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. 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 between the two lineages described for the species (*L.g. cacsilensis* and *L.g. guanicoe*).

Methods. We used maximum entropy to model lineage's climate niche from 3,321 locations throughout continental Chile, and develop future niche models under climate change for two extreme greenhouse gas emission scenarios (RCP2.6 and RCP8.5). We evaluated 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 were based on identity and background similarity tests.

Results. We show that: a) the current geographic distribution of lineages is associated to 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) a 3% decrease of areal protection is expected if the current distribution of protected areas is maintained, and this is expected to occur at the expense of a large reduction of high quality habitats under the best scenario; d) current and future distribution ranges of guanaco mostly adhere to phylogenetic niche divergence hypotheses between lineages.

Discussion. Associating environmental variables to species ecological niche seems to be an important aspect of unveiling the particularities of, both evolutionary patterns and ecological features that species face in a changing environment. We report specific descriptions of how these patterns may play out under the most extreme climate change predictions and provide a grim outlook of the future potential distribution of guanaco in Chile. From an ecological perspective, while a slightly smaller distribution area is expected, this may come with an important reduction of available quality habitats. From the evolutionary perspective, we describe the limitations of this taxon as it experiences forces imposed by climate change dynamics.

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20 ABSTRACT

21 **Background.** The main goal of this contribution was to define the ecological niche of the
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29 South America. Evaluation of niche conservatism and divergence were based on identity and
30 background similarity tests.

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32 different climatic requirements that are related to the geographic areas where these lineages
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34 both scenarios; c) a 3% decrease of areal protection is expected if the current distribution of
35 protected areas is maintained, and this is expected to occur at the expense of a large reduction
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41 these patterns may play out under the most extreme climate change predictions and provide a
42 grim outlook of the future potential distribution of guanaco in Chile. From an ecological
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44 important reduction of available quality habitats. From the evolutionary perspective, we
45 describe the limitations of this taxon as it experiences forces imposed by climate change
46 dynamics.

47   **Introduction**

48   Human induced climate change is imposing severe challenges to the equilibrium of natural

49   ecosystem functioning (IPCC, 2013). Organisms will either have to face extinctions or adapt

50   (Berg et al., 2010) by altering their seasonal activities, home ranges, migratory patterns,

51   abundances, and interspecific interactions (Lenoir et al., 2008; Araújo, Thuiller & Yoccoz, 2009;

52   Elith & Leathwick, 2009; Pecl et al., 2017). Global rise of temperatures will likely accelerate

53   extinction risks and threaten up to one in every six species (Urban, 2010). Studies on the impact

54   of climate change on ungulates have shown that changes in distribution ranges include

55   altitudinal shifts in mountain environments (Mason et al., 2014) and distributional shifts

56   towards equivalent habitats (Hu & Jiang, 2011). In more extreme cases, local extinctions will be

57   driven by environmental aridization (Thuiller et al., 2006; Duncan et al., 2012).

58   In Chile, current projections of greenhouse gas emissions proposed by the Intergovernmental

59   Panel on Climate Change (IPCC) indicate that temperature will increase in a North to South

60   gradient (IPCC, 2013). A large 2.5°C increase is expected in the Altiplano under the most

61   extreme emission scenario and a milder 0.5°C increase is projected in the southern region of

62   Magallanes for the period 2031-2050. Additionally, a 10-15% decrease in precipitation is

63   expected in the middle of the country (between 25° and 45° S), while forecasting a 5% rainfall

64   increase in Patagonia and a similar snowfall decrease in the Magallanes region (Rojas, 2012).

65   The guanaco (*Lama guanicoe*) is both the most abundant native ungulate and the largest (120

66   kg) artiodactyl in South America (Franklin, 1982). The species is widely distributed throughout

67   the Southern Cone, inhabiting cold, arid, and semi-arid environments from sea level up to 5,000

68   m a.s.l. extending from northwestern Peru to Tierra del Fuego and Isla Navarino in the southern

69   tip of the continent, with small populations roaming east of the Andes in the arid Chaco of

70   Bolivia and Paraguay (Franklin, 1982; González et al., 2006). Highest population densities are

71   found in the Andes and in Patagonia (Baldi et al., 2016). The species is characterized by specific

72   anatomical, physiological, and reproductive adaptations to thrive and survive in arid

73   environments despite the intense competition with livestock and severe degradation of their

74   habitat (González et al., 2013; Marin et al., 2013; Baldi et al., 2016). The guanaco has a defined

75   ecological role in each of its ecoregions either controlling vegetation growth or dispersing seeds

76   (González et al., 2006). These characteristics make the guanaco an important element within

77   the trophic chain. For instance, it is the main prey of the puma (*Puma concolor*) (Franklin et al.,

78   1999) and is the target of scavengers such as the chilla fox (*Lycalopex griseus*), the culpeo fox

79   (*Lycalopex culpeus*) and the Andean condor (*Vultur gryphus*) among others (Travaini et al.,

80   2001; González et al., 2006).

81   Two distinct subspecies of guanaco (*L.g. cacsilensis* and *L.g. guanicoe*) have been proposed

82   based on genetic studies. *L.g. cacsilensis* is distributed to the west of the Central Andean

83   Plateau throughout Peru and the northern tip of Chile with occurrences mostly explained by

84   elevation and precipitation seasonality. *L.g. guanicoe* is found on the southeastern slope of the

85   Andes, ranging throughout Patagonia and Tierra del Fuego with occurrences mostly explained

86   by annual precipitation, precipitation seasonality and grass cover (González et al., 2013; Marin

87   et al., 2013, 2017). The geographical limit between the northwestern and southeastern lineages

88   has been proposed to occur around 31° S in Chile (Marin et al., 2017) and the significant genetic

89   structure found among the two guilds has led to recommend to classify the two lineages as

90   evolutionary significant units (ESUs) following Moritz's (1994) criteria (González et al., 2013;

91   Marin et al., 2013). However, the two lineages are not completely separated from each other.

92   In fact, some populations have individuals of both lineages forming zones of mixed genetic

93   heritage (Marin et al., 2013). The distribution of this mixed population was predicted to occur

94   at the south end of the Altiplano, between 26° S and 32°S approximately, and is better

95   explained by annual precipitation and precipitation seasonality (González et al., 2013). As

96   reported by Marin et al., (2013), the Andean plateau could have acted as a biogeographical and

97   ecological barrier fostering vicariance processes that may be at the origin of the current

98   distribution of guanaco lineages. It is presumed that climate changes that occurred in the past,

99   allowed the establishment of populations over this geographic barrier, with periods of

100   connectivity and isolation allowing the establishment of populations with mixed genetic

101   heritage (Marin et al., 2013).

