Landscape connectivity among remnant populations of guanaco (*Lama guanicoe* Müller, 1776) in an arid region of Chile impacted by global change

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Connectivity between populations plays a key role in the long-term persistence of species in fragmented habitats. This is of particular concern for biodiversity preservation in drylands, since water limited landscapes are typically characterized by little suitable habitat cover, high habitat fragmentation, harsh matrices, and are being rapidly degraded at a global scale. In this study, we modelled landscape connectivity between 11 guanaco *Lama guanicoe* populations in Chile's arid Norte Chico, a region that supports the last remnant coastal populations of this emblematic herbivore indigenous to South America. We produced a habitat suitability model to derive a regional surface resistance map, and used circuit theory to map functional connectivity, investigate the relative isolation between populations, and identify those that contribute most to the patch connectivity network. Predicted suitable habitat for *L. guanicoe* represented about 25% of the study region (i.e. 29,173 km^2) and was heterogeneously distributed along a continuous stretch along the Andes, and discontinuous patches along the coast. As a result, we found that high connectivity current flows in the mid and high Andes formed a wide, continuous connectivity corridor, enabling connectivity between all high Andean populations. Coastal populations, in contrast, were more isolated. These groups demonstrate no inter-population connectivity between themselves, only with higher altitude populations, and for two of them, animal movement was linked to the effectiveness of wildlife crossings along the Pan-American highway. Our results indicate that functional connectivity is an issue of concern for *L. guanicoe* in Chile's Norte Chico, implying that future conservation and management plans should emphasize strategies aimed at conserving functional connectivity between coastal and Andean populations, as well as the protection of habitat patches likely to act as stepping stones within the connectivity network.

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9 **ABSTRACT**

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11 fragmented habitats. This is of particular concern for biodiversity preservation in drylands, since

12 water limited landscapes are typically characterized by little suitable habitat cover, high habitat

13 fragmentation, harsh matrices, and are being rapidly degraded at a global scale. In this study, we

14 modelled landscape connectivity between 11 guanaco *Lama guanicoe* populations in Chile's arid

15 Norte Chico, a region that supports the last remnant coastal populations of this emblematic

16 herbivore indigenous to South America. We produced a habitat suitability model to derive a

17 regional surface resistance map, and used circuit theory to map functional connectivity,

18 investigate the relative isolation between populations, and identify those that contribute most to

19 the patch connectivity network. Predicted suitable habitat for *L. guanicoe* represented about 25%

20 of the study region (i.e. 29,173 km^2) and was heterogeneously distributed along a continuous

21 stretch along the Andes, and discontinuous patches along the coast. As a result, we found that

22 high connectivity current flows in the mid and high Andes formed a wide, continuous

23 connectivity corridor, enabling connectivity between all high Andean populations. Coastal

24 populations, in contrast, were more isolated. These groups demonstrate no inter-population

25 connectivity between themselves, only with higher altitude populations, and for two of them,

26 animal movement was linked to the effectiveness of wildlife crossings along the Pan-American

27 highway. Our results indicate that functional connectivity is an issue of concern for *L. guanicoe*

28 in Chile's Norte Chico, implying that future conservation and management plans should

29 emphasize strategies aimed at conserving functional connectivity between coastal and Andean

30 populations, as well as the protection of habitat patches likely to act as stepping stones within the

31 connectivity network.

32   **INTRODUCTION**

33   Understanding and managing connectivity has become a key concern for the conservation of

34   biological populations and communities in the face of rapid habitat loss and fragmentation driven

35   by anthropogenic and climate change effects (Mitchell, Bennett & Gonzalez, 2013; Correa Ayram

36   et al., 2014; Riordan et al., 2015; Dilts et al., 2016). By facilitating genetic exchange between

37   habitat patches, connectivity plays a fundamental role in the long-term persistence of species in

38   fragmented habitats (Fahrig & Merriam, 1994; Coughenour, 2008; Kindlmann & Burel, 2008).

39   This is of particular concern in highly fragmented landscapes, where habitat loss results in

40   exponential increases in patch distances, and thus dramatically intensifies habitat isolation

41   (Andrén, 1994). Connectivity depends on both the proportion of suitable habitat across the

42   landscape as well as the permeability of the surrounding matrix. According to empirical and

43   theoretical evidence, patch isolation negatively impacts population size and species richness in

44   birds and mammals when suitable habitat cover is low (Andrén, 1994; Radford, Bennett &

45   Cheers, 2005). It is believed to become a significant factor when the amount of suitable habitat in

46   the landscape falls below 10-30% (Andrén, 1994; Betts et al., 2006), although this threshold may

47   be greatly underestimated for many species (Mönkkönen & Reunanen, 1999). The surrounding

48   matrix, on the other hand, may either facilitate or hinder patch connectivity by determining the

49   permeability of the landscape to species movement.

50   The guanaco, *Lama guanicoe* (Artiodactyla, Camelidae), is an emblematic herbivore

51   indigenous to South America, occurring in Peru, Bolivia, Chile, Paraguay and Argentina (Fig. 1).

52   *L. guanicoe* has disappeared from 75% of its original range during the last century due to

53   anthropogenic habitat disturbance and overhunting (Cunazza, Puig & Villalba, 1995; Ceballos &

54   Ehrlich, 2002; Baldi et al., 2016), and its distribution appears discontinuous along its northern

55   range (see map in Marín et al., 2013). While still classified as a species of least concern at the

56   continental scale (Baldi et al., 2016), its conservation status varies across its distribution range. In

57   Chile, *L. guanicoe* is considered vulnerable, particularly in the north of its distribution, where it

58   occurs in small and isolated populations (Marin et al., 2013; González & Acebes, 2016). Because

59   guanacos need expansive areas (Baldi et al., 2016), movements between habitat patches may not

60   only be necessary to maintain effective population sizes, and thereby the evolutionary potential

61   and long-term survival of the species, but also for individuals to meet their essential needs. *L.*

62   *guanicoe* is able to travel long distances, which is demonstrated by large home-ranges (up to 600

63   km^2 in the Payunia reserve, western Argentina) and the extensive migratory movements that have

64   been recorded (i.e. up to 160 km) (Novaro, 2010). Human development and pressures may act to

65   limit movement in this species, however, threatening populations in areas where resources are

66   heterogeneously distributed, scarce, or transitory (Hobbs et al., 2008).

67   In this study, we modelled functional connectivity for *L. guanicoe* over the semi-arid

68   region of Chile's Norte Chico (between 26ºS and 32ºS latitude), home to the last remnant

69   populations on the Pacific coast, comprising both cordilleran and pre-cordilleran groups. Chile's

70   Norte Chico is one of the most environmentally fragile areas in South America (Downing, 1994),

71   and has experienced accelerated rates of desertification exacerbated by human activities (i.e.

72   mining, agriculture, livestock production and tourism) and the overexploitation of scarce natural

73   resources such as scrublands and seasonal grasslands for firewood collection and livestock

74   grazing (Campos-Ortega & Jorquera-Jaramillo, 2008; Estevez et al., 2010). No information

75   regarding movement and dispersal by individuals between populations in this region is available.

