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Change of niche in guanaco (*Lama guanicoe*): The effects of climate change on habitat suitability and lineage conservatism in Chile

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**Background.** A fundamental problem in the biogeography of climate change is to understand and predict how environmental factors determine whether organisms will alter their seasonal activities, home ranges, migratory patterns, abundances, and interspecific interactions. The main goal of this contribution was to define the ecological niche of the guanaco (*Lama guanicoe*) to describe potential distributional changes and to assess the relative importance of niche conservatism and divergence processes among the two lineages described for the species.

**Methods.** We used current and future projections of climate change under two extreme GHG emission scenarios (RCP2.6 and RCP8.5) to evaluate changes of the environmental niche and future distribution of the largest mammal in the southern cone of South America. Evaluation of niche conservatism and divergence are based on identity and background similarity tests.

**Results.** We show that: a) the current geographic distribution of lineages and contact population prescribe different climatic requirements that are related to the geographic areas where these lineages are located; b) future distribution models predict a decrease in the distribution surface under both scenarios; c) the surface area predicted to be gained, lost, and unchanged is ~15%, 15-26%, and 85-75% respectively; d) a 3% increase of areal protection is expected if the current distribution of protected areas is maintained, however this is expected to occur at the expense of a large reduction of high quality habitats under the best scenario and; e) current and future distribution ranges of guanaco mostly adhere to phylogenetic niche divergence hypotheses between lineages (*L. g. cacsilensis* and *L. g. guanicoe*). However, both lineages and the contact population show niche conservatism given niche similarity tests.

**Discussion.** Associating environmental variables to species ecological niche seem to be an important aspect of unveiling the particularities of, both, evolutionary patterns and ecological features that species face in a changing environment. We have provided specific descriptions of how such patterns may play out under the most extreme climate change predictions, thereby, providing a grim outlook of the future potential distribution of guanaco. From an ecological perspective, while a slightly larger distribution area is expected, this may come with an important reduction of available quality habitats. From the evolutionary perspective, we describe the limitations of the contact population´s niche to merge with the northern and/or southern niche lineages of guanaco exposing the complexities of understanding evolutionary patterns across this taxon as it experiences climate change dynamics.
Change of niche in guanaco (*Lama guanicoe*): The effects of climate change on habitat suitability and lineage conservatism in Chile

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ABSTRACT

Background. A fundamental problem in the biogeography of climate change is to understand and predict how environmental factors determine whether organisms will alter their seasonal activities, home ranges, migratory patterns, abundances, and interspecific interactions. The main goal of this contribution was to define the ecological niche of the guanaco (Lama guanicoe) to describe potential distributional changes and to assess the relative importance of niche conservatism and divergence processes among the two lineages described for the species.

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Results. We show that: a) the current geographic distribution of lineages and contact population prescribe different climatic requirements that are related to the geographic areas where these lineages are located; b) future distribution models predict a decrease in the distribution surface under both scenarios; c) the surface area predicted to be gained, lost, and unchanged is ~15%, 15-26%, and 85-75% respectively; d) a 3% increase of areal protection is expected if the current distribution of protected areas is maintained, however this is expected to occur at the expense of a large reduction of high quality habitats under the best scenario and; e) current and future distribution ranges of guanaco mostly adhere to phylogenetic niche divergence hypotheses between lineages (L. g. cacsilensis and L. g. guanicoe). However, both lineages and the contact population show niche conservatism given niche similarity tests.

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Introduction

Since industrialization, the anthropogenic influence on natural environments has soared and human induced climate change is imposing severe challenges to the equilibrium of natural ecosystem functioning (IPCC, 2013). As a response to climate change, and in order to cope with altered environmental conditions, species may shift their geographic distribution (Pecl et al., 2017). As climate change progress, organisms will either have to face extinctions or adapt (Berg et al., 2010) by altering their seasonal activities, home ranges, migratory patterns, abundances, and interspecific interactions (Lenoir et al., 2008; Araújo, Thuiller & Yoccoz, 2009; Elith & Leathwick, 2009; Pecl et al., 2017). While many of these changes have already been observed (IPCC, 2013; Pecl et al., 2017), recent meta-analyses indicate that the global rise of temperatures will likely accelerate extinction risks and threaten up to one in every six species (Urban, 2010). Studies on the impact of climate change on ungulates have shown that changes in distribution ranges include altitudinal shifts in mountain environments (Mason et al., 2014) and distributional shifts towards equivalent habitats (Hu & Jiang, 2011). In more extreme cases, local extinctions will be driven by environmental aridization (Thuiller et al., 2006; Duncan et al., 2012).

In Chile, current projections of greenhouse gas emissions proposed by the Intergovernmental Panel on Climate Change (IPCC) indicates that temperature will increase in a North to South gradient (IPCC, 2013). A large 2.5°C increase is expected in the Altiplano under the most extreme emission scenario and a milder 0.5°C increase is projected in the southern region of Magallanes for the period 2031-2050. Additionally, a 10-15% decrease in precipitation is
expected in the middle of the country (between 25° and 45° S), while forecasting a 5% rainfall increase in Patagonia and a similar snowfall decrease in the Magellan region (Rojas, 2012).