102   While the discontinuity of the current geographical distribution of guanaco is mostly a

103   consequence of recent human activities (González et al., 2006), the macroevolutionary

104   processes leading to lineage divergence in guanaco should be taken into consideration when

105   deciding on the conservation actions required, as it has been discussed elsewhere for other

106   species (Hu et al., 2015). Current threats are mostly related to high competition for fodder with

107   cattle and introduced mammals (Mason et al., 2014); predation by feral dogs, illegal hunting,

108   and the reduction of available habitat due to the intensification of agriculture (González et al.,

109   2006; Baldi et al., 2016). The 14.5 million hectares protected by the Chilean System of

110   Protected Areas does not cover the entire species range (Baldi et al., 2016), prompting

111   important questions regarding the future distribution of guanaco. Mostly, *L. guanicoe* is well

112   adapted to a wide variety of habitats (González et al., 2006, 2013). However, at the intraspecific

113   level, each lineage may respond differently to changes. As evidence from guanaco's natural

114   history indicates, past changes in climate have clearly influenced the geographic distribution of

115   this species, particularly in the Altiplano and Puna where guanacos and vicuñas (*Vicugna*

116   *vicugna*) compete for resources since the Holocene (Marin et al., 2013, 2017). Thus, under the

117   possible climate change scenarios in Chile, we expect *L.g. cacsilensis* to expand (or to shift)

118   southward and overlap with the mixed genetic heritage population. On the other hand, we

119   predict that *L.g. guanicoe*, characterized by a wider climatic tolerance (González et al., 2013),

120   should mostly maintain its current geographic distribution.

121   From an evolutionary perspective, given the existence of these two lineages and the repeated

122   suggestions of their consideration as ESUs (Marin et al., 2013; Baldi et al., 2016), it would be of

123   great interest to evaluate the state of conservation of their niche to support with new evidence

124   this classification. From such perspective, it becomes relevant to assess whether phylogenetic

125   niche conservatism (PNC), the tendency of closely related species to differ less ecologically than

126   expected by chance, or otherwise, phylogenetic niche divergence (PND), the tendency of

127   closely related species to differ more ecologically than expected by chance may prevail under

128   current and predicted niche segregation patterns under future climate change (Pyron et al.,

129   2015; Meynard et al., 2017).

130   Based on the latest projections of climate change in the region (Rojas, 2012; IPCC, 2013) and

131   the understanding of *L. guanicoe* taxonomy and life history, we developed models based on

132   niche theory to assess the impact of climate change on guanaco's ESUs. By modeling the niche

133   of *L. guanicoe* and its lineages we here: a) estimated their current geographic distribution based

134 on bioclimatic variables; b) predicted their future distribution based on the projections of the

135 best and worst climate change scenario at two different time frames (2050, 2070); c) quantified

136 the area predicted to be gained, lost, or remain stable in the future for both guanacos lineages

137 and mixed population; d) evaluated and compared how much of the Chilean protected areas

138 will overlap with the future distribution area calculated for guanacos; and e) explored the

139 existence of niche conservatism or divergence between *L. guanicoe* lineages, in terms of their

140 niche equivalence (Graham et al., 2004) and similarity (Peterson, Soberón & Sánchez-cordero,

141 1999).

142 **METHODS**

143 **Species occurrence data**

144 We built a guanaco occurrence dataset of 3,321 records by complementing previous work by

145 the authors with 359 additional records (González et al., 2013). New records were collected

146 following the same procedures outlined in González et al., (2013), that is, from direct and

147 indirect evidence of guanaco presence collected between the years 2000 and 2016 across

148 several field campaigns. Indirect evidence of guanaco occurrence was assigned to a lineage by

149 genetic and morphological evaluation of biological samples such as feces and dead tissues.

150 Most of new records were collected in the northern section of the country in the Arica,

151 Parinacota (i.e. 17°S latitude) and Coquimbo region (30°S). Each record was assigned to a

152 1x1km cell defined by the resolution of the environmental datasets employed (see below). This

153 resulted in a total of 298 records for *L.g. cacsilensis*, 837 for the mixed population, and 2186 for

154 *L.g. guanicoe.*

155 **Climate predictors**

156 We limited the selection of environmental predictors to climatic variables (Thuiller et al., 2006;

157 Hu et al., 2015). Similarly to what has been described in the literature (Thuiller et al., 2004), our

158 previous work dismissed the importance of non-climate predictors for guanaco distribution

159 models in favor of exclusive climatic variables (González et al., 2013). We used all 19 bioclimatic

160 variables from WorldClim (version 1.4) summarizing temperature and precipitation information

161 worldwide (Hijmans et al., 2005). To reduce collinearity, model overfitting, and the number of

162 explanatory variables, we used a paired correlation analysis to inspect pairs of variables and

163 removed variables with large correlation coefficient (>0.8) (Beaumont, Hughes & Poulsen,

164 2005).

165 While the analysis was limited to the administrative bounds of Chile, all WorldClim variables

166 were projected to UTM 19 South, with a 1 squared-km of spatial resolution, spanning from

167 latitudes 15°S to 55°S and longitudes 60°W to 80°W and a total area of 5,921,578 km² covering

168 most of the Southern Cone.

169 **Future Climate Projections**

170 The projection of future geographic distribution of niches was performed using the outputs of

171 the Coupled Model Intercomparison Project 5 (CMIP5) of the IPCC's methodology for the Fifth

172 Assessment Report (AR5) (Taylor, Stouffer & Meehl, 2012). The two extreme greenhouse gas

173 (GHG) concentration scenarios, also known as Representative Concentration Pathway (RCP),

174 were used to project future climate niches. RCP2.6, the most optimistic scenario, considers a

175 lower GHG concentration and projects average increases of temperature between 0.3° to 1.6° C

176   with 0.26 to 0.55 m increases of sea levels. RCP8.5, the most pessimistic scenario, considers

177   higher GHG concentrations with a 2.6° to 4.8°C projected increase in mean global temperature

178   and a 0.45 to 0.82 m rise of sea levels (IPCC, 2013). We chose both extreme scenarios to

179   evaluate the minimum and maximum potential impact of climate change in the guanaco's

180   distribution.

