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Tell me where you live and I'll tell you who you are: Spatial segregation of southern species of *Eligmodontia* Cuvier in Patagonia, Argentina

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ABSTRACT

Eligmodontia morgani and *E. typus* are two small (<25 g) sigmodontine rodents that live in dry areas of southern Argentina. The species are very difficult to distinguish in the field, so their geographical delimitation has always been the subject of controversy. In this work we used sampling sites where each species has been previously identified by its karyotypes and mtDNA, and modeled their potential distribution using a maximum entropy analysis. Our results show a clear niche segregation between the two species, mainly driven by temperature. Ecological niche models show *E. morgani* is a more likely inhabitant of western Patagonia (the Steppe ecoregion), while *E. typus* is a more likely inhabitant of the eastern region (the Monte ecoregion). In ecotonal areas our models predict *E. morgani* occupies the highest and coldest areas at the top of plateaus, while *E. typus* occupies the Monte ecoregion. Our mathematical models show a habitat selection of average minimum temperatures of 1 °C and 5 °C for *E. morgani* and *E. typus*, respectively, and of average maximum temperatures of 22 °C and 27 °C for each species.

Eligmodontia morgani y *E. typus* son dos pequeños (<25 g) roedores sigmodontinos que habitan los ambientes áridos del sur de Argentina. Debido a que las especies son difíciles de distinguir en el campo, su delimitiación geográfica siempre ha sido controvertida. En este trabajo usamos registros donde las especies fueron identificadas por su cariotipo y ADN mitocondrial, y modelamos su distribución potencial usando análisis de máxima entropía. Nuestros resultados muestran una segregación en el nicho entre las especies, mayormente impulsado por la temperatura. Los modelos ecológicos de nicho muestran que *E. morgani* es un habitante del oeste y centro patagónico correspondientes con la ecorregión de la Estepa Patagónica, mientras *E. typus* es un habitante de las regiones centrales y el este patagónico, correspondientes con la ecorregión del Monte. En áreas de ecotono, nuestros modelos predicen que *E. morgani* ocupa las zonas altas y frías de las mesetas, mientras que *E. typus* ocupa zonas bajas con una matriz de vegetación de la Ecorregión del Monte. Nuestros modelos matemáticos muestran una selección de hábitat de temperaturas medias mínimas de 1 °C y 5 °C para *E. morgani* y *E. typus*, respectivamente, y de temperaturas máximas medias de 22 °C y de 27 °C para cada especie.

1. Introduction

Abiotic factors can affect or determine the distribution of organisms, being this distribution a good indicator of the ecological requirements of a species. Analyses of species distributions using climatic variables help understand why one species is present in a certain place and not in another, while providing opportunities to discuss species morphology and/or adaptations. This allows predicting areas that describe the appropriate environmental conditions for the survival of a species, that is, the potential distribution taken as the fundamental niche. In recent years, species distribution models have played an increasingly important role in the study of species distribution patterns (Guisan and Thuiller, 2005). Spatial modeling based on the analysis of environmental parameters and the presence of species is widely used in environmental,

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ecological and conservation studies, among others (Yanga et al., 2013; Matyukhina et al., 2014; Yuan et al., 2015).

There are species that, although genetically distinct, are morphologically difficult to separate/identify, leading to different interpretations on the number of species in a particular area, and their geographic distribution ranges. Many of these are sometimes considered "cryptic species", especially when they are split based on molecular analyses but unable to do so on morphologic/morphometric characters (Bickford et al., 2007). A particular case are rodents of the genus *Eligmodontia* F. Cuvier (Rodentia, Cricetidae, Sigmodontinae, Phyllotini), a group of small xerophytic-adapted rodents that inhabit arid and semi-arid habitats of South America from extreme southern Perú, western Bolivia, northern Chile and northwestern Argentina, south to southern Argentina and Chile, including the grasslands and scrublands of Patagonia, the Monte Desert, the Espinal, and the dry grasslands, scrublands, and Puna habitats of the high Andes (Hershkovitz, 1962; Musser and Carleton, 2005; Andrade and Monjeau, 2014; Lanzone et al., 2015). Species of this genus have several specialized characters for life in these regions (e.g., resistance to low water intake/water deprivation, high urine concentration, seed storage; Mares, 1977; Díaz and Ojeda, 1999; Giannoni et al., 2001), and a broad altitudinal range that goes from sea level in southern latitudes, to more than 4500 m in northern latitudes (Mares et al., 2008). However, there are no unique morphological characters to differentiate species, partly associated with the absence of integrative studies that include morphology, morphometrics and genetics (Mares et al., 2008; Lanzone and Ojeda, 2005; Lanzone et al., 2015). Species of *Eligmodontia* are highly variable in their morphology, overlapping in external and craniodental measurements, and also in qualitative characters which are age-dependent (Lanzone et al., 2015).

In Patagonia, *Eligmodontia morgani* has been registered sympatrically with *E. typus* in some areas, but mechanisms of coexistence between these sympatric populations remain unstudied (Lanzone et al., 2007; Andrade 2020). *Eligmodontia morgani* has been described as the species typically living in the Patagonian steppe ecoregion (*sensu* Burkart et al., 1999), while *E. typus* has been described as the species living in the Monte de Llanuras y Mesetas ecoregion, and both species have been considered as good surrogates for steppe and monte habitats throughout their distribution (Andrade 2020). Although these species are genetically distinct (Hillyard et al., 1997), the only way to separate them from a morphological point of view is through discriminant analyses of numerous external and cranial measurements (Sikes et al., 1997; Díaz et al., 2006). Due to this difficulty, most works consider species in this situation as a single unit or using an open taxonomy (*Eligmodontia* sp.; Andrade 2020), without making specific distinctions (Udrizar Sauthier, 2009, Udrizar Sauthier and Pardiñas, 2014; Formoso, 2013). Species distribution models can help us identify spatial overlap between these taxonomically distinct units, also providing information on their unique environmental requirements (Raxworthy et al., 2007). Our objectives were to find out if the species segregate spatially, if environmental and geographic variables can be used to separate the distribution of each species, and to ultimately determine the requirements of each species' ecological niche.

2. Materials and methods

2.1. Study area

Our study area included most of Patagonia, an area of Argentina characterized by a steep environmental gradient in the West, where annual precipitation ranges from ca. 4000 mm to less than 300 in ~100 km, gradually reduced to <200 mm towards the East (Prohaska, 1976; Paruelo et al., 1998). Elevation ranges from 3000 m to sea level, with several areas of intermediate to high altitude (e.g., northern and southern Patagonian plateaus as Somuncura, at ~2000 m), producing some of the sharpest biotic transitions known (Quintanilla Pérez, 1983; Veblen and Lorenz, 1988).