The guanaco (*Lama guanicoe*) is both the most abundant native ungulate and the largest (120 kg) artiodactyl in South America (Franklin, 1982). The species is widely distributed throughout the South American cone, inhabiting cold, arid, and semi-arid environments from sea level up to 5,000 m a.s.l. extending from northwestern Peru to Tierra del Fuego and Isla Navarino in the southern tip of the continent, with small populations roaming east of the Andes in the arid Chaco of Bolivia and Paraguay (Franklin, 1982; González et al., 2006). Highest population densities are found in the Andes and in Patagonia (Baldi et al., 2016). The species is characterized by specific anatomical, physiological, and reproductive adaptations that may explain its capability to thrive and survive in arid environments despite the intense competition with livestock and severe degradation of their habitat (González et al., 2013; Marin et al., 2013; Baldi et al., 2016) as well as the survival of the northern lineage through the mammal extinction in the late Pleistocene (Lessa & Fariña, 1996; Metcalf et al., 2016). In spite of this, the guanaco has a defined ecological role in each of its ecoregions either controlling vegetation growth or dispersing seeds (González et al., 2006). These qualities make the guanaco an important element within the trophic chain. For instance, it is the main prey of the puma (*Puma concolor*) (Franklin et al., 1999) and feeds scavengers such as the chilla fox (*Lycalopex griseus*), the culpeo fox (*Lycalopex culpeus*) and the Andean Condor (*Vultur gryphus*) among others (Travaini et al., 2001; González et al., 2006).

Two distinct subspecies of Guanaco (*L.g. cacsilensis* and *L.g. guanicoe*) have been proposed based on genetic studies (Marin et al., 2013, 2017). *L.g. cacsilensis* is distributed to the West of...
the Central Andean Plateau throughout Peru and the northern tip of Chile with occurrences mostly explained by elevation and precipitation seasonality. *L.g. guanicoe* is found on the southeastern slope of the Andes, ranging throughout Patagonia and Tierra del Fuego with occurrences mostly explained by annual precipitation, precipitation seasonality and grass cover (González et al., 2013). The geographical limit between the Northwestern and Southeastern lineages has been proposed to occur around 31° S in Chile (Marin et al., 2017) and the significant genetic structure found among the two guilds has led to recommend to classify the two lineages as evolutionary significant units (ESUs) following Moritz’s (Moritz, 1994) criteria (González et al., 2013; Marin et al., 2013). However, the two lineages are not completely isolated, in fact some populations have individuals of both lineages forming zones with individuals of mixed genetic heritage (Marin et al., 2013). The distribution of this “contact population” was predicted to occur at the south end of the Altiplano, between 26° S and 32°S approximately, and is related to annual precipitation and precipitation seasonality (González et al., 2013). As reported by Marin et al., (2013), the Andean plateau could have acted as a biogeographical and ecological barrier fostering vicariance processes that may be at the origin of the current distribution of guanaco lineages. It is presumed that climate changes that occurred in the past, allowed the establishment of populations over this geographic barrier, with periods of connectivity and isolation allowing the establishment of populations with mixed genetic heritage (Marin et al., 2013). An example of such is the small confined population between the Sechura and Atacama Desert discussed in (Marin et al., 2017), probably due to the increased environmental humidity between 16.2 - 10.5 Ma and 8-3 Ma which led to the growth vegetation in the desert (Betancourt, 2000).
While the discontinuity of the current geographical distribution of guanaco is mostly a consequence of recent human activities (González et al., 2006), the macroevolutionary processes leading to lineage divergence in guanaco should have important consequences when deciding on the conservation actions required for such species, as has been discussed elsewhere for other species. On the ecological end, it has been described that current threats are mostly related to high competition for fodder with cattle and introduced mammals (Mason et al., 2014); predation by feral dogs, illegal hunting, and the reduction of available habitat due to the intensification of the agriculture (González et al., 2006; Baldi et al., 2016). However, the impressive 14.5 million hectares protected by the Chilean System of Protected Areas only covers 5% of the species’ range (Baldi et al., 2016) and guanaco occurs in only four of the ten major arid habitats described for South America (González et al., 2013) prompting important questions regarding the future of its distribution. For instance, as a generalist, guanacos may not carry the necessary characteristics to adapt to the swift environmental changes predicted by climate change scenarios at large geographical scales. Nevertheless, evolutionary history molded specific adaptations to the environment at the intraspecific level, which could allow each lineage to respond differently to changes. Even considering that *L. guanicoe* is well adapted to a wide variety of habitats, evidence from its natural history indicates that past changes in climate have clearly influenced the geographic distribution of this species, particularly in the Altiplano and Puna where guanacos and vicuñas (*Vicugna vicugna*) compete for resources since the Holocene (Marin et al., 2013, 2017). Thus, under the possible climate change scenarios in Chile which forecast temperature increases and declining humidity values, we expect *L. g. cacsilensis* to expand (or to shift) southward and mix with the contact
population. On the other hand, we predict that \textit{L. g. guanicoe}, characterized by a higher phenotypic flexibility should mostly maintain its current geographic distribution.

From an evolutionary perspective, given the existence of these two lineages and the repeated suggestions of their consideration as ESUs (Marin et al., 2013; Baldi et al., 2016), it would be of great interest to evaluate the state of conservation of their niche to support with new evidence this classification. From such perspective, it becomes relevant to assess whether phylogenetic niche conservatism (PNC), the tendency of closely related species to differ less ecologically than expected by chance, or otherwise, phylogenetic niche divergence (PND), the tendency of closely related species to differ more ecologically than expected by chance may prevail under current and predicted niche segregation patterns under future climate change (Pyron et al., 2015).

Based on the latest projections of climate change in the region (Rojas, 2012; IPCC, 2013) and the understanding of \textit{L. guanicoe} taxonomy and life history, we developed models based on niche theory to assess the impact of climate change on guanaco’s ESUs. By modeling the niche of \textit{L. guanicoe} and its lineages we here: a) estimated their current geographic distribution based on bioclimatic variables; b) predicted their future distribution based on the projections of the best and worst climate change scenario at two different time frames (2050, 2070); c) quantified the surface area predicted to be gained, lost, or remain stable in the future for both guanacos lineages and contact population; d) evaluated and compared how much of the Chilean protected areas will overlap with the future distributional area calculated for guanacos; and e) explored the existence of niche conservatism or divergence between \textit{L. guanicoe} lineages, in
terms of their niche equivalence (Graham et al., 2004) and similarity (Peterson, Soberón & Sánchez-cordero, 1999).