181   Given the large uncertainties of future climate predictions, the computing power availability

182   and the exploratory nature of such models, we selected five General Circulation Models (GCM)

183   among the 19 models used to generate the AR5. GCM's are physical climate models that

184   simulate the interactive biophysical processes between the atmosphere, the ocean and the

185   land (Moss et al., 2010). Selected climate models were: (1) CCSM4 model of the National Center

186   of Atmospheric Research (Gent et al., 2011); (2) GFDL-CM3 model of the Geophysical Fluid

187   Dynamics Laboratory (Donner et al., 2011); (3) GISS-E2-R model of the NASA Goddard Institute

188   for Space Studies (Nazarenko et al., 2015); (4) HadGEM2 – AO atmosphere model and (5)

189   HadGEM2 – ES earth system model, both of the Met Office Hadley Centre (Collins et al., 2011).

190   Each scenario was evaluated for the short (2050) and medium term (2070).

191   **Niche Modeling**

192   Entropy maximization procedures in MaxEnt 3.3.3 k (Phillips, Anderson & Schapire, 2006) were

193   used to model current and future geographic distributions of *L. guanicoe* and its lineages.

194   MaxEnt uses a machine learning algorithm to generate predictions on the potential distribution

195   of species based on their presence, pseudo-absences and a set of environmental variables. The

196   software analyzes the multivariate distribution of environmental conditions of species

197   occurrences to generate a spatially explicit probability map of lineage occurrence (Franklin,

198   2009). Such modelling approach has shown to have a good statistical performance compared to

199   other types of modeling techniques (Elith et al., 2006) and is currently one of the most

200   commonly used methods to understand habitat suitability, niche structure, geographical

201   species distribution (Merow, Smith & Silander, 2013a) as well as to project environmental

202   niches to future scenarios (Hijmans & Graham, 2006).

203   We performed 100 cross-validated replicates for each current and projected distribution model

204   with logistic output, that unlike other outputs (i.e. raw and cumulative) assumes that a known

205   observation probability can be assigned to each pixel and has thus been considered as a true

206   approximation of presence (Merow, Smith & Silander, 2013a). The "fade by clamping" option

207   was used to avoid predictions beyond the observed geographical range during the training of

208   the future distributions model (Phillips, Anderson & Schapire, 2006). All other parameters were

209   kept at their default configuration (Phillips, Dudík & Schapire, 2004) as they have previously

210   shown good performance in ungulate modeling (Hu & Jiang, 2011; González et al., 2013; Hu et

211   al., 2015; Quevedo et al., 2016) and other taxonomic groups (Phillips & Dudík, 2008; Fourcade

212   et al., 2014).

213   We used an ensemble forecasting framework to minimize the inherent variability introduced by

214   the various forecast models employed, as proposed by Araújo and New (2007). Therefore, we

215   generated a model from the average of each bioclimatic variable produced by the five GCMs

216   (i.e. $Bio1_{CC}$+ $Bio1_{GF}$ $Bio1_{GS}$ + $Bio1_{HD}$ + $Bio1_{HE}$), and then evaluated an average value for each

217   variable from one hundred replicates for both extreme RCP emission scenarios for the years

218   2050 and 2070. Hence, 400 projected guanaco distribution models were generated (i.e. 2 RCPs

219   x 2 time frames x 100 replicates). The final results are four projected climate models for *L.*

220   *guanicoe,* one for each RCP2.6 and RCP8.5 scenarios evaluated for years 2050 and 2070.

221   **Model evaluation, prediction and spatial projection**

222   Generated niche models were evaluated using a threshold-independent analysis of the area

223   under the curve (AUC) provided by the Receiver Operator Curve (ROC) (Phillips, Anderson &

224   Schapire, 2006; Acevedo et al., 2010; Anderson & Raza, 2010). These sensitivity tests model

225   accuracy by calculating the proportion of true positives versus false positives. The resulting

226   values range from 0 to 1, where model predictions are considered fair when obtained AUC

227   values are above 0.7 (Swets, 1988; Merow, Smith & Silander, 2013b). A 3:1 ratio was used to

228   divide training and testing datasets (Phillips, Anderson & Schapire, 2006). AUC Jackknife

229   analysis allowed to identify the contribution of each variable to final current and future models,

230   and to allow the detection of those variables that significantly improve predictions for the

231   occurrences of each lineage (Phillips, Anderson & Schapire, 2006).

232   We reclassified predicted habitat using a 0.25 threshold interval to label three habitat suitability

233   classes: low suitability habitat when occurrence probability ranged between 25 and 50%;

234   suitable habitat if occurrence probability was in the 50 to 75% interval; and high suitability

235   habitat if occurrence probability was over 75%, values below 25% were considered as

236   inappropriate habitat (Hu & Jiang, 2012; González et al., 2013; Shrestha & Bawa, 2014).

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

238   The areal extent for each suitability class predicted by each model, current and projected, were

239   compared to determine habitat loss (or gains) under the various climate change scenarios

240   evaluated. We used the software BioSARN v.1 to calculate the amount of area gained or lost

241   and to estimate differences between models (Heap, 2016). These results were classified into

242   three categories: (a) Areal loss, when future prediction show a decrease of the areal extension

243   compared to current niche models; (b) Areal gain, produced when future prediction add area to

244   current niche models; (c) Unchanged areas, when climate change predictions show no impact

245   on current guanaco's distribution.

246   In addition, the fraction of future distribution covered by the system of protected area in Chile

247   (PA) was estimated. All categories offering some level of protection were considered: national

248   parks, national reserves, biosphere parks, national monuments, national patrimony, and private

249   PA as of 2011. RAMSAR sites (as of 2012) were also included as they constitute the most

250   important feeding grounds for guanaco in the hyper-arid north of Chile (Squeo et al., 2006).

