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Niche overlap and shared distributional patterns between two South American small carnivorans: *Galictis cuja* and *Lyncodon patagonicus* (Carnivora: Mustelidae)

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Abstract: Limiting abiotic conditions might shape boundaries of species distribution, while biotic factors influence such distributions through interspecific relationships. When two morphologically and or/ecologically similar species are geographically overlapped, a distribution displacement or a change in size or morphology is expected to minimize competition. Environmental niche modeling (ENM) might help us understand the relationship between distribution of a species' pair and their relationship with environmental conditions, allowing us to test the possible existence of shared distribution patterns and/or displacements across wide geographic ranges. In this work, distribution patterns and climatic and geographic overlap are analyzed between two South American small carnivorans, *Galictis cuja* and *Lyncodon patagonicus*, using geographic information systems and ENM. Environmental tolerance of the latter species seems to be enclosed within the range of the former, with high geographic overlap. No evidence of niche displacement was found between them. *G. cuja* seems to be a more generalist species than *L. patagonicus*, and size difference (e.g. body size, dentition size) might be the mechanism that allows coexistence between these highly similar species, although future field studies might be needed to support this statement.

Keywords: competition; distribution patterns; ENMTools; environmental niche modeling; MaxEnt.

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Introduction

The lesser grison *Galictis cuja* (Molina 1782) and the Patagonian weasel *Lyncodon patagonicus* (de Blainville 1842) are two sympatric South American small carnivorans, sharing several morphological features such as a reduced first upper molar, a reduced lingual portion of upper carnassials, and larger trigonids and small talonids in their lower carnassials, suggesting diets that rely mainly on vertebrate flesh (see Schiaffini and Prevosti 2014). Both species have thin, elongate bodies with short limbs (Yensen and Tarifa 2003, Prevosti et al. 2009), which allows them to enter burrows to seek refuge and/or food. They are also the closest relatives within Mustelidae in the southern cone of South America (Sato et al. 2012). *G. cuja* inhabits the south of Peru, Bolivia, Paraguay, and north-eastern Brazil to southern Chile and Argentina (Yensen and Tarifa 2003, Bornholdt et al. 2013). Although it is classified as "Least Concern" by the IUCN (Reid and Helgen 2008), population numbers and population trends are unknown, and it has also been considered "Vulnerable" by the "Libro rojo de mamíferos amenazados de la Argentina" (Soler and Aprile 2012). The geographic distribution range of *L. patagonicus* seems to be enclosed within the former, but restricted to the southern cone of South America and ranging from northern Argentina in the Salta province to southern Chile in the Magallanes region (Schiaffini et al. 2013). This species is classified as "Data Deficient" by the IUCN (Kelt and Pardiñas 2008) and "Near Threatened" by the "Libro rojo de mamíferos amenazados de la Argentina" (Díaz Isenrath et al. 2012). These two morphologically similar species with strongly overlapping geographic distributions seem highly adequate to study competition on a broad scale and niche overlap on a regional scale.

The area in which a species lives is determined by diverse factors acting on different scales (Gaston 2003): abiotic conditions (climate and physical environment that impose physiological limits to species), biotic factors (positive or negative interactions with other species), regions accessible to dispersal, and the evolutionary history of

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a species which allows it to cope with new conditions (Soberón and Peterson 2005). The study of the relationship between a species and its environment represents the core of predictive geographical modeling (Guisan and Zimmermann 2000). One of the main reasons to perform environmental niche modeling (hereafter ENM) is to understand the relationship between a species and its environment, for which several steps are necessary according to the scheme of Franklin (2009): 1) a conceptual model of how biotic and abiotic factors affect species distributions, 2) georeferenced data about species occurrence, 3) environmental variables, 4) a model linking species occurrence with environmental variables, and 5) tools for applying the model (see Franklin 2009).

