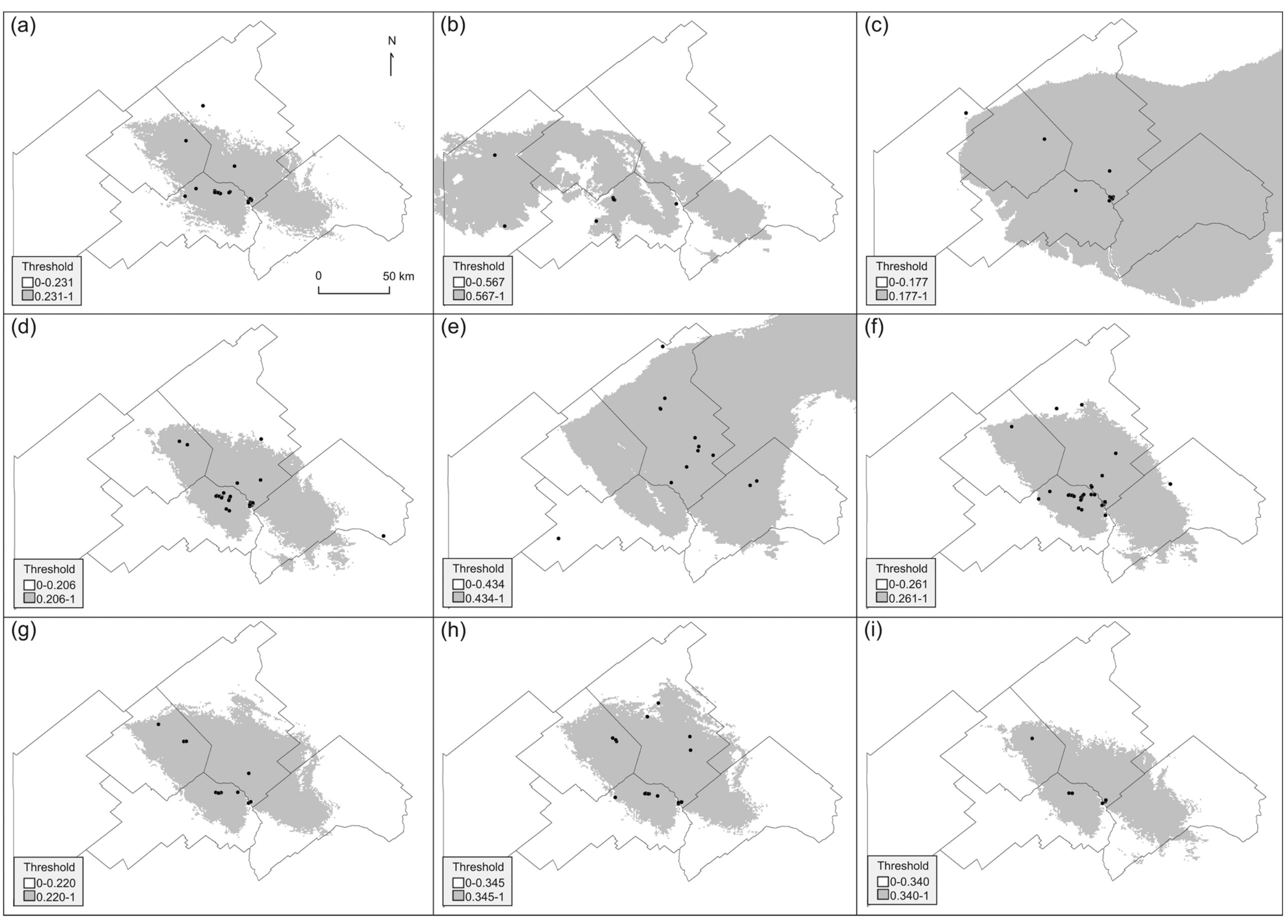

Fig. 2. Potential distribution models in binary output (suitable habitats) for *Bothrops alternatus* (a), *B. ammodytoides* (b), *Epictia australis* (c), *Erythrolamprus poecilogyrus* (d), *Lygophis anomalus* (e), *L. elegantissimus* (f), *Oxyrhopus rhombifer* (g), *Philodryas patagoniensis* (h), and *Xenodon dorbignyi* (i). Dots indicate the known localities of each species within the study area.