251   **Evaluation of PNC or PND**

252   PNC and PND among lineages and the mixed population were evaluated through their current

253   and projected niches for the most extreme scenario (i.e. RCP8.5) in 2070 using ENMTools

254   v.1.4.3 (Warren, Glor & Turelli, 2010). Niche overlap between lineages was calculated with the

255   statistical indices "*I*" (derivative of Hellinger's distance) and "*D*" (Shöener's D) which may take

256   values going from 0 (i.e. no overlap) to 1 (i.e. full overlap between lineages' niches). We used

257   the Identity test to evaluate the hypothesis of niche equivalence (Graham et al., 2004) and the

258   Background similarity test to evaluate the hypothesis of niche similarity (Peterson, Soberón &

259   Sánchez-cordero, 1999). Identity test quantitatively assesses whether the niche space for two

260   compared lineages are equivalent by comparing the actual niche to a null niche model

261   generated from a randomized pool of locations for each lineage. This allows to effectively

262   evaluate whether niche spaces are equal, under the premise that, if they are, they should be

263   able to predict each other (Warren, Glor & Turelli, 2010). Because the identity test strongly

264   depends on accurate representations of species habitat suitability, it is known to be sensitive to

265   the particular sampling scheme employed, and therefore less suitable to compare allopatric

266   niches (Warren, Glor & Turelli, 2010). The Background similarity test compares the niche

267   difference between allopatric lineages by contrasting the niche of a "focal" lineage to the niche

268   built from the background locations of a second lineage. If there is similarity between these, the

269   null model should predict the niche of the second lineage. We repeated each test 100 times to

270   produce a simulated distribution of I and D values and to evaluate significance using a threshold

271   of 0.1 (two-tailed for background similarity test, and one-tail for Identity test) (Warren, Glor &

272   Turelli, 2010; Guisan, Thuiller & Zimmermann, 2017). We considered outcomes as indicative of

273   PNC between lineages when observed I and D values fell within the simulated distribution. On

274   the other hand, when the observed values fell outside of the simulated distribution, they were

275   assumed to be indicative of PND between lineages.

276   **Results**

277   **Selection of climate variables and current distribution model**

278   After removing correlated variables, the final subset of independent bioclimatic variables used

279   in this analysis was composed of: annual mean temperature (Bio1), temperature seasonality

280   (Bio4), annual temperature range (Bio7), annual precipitation (Bio12) and precipitation

281   seasonality (Bio15). See correlation analysis in supplemental Fig. S1.

282   The major contribution to the current distribution of *L. guanicoe* was given by the annual range

283   of temperature (28.2%, AUC = 0.84), whereas *L.g. cacsilensis* was dominated by precipitation

284   seasonality (66.7%, AUC = 0.95), the mixed population by annual precipitation (36.7%, AUC =

285   0.93), and the southernmost *L.g. guanicoe* was mostly driven by annual mean temperature

286   (35.8%, AUC = 0.91). Detailed Jackknife's analysis can be seen in supplemental information, Fig.

287   S2.

288   All current distribution models generated for *L. guanicoe* and its lineages, presented a good

289   performance with mean AUC values over 0.89. The resulting geographic range for guanaco

290   spanned for about a third of the Chilean continental surface. The geographic areas covered by

291   *L.g. cacsilensis* and *L.g. guanicoe* were of 47,148 and 100,539 km^2 respectively. The mixed

292   population showed a geographic extent of 84,976 km^2. Interestingly, our models had a 20%

293   difference when comparing areas from the sum of lineages modeled independently and the

294   total area modeled with all the lineages pooled as if they were a single lineage (232,664 km^2 vs.

295   284,499 km^2 respectively). Full maps and predictions are available in supplemental information

296   Fig. S3.

297   **Projected distribution models**

298   As for current distribution models, the sensitivity analysis yielded a large mean AUC > 0.9. After

299   suitability categorization (Fig. 1), our results show that while the geographical distribution

300   pattern of guanaco is conserved, quantitative assessment of the distribution surface reveals a

301   downward trend in both scenarios of climate change for 2050 and 2070 (Table 1).

302 Marginal decreases of habitat suitability is observed under the RCP2.6 scenario for the years

303 2050 and 2070 (259,577 km² vs. 254,979 km² respectively). The small areal reduction under

304 both models is only of 6% and 7.6% of the current area. However, this decrease is more

305 pronounced under the RCP8.5 scenarios in which a 13% and 20.7% reduction is quantified for

306 the years 2050 and 2070 respectively (i.e. 240,505 km² and 218,841 km²).

307 **Surface change between current and projected distribution models**

308 Projected distribution models under the more optimistic scenario showed an increase of high

309 quality habitat and a net loss of medium and low quality habitat, while the projections under

310 the worst scenario indicate a generalized decrease in habitat suitability. Although no important

311 loss of potential distribution areas are apparent, a large decrease of areas with high quality

312 habitat may occur under the worst climate change scenario evaluated (Table 1).

313 Surface losses and gains under future climate projections are described in Table 2. Both

314 scenarios showed that a large fraction of the guanaco range will remain unchanged. The more

315 optimistic projection (i.e. RCP2.6) indicated an average loss of 67,042 km² between 2050 and

316 2070, and a niche displacement (i.e. gain) of 48,225 km² on average between such time periods.

317 A reversed trend was observed under the more pessimistic scenario (i.e. RCP8.5) with the larger

318 change predicted for 2070. Such prediction forecasts a reduction in guanaco's niche by 37%,

319 with a surface loss of 103,367 km² and a geographic distribution of 172,786 km². Likewise, the

320 smallest niche displacement was observed for this period, with 46,089 km² of areal gain (Fig. 2).

321 **Evaluation of PNC and PND**

322   Niche overlap and equivalence tests showed a large overlap between the contact population

323   and *L.g. cacsilensis* for niche models under current and worst scenarios (Table 3). While limited

324   niche overlap was reported, the overlap between the northern lineage and the mixed

325   population increased under future climate change scenarios. On the other hand, the overlap

326   between current and projected niches for *L.g. guanicoe* with the other groups was smaller,

327   particularly with the northern lineage (*L.g. cacsilensis*). When using the results of this latter

328   analysis as "empirical values" to perform identity and background similarity tests (Table 3 and

329   Table 4), we were able to show that statistical differences existed when comparing current

330   niches and projected niches. This indicates that the climatic requirements between the lineages

331   and mixed population are not equivalent.