Abiotic factors impose restrictions to species distributions. These "limiting factors" include temperature, wetness and dryness, and photoperiod, among others (Gaston 2003), and impose limitations to species survival and reproduction (Cox and Moore 2005). In this way, harsh climatic conditions influence the borders of a species' distribution, by physiological restrictions to range of temperatures and/or limitations in rainfall associated with primary productivity (Virgós et al. 2001 and references therein). As these variables are not uniformly distributed in space and time, they directly and indirectly influence the distribution of animals (Mackey and Lindenmayer 2001). Within this framework, ENM allows the study of relationship between a species' occurrence and spatial environmental characteristics (Guisan and Zimmermann 2000, Franklin 2009). So, ENMs are used to generate spatial estimates of habitat suitability, i.e. an estimate of a species' Grinnellian niche on regional scales (Soberón 2007, Wooten and Gibbs 2011).

A second determinant of species' distribution is biotic factors, mainly related to competition processes (Peers et al. 2013). Competition is thought to have a major role in structuring ecological communities, with ecologically overlapping species not being able to coexist (Dayan and Simberloff 2005). When two similar species are found in sympatry, a change in size or morphology is expected (Jones 1997) in order to minimize competition processes (see Dayan and Simberloff 1998, Palomares and Caro 1999, Dayan and Simberloff 2005) and it is mainly studied on small geographic scales (Soberón 2007). However, the analysis of possible abiotic niche displacements in geographic ranges across the entire area of distribution of a pair of species using ENM might help us understand competition process (Peers et al. 2013), with niche overlap as a surrogate for competition. This way, niche overlap will be analyzed with a dataset of "scenopoetic" variables on a regional scale, even when biotic factors are mainly related to "bionomic" variables on local scale (see Soberón 2007).

In the present work, the distribution patterns of *Galictis cuja* and *Lyncodon patagonicus* on regional scales were studied using ENM. Climatic determinants of distribution patterns and measures of niche breadth and niche overlap between sympatric and allopatric (*sensu* Rivas 1964) areas are also analyzed. Particular interest was given to answering whether niche displacement might exist between the studied species as a possible consequence of competition.

Materials and methods

Environmental niche modeling

ENMs were performed using MaxEnt v. 3.3.3k (Phillips et al. 2006). MaxEnt was chosen because it performs better than other alternative software using presence-only data (Elith et al. 2006). Nineteen bioclimatic variables and altitude data were downloaded from Worldclim (http://worldclim.org) at a spatial resolution of 30 arc-seconds or 1 km^2 (Hijmans et al. 2005a). GlobCover 2009 map provided 22 land cover classes at a 300-m resolution (see Bontemps et al. 2011), as a categorical variable of vegetation cover. MaxEnt models were created with the 19 bioclimatic variables, altitude and vegetation cover using 1 km^2 as resolution for all layers.

Data acquisition

Localities recorded for both species were taken from relevant literature and museum specimens. In the case of data lacking geographical coordinates, these were obtained with Global Gazetteer (http://www.fallingrain.com) and reference maps (e.g. roads, towns, rivers, lakes). In total, 240 localities were obtained for *Galictis cuja* and 54 for *Lyncodon patagonicus* (see Supplemental Table 1 and Supplemental Figure 1). Both datasets cover the actual known distribution of both species.

As the Worldclim database contains information from the year 1950 onwards, only localities posterior to this date were analyzed, given that to generate accurate models, species and environmental data should be contemporaneous (Myers et al. 2015). This way, 99 localities were analyzed for *Galictis cuja* and 38 for *Lyncodon patagonicus*. Using Convex Hull in QGIS 2.8.1- Wien (QGIS Development 2015), areas of distribution were created for each species from point localities (i.e. polygons) to define sympatric localities

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recorded of *G. cuja* with *L. patagonicus*. As the entire distribution area of *L. patagonicus* was enclosed within that of *G. cuja*, two datasets were delimited for the latter species: one for the entire distribution (from 1950 onwards) and the other using only sympatric localities. Although MaxEnt might not be particularly sensitive to spatial autocorrelation (Cheng 2008), museum localities derived from unplanned surveys are typically biased in geography (Radosavljevic and Anderson 2014). So localities were filtered, eliminating those that were less than 20 km from each other (a similar methodology has been employed in Pearson et al. 2007, Radosavljevic and Anderson 2014). Finally, three ENMs were created: A) one for *L. patagonicus* using all localities since 1950 (n = 28), B) one for *G. cuja* using all localities since 1950 (n = 73), and C) another for *G. cuja* using only sympatric localities since 1950 (n = 17).