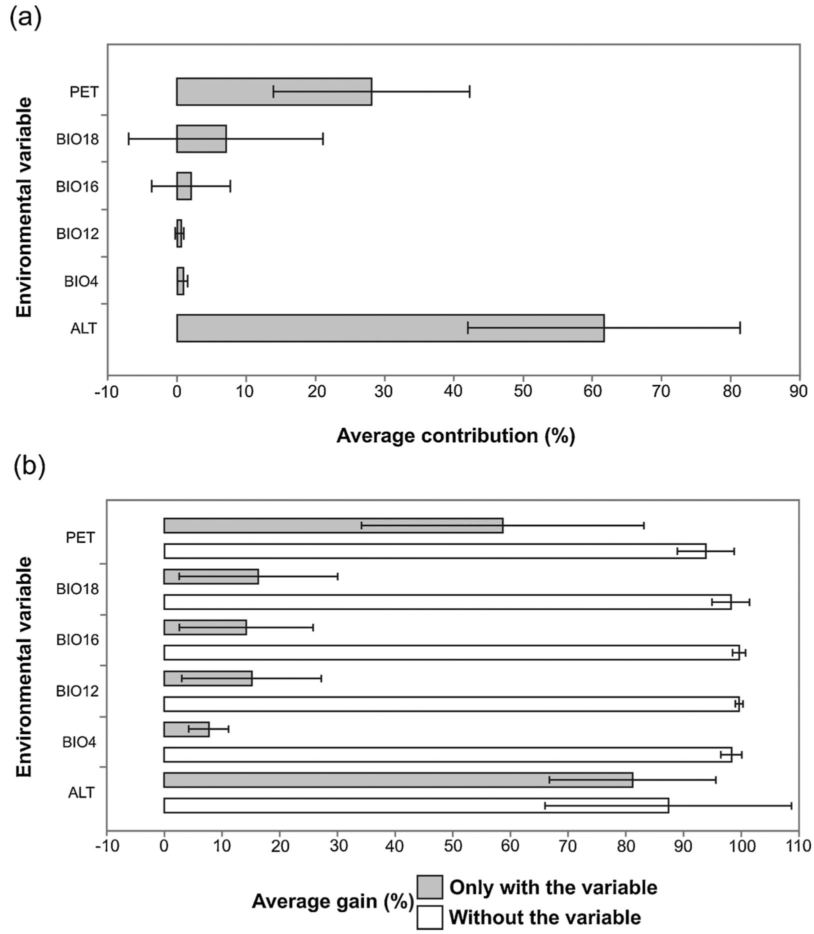

Fig. 3. Contribution of each environmental variable to the potential distribution models. Percentage contribution (a) and Jackknife method (b). Bars indicate the average gain of the models and lines show the standard deviation. References to variables are described in Table 1.

rhombifer and *X. dorbignyi* showed a sigmoid increment of probability of occurrence when ALT increased (Fig. 4c, g, i). However, this probability reached a maximum at different ALT levels in the other species (basal in *L. anomalus* and *B. ammodytoides* and intermediate in *B. alternatus*, *E. poecilogyrus*, *L. elegantissimus* and *P. patagoniensis*; Fig. 4).

3.2. Conservation proposal

Two conservation proposals were generated considering the priority areas obtained by alternative cell removal algorithms (ABF and CAZ; Fig. 5). These analyses revealed that the best areas to protect the snake assemblage (conservation values between 0.95 and 1) covered a total of 4176 km^2, representing only 1.3% of the Buenos Aires province territory.

The ABF algorithm indicated that the most important conservation areas were associated with the hilly environments in the Sierras de Ventania mountain range (south of Coronel Suárez department, west of Coronel Pringles department, east of Saavedra department, and northeast of Tornquist department; Fig. 5a, b). Alternatively, CAZ showed similar areas, although with smaller extension in the hilly environments at the expense of extending the priority areas to particular sectors of the surrounding plain (centre of Coronel Suárez and Puan departments; Fig. 5c, d). The distribution of both conservation areas was strongly influenced by the presence of endemic and/or threatened species (*L. elegantissimus*, *E. australis* and *P. agassizii*), which received a higher prioritization coefficient.

Comparison of the conservation areas selected for this study and the current ETPP areas of the province revealed that only 1.6% of the priority areas were represented in the ETPP. When the recently created SGPNR was considered, the percentage increased slightly to 2.2% (Fig. 5b, d). Although scarcely, both PNAs coincided geographically with the priority areas proposed here for the conservation of the Sierras de Ventania snake assemblage.

4. Discussion

4.1. Distribution models

The models obtained for the nine species with intermediate to extended distribution (six or more cells) had highly predictive AUC values (Phillips et al., 2006). It is widely known that AUC values vary in relation to the size of the area under study; therefore, this statistic should be avoided in distribution models comparing areas of variable size (Jiménez-Valverde, Lobo, & Hortal, 2008; VanDerWal, Shoo, Graham, & Williams, 2009). In the present study, species were modelled using the same area size. Accordingly, predictive AUC values as well as suitable habitat areas for each species were similar.