There are different interpretations of the term Patagonia, so there is no univocal and spatially explicit definition or landscape classification. Following the criteria used in Monjeau et al. (1998), Patagonia sensu lato extends from approximately 39°–55° South, roughly following the Colorado-Desaguadero rivers in the north and extending to the southernmost tip of the continent, including Tierra del Fuego, the Andes, and the mesas, plains and hills lying between the Andes and the Atlantic Ocean, including a small portion of Chile, adjacent but not included in our study. Cabrera (1971) distinguished three botanical provinces in Patagonia sensu lato: forest, monte and "Patagonia", using the term only from a phytogeographic point of view. Monjeau et al. (1998) clarified this nomenclatural issue by naming the floristic Patagonia of Cabrera "Patagonia sensu stricto". Inspired from a holistic perspective, del Valle et al. (1995) delimited two large areas within the semiarid or "Extra-Andean Patagonia" (see Monjeau et al., 1998 for comparison of both classifications): the Occidental Patagonia (coinciding with Patagonia sensu stricto of Cabrera) and the Oriental Patagonia (which is the portion of what Cabrera calls "monte", but south of the Colorado-Desaguadero river). These units were also considered by León et al. (1998) the Patagonian phytogeographic province, the Monte phytogeographic province, and the ecotone between the two. The study area of our paper comprises these areas explicit in del Valle et al. (1995) and León et al. (1998), and follows the ecoregional approach described by Burkart et al. (1999), in which the southern portion of Argentina includes, from East to West, the Monte de Llanuras y Mesetas (hereon Monte), Estepa Patagónica (hereon Patagonian steppe) and Bosques Patagónicos (hereon Subantarctic forests). Of these ecoregions, the species of *Eligmodontia* studied herein occupy habitats within the former two.

Our study area (i.e., Patagonia sensu lato) was chosen because it encompasses the distribution of both studied species with a similar set of environmental variables ("region A" as described in Soberón and Peterson, 2005), and following the indications of Soberón and Peterson (2005) and Barve et al. (2011) for selecting a "region M″ when modeling species distributions, to include areas accessible to each species in a period of time. Species of *Eligmodontia* have a well documented presence in the area, with information on their recent and past distribution (see Pardiñas, 1999; Udrizar Sauthier, 2009; Formoso, 2013; Andrade and Monjeau, 2014; Andrade, 2020; and literature cited therein).

2.2. Potential distribution models

We chose the maximum entropy algorithm (Maxent) because it generates optimal results using only points of presence, as is our case (Elith et al., 2006; Peterson et al., 2007). Maxent models were generated for *E. morgani* and *E. typus*, with presence records obtained from genetic analyses (Sikes et al., 1997; Hillyard et al., 1997), and with all records as a single taxonomic unit (patagonian *Eligmodontia*), using 25% test data, random seed, 1000 iterations, 10 replays, 10,000 background points, and the cumulative option as an output format following Merow et al. (2013) and Phillips et al. (2006), since Maxent's 'logistic output' greatly underestimates the probability of occurrence throughout the core of the species' range, and overestimates occurrence probability in regions where the species was never detected (Royle et al., 2012).

2.3. The variables selection

Our starting point was to use a total of 20 variables obtained from the WorldClim database (zone 43: South America) (www.worldclim.org), including elevation and 19 bioclimatic variables, with a resolution of 30 Arc-seconds ($0.93 \times 0.93 = 0.86$ km^2), and a projection at WGS 1984 following Hijmans et al. (2005). Environmental variables combining temperature and precipitation (e.g., Bio 8, 9, 18 and 19) were excluded because they show odd spatial anomalies in the form of odd discontinuities between neighboring pixels (Escobar et al., 2014; Astorga et al., 2018).

We used the modified soil adjusted vegetation index (MSAVI), because in areas with sparse vegetation surface reflectance and vegetation indices are influenced by exposed soil. Several vegetation indices incorporated with soil adjustment factors, such as SAVI, were designed to reduce the impact of soil brightness on canopy spectral signatures, and increase the index sensitivity to canopy biophysical characteristics (Huete, 1988; Qi et al., 1994; Huete et al., 2002). Unlike SAVI, which requires users to pre-specify the soil-adjustment factor L, the MSAVI equation contains a calculation of L using available red and NIR bands (Qi et al., 1994; Ji et al., 2014). This index was obtained by processing these bands from a series of MODIS satellite images, the MOD13Q1 images with dates between 18-02–2000 and 04-03-2000, obtained from www.earthdata.nasa.gov. Consecutive images from 16 days apart were merged using Idrisi software (Eastman, 1990), resulting in a layer at a spatial resolution of 250 m. Once images were generated, they were reprojected to WGS 1984 and multiplied by a scalar factor (Ruano, 2013). The MSAVI index was generated using the equation available in Qi et al. (1994), Ji et al. (2014) with the QGIS software raster calculator.

We performed an exploratory analysis using Maxent with selected environmental and MSAVI index, using three different approaches: the first including both species of *Eligmodontia* together, combining their known, genetically differentiated records as if it was a single species (A model), a second and third for each recognized species (B model for *E. morgani* and C model for *E. typus*), separately. Several studies recommend minimizing correlation among predictors, and identifying the appropriate feature shapes prior to model building, removing highly correlated predictors using correlation analysis, clustering algorithms, principal component analysis or some other dimension reduction method because the complex features created by Maxent are often already highly correlated (Dormann et al., 2012; Owens et al., 2013; Nuñez Penichet et al. 2016; Simões et al.). We performed a Pearson correlation analysis with R v.3.4.3 package (R Core Team, 2017) between variables for each model, with the values from environmental variables for each sampling locality (using the tool "Raster values to points" with QGis software, and then using these values to perform a correlation analysis). A correlation of 0.8 was considered high (Dormann et al., 2012), and we used the Jackknife test from the exploratory analysis of Maxent to select which variables showed the greatest explanatory contribution, considering also those with biological significance for each of the studied species. Following this procedure, we ended up with a total of 11 variables selected which we used in a second run of Maxent analyses with uncorrelated variables.

Also, we generated preliminary models using three regularization multipliers (i.e., $\beta = 0.5$, 1 and 2), since these values are known to generate different results (Warren and Seifert, 2011; Radosavljevic and Anderson, 2014), and used the area under the curve (AUC) as an estimator of the predictive power of each model. Generally, AUC values between 0.5 and 0.7 are considered of low precision, between 0.7 and 0.9 as reasonable predictions, and very good predictions are those with values greater than 0.9 (Swets, 1988). Model predictions were evaluated using the area under curve (AUC) and receiver operating characteristics (Phillips et al. 2004, 2006) for training and test values (i.e., AUC_{Train} and AUC_{Test}), and we present AUC_{Test} values since they are thought not to suffer from the same overfitting problems as the former (Warren and Seifert, 2011). To analyze our models for possible overfitting, which results in high AUC_{Train} but low AUC_{Test} values, we analyzed AUC differences (AUC_{Diff}) as proposed by Warren and Seifert (2011), and recently used by Gutiérrez et al. (2014), Giménez et al. (2015), and Ruiz Barlett et al. (2019). These AUC_{Diff} values were used to select the final models we analyzed.