Model fitting

Both Worldclim and GlobCover databases were downloaded and restricted to an area of South America including known occurrences and avoiding areas not inhabited by either species. ENMs were projected into this area.

Ten replicates were performed for each model, with 25% of the localities used as test data (and 75% as training data), random seed, 10,000 background points and auto features. Logistic output was avoided (see Merow et al. 2013) and the cumulative output was selected instead; suitability values of 100–76 (black, high prediction), 75–51 (dark gray, high-medium prediction), 50–26 (gray, medium prediction), 25–10 (light gray, low prediction), and 9–0 (white, very low-null prediction) were assigned. Model predictions were evaluated with a threshold-independent test [area under the curve (AUC, Phillips et al. 2004, 2006)] and a threshold-dependent test. The first, using AUC and as 25% of the data, was used as a test database; MaxEnt delivers two AUC values (i.e. $AUC_{training}$ and AUC_{test}). As the first AUC value is more prone to suffer from overfitting (Warren and Siefert 2011), AUC_{test} values are presented. The 10th percentile threshold was used to create binary maps (presence/absence) and to calculate the true skill statistic (see Allouche et al. 2006).

MaxEnt models were calibrated using 10 replicates with different values for regularization parameters (β): from 0.5 to 10 at 0.5 bins (e.g. 0.5, 1, 1.5, 2, 2.5; see Merow et al. 2013, Radosavljevic and Anderson 2014). Overfitting between all generated ENMs was evaluated with AUC_{diff}, expecting that overfitted models should perform well on training data, but poorly on test data (see Warren and Siefert 2011). A similar methodology was used in recent studies by Gutiérrez et al. (2014) and Giménez et al. (2015). A β of 5.5 yields the lowest AUC_{diff} (0.026 for model A, 0.022 for model B, and 0.024 for model C) and was selected and used to generate final ENMs and niche overlap analyses (see below).

Niche breadth and niche overlap

Niche breadth was calculated for the three datasets, based on Levins' (1968) metrics implemented in EMTools v. 1.4 (Warren et al. 2010, see also Nakazato et al. 2010), with niche breadth ranging from 0 (minimum niche breadth) to 1 (maximum niche breadth). Niche breadth mainly relates to the utilization of resources by a species, with maximum niche breadth when all resources are used equally (see Petraitis 1979).

Niche overlap was calculated twice between the three datasets, for models A–B and A–C (i.e. between *Lyncodon patagonicus* and the total range of *Galictis cuja* and between *L. patagonicus* and sympatric localities of *G. cuja*). ENMTools v. 1.4 (Warren et al. 2010) calculates a similarity measure called *I* (Warren et al. 2008) between habitat suitability measured for each grid cell using an ENM produced with MaxEnt (Phillips et al. 2006). The *I* statistic ranges from 0 (environmental tolerance for each species do not overlap) to 1 (when all grid cells are considered equally suitable for both species; see Warren et al. 2008, 2010). To study if ENMs generated for both species are identical or exhibit ecological significant differences, an identity test in EMTools (Warren et al. 2010) was performed only between models A and C, given that "identity" is expected only when two species tolerate the same environmental conditions and have the same suite of environmental conditions available (Warren et al. 2008). As this is a very strict condition, background test in EMTools (Warren et al. 2010) was also generated between two datasets (i.e. between *L. patagonicus* and *G. cuja* using all localities since 1950). The background test aims to determine if ENMs are more similar than expected by chance, given the underlying environmental differences between the regions the species inhabits (Warren et al. 2008, 2010). Both the Identity and background tests were performed with 100 replicates, which is assumed to be enough to reject a null hypothesis with $p < 0.01$ (Warren et al. 2008).

Importance of environmental variables

Importance of climatic variables in explaining distribution patterns was analyzed with two different approaches.