76   Although distances between coastal and cordilleran populations (< 200 km) are within the

77   movement range of this species, various landscape features potentially obstruct displacement

78   across the landscape, and in particular may result in isolation of coastal populations. These

79   include several human settlements, which are interspersed among the coastal populations, and a

80   fenced four-lane highway that transects the study zone from north to south, effectively

81   segregating inland and coastal populations. This connectivity issue has been identified in a recent

82   regional scale habitat modelling study (González et al., 2013), which predicted large areas of

83   unsuitable habitat between coastal and inland populations that potentially act as a

84   biogeographical barrier. Given that the predictive power of large scale models is often impaired

85   due to local niche variation (Osborne & Suárez-Seonane, 2002; Murphy & Lovett-Doust, 2007),

86   regional-scale studies are required to evaluate possible effects of local landscape characteristics

87   on animal movement. The goals of our study were thus to identify potential inter-population

88   migration routes between *L. guanicoe* populations in the region, assess the degree of connectivity

89   of coastal populations in particular, and to identify habitat patches that most contribute to the

90   network connectivity of the study area. To accomplish these objectives, we applied a resistance-

91   surface-based connectivity modelling approach, first generating a surface resistance layer using a

92   regional-scale habitat surface model, and finally mapping functional connectivity based on

93   circuit-theoretic connectivity models.

94

95   **MATERIALS AND METHODS**

96   **Study area**

97   The Norte Chico region in Chile is located between 26°S and 32°S (Fig. 1). It spans about

98   115,756 km^2 and encompasses five hydrologic basins (Fig. 2). It is characterized by steep

99   topography, with altitude increasing from zero to ~5,000 masl within a distance of only 200 km

100   inland from the coast (Squeo et al., 2008a; Zabala and Trigos, 2009). The climate is

101   predominantly arid, although average temperature, precipitation, and relative humidity vary

102   strongly according to both altitude and latitude (Juliá, Montecinos & Maldonado, 2008). The

103   vegetation is composed of xeric shrublands, woody-stemmed shrubs, spiny scrubs and columnar

104   and spherical cacti patchily distributed within an arid matrix (Novoa, Tracol & López, 2008).

105   Evergreen trees and shrublands dominate slopes, while elevations >2,800 masl are dominated by

106   cushion-forming plants, xeric herbs adapted to low temperatures, and high Andean wetland plant

107   species (Squeo et al., 2006; Arancio & Marticorena, 2008).

108   Chile's Norte Chico region is one of the most environmentally fragile areas in South

109   America (Downing, 1994); important climatic changes over the last century (Fiebig-Wittmaack et

110   al., 2012) have resulted in accelerated rates of desertification in the region, exacerbated by human

111   activities (i.e. mining, agriculture, livestock production and tourism) and the overexploitation of

112   scarce natural resources such as scrublands and seasonal grasslands for firewood collection and

113   livestock grazing (Campos-Ortega & Jorquera-Jaramillo, 2008; Estevez et al., 2010). The road

114   network includes a coastal highway with four-lanes that crosses the region from North to South

115   and various secondary roads.

116   ***Lama guanicoe* ocurrence data**

117   We collated presence data throughout the study zone, which includes eleven recorded *L.*

118   *guanicoe* populations, comprising three coastal (Pan de Azúcar National Park [1], Llanos de

119   Challe National Park [3] and Los Choros [6]), two mid-slope (El Calvario stream [7] and Oso

120   Negro sector [4]) and six high altitude populations (Nevado Tres Cruces National Park [2], El

121   Morro Private Protection Area [5], Tres Quebradas River Area of high conservation value [8], El

122   Tambo stream [9], Estero Derecho Private Protection Area & Nature Sanctuary [10], and

123   Pelambres Private Area [11]) (Fig. 2). While there have been no reports of any other coastal or

124   mid elevation populations in the northern or southern extents of the study area, eastern Andean

125   populations do exist on the Argentinean side. Both genetic (Marín et al., 2013) and telemetric

126   (ULS 2012-2015, unpublished data) data suggests that dispersal among the Chilean and

127   Argentinean populations can occur.

128   For populations 3, 6, 7, and 8, we took GPS coordinates of fresh fecal deposits in each

129   season from 2012 to 2014. Additionally, we considered geolocation data registered at ten day

130   intervals between December 2012 and December 2015 for three collared individuals, one in Los

131   Choros [6] (GPS-GSM Ecotone collars), and two in Tres Quebradas River Area [8] (Argos

132   satellite telemetry). Finally, we completed our occurrence database by incorporating information

133   from published sources (González et al., 2013; Bonacic et al., 2014) and observations recorded

134   by researchers of the Department of Biology at the University of La Serena. The occurrence data

135   were essentially recorded between 2002 and 2015 (Table S1), except for the El Tambo stream

136   sector which were observed between 1994 and 2008 (Table S1). To minimize spatial

137   autocorrelation issues, we filtered the records using ENMtools (Warren, Glor & Turelli, 2008;

138   Warren, Glor & Turelli, 2010), so that the distance between any two presence data was at least

139   500 m. The final occurrence dataset used in suitability modeling included 937 spatially unique

140   records, of which 12.8% were obtained from collared individuals (Table S1).

141   **Environmental variables**

142   Eight environmental variables were considered for the ecological niche models (Table 1), based

143   on *a priori* expectations of their influence on guanaco populations. All raster maps were prepared

144   and analyzed with a ~ 90 m spatial resolution. The landscape variables included characteristics of

145   topography and vegetation cover. Topographic factors were considered because available

146   evidence indicates that guanacos tend to prefer mountainous areas with high and medium slopes

147   (Travaini et al., 2007; Acebes et al., 2010; Pedrana et al., 2010). We derived elevation and slope

148   layers from Shuttle Radar Topography Mission digital elevation data (SRTM, Farr et al., 2007),

149   with a spatial resolution of 3 arc-seconds (http://srtm.csi.cgiar.org), using Spatial Analyst in

150   ArcGIS 10.2.1 (ESRI, 2014). In addition, we calculated the surface roughness as recommended

151   by Riley (1999) using the Geomorphometry and gradient metrics toolbox version 2.0 (Evans et

152   al., 2014) for ArcGIS. Since local vegetation plays a determinant role in habitat selection by

153   animals at fine spatial scales (Kotliar & Wiens, 1990; Chetkiewicz, St. Clair & Boyce, 2006),

154   including guanacos (Puig et al., 2008), we derived vegetation cover types from the classification

155   of Chilean vegetation communities (Luebert & Pliscoff, 2006). This information is summarized

156   in Table S2. Access to water and statutory protected status are both considered to positively

157   influence *L. guanicoe's* survival, and layers representing distance to both water sources and

158   protected areas were accordingly generated for use in habitat suitability modelling. Water sources

159   and protected area boundaries were identified based on the National Wetlands Inventory (MMA,

160   2011), and Coquimbo and Atacama red books (Squeo et al., 2001; Squeo et al., 2008a),

161   respectively. We used distance to both human settlements and roads as proxies for human

162   disturbances. The roads layer was generated based on data from the Ministerio de Obras Públicas

163   de Chile (MOP, 2013). Only paved roads were included. Finally, the distance to human

164   settlements raster was produced based on the Open Street Map database

165   (https://www.openstreetmap.org).