Maps for each species were generated using the median values provided by Maxent, representing the suitability values in a range of 100-75 for the highest prediction, 75-50 for a high prediction, 50-25 for a medium prediction, 25-10 for a low prediction, 10-1 for very low prediction, and 1-0 for a null prediction (Martin, 2010; Schiaffini et al., 2013; Giménez et al., 2015). As in Ruiz Barlett et al. (2019), median values were chosen because they represent a more robust statistical characterization than the mean, especially for the probability density function of a biological population, which has a natural lower boundary of zero. Using the median ensures that abnormally large values in the tail of the distribution do not skew the "typical" value of the distribution, as they would do in the case of the mean (Feller, 1967). We evaluated maps with the highest AUC_{Diff} for both species together and each species separately, based in our field experience, species distribution maps (e.g., Lanzone et al., 2015), and habitat types where species are known to occur (León et al., 1998; Pardiñas et al., 2003; Formoso, 2013). Finally, we generated a map showing the overlap between both species, using values of 0 or 1 for cumulative values between 0% and 50%, and from 51% to 100%, respectively, combining them with the Raster Calculator in QGis (QGIS Development Team, 2011).

A Scatter plot was made to visualize the distribution of species in the environmental space, between values of the annual average temperature (Bio 1) vs. annual precipitation (Bio 12) of the species' presence sites, on a background of the study area. In this way, the temperature and precipitation range in which each species is distributed can be observed preliminarily.

3. Results

We obtained a total of 65 records for *Eligmodontia*, 29 presence sites identified from genetic samples of *E. morgani* and 36 for *E. typus* (see Supplementary Material 1). The 3 distribution models generated with all sites taken together and separately for each species proved to be good predictive models with AUC_{Test} values between 0.891 and 0.778. The model with the lowest AUC_{Diff} for all records and each species separate had a β of 1 (values of 0.052, 0.02, and 0.061 for both species combined, *E. morgani* and *E. typus*, respectively), but after a close inspection of the generated maps we chose those with a β of 2 (values of 0.061, 0.027 and 0.067 for all, *E. morgani* and *E. typus*, respectively), which had similar values and presented what we believe are better interpretations of species' distributions. We found a clear separation in the distribution of both species, environmentally and spatially, with areas suitable for *E. typus* on the Atlantic coast, while *E. morgani* appears to have more suitable areas in central Patagonia and the Somuncura plateau. Our analyses also show that different variables contributed to each species' modeled distribution (Table 1).

The marginal occurrence records for *E. morgani* range between 34,18 and 48,99° south, and 66,31 and 71,73° west, while those of *E. typus* range between 28,86 and 47,86° south, and between 62.62 and 70,56° west. Our samples showed an altitudinal segregation between species, with *E. morgani* living at a range of 220–3300 m, and *E. typus* living from sea level to 1600 m (Fig. 1A).

The species are present in areas where rainfall per year is less than 930 mm for *E. morgani* (average of 354 mm) and 500 mm for *E. typus* (average of 294), *E. morgani* in areas with an annual average temperature of 8.6 °C (range between 20.4 °C and −5.5 °C) and *E. typus* in areas with annual average temperature of 13.4 °C (range between 27.9 °C and 1.3 °C (Fig. 1B). Average maximum and minimum temperatures are clearly distinct for *E. morgani* and *E. typus*, with maximum average values of 14.1 °C and 20.3 °C, respectively, and minimum average values of 3.1 °C and 7.1 °C, respectively (Supplemental Material 2).

The potential distribution model we generated combining both species of *Eligmodontia* shows a concentration of high prediction areas in central Patagonia, especially in central Chubut province, and north-central Santa Cruz and Río Negro provinces (Fig. 2A), consistent with areas of each species' localities and their models becoming closer and overlapped, respectively. Other areas of high prediction in this combined model overlap with high prediction areas for *E. typus* (Fig. 2C), especially towards the central and eastern distribution in Chubut province, and northern Santa Cruz province. As for the models generated for each species, independently, high to medium suitability areas (those

Table 1

Heuristic estimates of relative environmental variable contribution (in percentage) for the models generated for both species analyzed together, and each species analyzed separately. Bio 2 = mean diurnal range; Bio 3 = isothermality; Bio 4 = temperature seasonality; Bio 5 = Max temperature of warmest month; Bio 6 = Min temperature of coldest month; Bio 7 = Temperature annual range; Bio 11 = Mean temperature of coldest quarter; Bio 12 = Annual precipitation; Bio 14 = Precipitation of driest month; Bio 15 = precipitation seasonality; MSAVI = Modified Soil-adjusted Vegetation Index. Variable percentage (%) and permutation values (i.e., information not present in the rest of the variables; P) are presented for each of the models. Variables with the highest scores for % and P are indicated in bold.

E. morgani + E. typus			*E. morgani*			*E. typus*		
Variable	%	P	Variable	%	P	Variable	%	P
Bio12	**26.6**	9.3	**Bio11**	**51**	**63.7**	**Bio12**	**39.9**	**41.2**
MSAVI	21.4	19.1	Bio5	15.3	1.6	MSAVI	22	25.4
Bio4	20.6	8.9	Bio15	11.7	13.1	Bio5	19.9	6.2
Bio5	19.8	**26.5**	Bio7	11.1	2	Bio6	7.8	9.1
Bio15	4.8	11.3	Bio3	4.5	3.7	Bio2	6.9	7.9
Bio3	3.7	14	Bio12	3.9	14.3	Bio15	1.8	7.5
Bio2	1.7	3.1	MSAVI	2.4	1.6	Bio3	1.1	1.6
Bio6	0.8	2.1				Bio14	0.6	1.2
Bio14	0.6	5.8						
% explained by the two most important variables	48			66.3			61.9	
% explained by variables above 10%	88.4			89.1			81.8	
$\mathrm{AUC_{diff}}$	0,06			0,02			0,06	
$_{\text{Test}}$ AUC 0,778 ± 0.041			0.867 ± 0.041			0.827 ± 0.055		