332   Background similarity test showed that *L.g. cacsilensis* share climatic similarities with the mixed

333   population (Table 4). However, such similarity is not reciprocal when comparing the climatic

334   requirements of the mixed population to those of the northern lineage –a possibility

335   mentioned in Warren, Glor & Turelli (2010). A similar situation occurred when comparing

336   projected niches under the worst climate change scenario (RCP8.5), where results suggested

337   that *L.g. guanicoe´*s niche will closely resemble the future climatic niche of the mixed

338   population, in spite of not sharing any current similarity.

339   The remaining comparisons between climatic niches, current and future, showed that the

340   climatic requirements for each of the lineages analyzed are significantly different (Table 4).

341   **Projected distribution models and conservation in Chile**

342   The current network of PA in Chile covers a vast area of approximately 256,550 km², according

343   to 2016 data, and shows a limited overlap with modeled guanaco distribution. In fact, our

344   analysis shows that a 9.8% (i.e. 19,402 km²) of the species current distribution overlaps with a

345   PA. When looking at projected distributions for 2070, our results showed that such overlap will

346   decrease to 6.2% (15,772 km²) under the best scenario (RCP2.6). Similarly, under the worst

347   scenario (RCP8.5), the overlap will be of 5.7% (12,434 km²) (Fig. 3).

348   **Discussion**

349   Understanding species' response to climate change is crucial in order to adequately manage

350   conservation efforts (Thomas et al., 2004; Araujo & Rahbek, 2006; Warren et al., 2013). Several

351   authors have already warned about the dire consequences of climate change on ecosystems

352   and across a wide range of taxa (Walther et al., 2002; Quintero & Wiens, 2013; Muñoz-

353   Mendoza et al., 2017). Our worst-case scenario analysis suggests that the guanaco will have lost

354   up to a fifth (~21%) of its current geographic distribution by 2070. Although predicted changes

355   will barely be noticeable, the classification and quantification of suitable habitat provided

356   substantial insights on the vulnerability of this species to climate change showing that such

357   changes will additionally result in a confinement to sub-optimal quality habitats supporting

358   general trends outlined in the literature (Urban, 2010; Pecl et al., 2017). In particular, our

359   quantification of areal changes between current and future distribution under the worst-case

360   scenario, suggested an average loss of 34%, compared to 17% of areal gains (i.e. new

361   distribution areas available) between 2050 and 2070.

362   Our analysis strongly associated the northern lineage *L.g. cacsilensis* to precipitation seasonality

363   and predicted a southward shift in the future distribution of guanaco. However, our model

364   outputs essentially predicted an eastern distributional shift into areas of low suitability

365   between the Arica and Parinacota (18°S), and the Atacama regions (27°S)(Fig. 1). Other authors

366   have predicted similar changes in the distribution area of ungulates in arid and semi-arid

367   environments as for example, the silver dik-dik (*Madoqua piacentinii,* a small antelope), in the

368   southeastern coast of Somalia (Thuiller et al., 2006). In other cases, extinction risks have

369   increased with the intensification of drought episodes, as it has been seen for the hartebeest

370   (*Alcelaphus buselaphus*, an African antelope), and the waterbuck (*Kobus ellipsiprymnus*, a large

371   sub-Saharan antelope) (Duncan et al., 2012).

372   In the case of the guanaco in Chile, future distribution modeled here not only shows a

373   confinement to specific zones, such as coastal and central valleys in the Atacama region (27°S),

374   and coastal and Andes Mountains between Coquimbo (29°S) and Valparaíso (33°S) regions, but

375   also a reduction of the distribution extent of the mixed population. This roughly coincides with

376   a predicted 5-15% rainfall reduction for the next decades between the Copiapó River (27°S) and

377   the Aysén river basin (47°S) (Rojas, 2012; Garreaud et al., 2017).

378   In order to better understand spatial dynamics of guanaco's populations across their

379   distribution range, we seeked to address whether niche conservatism or divergence prevailed

380   under different climate change regimes. The basic assumption is that niches are diagnostic

381   traits that help us understanding how species deal with climate-induced changes in their

382   habitat (Wiens & Graham, 2005; Alvarado-Serrano & Knowles, 2014). For instance, sister

383   lineages should most likely exhibit closely similar niches, and point towards PNC (Webb et al.,

384   2002; Wiens & Graham, 2005; Losos, 2008; Warren, Glor & Turelli, 2008). Therefore, we

385   expected to find niche similarity (i.e. PNC) between the niches of guanaco lineages.

386   Nevertheless, we found stronger evidence for PND among *L.g. cacsilensis* and *L.g. guanicoe*,

387   hence supporting the existence of only two ESUs for the guanaco, as proposed by Marin et al.,

388   (2013): one lineage in the northwest represented by *L.g. cacsilensis* and another in the

389   southeast represented by *L.g. guanicoe* (see Table 3 and Table 4). Two interesting results

390   emerged when lineages' niches were compared with the mixed population: (i) The current

391   niche of northern *L.g. cacsilensis* is similar to the current niche of the mixed population; (ii) The

392   future niche of the southern *L.g. guanicoe* is projected to include, and resemble, the future

393   niche of the mixed population. Nevertheless, the current niche of the mixed population does

394   not share any statistically significant similarity with the northern nor the southern lineages (see

395   background similarity test results in Table 4). This suggests that *L.g. cacsilensis* is, given its

396   actual climatic requirements, more likely to adapt to current climatic conditions across the

397   mixed population's habitat, pointing towards the existence of PNC processes. Whereas when

398   we look at projected climate conditions, *L.g. guanicoe* will most likely experience a future

399   expansion of its environmental niche towards the projected mixed population's habitat.

400   Conversely, the mixed population will continue to limit its distribution to the small and

401   restricted areas of northern Chile, in spite of its recent dispersal history through extant barriers

402   (Marin et al., 2013). In summary, PNC seems to be more important when current niches are

403   analyzed, while PND emerges as the important process under future projections of climate

404   change.