METHODS

An analysis workflow is outlined in Figure 1 to explicitly show the different steps used in this work.

Specie occurrence data

We build a Guanaco occurrence dataset of 3,326 records by complementing previous work by the authors with 364 additional records (González et al., 2013). New records were collected following the same procedures outlined in Gonzalez et al. (González et al., 2013), that is, from direct and indirect evidence of Guanaco presence collected between the years 2000 and 2016 across several field campaigns. Most of new records were collected in the northern section of the country in the Arica, Parinacota (i.e. 17°S latitude) and Coquimbo region (30°S). Each record was assigned to a 1x1km cell defined by the resolution of the environmental datasets employed (see below). This resulted in a total of 298 records for L.g. cacsilensis, 837 for the contact population, and 2191 for L.g. guanicoe.

Climate predictors

To predict the distribution of L. guanicoe under possible climate change scenarios, we limited the selection of environmental predictors to climatic variables. In time of future anthropogenic landscape transformations (Thuiller et al., 2006; Hu et al., 2015). In fact, similarly to what has been described in the literature (Thuiller et al., 2004), our previous work dismissed the importance of non-climate predictors for Guanaco distribution models in favor of exclusive
climatic variables (González et al., 2013). We use the 19 bioclimatic variables from WorldClim (version 1.4) summarizing temperature and precipitation information worldwide (Hijmans et al., 2005). To reduce collinearity and the number of explanatory variables, we used a paired correlation analysis to inspect pairs of variables with large correlation coefficient (>0.8). This additionally allowed to reduce model overfitting by eliminating highly correlated variables (Beaumont, Hughes & Poulsen, 2005). Principal components analysis was then used to verify the independence of the selected set of bioclimatic variables.

While the analysis was limited to the administrative bounds of Chile, all WorldClim variables were projected to UTM 19 South, with a 1 squared-km of spatial resolution, spanning from latitudes 15°S to 55°S and longitudes 60°W to 80°W and a total area of 5,921,578 km² covering most of the southern cone of South America.

**Future Climate Projections**

The projection of future geographic distribution of niches was performed using the outputs of the Coupled Model Intercomparison Project 5 (CMIP5) of the IPCC's methodology for the Fifth Assessment Report (AR5) (Taylor, Stouffer & Meehl, 2012). The two extreme GHG concentration scenarios, also known as Representative Concentration Pathway (RCP), were used to project future climate niches. RCP2.6, the most optimistic (and unlikely) scenario, considers a lower GHG concentration and projects average increases of temperature between 0.3 ° to 1.6 ° C with 0.26 to 0.55 m increases of sea levels. While RCP8.5, the most pessimistic scenario, considers higher GHG concentrations with a 2.6° to 4.8°C projected increase in mean global temperature and a 0.45 to 0.82 m rise of sea levels (IPCC, 2013). We chose both extreme
scenarios to evaluate the minimum and maximum impact of climate change in the guanaco
distribution.

Given the large uncertainties of future climate predictions, and the exploratory nature of such
models, we selected five General Circulation Models (GCM) among the 19 models used to
generate the AR5. GCM’s are physical climate models that simulate the interactive biophysical
processes between the atmosphere, the ocean, and the land (Moss et al., 2010). Selected
climatic models were: (1) CCSM4 model of the National Center of Atmospheric Research (Gent
et al., 2011); (2) GFDL-CM3 model of the Geophysical Fluid Dynamics Laboratory (Donner et al.,
2011); (3) GISS-E2-R model of the NASA Goddard Institute for Space Studies (Nazarenko et al.,
2015); (4) HadGEM2 – AO atmosphere model and (5) HadGEM2 – ES earth system model, both
of the Met Office Hadley Centre (Collins et al., 2011). Each scenario was evaluated for the short
(2050) and medium term (2070) scenario.

**Niche Modeling**

Entropy maximization procedures in MaxEnt 3.3.3 k (Phillips, Anderson & Schapire, 2006) are
used to model current and future geographic distributions of *L. guanicoe* and its lineages.
MaxEnt uses a machine learning algorithm to generate predictions on the potential distribution
of species based on their presence, pseudo-absences and a set of environmental variables. The
software analyzes the multivariate distribution of environmental conditions of species
occurrences to generate a spatially explicit probability map of lineage occurrence (Franklin,
2009). Such modelling approach has shown to have a good statistical performance compared to
other types of modeling techniques (Elith et al., 2006) and is currently one of the most
commonly used methods to understand habitat suitability, niche structure, geographical
species distribution (Merow, Smith & Silander, 2013) as well as to project environmental niches
to future scenarios (Hijmans & Graham, 2006).

We performed 100 cross-validated replicates for each GCM with logistic output, that unlike
other outputs (i.e. raw and cumulative) assumes that a known observation probability can be
assigned to each pixel and has thus been considered as a true approximation of presence
(Merow, Smith & Silander, 2013). The "fade by clamping" option was used to avoid predictions
beyond the observed geographical range during the training of the future distributions model
(Phillips, Anderson & Schapire, 2006). All other parameters were kept at their default
configuration (Phillips, Dudík & Schapire, 2004) as they have previously shown good
performance in ungulate modeling (Hu & Jiang, 2011; González et al., 2013; Hu et al., 2015;
Quevedo et al., 2016) and other taxonomic groups (Phillips & Dudík, 2008; Fourcade et al.,
2014).