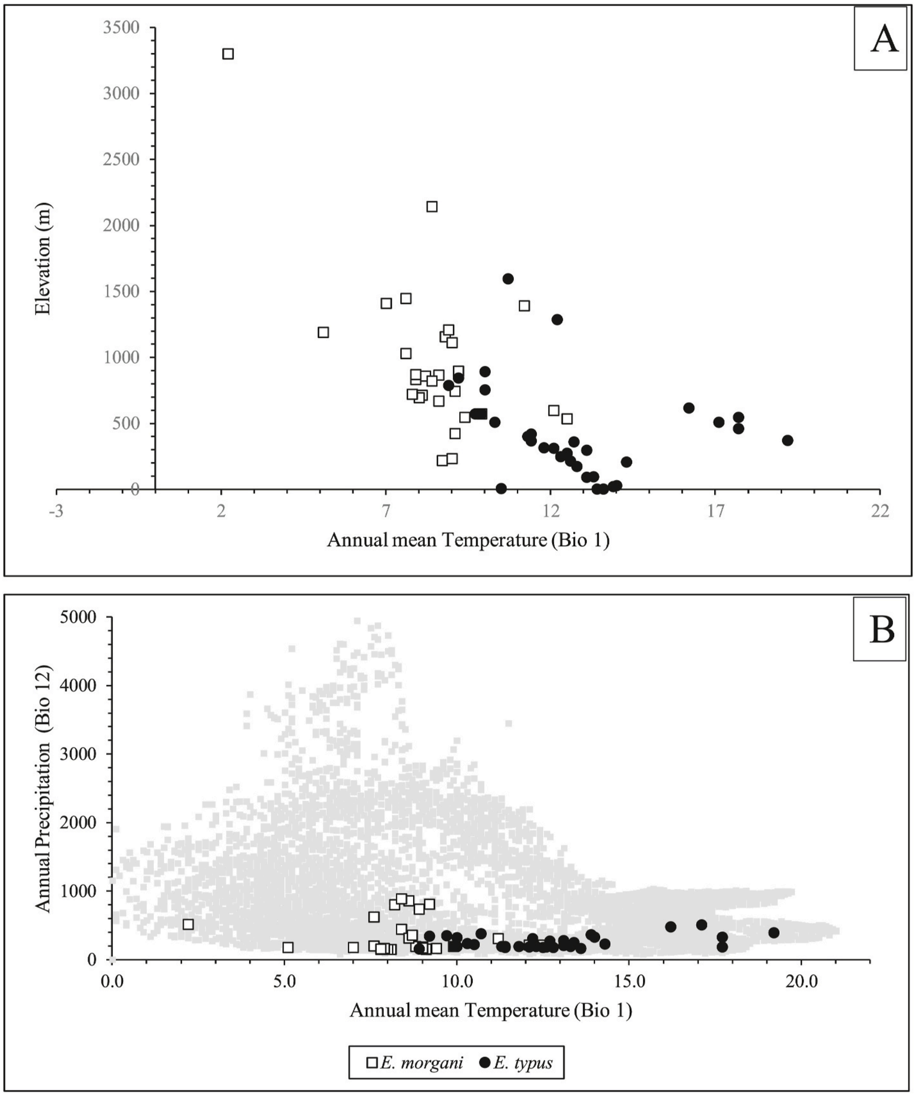

Fig. 1. (A) Altitudinal range vs. annual mean temperature from records of *E. morgani* (white squares) and *E. typus* (black circles), and (B) distribution of both species in the environmental space, with background data in grey, using values of annual mean temperature (BIO1) vs. annual precipitation (BIO12).

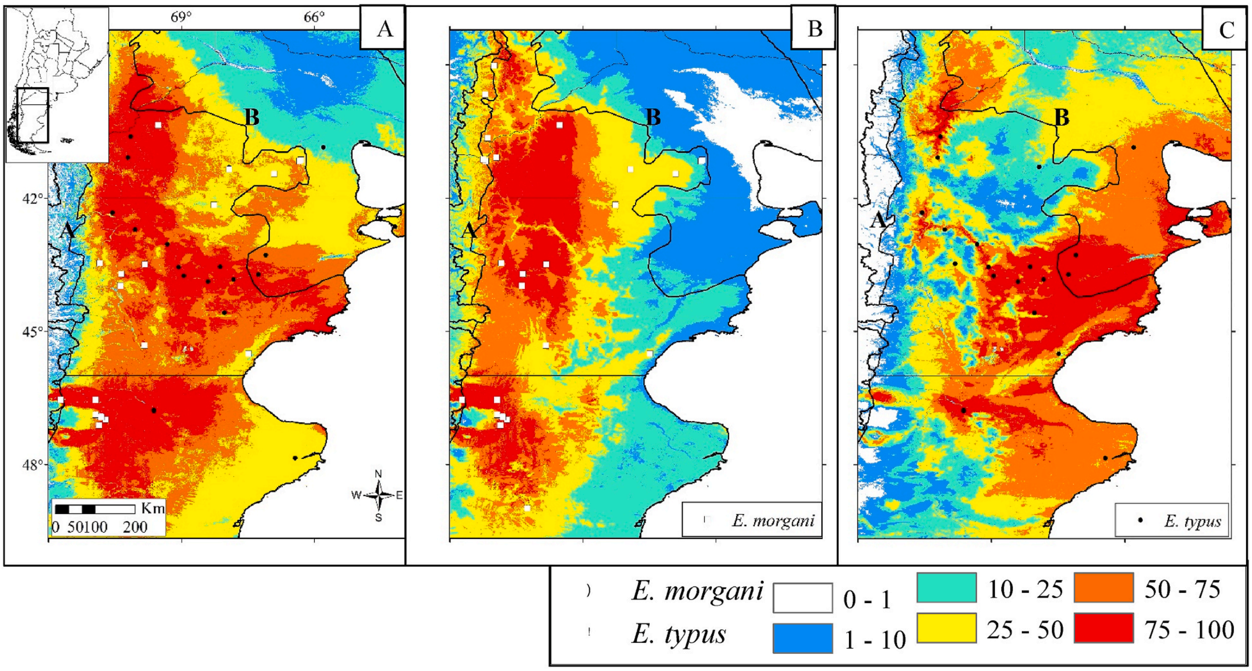

Fig. 2. Potential distribution model generated for: A-both species of *Eligmodontia*. B- *E. morgani,* C- *E. typus*. Black lines marked A and B represent the Eastern limit of the Subantarctic–Patagonian forests, and Patagonian Steppe sensu Burkart et al. (1999), respectively. White squares represent *E. morgani*, black dots *E. typus*.

above 50%) barely overlap, doing so only in areas of southern Chubut and north-central Santa Cruz provinces (similar to those of the combined model) (Fig. 2). Suitable areas for the presence of *E. morgani* are concentrated along the high areas of Somuncura plateau, central-western Chubut and Santa Cruz provinces (Fig. 2B). Contrary to this, suitable areas for *E. typus* are located in eastern Patagonia, in areas corresponding with the Monte de Llanuras y Mesetas ecoregion, clearly at lower altitudes and closer to the Atlantic ocean (Fig. 2C).

Areas with high environmental suitability (>50) for both species of *Eligmodontia* are located to the south of Patagonia, along river valleys with mixed altitudinal and vegetation coverage conditions (the Erial described by León et al., 1998), between 45° and 50°. Suitable environmental areas for *E. morgani* are mostly concentrated in central and western Patagonia, and in central and eastern Patagonia for *E. typus,* with little overlap between species (Fig. 3). When comparing the distribution models generated between species and a digital elevation model (DEM), suitable areas for *E. morgani* occur in high to mid-altitude areas in the western and central plateaus, while those for *E. typus* are mainly concentrated near sea level in the coast, and following river valleys and other low-altitude areas into the west (Fig. 4).