The projection of our distributional models into the geographic space of the study area diverged into two opposite patterns of suitable habitats according to the snake assemblage species studied: (1) suitable habitats for *B. alternatus*, *E. australis*, *E. poecilogyrus*, *L. elegantissimus*, *O. rhombifer*, *P. patagoniensis* and *X. dorbignyi* at relatively high altitude in the hills, and (2) suitable habitats for *B. ammodytoides* and *L. anomalus* at relatively low altitude in the surrounding hill plain. Most species corresponding to the first pattern (*E. poecilogyrus*, *O. rhombifer*, *P. patagoniensis* and *X. dorbignyi*) are present throughout the entire province of Buenos Aires (Williams, 1991), making it difficult to draw comparisons. However, the first pattern confirmed previous records of

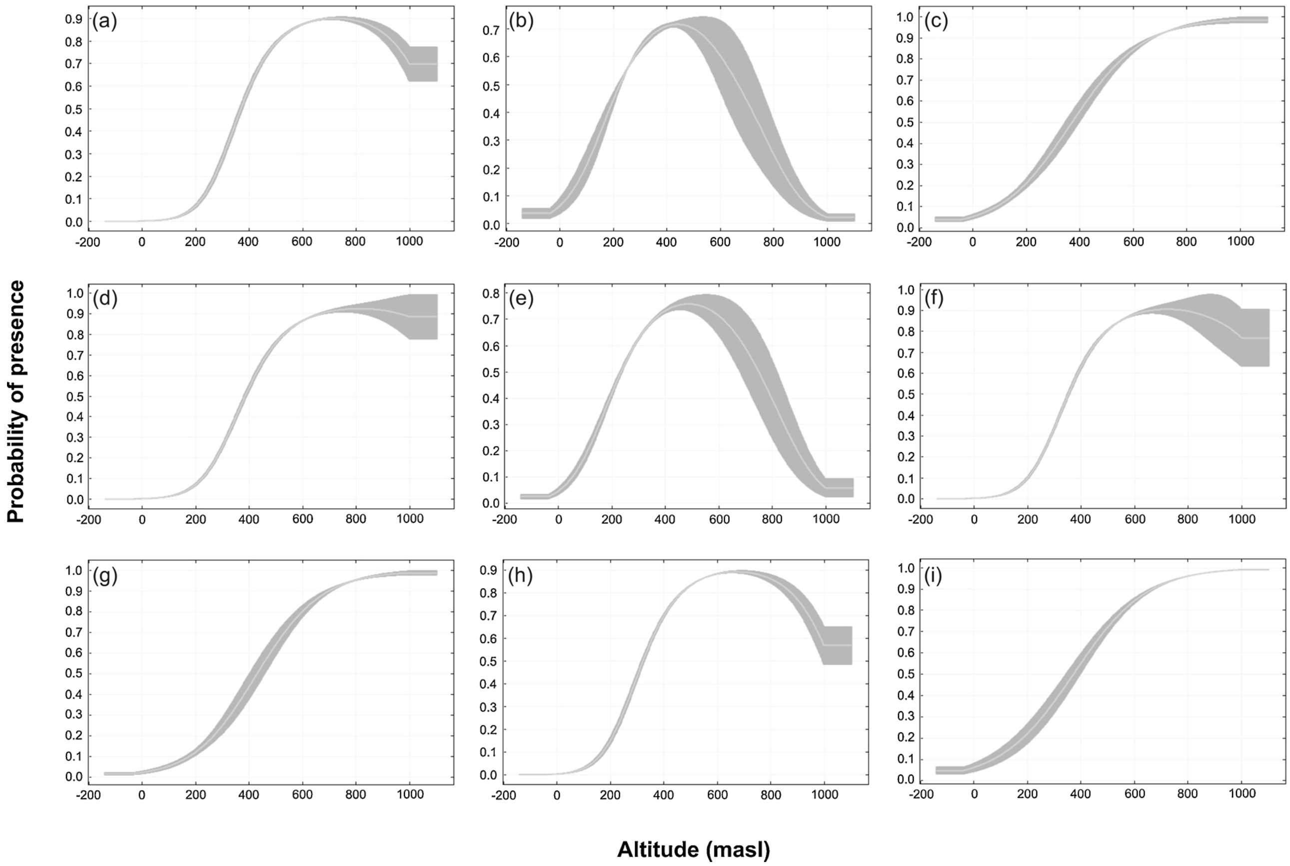

Fig. 4. Response curves of *Bothrops alternatus* (a), *B. ammodytoides* (b), *Epictia australis* (c), *Erythrolamprus poecilogyrus* (d), *Lygophis anomalus* (e), *L. elegantissimus* (f), *Oxyrhopus rhombifer* (g), *Philodryas patagoniensis* (h) and *Xenodon dorbignyi* (i) using only altitude as predictor of the distribution. Lines indicate the average values and the shaded area the standard deviation.

microendemic species such as *L. elegantissimus* (Cranwell, 1942) and isolated populations as *B. alternatus* (Barrio & Miranda, 1966; Barrio, 1961) and *E. australis* (Scrocchi, 1990) in the study area. Probably, the same applied for *P. aestiva* and *P. agassizii* (Couturier & Grisolia, 1989; Viñas et al., 1989, respectively), although it could not be confirmed with precise models due to the scarcity of data for these species.