We use an ensemble forecasting framework to minimize the inherent variability introduced by
the various forecast models employed, as proposed by Araújo and New (Araújo & New, 2007).
That is, we evaluated one hundred replicates for each of the five GCMs under both extreme
RCP emission scenarios for the years 2050 and 2070. We hence generated 2,000 projected
distribution models for the Guanaco (5 GCMs x 2 RCPs x 2 times slices = 20 models x 100
replicates) and used the average model over these 100 replicates for each GCM (Araújo & New,
2007). The final results are four projected climate models for L. guanicoe, under RCP2.6 and
RCP8.5 scenarios evaluated for years 2050 and 2070.

Two methods are used to generate forecast models: (i) Forecast-model 1 [(100 replicates x 5
cross-validated replicates for each GCM with logistic output, that unlike
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of MaxEnt for each 5 GCMs selected in this work. We average these five final models generating four ensemble models under the best (RCP2.6) and worst (RCP8.5) scenario, for both periods (2050 and 2070) (Fig. 1, method 1). (ii) Forecast-model 2 [(100 replicates x 5 GCMs) x 1 RCP x 1 time frame]. This model was generated from the average of each bioclimatic variable generated by each GCMs (i.e. [Bio1_{CC} + Bio1_{GF} + Bio1_{GS} + Bio1_{HD} + Bio1_{HE}] x 5). We then used the average of 100 replicates. As a result, only one model was evaluated in the worst scenario at 2070 (Fig. 1, method 2).

Forecast-model 1 was later employed to evaluate areal gains for each projected model (see below) (Heap, 2016), while Forecast-model 2 was used in the PNC analyses (see below) (Warren, Glor & Turelli, 2010). A comparison of the predictions of both forecast models is available in Supplemental Fig. S1.

**Model evaluation, prediction and spatial projection**

Generated niche models were evaluated using a threshold-independent analysis of the area under the curve (AUC) provided by the Receiver Operator Curve (ROC) (Phillips, Anderson & Schapire, 2006; Acevedo et al., 2010; Anderson & Raza, 2010). This sensitivity tests model accuracy by calculating the proportion of true positives versus false positives. The resulting values range from 0 to 1, where model predictions are accepted when obtained AUC values are over 0.7 (Merow, Smith & Silander, 2013). A 3:1 ratio was used to divide training and testing datasets (Phillips, Anderson & Schapire, 2006) for such purpose. AUC Jackknife analysis allowed to identify the contribution of each variable to final current and future models, and allow the detection of those variables that significantly improve predictions for the occurrences of each lineage (Phillips, Anderson & Schapire, 2006).
We reclassified predicted habitat using a 0.25 threshold interval to label three habitat suitability classes: low suitability habitat when occurrence probability ranges between 25 and 50%; suitable habitat if occurrence probability is in the 50 to 75% interval; and high suitability if over 75% of occurrence probability, values below 25% were considered as inappropriate habitat (Hu & Jiang, 2012; González et al., 2013; Shrestha & Bawa, 2014).

**Changes in distribution surface and incidence in protected areas**

The areal extent predicted by each model, current and projected, were compared to determine habitat loss (or gains) under the various climate change scenarios evaluated. The areal surface of each model was calculated from the suitability threshold defined above. We used software BioSARN v.1 (Heap, 2016) to estimate differences between models. These results were classified into three categories: (a) Areal loss, when future prediction show a decrease of the areal extension compared to current niche models; (b) Areal gain, produced when future prediction add area to current niche models; (c) Unchanged areas, when climate change predictions show no impact on current guanaco distribution.

In addition, the fraction of future distribution covered by the system of protected area in Chile (PA) was estimated. All categories of PAs were used: national parks, national reserves, biosphere parks, national monuments, national patrimony, RAMSAR sites (as of 2012) and private PA as of 2011 (IDE, 2016).

**Evaluation of PNC or PND**

PNC and PND among lineages and the contact population was evaluated through their current and projected niches using Forecast-model 1 for the most extreme scenario (i.e. RCP8.5) in
290 2070 and ENMTools v.1.4.3 (Warren, Glor & Turelli, 2010). As proposed in Warren et al.
291 (Warren, Glor & Turelli, 2008, 2010), niche overlap between lineages was calculated with the
292 statistical indices “I” (derivative of Hellinger’s distance) and “D” (Shöener’s D). These indices
293 quantitatively assess whether the niche space for two compared lineages are equivalent by
294 comparing the actual niche to a null niche model generated from a randomized pool of
295 locations for each lineage. This allows to effectively evaluate similarity under the premise that if
296 niche spaces are in fact similar, they should be able to predict each other (Warren, Glor &
297 Turelli, 2010). Because the identity test strongly depends on an accurate representation of
298 species habitat suitability in the construction of the niche model, it has been described to be
299 sensible to the particular sampling scheme employed and therefore less suitable to compare
300 allopatric niches (Warren, Glor & Turelli, 2008). We hence use the background test to compare
301 niche differences between allopatric lineages. The latter uses a null distribution of expected
302 niche differences drawn from random points within the range of the compared lineages. This is
303 repeated 100 times producing a distribution of I and D values to which empirical difference is
304 compared against using a two-tailed significance threshold of 0.1 for such background
305 similarity test. We used the identity test to evaluate the hypothesis of niche equivalence
306 (Graham et al., 2004); and the background similarity test to evaluate the hypothesis of niche
307 similarity (Peterson, Soberón & Sánchez-cordero, 1999). We consider positive outcomes for
308 these test as indicative of PNC between the lineages. On the contrary, the failure to show
309 statistically significance for niche equivalence or overlap as indicative of PND between lineages.