Analyses of environmental variable contributions to each of the models is different between species, and also when they are modeled together. In the model generated with both species (A model), Annual precipitation (Bio 12) and MSAVI (Modified Soil-adjusted Vegetation Index) are the two most important variables (temperature seasonality (Bio 4) and maximum temperature of the warmest month (Bio5) follow closely), while maximum temperature of the warmest month (Bio 5) is the variable with most information not contained in the rest (Table 1). The most important variable in the model generated for *E. morgani* was mean temperature of the coldest quarter (Bio 11) with more than a 50% contribution and also being the variable with most information not contained in the rest. The most important variables for *E. typus* were annual precipitation (Bio 12), MSAVI and temperature of the warmest month (Bio 5), while Bio 12 was also the variable with more information not contained in the rest (Table 1). Only 7 variables explained more than 98% of the models generated for each species individually and both species combined, while 4 (model for both species and *E. morgani*) and 3 (model for *E. typus*) environmental variables with values above 10%

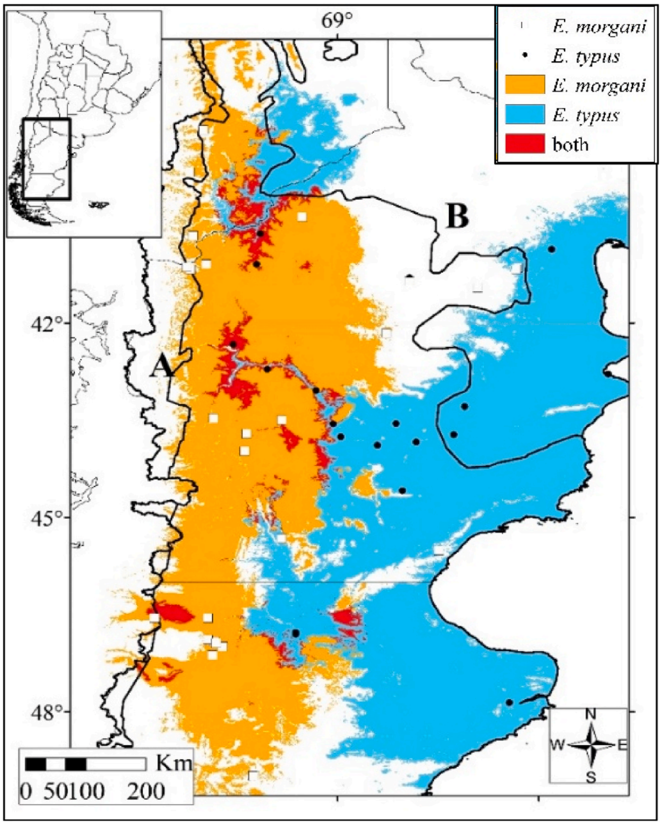

Fig. 3. Areas with high environmental suitability (>50%) for the two studied species of *Eligmodontia*. Black lines marked A and B represent the Eastern limit of the Subantarctic–Patagonian forests, and Patagonian Steppe sensu Burkart et al. (1999), respectively. White squares represent *E. morgani*, black dots *E. typus*.

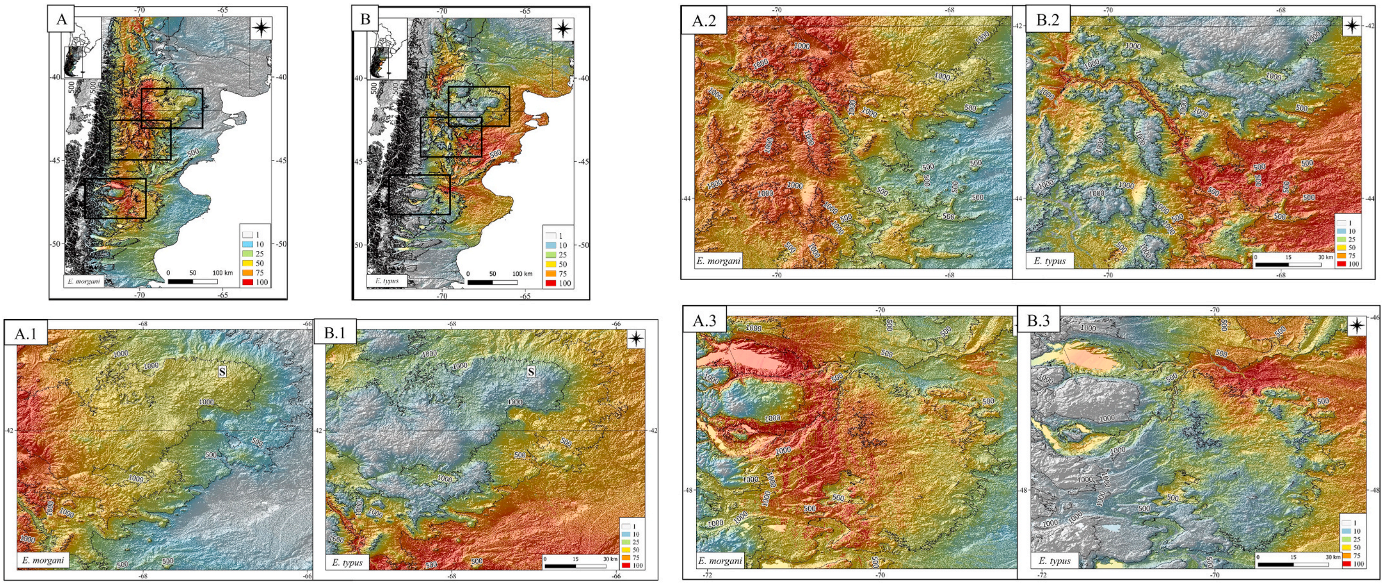

Fig. 4. Extended areas of the distribution models generated with the overlay of a digital elevation model (MDE) and contour lines. S represent the Somuncura Plateau. A: *E. morgani* model, B: *E. typus* model. Extended areas: 1: Samuncura plateau (S), 2: Chubut river, 3: north of Santa Cruz province.

explained over 81% of the models (Table 1).

3.1. Species habitat selection

We used the concept of Johnson (1980) to compare selected habitats between *E. morgani* and *E. typus*, in which habitats and their components are used disproportionately to their availability. This is different to the concept of preference, which results from choosing a habitat if offered on an equal basis with others.