With respect to the second distribution pattern, our models in general agreed with the maps by Dixon (1985) and Williams (1991) for *L. anomalus* and Barrio (1961) for *B. ammodytoides*. However, they predicted a range extension for the former species and, conversely, a range restriction for the latter. Further, the probability of presence of both species in hilly environments was notably low. Regarding *B. ammodytoides*, a similar situation was observed in several localities of the Sierras de Tandilia, Argentina, where this species was never recorded, although it is present in the surrounding plains (Vega & Bellagamba, 1990).

We found that ALT was the most informative variable for the construction of the distribution models, followed by PET and BIO18. Typically, ALT involves non-random changes in numerous components of the climate and local environment, which ultimately determine diversity patterns along the altitudinal gradient (Lomolino, 2001). Considering the available data for this study, the altitude of the Sierras de Ventania and surrounding areas is strongly correlated with three climatic variables (BIO1, BIO9 and BIO11; see Table 1). Together, they reflect the environmental characteristics determining the potential distribution of several snake species (González-Maya et al., 2014; Mesquita et al., 2013; Nori, Carrasco et al., 2013; Paredes-García et al., 2011; Rivera et al., 2011; Urbina-Cardona & Flores-Villela, 2010). However, the selection of variables was limited by data availability and resolution. According to Kristensen and Frangi (1995), and accepting the life zones proposed by Holdridge (1987), the basal localities in the area of Sierra de la Ventana (e.g., Sierra de la Ventana, Tornquist) correspond to the warm temperate dry forest, while the lower limit (12 °C) of the mountain floor is at 750 masl, where communities of hilly grasslands such as meadows of height and grasslands of *Festuca pampeana* and *F. ventanicola* are more important. Excluding all variables and considering only ALT as a predictor variable of distribution, the probability of presence of most species (including the microendemic species *L. elegantissimus* and the isolated population of *B. alternatus*) reaches a maximum peak at basal or intermediate altitudes, corresponding to the warm temperate dry forest (approximately 400 masl for *B. ammodytoides* and *L. anomalus* and 700 masl for *B. alternatus*, *E. poecilogyrus*, *L. elegantissimus* and *P. patagoniensis*). The unimodal relationship pattern between species richness and elevation, with a peak at low or medium altitudes, would be applicable to a wide variety of taxa, including snakes (Fu et al., 2007; Lomolino, 2001; McCain, 2010). In the rest of the species modelled here, including the partially endemic species *E. australis*, the probability of presence showed a sigmoid-type response function and reached a maximum at higher altitudes, in concordance with the warm temperate mountain floor (approximately 1000 masl for *E. australis*, *O. rhombifer* and *X. dorbignyi*).

4.2. Conservation proposals

Our results revealed that mountain areas presented greater diversity than adjacent plains as a result of physical heterogeneity, making it feasible to conserve large amounts of diversity in a relatively concentrated geographic space (Fu et al., 2007; Lafon, 2004). In the present study, we compared two conservation proposals based on different algorithms or cell removal rules in order to determine the most