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The first performed with MaxEnt's jackknife tests to evaluate variable contribution to each ENM, and the second with principal component analysis (PCA), extracting climatic information of altitude and 19 bioclimatic variables (Hijmans et al. 2005a) for each record locality (from 1950 onwards) for both species in DIVA-GIS v. 7.5 (Hijmans et al. 2005b), on a correlation matrix in the software InfoStat v. 2010 (Di Rienzo et al. 2010). This way, possible correlated variables are converted into uncorrelated principal components (PCs, see Jollife 2002), which in this case allowed the evaluation of the occurrences of the species in a climatic space (Broennimann et al. 2007).

Results

Environmental niche modeling

ENM projection for *Lyncodon patagonicus* is shown in Figure 1A. Three areas of high predictive values are seen in model A: 1) in eastern and central Patagonia (*sensu lato*), 2) in northwestern Patagonia (*sensu lato*), and 3) in northwestern Argentina. These three areas are connected by areas with medium predictive values, and in a biogeographic context, the potential distribution of *L. patagonicus* seems to be enclosed within the Andean Region and the South American Transition Zone (*sensu* Morrone 2001, 2006). ENM for *Galictis cuja* using all known localities since 1950 is shown in Figure 1B. High predictive values in model B are seen in Uruguay, Buenos Aires province, south-central Patagonia in Argentina, and in central Chile. These areas are both included in the Andean and Neotropical Regions (*sensu* Morrone 2001, 2006). Lastly, ENM for *G. cuja* using only sympatric localities with *L. patagonicus* is seen in Figure 1C. This model is highly similar to the one of *L. patagonicus*, with the same three areas with high predictive values, but reduced in extent (model C).

AUC values were high (i.e. a useful amount of discrimination, Elith et al. 2006) for the three models: 0.814 ± 0.030 (mean ± SD, model A), 0.775 ± 0.043 (mean ± SD, model B), and 0.831 ± 0.053 (mean ± SD, model C). True Skill Statistic was also high for the three ENMs: 0.714 for model A, 0.835 for model B, and 0.705 for model C.

Niche breadth and niche overlap

Niche breadth for *Lyncodon patagonicus* was 0.325, while for *Galictis cuja* it was 0.5 using all localities since 1950 and 0.286 using only sympatric localities.

Niche overlap was high in both analyses, reaching 0.776 between ENMs of *Lyncodon patagonicus* and *Galictis cuja* (models A and B), and 0.975 between ENMs of *L. patagonicus* and sympatric localities of *G. cuja* (models A and C). The identity test indicates that there were no significant ecological differences between ENMs generated for *L. patagonicus* and *G. cuja* using only sympatric recorded localities (Figure 2A), indicating niche equivalency. The background test showed that ENMs of *L. patagonicus* can be explained by environmental conditions of the background area of *G. cuja* (Figure 2B), but the opposite does