For each temperature found in the map, we define the selection of species s for temperature T, as a stochastic variable:

$$selection(s,T)=M_i(s,r),\ such\ that\ i\in U(T),$$

where the sites i are in the subset $U(T)$ of the map where T is the mean temperature of the coldest quarter (Bio 11) or the maximum temperature of the warmest month (Bio 5). The variable M is the median given by the Maxent algorithm, as described, of species s calculated at regularization r ($r = 2$ used throughout this analysis). Selection can be normalized as a percentage, and characterized by its probability distribution. Examples of these functions are shown in Fig. 5, for both species and for 1 °C and 5 °C for Bio 11 and 21 °C and 27 °C for Bio 5, chosen because they display the characteristic selection of *E. morgani* and *E. typus*. A peak at a certain value in one of these probability distributions means that the corresponding species would occupy that fraction of all the sites with such Bio 11 or Bio 5 temperature.

For Bio 5, the histograms corresponding to 21 °C (Fig. 5A, left) show that these sites are preferred by *E. morgani* more than *E. typus*. On the other hand, the histograms of 27 °C (Fig. 5A, right) show that these sites are preferred by *E. typus*. For Bio 11, the histograms corresponding to 1 °C (Fig. 5B, left) show that these sites are preferred by *E. morgani* more than *E. typus*. On the other hand, the histograms of 5 °C (Fig. 5B, right) show selection by *E. typus*. Observe, nevertheless, that the peaks in these probability distributions are broad, and even multimodal, reflecting the fact that Bio 5 and Bio 11 are just two of the several variables that enter in the Maxent calculation of the potential distribution. In other words, the fact that they allow to distinguish the two species shows that they are a reasonable proxy for selection, but that the other variables used in the Maxent computation also play a role. An animated version of these histograms, changing the value of the temperature throughout the range preferred by Eligmodontia, can be downloaded from the Supplementary material 3 (videos 1 and 2).

Supplementary video related to this article can be found at https://doi.org/10.1016/j.jaridenv.2020.104411

These probability distributions are clearly not Gaussian or even unimodal, so it is difficult to characterize them by a single parameter for a more compact representation of selection as a function of temperature. An alternative approach is the use of the potential distribution summed over the subset of sites of a given temperature, with the formula:

$$R(s,T)=\sum_{i\in U(T)}M_i(s,r).$$

This variable provides a simpler visualization of species selection, alternative to the histograms, that we show in Fig. 6A as spheres of radius R, for both species and for a set of temperatures. When analyzed in such a way, both species appear confined to a range of 15 °C: between 15 °C and 30 °C of the maximum temperature of the warmest month (Bio 5, Fig. 6A, up); and a range of 12 °C: between −2 °C and 10 °C of the mean temperature of the coldest quarter (Bio 11, Fig. 6A, bottom). An animated version of this representation can be found in the Supplementary material 4 (videos 3 and 4), covering the values missing in this selection. The corresponding normalized function $R(T)$ for both species, as a function of the temperature, is shown in Fig. 6B, right (for Bio 5), and Fig. 6B, left (for Bio 11). In the case of Bio 5 our analysis shows *E. morgani* preferring sites with a peak of 22 °C, and *E. typus* preferring sites with a warmer peak 25 °C, and the whole distribution shifted towards warmer temperatures. *E. morgani* displays a broader selection in its distribution, covering a range between 10 °C and 35 °C. *E. typus* is absent or very scarce when temperatures are below 15 °C.

Supplementary video related to this article can be found at https://doi.org/10.1016/j.jaridenv.2020.104411.

E. morgani prefer sites with Bio 11 in a range of 1 °C–2 °C, with a bell-shaped probability distribution. On the other hand, *E. typus* displays a broader selection in its distribution, in a range between 4 °C and 8 °C, with a mean of 5.2 °C.

4. Discussion

Our predictive models show a clear separation in the distribution of both studied species, spatially and environmentally. The models for each species separately are quite consistent with a single environmental variable needed to explain >40% of their potential distributions, even

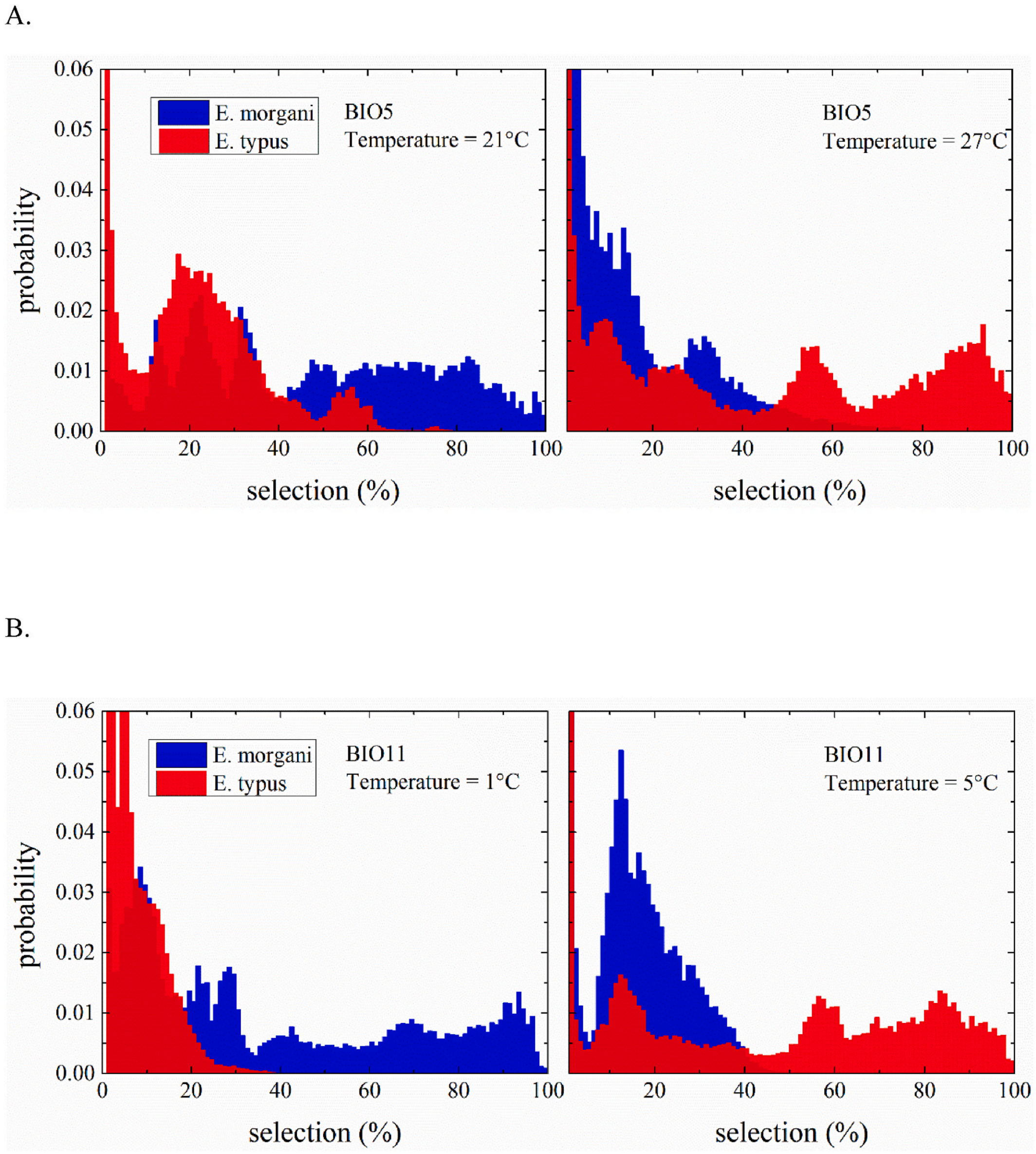

Fig. 5. Probability distribution of the habitat selection, for both species, corresponding to two temperatures as shown for Bio 5 (A) and Bio 11 (B). An animated version of this plot can be found in Supplementary material, videos 1 and 2.