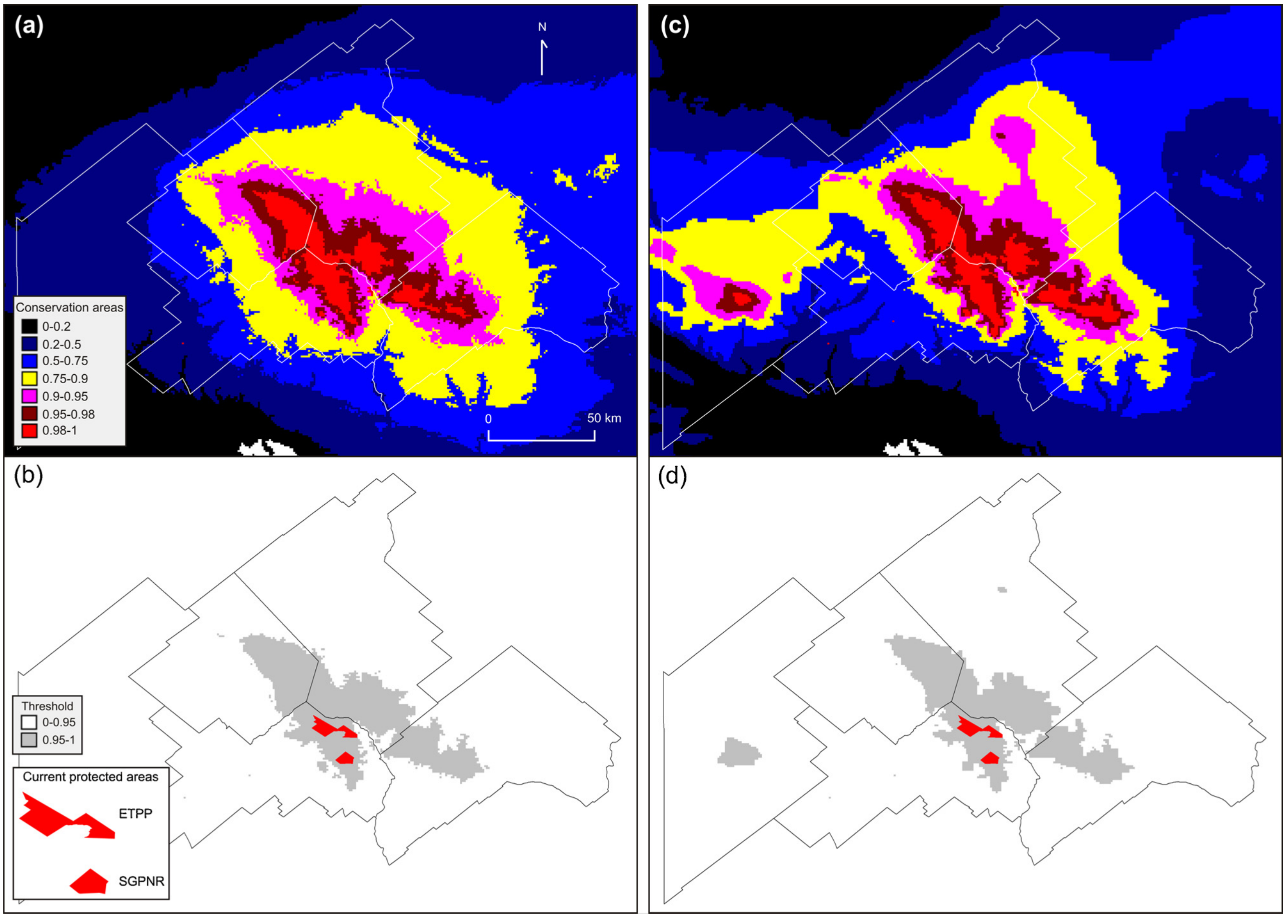

Fig. 5. Conservation priority areas based on ABF (a, b) and CAZ (c, d) Zonation algorithms. Values close to one indicate more priority areas. Detail of the selected area to protect the snake assemblage with values between 0.95 and 1, and polygons of the PNAs (b, d). See references for departments in Fig. 1.

appropriate option for the area of interest (Moilanen et al., 2014). The ABF algorithm favoured hilly species since all cells containing the species that occupy the surrounding plain environment were discarded in the analysis, minimizing the extinction rate and prioritizing areas with high specific richness. On the other hand, the CAZ algorithm prioritized the occurrence of all species, giving importance to the geographic distribution core areas (high probability of presence), and therefore also indicating specific low richness areas in the surrounding plain, thus minimizing biological loss. Due to the biogeographic island condition of the Sierras de Ventania (Cranwell, 1942; Crisci et al., 2001) and the fact that snakes were proposed as a good surrogate species for biodiversity conservation (Arzamendia & Giraudo, 2004; Giraudo, 2001), we considered that the ABF-based proposal was the most appropriate (Moilanen et al., 2014). Although environments of some species were missing in the surrounding plain (*B. ammodytoides*, *L. anomalus* and *X. semicinctus*), the ABF algorithm better represented the habitat of endemic and/or threatened species (*L. elegantissimus*, *E. australis* and *P. agassizii*), which received a higher prioritization coefficient. In addition, this conservation proposal fitted the objectives of size, shape and distance between reserves settled by the theory of island biogeography and associated biogeographic theories (Diamond, 1975; MacArthur & Wilson, 1967; Wilson & Willis, 1975).

It has been proposed that PNAs play a key role in the conservation of viable snake populations, mostly due to direct snake removal by most people who regard them as dangerous animals (Arzamendia & Giraudo, 2004, 2012; Giraudo, 2001). However, our models showed that the existing PNAs are not very effective in protecting the snake assemblage of Sierras de Ventania. The current PNAs limits were established primarily as a result of logistic reasons based on anthropic or geographic elements, which do not necessarily reflect suitable habitats and proper conditions to favour the species (Araújo & Williams, 2000). We found that in protection areas with conservation values between 0.95 and 1 (5% of the highest species richness areas using ABF, or 5% of the core area of all species using CAZ), the operative ETPP of Sierras de Ventania represented only 1.6% of these priority areas. If the recently created SGPNR area was also considered, then the percentage increased to 2.2%. Although the conservation value for the requirements of the studied snake assemblage was low, the current natural reserves of the area are located in areas of high conservation impact. Nevertheless, our results highlight the need of assigning a larger area for conservation purposes (e.g., Corbalán et al., 2011; Nori, Lescano et al., 2013; Tognelli et al., 2011; Urbina-Cardona & Flores-Villela, 2010).