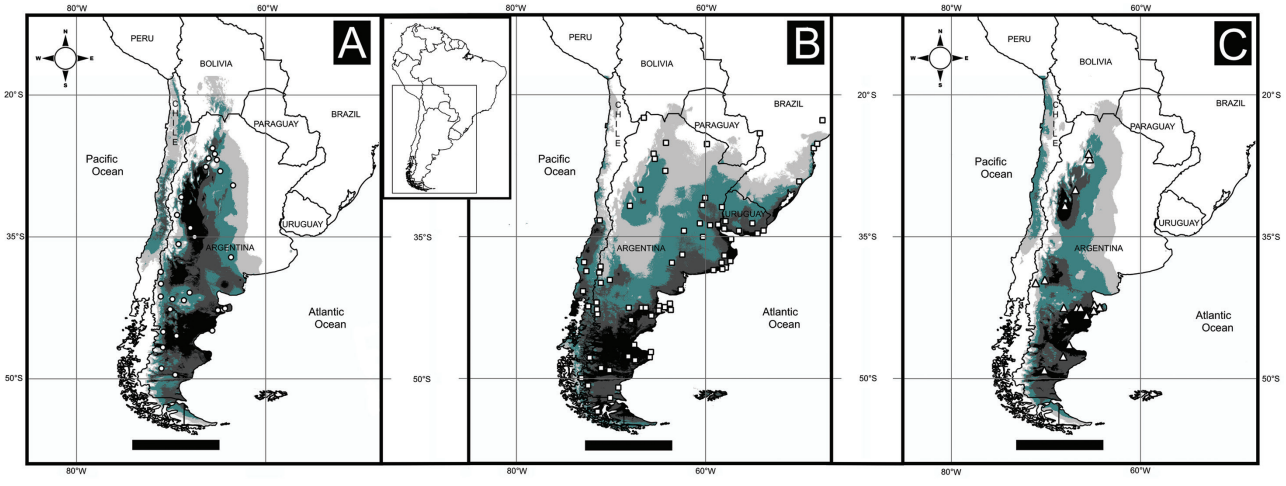


Figure 1: ENMs for (A) *Lyncodon patagonicus* using recorded localities after 1950 (white circles), (B) for *Galictis cuja* using recorded localities after 1950 (white squares), and (C) using only sympatric localities (white triangles) with *L. patagonicus*. Climate suitability values are 100–76 (black, high prediction), 75–51 (dark gray, high-medium prediction), 50–26 (gray, medium prediction), 25–10 (light gray, low prediction), and 9–0 (white, very low-null prediction). Scale (black bar): 1000 km.

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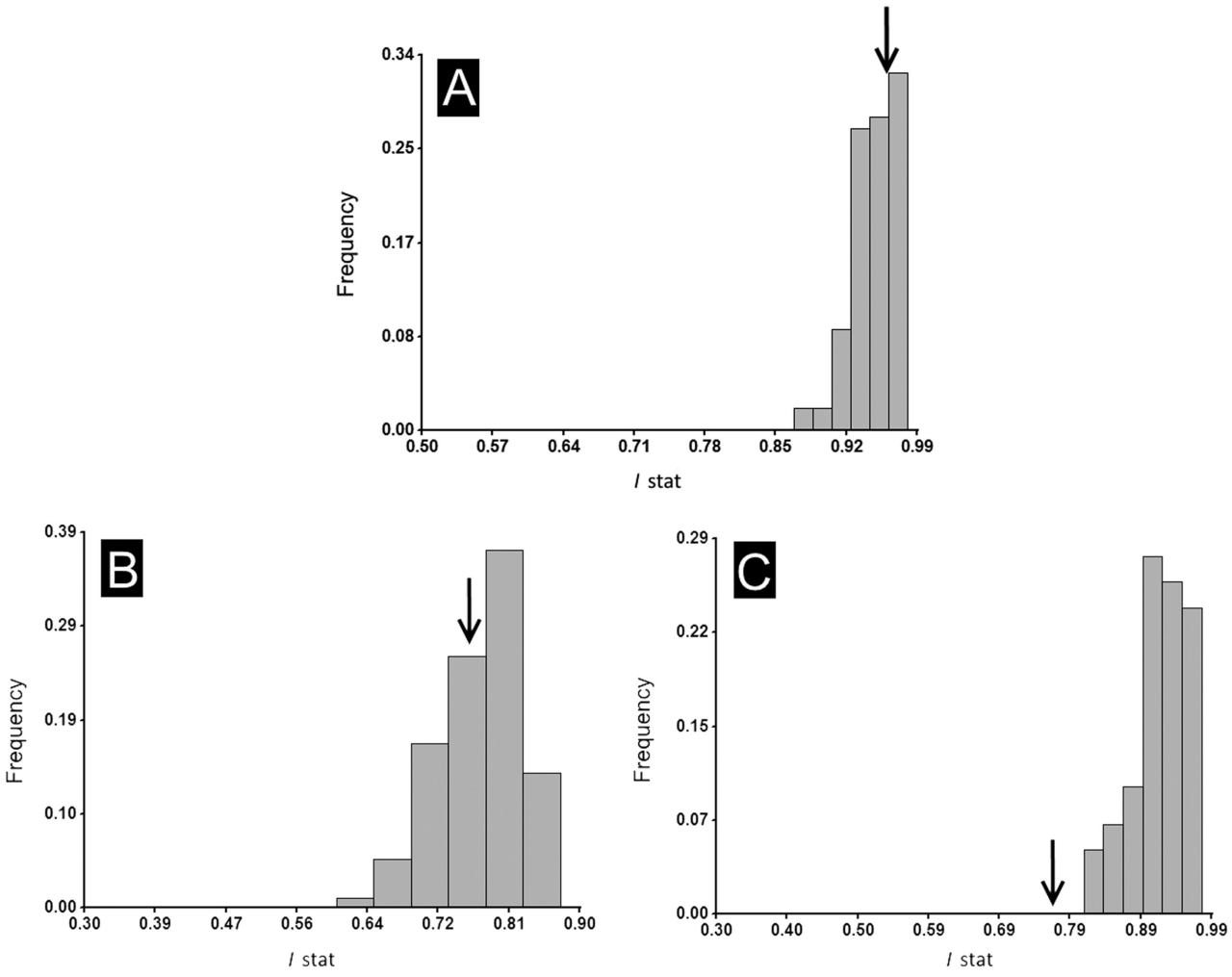