310 Results

311 Selection of climate variables and current distribution model
After removing correlated variables, the final subset of independent bioclimatic variables used in this analysis was composed by: annual mean temperature (Bio1), temperature seasonality (Bio4), annual temperature range (Bio7), annual precipitation (Bio12) and precipitation seasonality (Bio15). See supplemental Fig. S2 and Fig. S3 for results on correlation and principal component analysis.

The major contribution to the current distribution of *L. guanicoe* is given by the annual range of temperature (28.2%, AUC = 0.84), whereas *L. g. cacsilensis* is dominated by precipitation seasonality (66.7%, AUC = 0.95), the contact population by annual precipitation (36.7%, AUC = 0.93), and the southernmost *L. g. guanicoe* is mostly driven by annual mean temperature (35.8%, AUC = 0.91). Detailed analysis of variable contribution (%) and Jacknife’s analysis can be seen in supplemental information, Fig. S4.

All current distribution models generated for *L. guanicoe* and their lineages, presented a good performance with mean AUC values over 0.89. The resulting geographic range for guanaco spans for about a third of the Chilean continental surface. The geographic areas covered by *L.g. cacsilensis* and *L. g. guanicoe* are of 47,148 and 100,539 km$^2$ respectively. The contact population show a geographic extent of 84,976 km$^2$. Interestingly, our models show a 20% difference when comparing areas from the sum of lineages modeled independently and the total area modeled with all the lineages pooled as if they were a single lineage (232,664 km$^2$ vs. 284,499 km$^2$ respectively). Full maps and predictions are available in supplemental information Fig. S5.
Projected distribution models

As for current distribution models, the sensitivity analysis for all forecast-models yielded a large mean AUC > 0.9. After suitability categorization (Fig. 2), our results show that while the geographical distribution pattern of guanaco is conserved, quantitative assessment of the distribution surface reveals a downward trend in both scenarios of climate change for 2050 and 2070. See Table for an outline of workflow and in-depth description of these quantitative analyses.

Marginal decreases are observed among habitat suitability probabilities under the RCP2.6 scenario for the years 2050 and 2070 (273,833 km² vs. 273,573 km² respectively). The small areal reduction under both models is only of 0.8% and 0.9% of the current surface area. However, this decrease is more pronounced under the RCP8.5 scenarios in which a 6.5% and 16.4% reduction is quantified for the years 2050 and 2070 respectively (i.e. 258,141 km² and 230,905 km² respectively).

Surface change between current and projected distribution models.

Projected distribution models show a net loss of high quality habitat (> 75%) and an increase of low quality ones (25-50%) predicting that, while no significant loss of potential distribution areas are apparent, a significant decrease of areas of high quality habitat may occur under both climate change scenarios evaluated here (Table 1).

Surface loss and gains under future climate projections are described in Table 2. Both scenarios show that a large fraction of the guanaco range will remain unchanged. However, it is interesting to note that while similar areal losses and gains are observed under each scenario
for both forecasted time slices, we see larger losses and lower gains for 2070. The more optimistic projection (i.e. RCP2.6) indicates an average loss of 44,234km$^2$ between 2050 and 2070, and a niche displacement (i.e. gain) of 41,225 km$^2$ on average between such time periods. A reverse trend is observed under the more pessimistic scenario (i.e. RCP8.5) with the larger change predicted for 2070. Such prediction will reduce guanaco’s niche by 30%, with a surface loss of 84,008 km$^2$ and a geographic distribution of just about 192,623 km$^2$. Likewise, the smallest niche displacement is observed in this period, with only 38,255 km$^2$ of areal gain (Fig. 3).

Evaluation of PNC and PND

Niche overlap and equivalence tests in Table 3 show a large overlap between the contact population and *L.g. cacsilensis* for niche models under the current and the worse scenario. While limited niche overlap is reported, interestingly, the overlap between the northern lineage and the contact populations increases under future climate change scenarios. On the other hand, the overlap between current and projected niches for *L.g. guanicoe* and other lineages is smaller, particularly with the northern lineage (*L.g. cacsilensis*). When using the results of this latter analysis as “empirical values” to perform identity and background similarity tests (Table 3 and Table 4), we are able to show that statistical differences exist when comparing current niches and projected niches. This indicates that the climatic requirements between the lineages and contact population are not equivalent.

Background similarity test shows that *L.g. cacsilensis* share climatic similarities with the contact population (Table 4). However, such similarity is not reciprocal when comparing the climatic requirements of the contact population to those of the northern lineage – a possibility
mentioned in (Warren, Glor & Turelli, 2010). A similar situation happens when comparing projected niches under the worst climate change scenario (RCP8.5). In such latter case, our results suggest that \textit{L.g. guanicoe} will closely resemble the future climatic niche of the contact population, but this population shows no similarity to the southern lineage.

In spite of this, the remaining comparisons between climatic niches, current and future, exhibit important statistical differences and show that, except for the previous two cases, the climatic requirements for each of the lineages analyzed here are significantly different.

**Projected distribution models and conservation in Chile**

The current network of PA in Chile covers a vast area of approximately 256,550 km\(^2\), according to 2016 data and show a limited overlap with modeled guanaco distribution. In fact, only a 9.8% (i.e. 19,402 km\(^2\)) of current distribution overlaps with a PA. When looking at projected distributions for 2070, our results show that such overlap will increase just slightly to 11.2% (20,630 km\(^2\)), and under the best scenario (RCP2.6). Similarly, under the worst scenario (RCP8.5), the overlap will be of only 10.7% (16,036 km\(^2\)) (Fig. 4).