Finally, we found that the zone of higher interest for conservation of the studied snake assemblage represents a continuous and very extensive amount of land mostly corresponding to private farms that, unfortunately, would never be entirely set apart for conservation purposes. Nevertheless, if our conservation proposal were taken into account by government agencies, the protection of the Sierras de Ventania snake assemblage should be carried out both inside and outside the PNAs. The design of an appropriate social and economic incentive system together with the execution of innovative and biodiversity-friendly land management systems would be necessary to achieve this goal.

Competing interests

The authors declare no competing interests.

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Appendix A. Specimens studied and voucher information

Scolecophidia, Leptotyphlopidae

Epictia australis (Freiberg's Blind Snake). Argentina: Buenos Aires province: Coronel Suárez department, Villa La Arcadia, around of Cerro Ceferino, MLP.R.6217–18, 6221–35; Sierra de las Tunas and Provincial Route 76, Ea. la Morocha, MACN 34548. Puan department, Cerritos de Puan, MACN 36774 A, B. Saavedra department, Cerro Cura Malal, 10 km E Dufaur, MACN 36773. Tornquist department, Sierra de la Ventana, MACN 25080, 32564, 32909–17, 32942–54, 34521, 36775, FML 01609 A, B; Ernesto Tornquist Provincial Park, base of Cerro Ventana and Provincial Route 76, MLP.R.6219.

Epictia munoai (Rio Grande do Sul Blind Snake). Argentina: Buenos Aires province: Coronel Suárez department, Villa La Arcadia, around of Cerro Ceferino, MLP.R.6220. Saavedra department, Saavedra, MLP.JW.1018. Tornquist department, Sierra de la Ventana, MACN 12487 (paratype).

Colubridae, Dipsadinae

Erythrolamprus poecilogyrus. Argentina: Buenos Aires province: Coronel Pringles department, Indio Rico, MLP.R.6163. Coronel Suárez department, Quiñihual, headwaters of Quiñihual stream, MACN 27316; D´Orbigny, MACN 28811, 32261; Sierra de las Tunas and Provincial Route 76, MLP.R.6173; Villa La Arcadia, around of Cerro Ceferino, MLP.R.6138, 6148–49, 6152–53, 6157–58, 6164–65, 6169–70, 6174, 6177, 6180, 6182–84, 6186–87. Saavedra department, Cerro Cura Malal Chico, MLP.JW.0309; base of Cerro Cura Malal Grande, MLP.R.6189. Tornquist department, Abra de la Ventana, MACN 7442, 20830, MLP.JW.0751; Cerro Tres Picos, MACN 24873, 25885–86; Cerro Tres Picos rocky pools, MACN 9689; Ernesto Tornquist Provincial Park, MLP.JW.0442, MLP.R.6151, 6156, 6162, 6167–68, 6175–76, 6181; Ernesto Tornquist Provincial Park, base of Cerro Bahía Blanca and Provincial Route 76, MLP.R.6155, 6185, 6188; Ernesto Tornquist Provincial Park, base of Cerro Ventana and Provincial Route 76, MLP.R.6150, 6160; Ernesto Tornquist Provincial Park, road to Cueva del Toro, MACN 32820, 32822; Ernesto Tornquist Provincial Park, Villa Ventana, Belisario stream, MLP.R.6166; Ernesto Tornquist Provincial Park, between Cuesta de la mesa and park refuge, MACN 32819, 32828–29; Sierra de la Ventana, MACN 22168, 34476, 34488, 34505 A, B, MLP.JW.0156, 0474, 0811, 1515, 1529, 1545, 1561, 1593, 1695, 1715, 1801, 1866, 1868, MLP.R.6161, 6172; Sierra de la Ventana, Abra de los Vascos, MACN 28810; Sierra de la Ventana, Atravesado stream, MACN 28813; Sierra de la Ventana, El Paraíso camping, MLP.R.6159; Sierra de la Ventana, Sierra Ventura camping, MLP.R.6154; Sierra de la Ventana, Yamila camping, MLP.R.6179; Sierra de la Ventana, Sauce Grande river, MACN 7341–42, MLP.JW.1502–03, MLP.R.6171, 6178; Villa Ventana, road to Hotel Provincial, MLP.JW.0961; Villa Ventana, dam of Belisario stream, MACN 14279.