166   **Habitat suitability modelling and resistance surface**

167   Habitat suitability was modelled based on a maximum entropy approach using MaxEnt version

168   3.3.3k (Phillips, Anderson & Schapire, 2006). MaxEnt is a machine-learning method that

169   minimizes the relative entropy between the probability density at the presence sites and the

170   probability density at background locations, the latter representing a random sample of the

171   available environment (Elith et al., 2011). It is widely recognized as the most reliable approach in

172   cases where only presence data are available (Phillips, Anderson & Schapire, 2006; Elith,

173   Kearney & Phillips, 2010; Yackulic et al., 2013). The logistic output of MaxEnt provides a

174   habitat suitability index (HSI) ranging from 0 to 1 (Phillips & Dudík, 2008; Anderson et al.,

175   2016). We generated MaxEnt models using a bootstrap approach, where 70% of the occurrence

176   data (i.e. 656 points) were used for training, while the remaining 30% (i.e. 281 points) were used

177   to validate the model. A mask was applied to the study area, excluding non-continental areas and

178   large areas with no historical occurrence data, in order to force MaxEnt to pick background

179   information in areas within which the presence data were collected so that all the modelled data

180   (presence and background) contained the same collection bias (Elith et al., 2010; Elith et al.,

181   2011). We used the default number of background (or pseudo-absence) locations, 10,000.

182   To identify the best solution, MaxEnt uses a regularization multiplier and a set of features

183   (i.e. transformations of the original predictor variables). Because the default settings can generate

184   highly complex models (Kumar, Neven & Yee, 2014a; Kumar, Neven & Yee, 2014b), we first

185   explored different combinations of features and various regularization multiplier values. For the

186   selection of the features, we inspected the species responses (i.e. curves showing the probability

187   of occurrence in relation to each predictor) obtained from various feature combinations. We opted

188   for the linear and product features because their combined use resulted in simpler, more

189   interpretable variable effects. The regularization multiplier is a smoothing parameter designed to

190   reduce model overfitting and complexity (Radosavljevic & Anderson, 2014). To identify the

191   optimal parameter value, we generated models with regularization multipliers varying from one

192   to 20 with increments of one. Based on the Akaike Information Criteria corrected for small

193   sample sizes (AICc), calculated using ENMTools (Warren, Glor & Turelli, 2008; Warren, Glor &

194   Turelli, 2010; Warren & Seifert, 2011), optimal model performance was achieved using a

195   regularization parameter of two. The collinearity of the variables was then analyzed by

196   calculating Pearson correlations using the "raster" R-package (Hijmans et al., 2016). In cases

197   where two variables were strongly correlated ($|r| \geq 0.75$), we discarded the variable with the least

198   ecological significance. The final set of environmental variables comprised elevation, distance to

199   wetlands and rivers, vegetation communities, distance to protected areas, distance to urban

200   settlements, and slope.

201   To construct the habitat suitability model, we ran 20 different bootstrap replicates and

202   used the average results and area under the curve (AUC) scores. AUC scores are used to evaluate

203   model performance, with values of one indicating a perfect fit of the presence data, and values

204   close to 0.5 indicating that the model does not better predict the presence data than random

205   background locations (Elith et al., 2011). The suitable habitat threshold was defined as the HSI

206   value that maximized the sum of sensitivity (correct predictions of the occurrence) and specificity

207   (correct predictions of the absence), as recommended by Liu, White & Newell (2013). To assess

208   the performance of the model, we tested the significance of the extrinsic omission rate (i.e. the

209   fraction of test localities falling outside the predicted suitable habitat) with a one-tailed binomial

210   test (Phillips, Anderson & Schapire, 2006).

211   We derived the resistance surface from the habitat suitability scores by inverting and

212   rescaling the HSI values into a continuous scale from one (low resistance / highly suitable for

213   movement) to 100 (high resistance / low suitability for dispersal) using a linear scaling function

214   available in ArcGIS 10.2.1 (ESRI, 2014). A barrier layer was then incorporated to generate the

215   final dispersal cost map. We defined areas of intensive agriculture, towns and cities, mining

216   extraction sites and large dams as impenetrable barriers to guanaco movement. Because vehicle

217   collision is a leading cause of *L. guanicoe* mortality in the region (Vargas, Bonacic & Moraga,

218   2016), we considered unfenced highways as major barriers with a very low permeability,

219   allocating them a very high resistance value (i.e. 95). Fencing potentially presents an absolute

220   barrier to mammal movement (van Langevelde, van Dooremalen & Jaarsma, 2009) and decreases

221   the survival probability of ungulates crossing highways, even in low traffic conditions

222   (Harrington & Conover, 2006). We therefore allocated the maximum resistance value of 100 in

223   fenced sections of the highway.

224   **Modelling landscape connectivity for *L. guanicoe***

225   We used Circuitscape 4.0 (McRae et al., 2008) to model connectivity and routes of dispersal

226   across the landscape. Circuitscape, based on circuit theory, treats the landscape as a conductance

227   surface, where each pixel represents a resistor with an assigned resistance (or, conversely,

228   conductance) value. Pairwise electrical resistances between locations (McRae, 2006; McRae et

229   al., 2008) are calculated by running a theoretical electrical current between each population pair,

230   with one population being set as the current source and the other as the ground. Contrary to least

231   cost resistance methods, Circuitscape does not assume that animals disperse according to

232   previous knowledge of the surroundings, but is based on random walks (McRae, Shah &

233   Edelman, 2016). It thus links populations through multiple pathways (McRae et al., 2008), such

234   that connectivity between habitat patches increases according to the number of connected

235   pathways, and the effective resistance between two populations is derived from the overall

236   resistance across all pathways. To estimate effective resistance and densities, one ampere of

237   current was injected to the current sources using the resistance surface derived from the habitat

238   suitability model. A cumulative flow map based on all possible pairs of nodes was constructed

239   displaying the amount of current flowing through each pixel according to the model. A map of

240   maximum current densities between any pair of populations was also generated to identify areas

241   that facilitate the most efficient movement between populations, and to identify pinch points,

242   which correspond to areas where connectivity is most tenuous (MacRae & Shah, 2009), and

243   therefore essential for connectivity due to the lack of alternative pathways (i.e. McRae et al.,

244   2008).

245   We used Linkage Mapper Connectivity Analysis Software (available at:

246   *www.circuitscape.org/linkagemapper*) to build a network of least-cost corridors (McRae &

247   Kavanagh, 2011). The resulting linkage network was then analyzed with the Centrality Mapper

248   module to calculate current flow centrality (CFC) across the networks. CFC is a measure of the

249   amount of dispersal passing through any given link or population as a function of its position in

250   the network topology, thus allowing the contribution of each population and least-cost corridors

251   to the linkage network to be assessed.

252   **Ethics Statement**

253   The capture and handling of guanacos for installation of tracking devices were performed

254   according to the highest standards designed to ensure the safety of the animals. Prior

255   approval was obtained from the Chilean authority for wildlife management (Servicio Agrícola y

256   Ganadero – SAG; authorization N°: 3346/2013 and 7899/2014), whose agents controlled all field

257   manipulations of guanacos to ensure strict compliance with standards and regulations.