**Discussion**

Understanding species response to climate change is crucial in order to adequately manage conservation efforts (Thomas et al., 2004; AraÚjo & Rahbek, 2006; Warren et al., 2013). Several authors have already warned about the dire consequences of climate change on ecosystems and across a wide range of taxa (Walther et al., 2002; Quintero & Wiens, 2013; Muñoz-Mendoza et al., 2017). Our worst-case scenario analysis suggests that the guanaco will have lost up to ~16% of its current geographic distribution by 2070. Although, predicted changes will
barely be noticeable (Fig. 2), the classification and quantification of suitable habitat provides substantial insights on the vulnerability of this species to climate change. In fact, our results indicate that the net effect of climate change on guanaco habitats will result in a reduction of its geographic distribution and, most importantly, to a confinement to sub-optimal quality habitats (Table 1) supporting general trends outlined in the literature (Urban, 2010; Pecl et al., 2017). In fact, our quantification of surface changes between current and future distribution under the worst-case scenario, suggests an average loss of 26% of its current area, compared to 15% of areal gains (i.e. new distribution areas available) between 2050 and 2070 (Table 2) supporting claims describing how climate change will modify species ranges, decrease abundances, and increase exposure to local and global extinction (Lenoir et al., 2008; Urban, 2010; Pecl et al., 2017).

For instance, our analysis strongly associates the northern lineage *L.g. cacsilensis* to precipitation seasonality of an habitat that has recently been exposed to a succession of rainy years interspersed by multiannual droughts (Ortega et al., 2012) hinting to a southward shift in future guanaco distribution. However, our model outputs essentially predict an eastern distributional shift into areas of low suitability between the Arica and Parinacota (18°S), and the Atacama regions (27°S)(Fig. 2). This closely matches descriptions in ungulates research describing substantial reductions of their distribution areas in arid and semi-arid environments. Such is the case for the silver dik-dik (*Madoqua piacentinii*, a small antelope), in the southeastern coast of Somalia (Thuiller et al., 2006). In other cases, extinction risks have increased with the intensification of drought episodes, as it has been seen for the hartebeest.
(Alcelaphus buselaphus, an African antelope), and the waterbuck (Kobus ellipsiprymnus, a large sub-Saharan African antelope) (Duncan et al., 2012).

As for the guanaco, future distribution modeled here not only shows a confinement to coastal and central valleys between the Atacama (27°S) and Valparaíso (33°S) regions (Fig. 2), but also a reduction of the distribution extent of the contact population. This roughly coincides with a predicted 5-15% rainfall reduction for the next decades between the Copiapó River (27°S) and the Aysén river basin (47°S) (Rojas, 2012; Garreaud et al., 2017).

Given the disparate exposures of guanaco’s lineage distribution to different climate change regimes, we have additionally seek to address whether phylogenetic conservatism or niche divergence may prevail under such regimes. This is possible if we assume that niches are a diagnostic traits contributing to understand how species complexes bear with climate-induced changes in their habitat as proposed (Wiens & Graham, 2005; Alvarado-Serrano & Knowles, 2014). Understanding this, should allow us to better describe spatial patterns of speciation and to help crafting species management plans for guanaco conservation. For instance, sister lineages should most likely exhibit closely similar niches pointing towards PNC hypotheses (Webb et al., 2002; Wiens & Graham, 2005; Losos, 2008; Warren, Glor & Turelli, 2008). As such, we expected to find niche similarity (i.e. PNC) between the niches of guanaco lineages. We nevertheless, found stronger evidence for PND among L.g. cacsilensis and L.g. guanicoe rejecting the hypothesis of Graham et al. (2004) and Peterson, Soberón & Sánchez-cordero (1999) based on the results of the identity and similarity test, as proposed by Warren, Glor & Turelli (2010). This information hence supports the classification of Moritz (1994) and proposes the existence of only two significant evolutionary units for the guanaco from this ecological
perspective. One to the north represented by *L. g. cascilensis* and another to the South represented by *L. g. guanicoe* (Marin et al., 2013) (see Table 3 and Table 4). Now, when we compared lineages' niches with the contact population's niche, two interesting results show that: (i) The current niche of northern *L. g. cascilensis* is similar to the current niche of the contact population; (ii) The future niche of the southern *L. g. guanicoe* is projected to include, and resemble, the future niche of the contact population. (iii) Nevertheless, the niche of the actual contact population does not share any statistically similarities with the north and south lineages (see background similarity test results in Table 4). This suggests that *L. g. cascilensis* is, by their climatic requirements, more likely to adapt to current climatic conditions across the contact population’s habitat favoring PNC processes, as shown by our background similarity results (Table 4). While *L. g. guanicoe*, on the other hand, will most likely experience an expansion of its environmental niche towards the contact population’s habitat. Conversely, the contact population will continue to limit its distribution to the small and restricted areas in northern Chile, in spite of its recent dispersal history through extant barriers across its evolutionary history (Marin et al., 2013).

Since, genetic evidence indicates that Patagonia has functioned as a climatic refuge for this species (Fuentes & Jaksic, 1979) and a great genetic variation has been observed among populations of this lineage (González et al., 2013), we would expect that conservation efforts should consider projected distributions of guanaco lineages to protect future habitats and thereby safeguard evolutionary potential of the species (Pecl et al., 2017). From our results, and under the best scenario, the current distribution of protected areas (PA) will only protect about a 11% of the future guanaco distribution (Fig. 4). While this represents a 2% increase with
respect to actual protection figures, such increase will come with the cost of conserving lower quality habitat as discussed above.