Lygophis anomalus. Argentina: Buenos Aires province: Coronel Pringles department, Coronel Pringles, Pillahuincó stream, MLP.R.5503, 6119. Coronel Suárez department, las Tunas stream and Provincial Route 76, MLP.R.6116–18, 6133; D´Orbigny, MACN 24469, 31303, 31438, 32262, 32279–80; Ea. El Relincho, MACN 36079; Ea. El Triunfo, MACN 27841–42, 28799; Huanguelen, Ea. Las Nenas, MACN 24444; headwaters of las Tunas stream, MACN 27315; Quiñihual, MACN 28305. Tornquist department, Chasicó, MLP.JW.0856.

Lygophis elegantissimus. Argentina: Buenos Aires province: Coronel Pringles department, Coronel Pringles, Pillahuincó stream and Provincial Route 51, MLP.R.6216. Coronel Suárez department, las Tunas stream and Provincial Route 85, MLP.R.6195; Cerro las Tunas, MACN 24470, 33009; Cerro las Tunas, Ea. El Relincho, MACN 32956–57; Coronel Suárez, MLP.JW.0097; Cura Malal, MACN 195 A; Sierra de las Tunas, MACN 29185; Sierra de las Tunas, headwaters of las Tunas stream, Ea. Peñaflor, MACN 27315; Sierra de las Tunas and Provincial Route 76, MLP.R.6191; Sierra de las Tunas, Provincial Route 76, Ea. El Perdido, MACN 34563; Sierra de las Tunas, Provincial Route 76, Ea. El Relincho, MACN 34564; Villa La Arcadia, around of Cerro Ceferino, MLP.R.6005, 6192–93, 6197–02, 6204, 6206–11, 6213, 6241. Saavedra department, Pigüé, MACN 2747; Pigüé, Sierra de Cura Malal, Ea. La Bloqueada, MACN 34540. Tornquist department, Abra de la Ventana, MACN 7440–41, 20829; Cerro Tres Picos, MACN 24874; Cerro Tres Picos rocky pools, MACN 9691; Cordón Esmeralda, Provincial Route 72 intersection with Provincial Route 76, MLP.R.6205, MACN 32541–42; Ernesto Tornquist Provincial Park, MLP.JW.0946, MLP.R.6215; Ernesto Tornquist Provincial Park, base of Cerro Bahía Blanca and Provincial Route 76, MLP.R.6196; Ernesto Tornquist Provincial Park, base of Cerro Ventana and Provincial Route 76, MLP.R.6203, 6214; Ernesto Tornquist Provincial Park, Cordón Esmeralda, MLP.R.6194; Ernesto Tornquist Provincial Park, Villa Ventana, Belisario stream, MLP.R.6212; Saldungaray, MACN 6446; Sierra de la Ventana, MACN 195 B, 2658, 3007, 6447, 16775, 27305, 34504, MLP.JW.0713, 0715, 0835, 1930, MLP.R.6190; Sierra de la Ventana, Ea. Fortín Chaco, MACN 30303; Sierra de la Ventana, Ea. Montoriano, MLP.JW.0714; Tornquist, MACN 1259; Villa Ventana, MACN 32832; Villa Ventana, dam of Belisario stream, MACN 14280; Villa Ventana, Hotel Provincial, MLP.JW.0472–73. No specific collection locality, MACN 0850, 30008.

Oxyrhopus rhombifer (Amazon False Coral Snake). Argentina: Buenos Aires province: Coronel Suárez department, Sierra de las Tunas, MACN 29626, 33464; Villa La Arcadia, MLP.R.6552–53. Saavedra department, Pigüé, MACN 44822; Sierra de Cura Malal, 46 km E Saavedra, MACN 29059; base of Cerro Cura Malal Grande, MLP.R.6132. Tornquist department, Abra de la Ventana, MACN 9690, 20832–33; Ernesto Tornquist Provincial Park, MACN 12783; Ernesto Tornquist Provincial Park, base of Cerro Bahía Blanca, MLP.R.6120; Sierra de la Ventana, MACN 34497; Sierra de la Ventana, Cordón Esmeralda, MLP.R.5504; Sierra de la Ventana, Ea. Laurina, MACN 37232.

Paraphimophis rusticus. Argentina: Buenos Aires province: Coronel Suárez department, Sierra de las Tunas and Provincial Route 76, MLP.R.6127. Saavedra department, base of Cerro Cura Malal Grande, MLP.R.6128. Tornquist department, Cerro Tres Picos, MACN 33555; Sierra de la Ventana, MACN 34583.

Phalotris bilineatus. Argentina: Buenos Aires province: Tornquist department, Ernesto Tornquist Provincial Park, MACN 32886; Sierra de la Ventana, MLP.JW.0620, MLP.R.5640, 6129.

Philodryas aestiva (Common Green Racer). Argentina: Buenos Aires province: Tornquist department, Complejo Turístico el Pinar, MACN 33197; Hotel La Espadaña, MACN 31675; Sierra de la Ventana, MACN 37430, MLP.R.6051.