258   **RESULTS**

259   **Habitat suitability model generated by MaxEnt**

260   The final model of habitat suitability for *Lama guanicoe* across the study area performed better

261   than random, with an average test AUC value of 0.87 (95% confidence interval: 0.84 - 0.88;

262   standard error: ± 0.009). Extrinsic omission rate was 0.13 ($P < 0.01$), indicating that the variables

263   of the pruned model contributed significantly to the habitat suitability predictions. Elevation,

264   distance to wetlands, and vegetation communities were the most important predictors of habitat

265   suitability, with a combined contribution of 87.7% to the final MaxEnt model (Table 2). The

266   occurrence probability response of *L. guanicoe* to each predictor variable varied considerably,

267   showing a strong negative association with distance to wetlands, distance to protected areas, and

268   elevation (Fig. 3A,B,F), a positive association with scrubland vegetation communities (Andean

269   Mediterranean sclerophyll forest, Andean Mediterranean underbrush, Andean tropical

270   Mediterranean underbrush, Mediterranean pastureland, Mediterranean Coastal Desert Thicket*,

271   Mediterranean interior desert scrubland, Fig. 3D), and a weak positive association with slope and

272   distance to urban settlements (Fig. 3C,E). Maps of the six environmental variables, including

273   guanaco occurrences, are provided in Fig. S1. Overall, our model predicted 29,173 km^2 of

274   suitable habitat heterogeneously distributed throughout the landscape, equivalent to

275   approximately 25% of the total study area (Fig. S2A). Medium to high HSI values were found all

276   along the Andes, forming a continuous stretch of suitable habitat from south to north of the study

277   area up to the Nevado Tres Cruces National Park (Fig. S2B). By contrast, non-continuous patches

278   of high HSI values surrounded by extensive zones of unsuitable habitat were predicted along the

279   coast, particularly in the Limarí, Huasco, and Copiapó basins (Fig. S2A,B).

280   **Habitat resistance map of the study region for *L. guanicoe***

281   The resistance surface derived from the HSI scores showed a gradient of increasing resistance

282   costs from south to north of the study area, with marked intermediate zones of high resistance

283   costs within each river basin, being continued north of the Copiapó river basin (Fig. 2). Most of

284   the areas of lower resistance cost were spatially coincident with high HSI value areas (see Fig. 2

285   and Fig. S2B), forming a contiguous expanse along high and mid elevation zones as far as the

286   Copiapó river basin, and discontinuous patches along the coast, separated by all major transverse

287   river basins except the Limarí. The Copiapó basin also represents the northern limit of the large

288   predicted coastal areas with low habitat resistance, above which only a few discrete low

289   resistance patches were identified (Fig. 2).

290   **Patterns of landscape connectivity for *L. guanicoe* across the study area**

291   The cumulative current density map based on all possible pairwise combinations between the 11

292   populations in the study area shows different current density patterns between coastal and

293   mountainous areas. Similar to what was observed in the HSI and habitat resistance maps, highest

294   cumulative current flow occurred within a wide corridor encompassing the mid and high

295   elevation Andean sectors (28°00'02"–30°20'25" S and 69°45'0"–70°26'35" W), which harbor

296   five guanaco populations (El Morro (5), Calvario (7), Tres Quebradas (8), El Tambo (9) and

297   Estero Derecho (10); Fig. 4). Relatively high cumulative current flow was also found between the

298   populations of Pelambres (11) and Estero Derecho (10) in the south of the study area. By

299   contrast, current flows appeared discontinuous along the coast. Other areas with middle to high

300   movement probabilities were revealed in the center of the study region between and along the

301   transversal Elqui, Huasco and Copiapó valleys, as well as along the highway (Fig. 4). Overall,

302   lowest current flows included the Pan de Azúcar (1) and Nevado Tres Cruces (2) national parks in

303   the north and the Limarí and Choapa river basins in the south (Fig. 4). Seven pinch-points were

304   identified by our maximum current flow model: one in the high Andes, two at mid altitudes, three

305   at wildlife crossings located on the highway, and one in the coastal region (Fig. 5).

306   **Current flow centrality analysis between _L. guanicoe_ populations across the study area**

307   Our linkage map revealed a greater density of corridors connecting habitat patches above 600

308   masl between the Copiapó and Elqui river basins (Fig. 5). All three coastal populations were

309   associated with relatively low centrality scores (Fig. 5). They connected to other populations by

310   only one or two least resistance routes that crossed the highway, and which, in most cases (four

311   out of five), harbored a pinch point (Fig. 5). No corridors directly linking coastal habitat patches

312   were generated. Most pre-cordilleran and cordilleran habitat patches showed higher centrality

313   scores and connected to other geographically close patches by at least two corridors. Only the

314   northern and southernmost high Andean populations of Nevado Tres Cruces (2) and Pelambres

315   (11), respectively, displayed low current flow centrality scores (Fig. 5), only receiving least cost

316   paths with low or medium centrality scores.

317   **DISCUSSION**

318   **Habitat suitability of _Lama guanicoe_ in Chile's Norte Chico**

319   In this study, we identified connectivity pathways for _L. guanicoe_ in a region of Chile

320   characterized by small and fragmented populations (Marín et al., 2013). To achieve this goal, we

321   first developed a regional scale habitat suitability model. Consistent with González et al. (2013),

322   we identified areas of suitable habitat along both the coastline as well as the Andes. Overall,

323   predicted habitat suitability comprises an area of 29,173 km^2, which slightly exceeds the

324   prediction of González et al. (2013) for the same region (i.e. 23,481 km^2). Differences in the

325   predictor variables, the definition of the habitat suitability threshold or resolution of the models

326   may explain the observed discrepancy. Because González et al. (2013) aimed to evaluate habitat

327   suitability across the entire *L. guanicoe* distribution range in Chile, they used data layers of a

328   much lower resolution (3 x 3 km) than ours (90 x 90 m). Models built over large areas are

329   expected to have weak local predictive power due to regional niche variation (Osborne & Suárez-

330   Seoane, 2002; Murphy & Lovett-Doust, 2007), and higher resolution models are therefore better

331   suited for regional scale applications (Carroll, McRae & Brookes, 2012), as was the case here.

332   We found that resource factors most strongly influenced *L. guanicoe* distribution in

333   Chile's Norte Chico, followed by elevation and then disturbance factors. Vegetation and distance

334   to water resources accounted for 72% of the predictive ability of the Maxent model; constraining

335   *L. guanicoe*'s presence to seven of the 33 vegetation communities of the study area (Luebert &

336   Pliscoff, 2006), and to areas located less than 5 km from water resources. The seven vegetation

337   communities included at least one plant species foraged by *L. guanicoe* (Table S3). The

338   importance of the resource factors identified in this study is consistent with Lucherini et al.

339   (2000)'s habitat use study in a high Andean ecosystem of North-Eastern Argentina, which

340   showed that free-ranging guanacos most often occurred in vegetation-rich areas close to streams.

341   Overall, these results suggest that forage and water availability are key drivers of guanaco

342   distribution patterns, at least in environments where resources are limited and heterogeneously

343   distributed. In the study area, these factors resulted in a heterogeneous distribution of habitat

344   suitable for *L. guanicoe*. The largest sector was predicted in the foothills of the mid and high

345   elevation areas (2,000 – 4,500 masl), where four of the influential vegetation communities

346   (Andean Mediterranean sclerophyll forest of *K. angustifolia* and *G. trinervis,* Mediterranean

347   pastureland of *N. spathulatus* and *M. spathulata*, Andean tropical Mediterranean underbrush *A.*

348   *subterranea* and *A. echinus*, Andean Mediterranean underbrush *Laretia acaulis* and *Berberis*

349   *empetrifolia*) as well as numerous Andean wetlands occur (Squeo, Arancio & Gutierrez, 2001;

350   Squeo et al., 2006; Squeo et al.,2008b). High Andean wetlands may not only provide water

351   supply for *L. guanicoe,* but also fulfill various other needs such as food and shelter (Torres,

352   1992). The other three influential vegetation communities (Mediterranean Coastal Desert Thicket

353   *O. gigantean* and *E. breviflora,* Mediterranean Coastal Desert Thicket *H. stenophyllum*,

354   Mediterranean interior desert scrubland *H. stenophyllum* and *F. thurifera*) are constrained to

355   coastal areas, and in a section excluding the southernmost and northernmost regions. In the

356   coastal areas, water resources are sparse and scattered, resulting in large stretches of unsuitable

357   habitat along the coast.