It is important to mention that the projected distributions models proposed here under future climates are by no means a prognosis of the fate of guanacos in Chile. They rather outline the distribution probabilities based on possible scenarios given the future GHG emissions (IPCC, 2013). As such, uncertainties associated to GCMs (Buisson et al., 2010), will certainly permeate our predictions (Moss et al., 2010). However, just as GCMs, the work presented here is based on the best knowledge of the species natural history and species distribution modelling and should be scrutinized by expert judgments according to the environmental, socioeconomic, political and technological trends observed in the last decades (Moss et al., 2010).

Conclusions

While current climate projections show a variety of possible climate conditions for the near future, they offer the opportunity to explore and understand how such change will impact wildlife. Actions undertaken today, together with the evolving directions of global society, will certainly determine the future of ecosystems and their species. We hope that our analyses and findings will contribute to the management of long term conservation plans seeking to address local impacts of climate change on the habitat of this ungulate. We see this as a first and broad scale attempt to expose not only the environmental requirements of each lineage, but also to preserve its genetic variability and protecting ongoing evolutionary processes of this species.
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Figure 1 (on next page)

Analysis workflow

Workflow followed for the generation of the current and projected climate models of the *L. guanicoe* distribution and their linages. We have used four software for the generation, analysis and cartographic projection of our models. In a first stage, we used MaxEnt (Phillips et al., 2006) to generate the current and projected climatic models of *L. guanicoe* and its lineages; in a second stage, ENMTools (Warren et al., 2008) was used to evaluate niche conservatism hypotheses between lineages using the Identity test and Background similarity test. Finally, we used BioSARN (Heap, 2016) to quantify the surface change between current and projected distribution of *L. guanicoe*, which additionally helped to compare these surface with the protected areas in Chile. We applied two different methods in the generation of the models: (1) We averaged the result of 5 models generated under different GCMs and obtained an average final model; and (2) We averaged the bioclimatic variables of the GCMs, and with this set of data we generated the final model. The GCM names used in these analyzes were abbreviated as follows: CC= Community Climate System Model version 4; GF= Geophysical Fluid Dynamics Laboratory’s Coupled Model 3; GS= Goddard Institute for Space Sciences’ Russell ocean model E2; HD= Hadley Centre Global Environmental Model version 2 for atmosphere system; and HE= Hadley Centre Global Environmental Model version 2 for earth system.
Niche modeling
(MaxEnt by Phillips et al., 2006)

Inputs
3,326 records
298 L. g. cacsilensis
837 Contact population
2,191 L. g. guanicoe

+ CURRENT VARIABLES
Bioclimatic variables (Worldclim)
- Bio1  Bio12
- Bio4  Bio15
- Bio7

+ PROJECTED VARIABLES
- 5 Bioclimatic variables
- 5 GCMs (CC, GF, GS, HD, HE)
- 2 RCPs (RCP2.6, RCP8.5)
- 2 Time slices (2050, 2070)

Outputs

(A) Current model
L. guanicoe
L. g. cacsilensis
Contact population
L. g. guanicoe

(B) Projected models
1 average GCM
×
2 RCPs
×
2 time slices
= 4 Projected models

PNC and PND analyses
(ENMTools by Warren et al., 2008)

Similarity measures
Niche overlap (empirical value) (2)

Niche conservatism tests
Identity test → Niche equivalence (Graham et al., 2004)
Background similarity test → Niche similarity (Peterson et al., 1999)

Quantification of Surface Changes
(BioSARN by Heap, 2016)

Comparison between protected areas in Chile (IDE, 2016)

Outputs
- Areal loss
- Unchanged area
- Areal gains

Average Model
(Method 2)

(Average Model)

(ModelCC + ModelGF + ModelGS + ModelHD + ModelHE) / 5 = ModelGCM (Method 1)

(Mathematics)

Average Model

(ModelCC + ModelGF + ModelGS + ModelHD + ModelHE) / 5 = ModelGCM (Method 1)

(Mathematics)

Average Model

(ModelCC + ModelGF + ModelGS + ModelHD + ModelHE) / 5 = ModelGCM (Method 1)

(Mathematics)
Current and projected distribution model of guanaco lineages in South America.

A) current distribution; and projected distributions B) under RCP2.6 to 2050; C) under RCP2.6 to 2070; D) under RCP8.5 to 2050; E) under RCP8.5 to 2070. These surfaces were classified according to habitat suitability.
Figure 3 (on next page)

Cartographic projection of distribution surface change analysis.

Pink surface corresponds to areal loss and representing the areal fraction of the climatic niche that exists only in the current model. Olive surface corresponds to areal gains and represents the climatic niche area that exists only in the projected model. Finally, the orange surface corresponds to the area that has remained unchanged and represents the surface of the climatic niche that exists in both models (current and projected models). Panel A is the comparison between current and projected model under RCP2.6 to 2050; B, the comparison between current and projected model under RCP2.6 to 2070; C, the Comparison between current and projected model under RCP8.5 to 2050; D, is the comparison between current and projected model under RCP8.5 to 2070.
Figure 4 (on next page)

Overlap between projected environmental niche models under two extreme climate scenarios and distribution of protected areas in Chile.

A1 and A2 are projections based on RCP2.6 scenarios; B1 and B2 correspond to RCP8.5 scenarios. Protected categories consider National Parks, National Reserves, Biosphere Reserves, National Monuments, Protected National Heritage, RAMSAR sites (2012), and Private Protected Areas (2011) (IDE, 2016).
Table 1 (on next page)

Geographic distribution area (km$^2$) of current potential distribution of *L. guanicoe* across habitat suitability categories.