405   The high genetic variation observed for the guanaco lineage in Patagonia indicates that this

406   area may have functioned as a climatic refuge for the species (Fuentes & Jaksic, 1979; González

407   et al., 2013). In order to safeguard the evolutionary potential of the species, conservation

408   efforts should take into consideration the projected distributions of guanaco lineages (Pecl et

409   al., 2017).

410   From our results, and under the best scenario, the current location of protected areas (PA) will

411   only decrease a 3% of guanaco's protected distribution range, but will shift to lower quality

412   habitat, as discussed above. Projected distributions models proposed in this study are by no

413   means a prognosis of the fate of guanacos in Chile, as they outline the distribution probabilities

414   based on possible scenarios given the future GHG emissions (IPCC, 2013). Furthermore, the

415   limited geographic locations that fed our models and the uncertainties associated to GCMs

416   (Buisson et al., 2010) have likely permeated our predictions (Moss et al., 2010). In fact, the net

417   effect of our conservative forecasts may underestimate current and future species distribution

418   both within the boundaries of Chile and beyond. For instance, the species may be influenced by

419   a range of environmental conditions outside Chile that are currently not represented among

420   the presence localities in Chile. Thus, when projecting the future distribution within Chile, these

421   areas may appear as not environmentally suited for the presence of the species, altering the