358   Elevation accounted for 16% of the model's predictive ability, with occurrence

359   probabilities gradually declining with increases in elevation. However, even at the highest

360   elevations, the HSI values did not fall below the habitat suitability threshold. This finding is

361   consistent with literature reports of physiological and physical adaptations of guanacos to high

362   altitude (Wilson, 1989; Starck & Wang, 2005). Compared to resource factors and elevation,

363   disturbance factors only moderately influenced *L. guanicoe* distribution. Distance to urban

364   settlements and distance to protected areas accounted for a combined 10.6% of the predictive

365   ability of the model; as anticipated, proximity to protected areas exerted a positive effect on

366   occurrence probability, while proximity to human settlements had the opposite effect. While none

367   of the distance to human settlements was associated with HSI corresponding to unsuitable

368   habitat, the fact that adverse effects were detected suggests that the current growth in

369   urbanization in the region (INE, 2012) may become a serious threat for *L. guanicoe* in the near

370   future.

Landscape connectivity and conservation priorities

The proportion of predicted suitable habitat (i.e. 25%) fell below the threshold at which patch

isolation increases the risk of extinction in bird and mammal populations (Andrén, 1994; Betts et

al., 2006), indicating that population connectivity is an issue of concern for *L. guanicoe* in Chile's

Norte Chico. In this context, our study contributes pertinent knowledge. Clear connectivity

patterns were identified, including both connectivity corridors and hotspots, as well as areas of

low movement probability and functionally isolated populations. The area most permeable to *L.

guanicoe* movement was predicted in the Andes, in a sector spanning about 2/3 of the latitudinal

extent of the study area. This corridor enables movement between all the high Andean

populations, of which five (Estero Derecho, El Tambo, Calvario, Tres-quebradas and El Morro)

in particular demonstrate high probability of inter-population movement, being crossed by

multiple pathways. Only a single pinch point was detected in this area, located upstream of the

Elqui river, but did not affect connectivity since it was not located on any connectivity pathway.

Altogether, these results suggest a relatively high resilience of the population network in the pre-

cordilleran and cordilleran regions, which could further benefit from transboundary movements

with the Argentinean populations.

Population connectivity nevertheless remains an issue of concern in the Andean region,

which is facing multiple threats due to mining (Squeo et al., 2006, Table S4) including habitat

loss and water contamination, exacerbated by the high density of mining concessions located

close to important water resources such as high-altitude wetlands (Troncoso et al., 2017). In the

absence of adequate regulation, mining therefore has the potential to significantly increase habitat

fragmentation in this sector. Environmental impact assessments and mitigation programs should

thus consider population connectivity in future baseline studies, and particularly for those

populations that may be at higher extinction risk, such as El Tambo and Nevado Tres Cruces

395   National Park, which may be less resilient to local threats due to small population size (i.e. N <

396   80, Table S4), and Nevado Tres Cruces National Park, which displayed a low centrality score.

397   Because our estimates did not consider populations outside the study area, some neighborhood

398   populations of the Andean sites might have been omitted, which may have resulted in an

399   underestimate of the centrality scores in the cordilleran region. Further analyses, such as

400   population genetic studies, are needed to confirm the isolation status of the Nevado Tres Cruces

401   National Park.

402   Connectivity patterns along the coast contrasted strongly with those observed in the

403   Andes. The coastal landscape was essentially dominated by low to medium current areas. Low

404   current areas reflect either barriers to movement or very large corridors (Cushman, Chase &

405   Griffin, 2010). In the present case, they occurred in high-resistance areas (i.e. low quality

406   habitat), coinciding with urban areas or areas of intensive agriculture (Novoa & López, 2001). As

407   a result, no connectivity was detected between coastal populations themselves, only to

408   populations at higher altitudes. The actual effectiveness of these connections was unclear,

409   however. Indeed, they implied crossing the four-lane highway that extends vertically across the

410   study area. Fenced highways increase animal mortalities due to vehicle collisions and animals

411   becoming trapped in the barbed wire (Vanak, Thaker & Slotow, 2010). Besides, two pinch points

412   along the highway were coincident with locations of wildlife underpasses, located in the

413   pathways linking Llanos del Challe to Oso Negro and Los Choros to El Cavario. To date, it is

414   unknown if guanacos utilize these structures effectively. This should be a topic of future research,

415   particularly since evidence suggests that ungulates tend to demonstrate a preference for utilizing

416   overpasses rather than underpasses (Simpson et al., 2016). Overall, our results suggest that the

417   coastal populations may be functionally isolated, a situation that would endanger their long-term

418   persistence. This threat could be further compounded if anthropogenic activities like mining were

419   developed in the mid elevation sector, which could severely affect the few remaining connectivity

420   links of the coastal populations. Actions to protect or restore connectivity might thus be crucial

421   for the conservation of the remnant coastal populations of *L. guanicoe*.

422   Other areas that should be prioritized are those playing a key role in the connectivity

423   network. Our model recognized El Morro and Calvario patches as the most important habitat

424   patches for overall connectivity, facilitating individuals' dispersal between several pairs of

425   populations. If these resource patches were to be lost, it would result in considerable increases in

426   the distance and/or transit times between populations (Carroll, McRae & Brookes, 2012). Future

427   regional planning should consider maintaining their integrity for the long-term persistence of this

428   emblematic species in this region of Chile.

429   **CONCLUSIONS**

430   The identification of biological corridors, defined as areas of natural habitat that allow species

431   dispersal processes essential for their persistence in a landscape, is of prime importance for the

432   conservation of endangered species, and also has implications for the maintenance of important

433   biological patterns and processes at large regional scales (Chetkiewicz, Clair & Boyce, 2006;

434   Rouget et al., 2006). In this study, we used a resistance-surface-based connectivity modelling

435   approach to investigate functional connectivity of *L. guanicoe* in Chile's Norte Chico. To

436   appraise the actual pertinence of our results in terms of dispersal, future studies contrasting our

437   connectivity model predictions against gene flow would be needed (Baguette et al., 2013). Yet,

438   our study suggests that functional connectivity is an issue of concern for *L. guanicoe* in Chile's

439   Norte Chico. Indeed, we found that isolation may jeopardize the viability of the three coastal

440   populations, which are the last remaining in Chile. Very few of the connectivity pathways may in

441   fact facilitate access to these populations, and the effectiveness of these routes needs to be

442   investigated, since their functionality appears to be wholly dependent on wildlife crossing

443   structures that may or may not be appropriate for *L. guanicoe*. Our results were rather comforting

444   for most Andean populations, for which we predicted high connectivity levels; and two

445   populations in particular were found to play a central role in the connectivity network.

446   Collectively, these results indicate that future conservation and management plans involving *L.*

447   *guanicoe* in the region should adopt a landscape strategy designed to conserve functional

448   connectivity between coastal and Andean populations, as well as protect habitat patches that

449   likely function as stepping stones within the connectivity network.

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Table 1(on next page)

Environmental variables used for habitat suitability modeling of *Lama guanicoe* in Chile's Norte Chico.