Philodryas agassizii (Burrowing Night Snake). Argentina: Buenos Aires province: Tornquist department, Ernesto Tornquist Provincial Park, FML 16269, MACN 31773; Sierra de la Ventana, MACN 31772, 31774.

Philodryas patagoniensis (Patagonia Green Racer). Argentina: Buenos Aires province: Coronel Suárez department, Bajo del Cura, between Sauce Corto and Cura Malal streams, MACN 27840; Coronel Suárez, MACN 28117, 38737; Provincial Route 76 intersection with Provincial Route 85, MLP.R.6140; D´Orbigny, MACN 14281, 23527, 27467, 32236, 35339, 35742–43; D´Orbigny, Ea. Sauce Corto, MACN 18575; D´Orbigny, Ea. Santa Marta, MACN 21728; D´Orbigny, Ea. San Pablo, MACN 27317; Villa La Arcadia, around of Cerro Ceferino, MLP.R.5926, 5955, 6136–37. Saavedra department, base of Cerro Cura Malal, MLP.R.6142–44, 6146–47. Tornquist department, Abra de la Ventana, MACN 20831, 30012; Ernesto Tornquist Provincial Park, base of Cerro Bahía Blanca and Provincial Route 76, MLP.R.6240; Ernesto Tornquist Provincial Park, base of Cerro Ventana and Provincial Route 76, MLP.R.6134–35, 6139, 6141; Ernesto Tornquist Provincial Park, between Cuesta de la mesa and park refuge, MACN 32830–31; Sierra de la Ventana, MACN 32941, 35401, 38705, MLP.JW.1901–03, 1905, MLP.R.6145; Sierra de la Ventana, Ea. Laurina, MACN 38694; Tornquist, MLP.JW.1655; Villa Ventana, MACN 34822.

Xenodon dorbignyi (South American Hognose Snake). Argentina: Buenos Aires province: Coronel Suárez department, Villa La Arcadia, MLP.R.6125, 6554–55. Saavedra department, Cerro Cura Malal Chico, MLP.JW.0508. Tornquist department, Ernesto Tornquist Provincial Park, base of Cerro Bahía Blanca, MLP.R.6121, 6124, 6126; Ernesto Tornquist Provincial Park, base of Cerro Ventana and Provincial Route 76, MLP.R.6122–23; Sierra de la Ventana, Ea. El Pantanoso, MACN 44543.

Xenodon semicinctus (Ringed Hognose Snake). Argentina: Buenos Aires province: Tornquist department, Chasicó, MACN 27451; Tornquist and National Route 33, MLP.R.6239.

Viperidae, Crotalinae

Bothrops alternatus (Urutu). Argentina: Buenos Aires province: Coronel Suárez department, Cura Malal, MACN 0189; Sierra de las Tunas and Provincial Route 76, MLP.R.6108, 6113; Villa La Arcadia, around of Cerro Ceferino, MLP.R.6105, 6109, 6114–15. Saavedra department, base of Cerro Cura Malal, MLP.R.6130–31. Tornquist department, Abra de la Ventana, MACN 7439, 20834, 27318, MLP.JW.1740, MLP.R.5875; Ernesto Tornquist Provincial Park, MACN 9692 A, B, MLP.JW.0039, 0470, 0749, MLP.R.6104, 6110–12; Ernesto Tornquist Provincial Park, base of Cerro Bahía Blanca, MLP.R.6106–07, 6098; Ernesto Tornquist Provincial Park, base of Cerro Ventana, MACN 43252, MLP.R.6099, 6101, 6103; Ernesto Tornquist Provincial Park, Cordón Esmeralda, MLP.R.6100; Ernesto Tornquist Provincial Park, near park refuge, MLP.JW.0750; Ernesto Tornquist Provincial Park, Villa Ventana, MLP.R.6102; Sierra de la Ventana, MACN 6905–07, 33463, 40018, 43088, 43268, 44202, MLP.JW.0484, 0773; Sierra de la Ventana, Ea. Laurina, MACN 39209; Sierra de la Ventana, Fortín Chaco, MACN 26097; Sierra de la Ventana, Sauce Grande river, MACN 7340, 33029; Sierra de la Ventana, Campo Vineto, MLP.JW.0507; Sierra de la Ventana, Vivero Agrario, MLP.JW.0781; Tornquist, MLP.JW.0710–11, 0783, 0793, 0899–02, 1578.

Bothrops ammodytoides (Patagonia Lancehead). Argentina: Buenos Aires province: Puan department, Bordenave, Ea. Las Glicinas, MACN 34371; San Germán, MLP.JW.0595. Tornquist department, Sierra de la Ventana, MACN 44276; Tornquist, MACN 34648, 39068, 46306; Tornquist and National Route 33, MLP.R.6238.

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