after using only genetically differentiated records. The model generated with both species combined showed the need of 4 variables contributing almost equally to the model, while models for individual species responded highly to a single variable (Table 1). Our data shows that the potential distribution model of *E. morgani* is mostly conditioned by a temperature variable (mean temperature of the coldest quarter, Bio 11), while the model for *E. typus* is mostly conditioned by a precipitation variable (annual precipitation, Bio 12) (Table 1). This is consistent with the geographic characteristics of the ecoregions where both species inhabit, *E. morgani* in the Patagonian steppe with its cold temperatures and frosts throughout the year, and *E. typus* in the Monte de Llanuras y Mesetas where precipitation is the main limiting factor (Paruelo et al., 1998).

The model generated for *E. typus* shows the species is distributed in the Monte de Llanuras y Mesetas ecoregion, and eastern and southern portions of the Patagonian steppe, where the species is found mostly between 40° and 50° South, overlapping in areas where *E. morgani* is found (Fig. 3). *Eligmodontia typus* is mostly present in low areas with bare soil and dry habitats, where the mean annual temperature can reach 13.4 °C, and the coldest months are near 7.1 °C (Supplemental Material 2). These averages are clearly above those found for *E. morgani*, for which we found an average mean annual temperature of 8.6 °C, and an average minimum temperature of 3.1 °C. The use of MSAVI in our models allowed for a better discrimination of bare soil patches which are more commonly found in the Monte de Llanuras y Mesetas, and that are apparently selected by *E. typus*. This agrees with Mares et al. (2008), who mentioned the species lives in eastern Argentina through the pastures and scrublands of the Pampa through the Patagonian lowlands, but not to the foothills of the Andes. Our models show that the areas of highest selection for *E. morgani* are mostly in western Patagonia, east of the limit for the Subantarctic forests (Bosques Patagónicos ecoregion sensu Burkart et al., 1999) (line A in Fig. 3), and the central Patagonian steppe ecosystems, extending only sparsely to the optimal areas modeled for *E. typus* (Fig. 3). These models are different from those generated by Ruiz Barlett et al. (2019), where more constrained distributions were modeled for each species, with little to no overlap between them. These differences and those between environmental variables show the importance of selecting localities based on the species distribution and

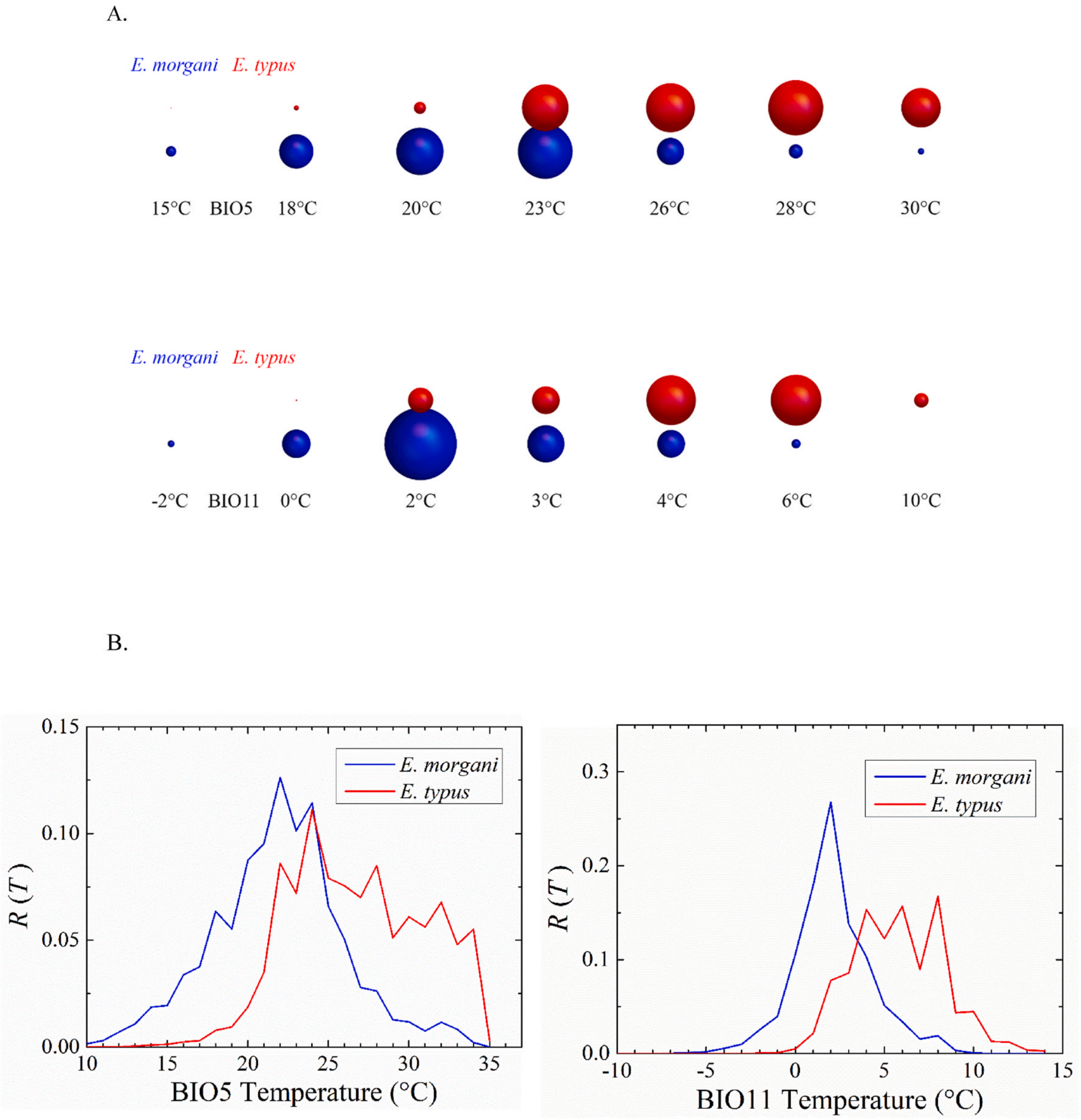

Fig. 6. A. Habitat selection represented as the radius of spheres, for several temperatures of the variable Bio 5 and Bio 11. B. Total normalized preference $R(T)$ for both species.