Table 1. Environmental variables used for habitat suitability modeling of *Lama guanicoe* in Chile's Norte Chico

GIS data layer	Description	Potential relevance for guanacos	Reference
Elevation	Altitude above sea level	Preference for mountainous areas	Travaini et al., 2007; Acebes et al., 2010
Roughness	Surface roughness	Surface roughness influences terrestrial animal movement	Dickson et al., 2005
Slope	Rate of maximum change in z-values	Preference for high and medium slopes	Travaini et al., 2007; Acebes et al., 2010
Distance to urban areas	Euclidean distance to nearest urban area	Negative impact of dog attacks, poaching, competition with livestock and human activities in general	Vargas, Bonacic & Moraga, 2016
Distance to water bodies	Euclidean distance to nearest water bodies	Water is necessary for survival and physiological functions	Lautier, Dailey & Brown, 1988; Packard, 1991; Prenda, López-Nieves & Bravo, 2001
Distance to roads	Euclidean distance to nearest paved roads	Vehicle collisions constitute an important threat in northern Chile	Vargas, Bonacic & Moraga, 2016
Vegetation communities	Main vegetal communities described in the study region	Determinant role of local vegetation in habitat selection	Puig et al., 2008
Protected areas	Protected areas along the Coquimbo and Atacama regions	Protected areas bring safety, stability and resources to the fauna	Geldmann et al., 2013; Gray et al., 2016

Table 2 (on next page)

Relative contribution of the environmental variables to the final habitat suitability model of *Lama guanicoe* in Chile's Norte Chico.

1   **Table 2**. Relative contribution of the environmental variables to the final habitat suitability model of

2   *Lama guanicoe* in Chile's Norte Chico

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Environmental variable	Contribution (%)
Vegetal communities	58.9
Elevation	15.6
Distance to wetlands and rivers	13.2
Distance to urbane settlements	7.2
Distance to protected areas	3.4
Slope	1.7

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Figure 1

Distribution range of *Lama guanicoe* according to Baldi *et al.* (2016) and location of the study area.
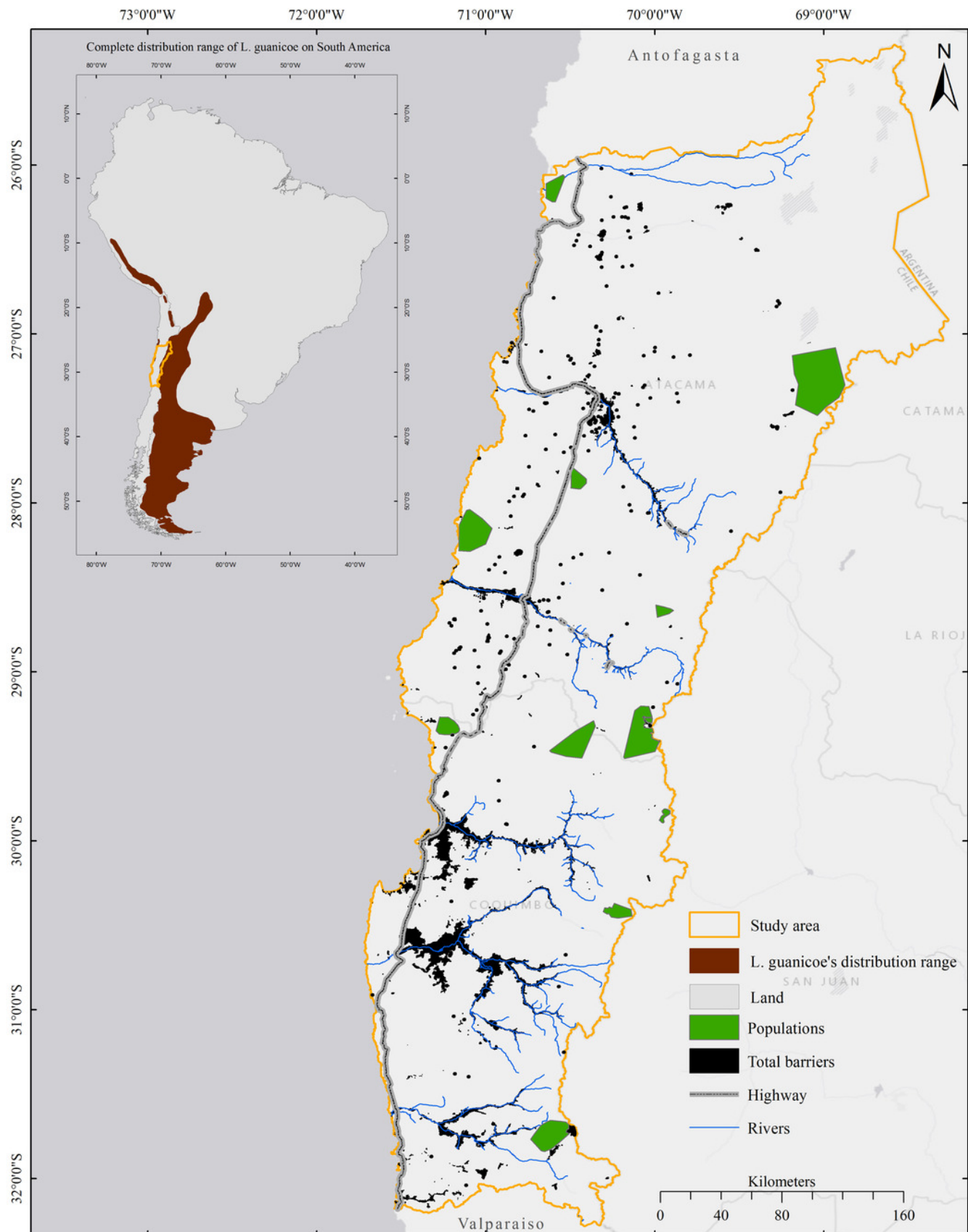
Figure 2

Map of landscape resistance for the guanaco *Lama guanicoe* in Chile's Norte Chico.