422   correct estimation for the area (or percentage) of range contraction and the area (or

423   percentage) of the range in protected areas. Furthermore, addressing congruence between

424   restricted and broad scale predictions, Titeux et al., (2017) suggested that local models might

425   omit the warmest and coldest parts of future distribution, projecting a larger decrease in future

426   species richness at warmer temperatures. Therefore, the validity of the proposed distribution

427   of guanaco's future range in Chile likely depends on the consistency between the

428   environmental niche used and the values present elsewhere, as well as on the extension of

429   guanaco's presence in extreme temperatures areas. Understanding how these observations

430   could translate to guanaco's species and lineage distribution will certainly contribute to the

431   ongoing research efforts currently underway in Argentina and Chile. Hence, it is likely that

432   efforts to expand the sampling dataset to consider guanaco's full range will also increase its

433   climate niche definition and improve the predictions of the future distribution of the species. As

434   is, the work presented represents a conservative view of guanaco's range that allows to

435   evaluate the evolutionary aspect of niche conservatism hypotheses based on the best

436   knowledge of the species natural history.

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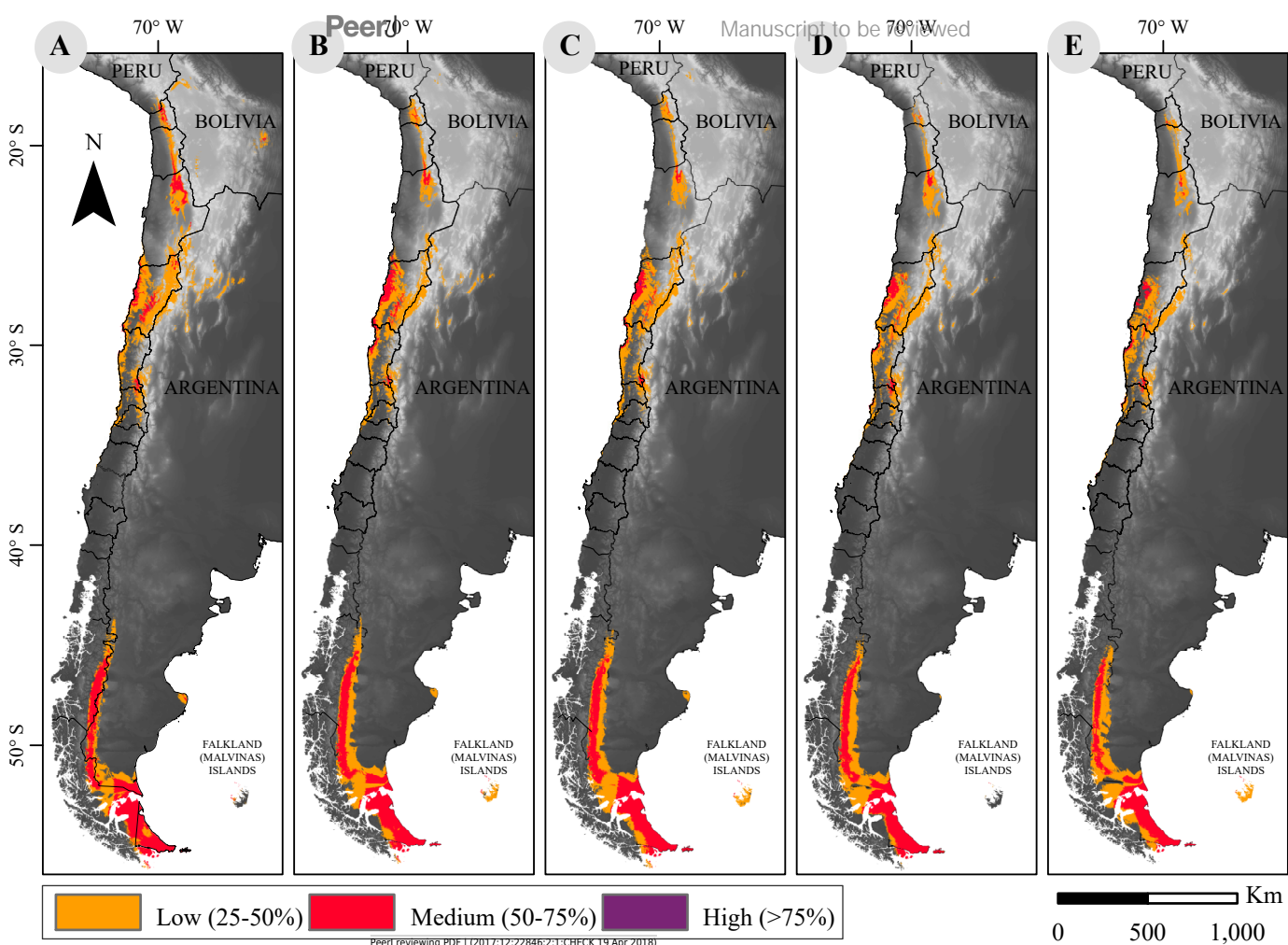
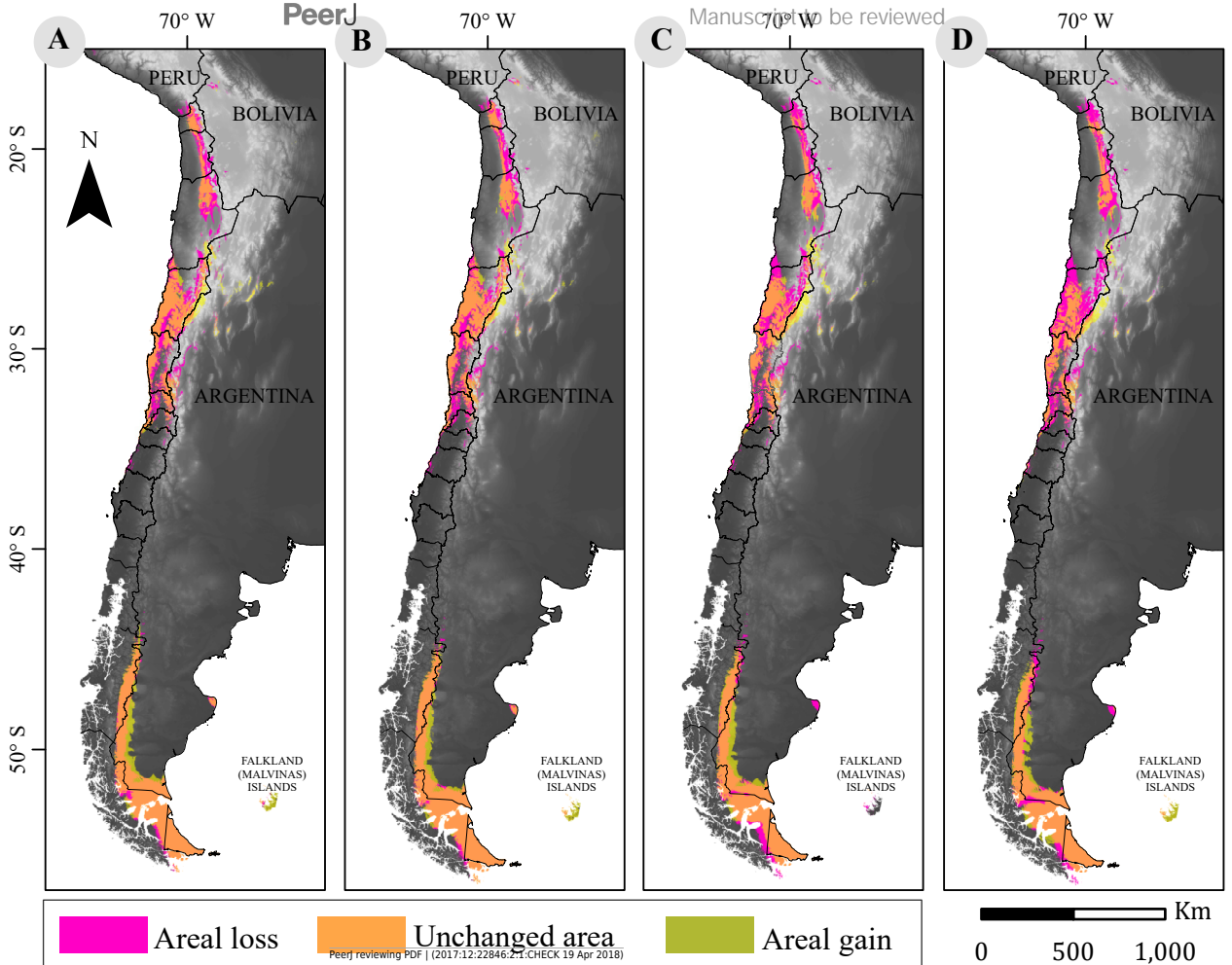
Current and projected distribution model of guanaco lineages in South America.