area of extension, with a clear idea of the objectives behind the modeling (e.g., potential distribution, environmental limiting factors, species overlap). In this respect, the area of overlap at the southern extension of both species seems odd, because the climate is more extreme in the southern Patagonia. However, this might be the result of appropriate landscape (i.e., local) conditions favoring the spatial separation of both species, while allowing them to coexist. We also expect this spatial segregation would be accompanied/coupled with changes in the average size and weight of these species, enhancing the separation between larger and smaller individuals of *E. morgani* and *E. typus*, respectively. On the other hand, a tendency to a larger size (and associated weight) in *E. typus* would be a "typical" response following a clinal gradient, especially towards the South, where it would become even harder to separate from *E. morgani* on morphological and morphometric grounds. To our knowledge, no analysis has put these hypotheses to the test.

Our study shows that *E. morgani* is present in arid areas with higher elevation, and lower temperatures in the cold months than those apparently tolerated by *E. typus*. These results coincide with Hillyard et al. (1997), Kelt et al. (1991) and Mares et al. (2008), who concluded that *E. morgani* is more restricted to western Patagonia, while *E. typus* is present in central and eastern Patagonia sensu lato, and is abundant along the Atlantic coast. In our models, the marginal limit to the east of *E. morgani* is found on the Somuncura plateau (Fig. 4), a Protected Natural Area located in the center-south of the province of Río Negro/northern Chubut province, with exceptional geographical, botanical and zoological characteristics (Sikes et al., 1997; Hillyard et al., 1997). Somuncura is an area with extensive patches within a transition-zone matrix, between the Patagonian steppe and high altitude pastures, and between the Patagonian steppe and the Monte de Llanuras y Mesetas (Forman and Gordon, 1986). This area has *mesas* and hills that approach 1900 m above sea level, being an area with favorable environmental conditions for the presence of *E. morgani* but very low for the presence of *E. typus*. As altitude increases and temperature decreases the environmental suitability of *E. morgani* increases; the opposite was seen in the models generated for *E. typus*, where habitat suitability increases at lower altitudes (Fig. 2). The MSAVI values in the presence sites of *E. typus* vary from −0.2 to 0.2, implying the species' suitability increases in areas of very low vegetation cover (MSAVI values closer to 0 indicate larger areas without any vegetation). Although *Eligmodontia* as a genus has always been associated with areas of bare soil or low coverage, our work points out to a substantial difference between *E. morgani* and *E. typus*, in which the latter species seems to select more open areas than it's partially sympatric species. Studies based on cytogenetics (Kelt et al., 1991; Ortells et al., 1989; Tiranti, 1997; Zambelli et al., 1992), morphology (Sikes et al., 1997) and molecular data (Hillyard et al., 1997; Lessa et al., 2010) have allowed a better understanding of the geographical distribution of *Eligmodontia* species. These studies clearly demonstrated the presence of 2 different *Eligmodontia* species in the southern cone, providing data on the ecological relations of *E. morgani* with *E. typus* in the region (Mares et al., 2008). Although *E. morgani* presents a southern distribution in Chile and Argentina and overlaps its geographical range with *E. typus* in part of the Patagonian steppe (Hillyard et al., 1997), the areas where both species overlap are modeled on a regional scale, which can be predicted with acceptable precision using only precipitation and temperature variables, a similar result to that reached by Monjeau et al. (1997, 1998). When moving down from regional to a local scale, it is likely that the climatic indicators lose variability (that is, temperature and precipitation are the same in each pixel), and it is at this scale where "local" variables become more important indicators than climatic variables (Ruiz Barlett et al., 2019). In some areas, we found small distances horizontally can have large altitude differences, which may not be differentiated at a regional scale as predicted by Maxent. This is shown in our analyses at local scales of altitude maps and preferences (Fig. 4), where *E. morgani* appears present in higher altitudes while *E. typus* in lower. Other local conditions which could influence the distribution at a local scale include landscape roughness, soil impermeability, and vegetation structure and coverage (MSAVI is a good example, as previously described). Andrade and Monjeau (2014) made an altitudinal transect in Somuncura mentioning *Eligmodontia* spp. In their study, due to the impossibility of separating one species from the other with the available data. The tools used in this work now allow us to discriminate, indirectly, the habitat of one species from another, and we could assume that the samples in the high steppes of that study belong to *E. morgani* and the samples from the lower, more open sites and with Monte vegetation would be *E. typus*. This is consistent with what was found on the same site by Sikes et al. (1997) and Hillyard et al. (1997). If we corrected the results of Andrade and Monjeau (2014) discriminating *E. typus* from *E. morgani*, their described pattern of species turnover with elevation would be even more remarkable than that presented by these authors.

We expect to find the following physiological differences between *E. morgani* and *E. typus*, based on our modeling results: (1) following Bergman's rule, *E. morgani* should be consistently larger than *E. typus*, and also have a larger concentration of brown adipose tissue than *E. typus*; (2) due to the aridity difference between the Monte and Patagonia ecoregions, the kidneys of *E. typus* should have larger medullary areas (and therefore longer Henle loops) and higher renal indices than *E. morgani* (Díaz and Ojeda, 1999).

Despite current studies, the confusing situation of the taxonomy and distribution of the genus *Eligmodontia* is a common denominator of some sigmodontine rodents in South America (Lanzone and Ojeda, 2005; Lanzone et al., 2015). It is clear that more studies of *Eligmodontia* are needed, not only for *E. morgani* and *E. typus*, but also for other species such as *E. moreni* and *E. puerulus,* species that also inhabit dry areas of South America and occur sympatrically, and have similar identification problems as the ones described herein for *E. morgani* and *E. typus* (see Lanzone et al., 2015). Similarly, *E. moreni* and *E. typus* occur sympatrically in much of the northern and central Monte de Llanuras y Mesetas ecoregion (Lanzone and Ojeda, 2005; Mares et al., 2008; Lanzone et al., 2007), providing a good opportunity to make analyses as the ones we presented herein.

Finally, we hope potential distribution models generated from presence records of genetically differentiated individuals and a differential environmental selection (especially related to temperature variables), can help clarify the distribution limits between both species for a preliminary identification of individuals, providing data to solve this problem.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jaridenv.2020.104411.

Credit author statement

TRB did Maxent's analyzes and wrote most of the manuscript. GA, wrote part of the manuscript and made the temperature model for the two species, including the animation. FL wrote part of the manuscript and made the temperature model for the two species, including the animation. GM participated in the methodology and wrote part of the manuscript. AM participated in the design of the research and wrote part of the manuscript

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