Resistance values were estimated by inverting and rescaling the habitat suitability values, generated with MaxEnt, to a continuous scale from 1 (low resistance / high suitability for dispersal) to 100 (high resistance / low suitability for dispersal). Numbers represent patches of habitat corresponding to the guanaco populations (**1.** Pan de Azúcar National Park; **2.** Nevado Tres Cruces National Park; **3.** Llanos de Challe National Park; **4.** Oso Negro sector; **5.** El Morro; **6.** Los Choros; **7.** Calvario stream; **8.** Tres Quebradas river; **9.** El Tambo stream; **10.** Estero Derecho nature sanctuary; **11.** Pelambres area).
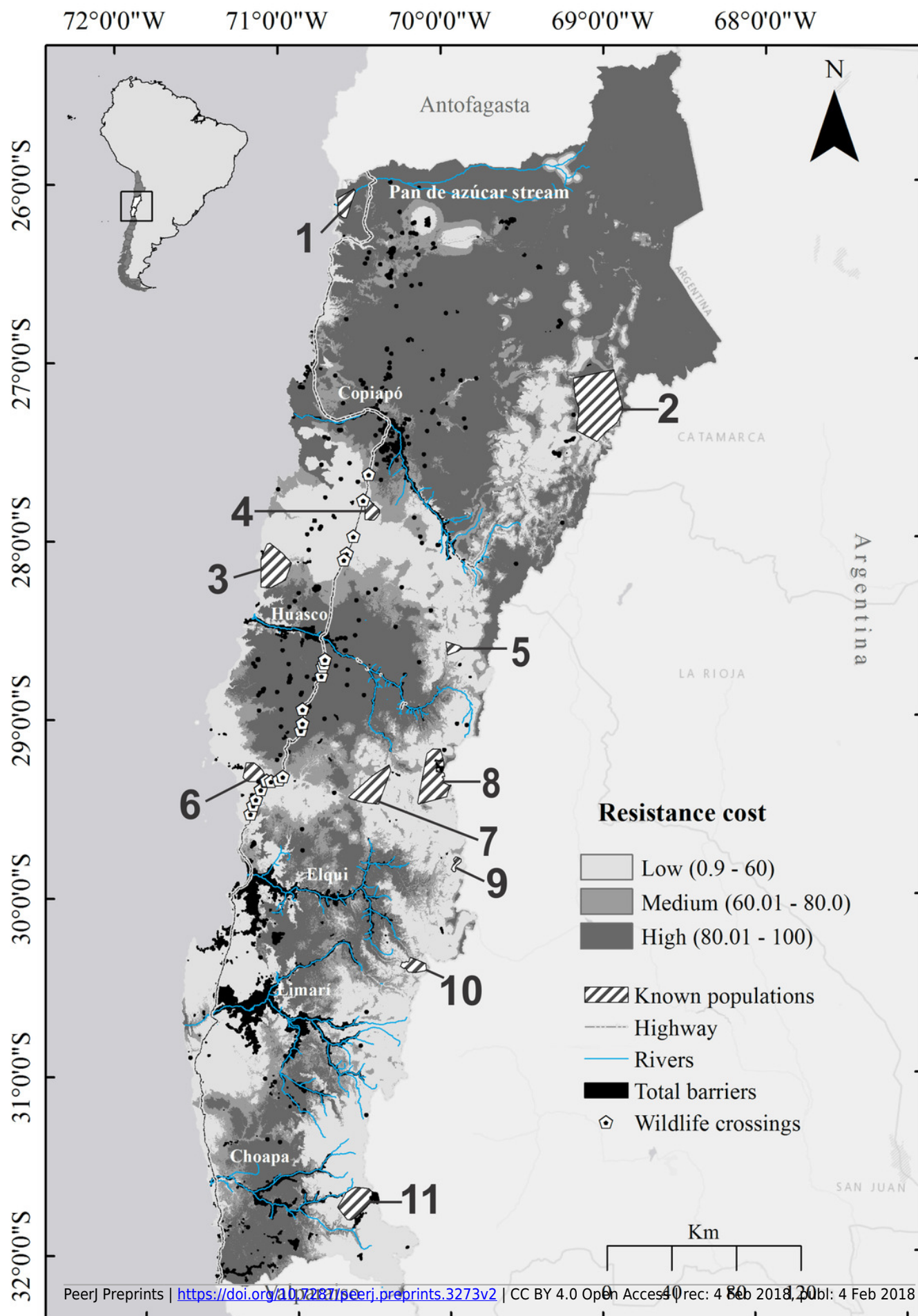
Figure 3

Response curves and predictive power of the environmental variables for the pruned habitat suitability model for *Lama guanicoe* generated by MaxEnt.

Marginal response curves generated for each predictor are shown for continuous predictors (A) Distance to wetlands. (B) Distance to protected areas. (C) Slope. (E) Distance to human settlements. (F) Elevation. Single-variable response curve is shown for the categorical predictor. (D) Vegetal communities, each of them being described in Table S2. The predictive power of the variables, reported within the plot area in each case, is given by a Jackknife test of the variable importance using AUC on test data for each environmental variable retained in the MaxEnt model.
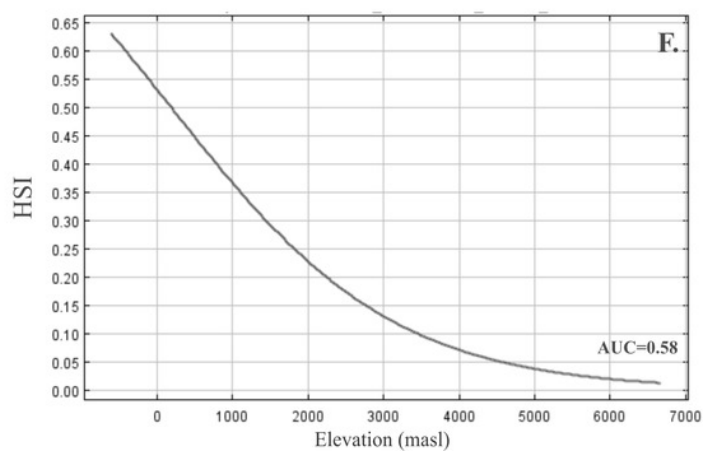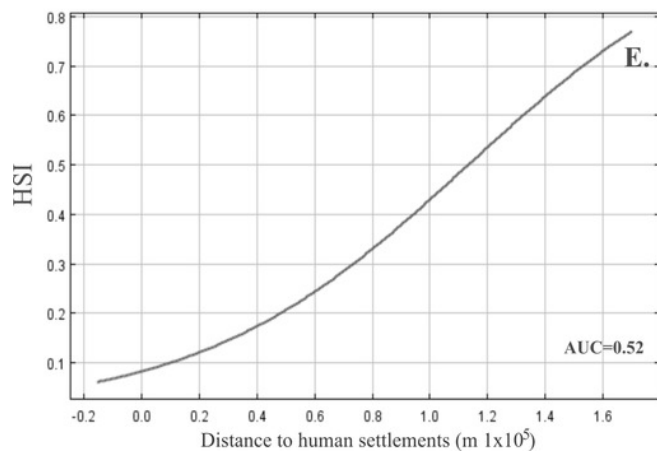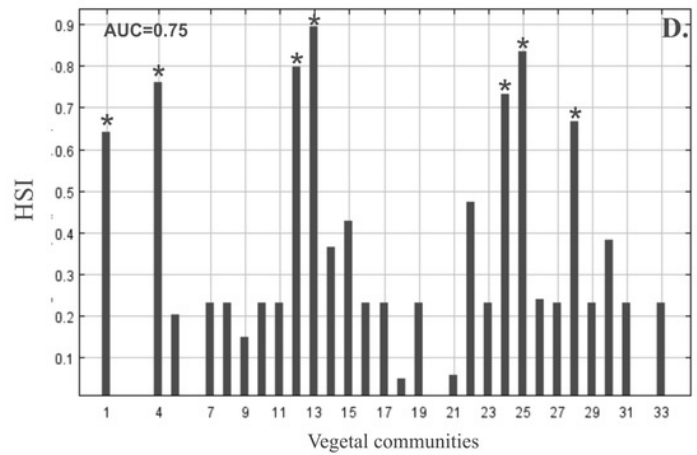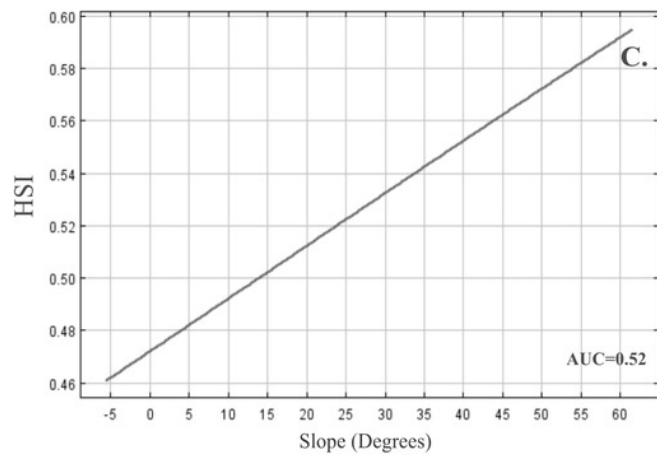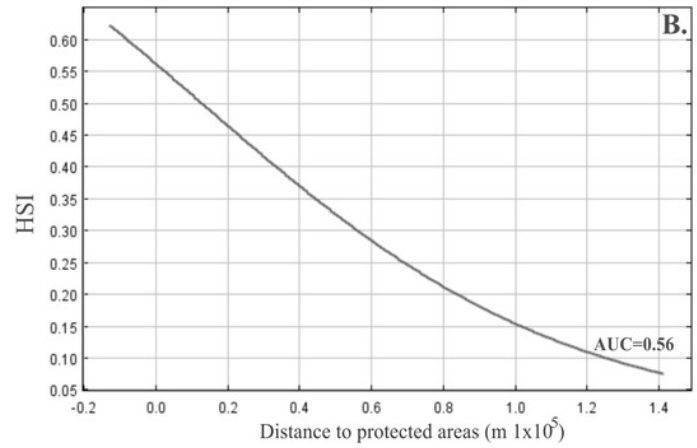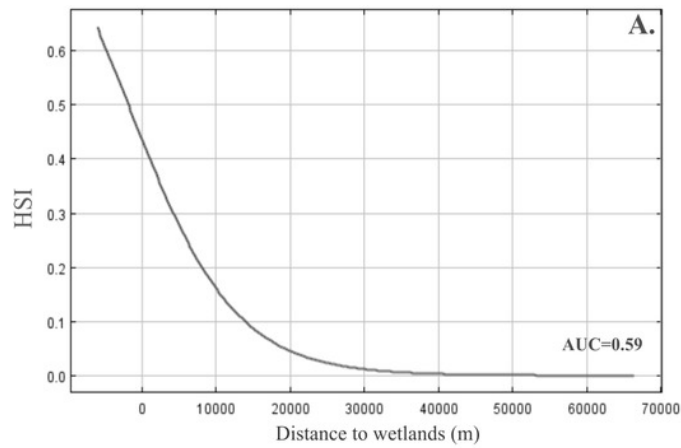
Figure 4