Environmental niche models are projected models to years 2050 and 2070 under the most extreme GHG emission scenarios. RCP2.6 represents climate model under the less severe emission scenario and RCP8.5 the scenario under the largest GHG emission. Letters in parentheses show corresponding panel in Fig. 2.
<table>
<thead>
<tr>
<th>Suitability category</th>
<th>Current (A)</th>
<th>2050 (B)</th>
<th>2070 (C)</th>
<th>2050 (D)</th>
<th>2070 (E)</th>
</tr>
</thead>
<tbody>
<tr>
<td>High (&gt;75%)</td>
<td>23</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Medium (50-75%)</td>
<td>102,693</td>
<td>78,529</td>
<td>72,236</td>
<td>61,560</td>
<td>35,389</td>
</tr>
<tr>
<td>Low (25-50%)</td>
<td>173,353</td>
<td>195,304</td>
<td>201,336</td>
<td>196,580</td>
<td>195,515</td>
</tr>
</tbody>
</table>
Table 2 (on next page)

Percent change of distribution area between current and projected models for 2050 and 2070 under the most extreme climate change projections.

RCP2.6 model represents climate change under the less severe emission model and RCP8.5 the projection assuming the largest GHG emission scenario. The amount of areal losses, unchanged and gains in square kilometers are shown in parentheses. Letters at years columns head show corresponding panel in Fig. 3.
<table>
<thead>
<tr>
<th></th>
<th>RCP2.6</th>
<th></th>
<th>RCP8.5</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>2050 (A)</td>
<td>2070 (B)</td>
<td>2050 (C)</td>
</tr>
<tr>
<td>Losses (km²)</td>
<td>16% (45,193)</td>
<td>15% (43,276)</td>
<td>23% (62,800)</td>
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<tr>
<td>Unchanged (km²)</td>
<td>84% (231,438)</td>
<td>85% (233,355)</td>
<td>77% (213,831)</td>
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<tr>
<td>Gains (km²)</td>
<td>15% (42,396)</td>
<td>14% (40,055)</td>
<td>16% (44,310)</td>
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</table>
Table 3 (on next page)

Niche identity test.

First column indicates whether the analysis was applied on current or projected niche models. Second column indicates the pair of lineages compared. This test generates new models for the comparative lineages, using the set of climatic variables defined in this work, but mixing the occurrences of the lineages. The results in the table correspond to the comparison between the empirical values (niche overlap results) and values of percentiles 0.01 of the null distribution (one tailed, Warren, Glor & Turelli, 2010). The “I” and “D” statistics allow to compare the overlap between the replicas of this test. If the empirical value is within the range of values observed in the percentages, the hypothesis of niche equivalence is approved. The values in this situation have been darkened.
<table>
<thead>
<tr>
<th>Niche model</th>
<th>Compared lineages</th>
<th>Empirical value (Niche overlap)</th>
<th>Identity test (Niche equivalence)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>I</td>
<td>D</td>
</tr>
<tr>
<td>Current</td>
<td>L. g. cacilensis – Contact population</td>
<td>0.283</td>
<td>0.089</td>
</tr>
<tr>
<td></td>
<td>L. g. guanicoe – Contact population</td>
<td>0.178</td>
<td>0.058</td>
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<tr>
<td></td>
<td>L. g. cacilensis - L. g. guanicoe</td>
<td>0.133</td>
<td>0.033</td>
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<tr>
<td>Projected (2070)</td>
<td>L. g. cacilensis – Contact population</td>
<td>0.471</td>
<td>0.208</td>
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<tr>
<td></td>
<td>L. g. guanicoe – Contact population</td>
<td>0.135</td>
<td>0.039</td>
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<td></td>
<td>L. g. cacilensis - L. g. guanicoe</td>
<td>0.090</td>
<td>0.015</td>
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</table>
Table 4 (on next page)

Background similarity test.

The first column indicates whether the analysis was applied on current or projected niche models. Second and third columns indicate compared lineages and focal lineage used for the comparison. This test generates new models for the compared lineages, using the set of climatic variables defined in this work, but omitting the climatic space where the niche of the “background species” is located. In this way, it is modeled in the background area with the occurrence of the focal species. We hence show the comparison between the empirical values (niche overlap results) and 0.01 and 0.9 percentiles of the null distribution (two tailed) delivered by the test. If the empirical value is within the range of values observed in the percentages, the hypothesis of niche similarity is approved. The values in this situation have been darkened.
<table>
<thead>
<tr>
<th></th>
<th>Pair compared</th>
<th>Niche overlap</th>
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<tr>
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<td>Focal</td>
<td>Background</td>
<td>D</td>
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<tr>
<td>Current</td>
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<td>Contact population</td>
<td>0.089</td>
</tr>
<tr>
<td></td>
<td>Contact population</td>
<td><em>L. g. cacsilensis</em></td>
<td>0.089</td>
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<tr>
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<td><em>L. g. guanicoe</em></td>
<td>Contact population</td>
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<tr>
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<tr>
<td></td>
<td><em>L. g. cacsilensis</em></td>
<td><em>L. g. guanicoe</em></td>
<td>0.033</td>
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<td><em>L. g. guanicoe</em></td>
<td><em>L. g. cacsilensis</em></td>
<td>0.033</td>
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<tr>
<td>Projected (2070)</td>
<td><em>L. g. cacsilensis</em></td>
<td>Contact population</td>
<td>0.208</td>
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<td><em>L. g. guanicoe</em></td>
<td>Contact population</td>
<td><strong>0.039</strong></td>
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<td>Contact population</td>
<td><em>L. g. guanicoe</em></td>
<td>0.039</td>
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<td>----------------</td>
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</tr>
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<td>L. g. cacsilensis</td>
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<tr>
<td>L. g. guanicoe</td>
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