Figure 2: Histogram of similarity (*I* stat) obtained from 100 replicates with identity test for ENMs of *L. patagonicus*-*G. cuja* (A). Histogram of similarity (*I* stat) obtained from 100 replicates with background test for ENMs of *L. patagonicus*-*G. cuja* using all known localities (B) and for *G. cuja*-*L. patagonicus* using all known localities (C). Black arrows represent niche overlap values from original ENMs.

not hold (i.e. the background area of *L. patagonicus* does not explain the ENM of *G. cuja* using all known localities, Figure 2C).

Importance of environmental variables

MaxEnt's jackknife test shows that the most important variables for explaining the distribution of *Lyncodon patagonicus* were minimum temperature of the coldest month (52.3%) and precipitation of the driest month (34.8%). Annual precipitation and isothermality were also important variables with a smaller contribution (< 5%).

The most important variables for explaining the distribution of *Galictis cuja* using known localities from 1950 were isothermality (59.5%) and mean temperature of the coldest quarter (9.4%). Other important variables with smaller contribution were altitude and minimum temperature of coldest month (< 8%). For the analysis using only sympatric localities for *G. cuja*, the most important variables were minimum temperature of the coldest month (39.3%), precipitation of the driest quarter (18.7%), and precipitation of the wettest quarter (16.9%). Other important variables with smaller contribution were annual precipitation and altitude (< 10%).

According to the vegetation types of the GlobCover 2009 map (Bontemps et al. 2011), most (32%) of the localities for *Lyncodon patagonicus* come from "Closed to open (> 15%) (broadleaved or needle-leaved, evergreen or deciduous) shrubland (< 5 m)", followed by "Mosaic forest or shrubland (50–70%)/grassland (20–50%)" with 21%, and by "Sparse (< 15%) vegetation" with 16% (Bontemps et al. 2011). *L. patagonicus* is primarily distributed, based on the recording localities from 1950, in areas of 835 m of mean

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altitude with an altitudinal range of 0–1906 m, 12.4°C of mean annual temperature with a range of 6.7°C–19.6°C, and 378 mm of annual precipitation with a range of 121–1081 mm. If all recorded localities are to be considered, the upper limit of the mean annual temperature range would extend to 20.2°C.

As for *Galictis cuja*, the majority of records (25%) also come from "Closed to open (>15%) (broadleaved or needle-leaved, evergreen or deciduous) shrubland (<5 m)", followed by "Sparse (<15%) vegetation" with 16%, and from "Closed to open (>15%) broadleaved evergreen or semi-deciduous forest (>5 m)" with 10% (Bontemps et al. 2011). Using the data from 1950 onwards, the lesser grison is distributed in areas of 653 m of mean altitude, with an altitudinal range of 0–4182 m, 12.8°C of mean annual temperature with a range of 4°C–22°C, and 669 mm of annual precipitation with a range of 113–2135 mm. If all recorded localities are used, the upper altitude limit would extend to 4654 m, 27.4°C of mean annual temperature, and 4000 mm of annual precipitation.

The first four PCs explained 89% of the variance, with 40%, 24%, 18%, and 7% for factors 1–4, respectively. Minimum temperature of the coldest month explained most of the variation for PC1 (i.e. the one with the highest loads), followed by annual precipitation. Maximum temperature of the warmest month and precipitation of the coldest quarter explained most of the variation of PC2. The entire climatic range plotted in a PCA of *Lyncodon patagonicus* was included within that of *Galictis cuja*, analyzing PC1 vs. PC2 (Figure 3), PC2 vs. PC3, and PC3 vs. PC4 (figures not shown).