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. Base Map Elevation Data: CIAT-CSI SRTM (http://srtm.csi.cgiar.org).

Low (25-50%)   Medium (50-75%)   High (>75%)

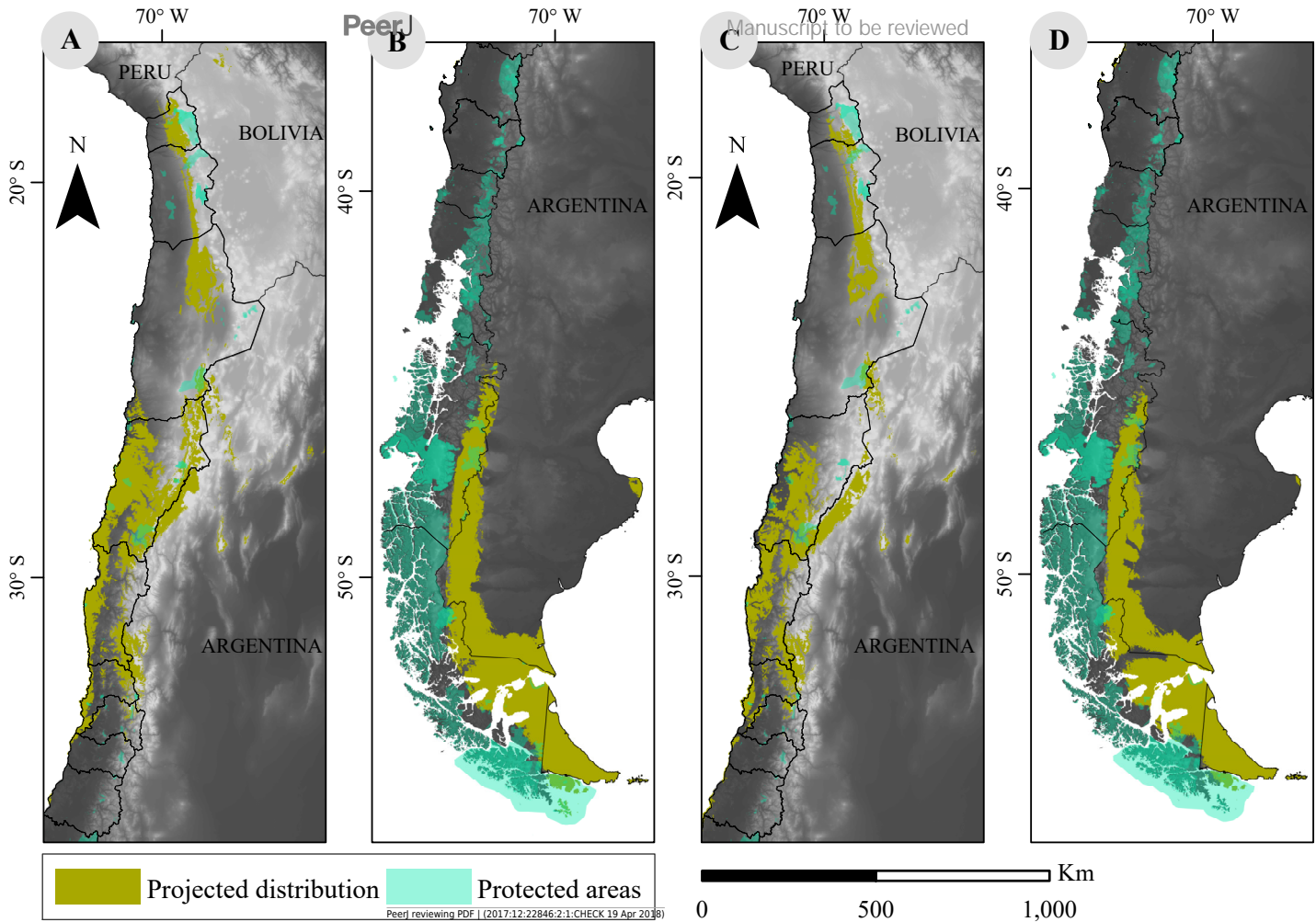
Km

0   500   1,000

Cartographic projection of changes in distribution.

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. 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. Base Map Elevation Data: CIAT-CSI SRTM (http://srtm.csi.cgiar.org).

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

A and B are projections based on RCP2.6 scenarios; C and D 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). Base Map Elevation Data: CIAT-CSI SRTM (http://srtm.csi.cgiar.org).

Projected distribution   Protected areas

0   500   1,000   Km

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

Environmental niche models are projected to years 2050 and 2070 under the most extreme greenhouse gas emission scenarios. RCP2.6 represents climate model under the less severe emission scenario and RCP8.5 the scenario under the largest greenhouse gas emission. Letters in parentheses show corresponding panel in Fig. 1.

Suitability category	Current (A)	RCP2.6		RCP 8.5	
		2050 (B)	2070 (C)	2050 (D)	2070 (E)
High (>75%)	23	71	258	3	0
Medium (50-75%)	102,693	94,574	88,295	80,653	66,344
Low (25-50%)	173,353	164,932	166,427	159,849	152,497
Total	276,069	259,577	254,979	240,505	218,841

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

Areal losses, unchanged and gains in square kilometers for each RCP model with respect to current potential distribution of guanaco. Percentage changes are shown in parentheses. Letters in parentheses after the year, refer to panels of Fig. 2.

	RCP2.6		RCP8.5	
	2050 (A)	2070 (B)	2050 (C)	2070 (D)
Losses (km^2)	66,634 (24%)	67,450 (24%)	86,540 (31%)	103,367 (37%)
Unchanged (km^2)	209,519 (76%)	208,703 (76%)	189,613 (69%)	172,786 (63%)
Gains (km^2)	50,106 (18%)	46,343 (17%)	50,968 (18%)	46,089 (17%)

Niche identity test.

These results correspond to the comparison between the empirical values (niche overlap) and values of percentiles 0.1 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 supported (shown in bold type).

Niche model	Compared lineages	Empirical value (Niche overlap)		Identity test (Niche equivalence)	
		I	*D*	*I*	*D*
Current	*L. g. cacsilensis* – Mixed population	**0.283**	**0.089**	0.923	0.686
	L. g. guanicoe – Mixed population	0.178	0.058	0.922	0.711
	L. g. cacsilensis - L. g. guanicoe	0.133	0.033	0.922	0.596
Projected (2070)	*L. g. cacsilensis* – Mixed population	**0.471**	**0.208**	0.930	0.760
	L. g. guanicoe – Mixed population	0.135	0.039	0.950	0.800
	L. g. cacsilensis - L. g. guanicoe	0.090	0.015	0.890	0.630

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. These results show the comparison between the empirical values (niche overlap results) and 0.1 and 0.9 percentiles of the null distribution (two tailed, Warren, Glor & Turelli, 2010) delivered by the test. If the empirical value is within the range of values observed in the percentages, the hypothesis of niche similarity is supported (shown in bold type).

	Pair compared		Niche overlap		Background similarity test			
Niche					p = 0.01		p = 0.90	
Model	Focal	Background	D	I	D	I	D	I
Current	*L. g. cacsilensis*	Mixed population	**0.089**	**0.283**	**0.082**	**0.260**	**0.115**	**0.320**
	Mixed population	*L. g. cacsilensis*	0.089	0.283	0.094	0.304	0.108	0.336
	L. g. guanicoe	Mixed population	0.058	0.133	0.136	0.358	0.140	0.366
	Mixed population	*L. g. guanicoe*	0.058	0.133	0.091	0.302	0.107	0.332
	L. g. cacsilensis	*L. g. guanicoe*	0.033	0.178	0.091	0.273	0.124	0.332
	L. g. guanicoe	*L. g. cacsilensis*	0.033	0.178	0.136	0.359	0.141	0.368
Projected (2070)	*L. g. cacsilensis*	Mixed population	0.208	0.471	0.158	0.387	0.169	0.410
	Mixed population	*L. g. cacsilensis*	0.208	0.471	0.055	0.211	0.074	0.251
	L. g. guanicoe	Mixed population	**0.039**	**0.135**	**0.033**	**0.123**	**0.042**	**0.148**
	Mixed population	*L. g. guanicoe*	0.039	0.135	0.011	0.055	0.016	0.072

	L. g. cacsilensis	*L. g. guanicoe*	0.015	0.090	0.006	0.042	0.010	0.058
	L. g. guanicoe	*L. g. cacsilensis*	0.015	0.090	0.018	0.080	0.020	0.085