Cumulative current flow density map for the guanaco *Lama guanicoe* across Chile's Norte Chico.

Current flows represent passage probabilities calculated between all pairs of habitat patches corresponding to the guanaco populations by injecting 1 Ampere of current. Habitat patches corresponding to the guanaco populations are numbered as follow: **1.** Pan de Azúcar National Park; **2.** Nevado Tres Cruces National Park; **3.** Llanos de Challe National Park; **4.** Oso Negro sector; **5.** El Morro; **6.** Los Choros; **7.** Calvario stream; **8.** Tres Quebradas river; **9.** El Tambo stream; **10.** Estero Derecho nature sanctuary; **11.** Pelambres area.
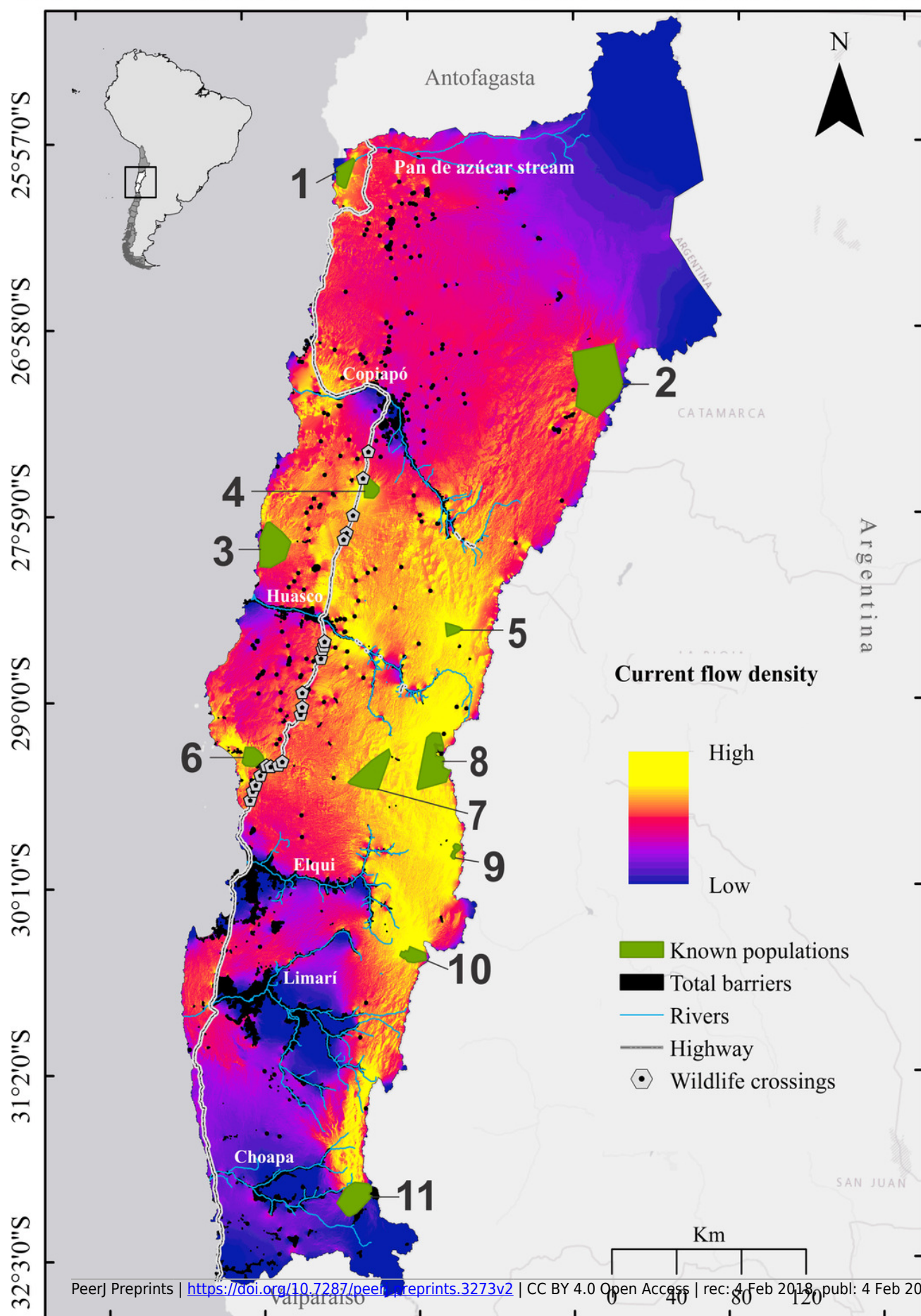
Figure 5

Linkage network map of *Lama guanicoe* populations in Chile's Norte Chico, produced with the Linkage Mapper Connectivity Analysis software.

Centrality score of patches and routes are represented on the map. White arrows indicate locations identified as pinch points by the maximum cumulative current flow map generated by Circuistcape. Habitat patches corresponding to the guanaco populations are numbered as follow: **1.** Pan de Azúcar National Park; **2.** Nevado Tres Cruces National Park; **3.** Llanos de Challe National Park; **4.** Oso Negro sector; **5.** El Morro; **6.** Los Choros; **7.** Calvario stream; **8.** Tres Quebradas river; **9.** El Tambo stream; **10.** Estero Derecho nature sanctuary; **11.** Pelambres area.