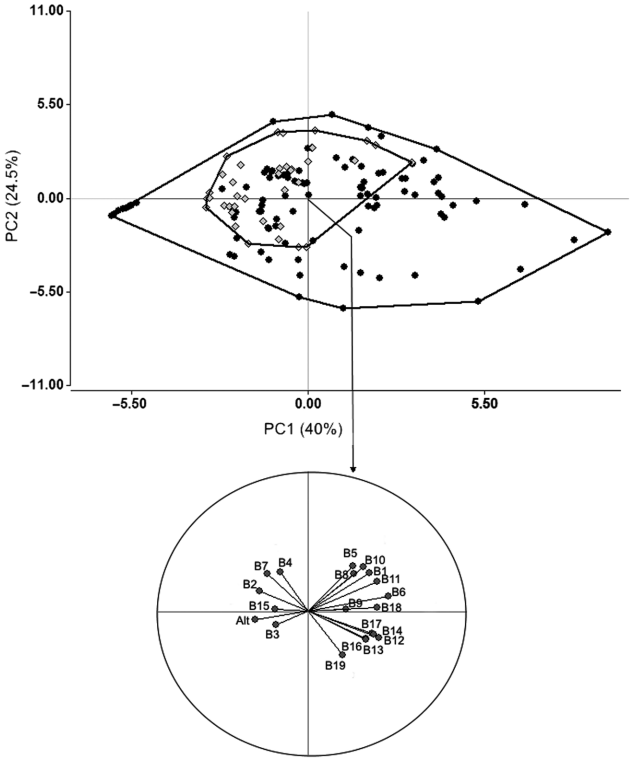


Figure 3: Scatterplot of PC1 and PC2 of PCA performed on environmental variables extracted from recorded localities for *G. cuja* (black dots) and *L. patagonicus* (gray diamonds). Polygons include specimens for each species. Variable names represent altitude (Alt) and the 19 bioclimatic variables (B1–B19), from Hijmans et al. (2005a).

Discussion

Lyncodon patagonicus's range extends mainly throughout northwestern Argentina and Patagonia (*sensu lato*), following dry and cold climates, with altitudes lower than 2000 m (see Prevosti and Pardiñas 2001, Prevosti et al. 2009, Schiaffini et al. 2013). The distribution pattern presented herein is similar to the ones presented previously (Schiaffini et al. 2013), as expected given that many of the localities recorded have been re-analyzed (with an updated methodology) in the present work. The use of different β multipliers might explain the differences found between this and the previous study, particularly on the extent of high suitability values.

Galictis cuja distribution extends from northeastern Brazil (Ceara state) from 5°29′S to the southern tip of Chile ("Península de Brunswick") at 53°30′S. The map of localities recorded for *G. cuja* (see Supplemental Figure 1) is very similar to the ones presented in Yensen and Tarifa (2003) and Bornholdt et al. (2013). This is the first attempt to model *G. cuja*'s potential distribution using MaxEnt. Unfortunately, many of the published localities lack date of collection, and hence had the problem of not being temporally allocated with certainty within the climatic database used. Higher predictive values were seen along southern Brazil, Uruguay, Buenos Aires province, and Patagonia, in areas composed mainly of shrubs with low vegetation cover, but with highly variable precipitation and temperature (Dinerstein et al. 1995, Burkart et al. 1999). This makes it possible to think of *G. cuja* as a generalist species regarding habitat requirements, which seems to be confirmed by a wider niche breadth.

Environmental tolerance of *Galictis cuja* includes the areas and climate of *Lyncodon patagonicus*, as shown by the background test and PCA, with minimum temperatures and annual precipitation as important variables to explain their distribution patterns. Previous works had stated the importance of minimum temperatures as a limiting factor for species distribution (see Birney and Monjeau 2003

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for South American marsupials and Monjeau et al. 2009 for South American carnivores), mainly related to energy availability. If we take into account that both species have a long and thin body and might present poor thermal balance (i.e. large body surface related to metabolically active tissue, see Brown and Lasiewski 1972), their presence in cold zones might be explained by the possibility of obtaining a large number of prey to maintain a somehow constant body temperature (or at least with minor fluctuations), as has been proposed for *Mustela nivalis* (see Sheffield and King 1994). As *G. cuja* is larger (see Schiaffini and Prevosti 2014), it might present a wider range of available prey sizes (Schoener 1969), and extend its southern distribution more than *L. patagonicus*.

Niche overlap of these two species was high, and geographic overlap might be thought of as a surrogate for competition. Highly overlapping species in geographic and ecologic space would have to co-evolve to minimize competition between them (Dayan and Simberloff 1998). Through this process, direct interspecific interactions would be low, even when geographic overlap is great, due to different microhabitat use, different activity cycles, or trophic preferences (Davies et al. 2007). Although the distribution of these species on a microhabitat scale was not analyzed herein, several localities seem to be syntopic (*sensu* Rivas 1964), especially in eastern and northwestern Patagonia, and northwestern Argentina. Activity cycles of *Galictis cuja* seem to indicate that it is active during day and night (Yensen and Tarifa 2003 and references therein), while *Lyncodon patagonicus* is assumed to be active during crepuscular times and at night (Larivière and Jennings 2009). Both *G. cuja* and *L. patagonicus* display morphological features of "hypercarnivorous" morphotypes within Mustelidae (see Ewer 1973), with large canines and developed shearing edges in carnassial teeth (i.e. adapted for feeding from vertebrate flesh) and occupying similar positions in the morphological space (see Schiaffini and Prevosti 2014). However, there are strong size differences among them, with condylobasal length and length of lower carnassial averaging 75.24 mm and 8.29 mm for *G. cuja*, and 53.87 mm and 6.78 mm for *L. patagonicus*, respectively (taken from Schiaffini 2014). Results from this study seem to be in accordance with those obtained by Davies et al. (2007), who found that range overlap might be large in carnivoran species that differ in some morphological traits such as size and/or shape of carnassial teeth. Size differences might allow these two mustelid species to co-occur. The diet of *G. cuja* in Argentina is composed mainly of introduced lagomorphs and native rodents (Diuk-Wasser and Cassini 1998, Delibes et al. 2003, Zapata et al. 2005, Sade et al. 2012), while that of *L. patagonicus* is virtually unknown but supposed to comprise fossorial rodents, particularly *Microcavia* and/or *Ctenomys* species (Prevosti et al. 2009 and references therein). However, these items are also found in *G. cuja*'s diet, with variable contributions of these items according to different localities (see Diuk-Wasser and Cassini 1998, Delibes et al. 2003, Zapata et al. 2005, Sade et al. 2012). Future studies should focus on gathering information on the diet of *L. patagonicus*.

Although size differences could be the result of character displacement, regrettably only a few *Galictis cuja* specimens from sympatric areas with *Lyncodon patagonicus* had voucher specimens deposited in museum collections, for which no statistical test of size variation could be performed yet. However, previous works have detected that most of the size variation between these species might be the result of historical processes, particularly related to cladogenetic events (Schiaffini and Prevosti 2014). The acquisition of more voucher specimens from sympatric areas might allow future lines of research to specifically address the possible existence of character displacements between these species.

In conclusion, no evidence for niche displacement between these species was found. Instead, they both share major areas of geographic and potential distribution. *Galictis cuja* seems to be more of a generalist species, based on niche breath and environmental tolerance. The process that allows coexistence between these species seems to be related to prey-size range, with *Lyncodon patagonicus* specialized on fossorial rodents as the main food item, indicating that geographic overlap is not the only necessary surrogate for estimating competition processes. As ecological overlap between *G. cuja* and other predators from the South American southern cone has been previously studied (see Ebensperger et al. 1991), further research might address other important questions regarding the existence of ecological overlap between *G. cuja* and the major grison *Galictis vittata* in sympatric areas (see Bornholdt et al. 2013), or even between *L. patagonicus* and the Patagonian opossum *Lestodelphys halli*, sympatric in patagonia (*sensu lato*, see Formoso et al. 2015).

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