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Espinosa MI, Gouin N, Squeo FA, López D, Bertin A. 2018. Landscape connectivity among remnant populations of guanaco (*Lama guanicoe* Müller, 1776) in an arid region of Chile impacted by global change. PeerJ 6:e4429 <https://doi.org/10.7717/peerj.4429>

# 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. It is an issue of concern for the preservation of biodiversity in drylands since landscapes in water limited environments are characterized by low habitat cover, high habitat fragmentation and harsh matrices, and are being rapidly degraded at the global scale. In this study, we modelled landscape connectivity between the 11 remnant coastal and Andean populations of the guanaco *Lama guanicoe*, an emblematic herbivore indigenous to South America, in Chile's arid Norte Chico. We first produced a habitat surface model to derive a regional surface resistance map; and we then used circuit theory to map functional connectivity, investigate the degree of isolation of the populations, and identify those that most contribute to the network patch connectivity. Predicted suitable habitat for *L. guanicoe* represented about 25% of the study region (i.e. 29,173 km<sup>2</sup>), 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 the high Andean populations. Coastal populations, in contrast, were predicted to be more isolated. They only connect to medium and high altitude populations, and for two of them, animal movement was linked to the effectiveness of wildlife crossings. Based on the degree of connectivity, population size, and local threats, the coastal and the northernmost populations were identified as being most vulnerable, while the Andean populations appeared to be least at risk, even when located near areas of mining activity. Collectively, our results suggest that functional connectivity is an issue of concern for *L. guanicoe* in Chile's Norte Chico, and that future conservation and management plans should adopt a landscape strategy aiming at

conserving the functional connectivity between the coastal and Andean populations, and at protecting the habitat patches likely to act as stepping stones within the connectivity network.

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# 10 ABSTRACT

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12 fragmented habitats. It is an issue of concern for the preservation of biodiversity in drylands since  
13 landscapes in water limited environments are characterized by low habitat cover, high habitat  
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27 crossings. Based on the degree of connectivity, population size, and local threats, the coastal and  
28 the northernmost populations were identified as being most vulnerable, while the Andean  
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30 Collectively, our results suggest that functional connectivity is an issue of concern for *L.*  
31 *guanicoe* in Chile's Norte Chico, and that future conservation and management plans should  
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33 and Andean populations, and at protecting the habitat patches likely to act as stepping stones  
34 within the connectivity network.

35 Keywords: Animal movement, Circuitscape, functional connectivity, guanaco, habitat modelling,

36 *Lama guanicoe*

## 37 INTRODUCTION

38 Understanding and managing connectivity has become a key concern for the conservation of  
39 biological populations and communities in the face of rapid habitat loss and fragmentation driven  
40 by anthropogenic and climate change effects (Mitchell, Bennett & Gonzalez, 2013; Correa Ayram  
41 et al., 2014; Riordan et al., 2015; Dilts et al., 2016). By facilitating genetic exchange between  
42 habitat patches, connectivity plays a fundamental role on the long-term persistence of species in  
43 fragmented habitats (Fahrig & Merriam, 1994; Coughenour, 2008; Kindlmann & Burel, 2008).  
44 This is of particular concern in highly fragmented landscapes, where habitat loss results in  
45 exponential increases in patch distances, and thus dramatically intensifies habitat isolation  
46 (Andrén, 1994). In these cases, connectivity is a factor of both the proportion of suitable habitat  
47 across the landscape as well as the permeability of the surrounding matrix. According to  
48 empirical and theoretical evidence, patch isolation negatively impacts biodiversity when habitat  
49 cover is low (Andrén, 1994; Radford, Bennett & Cheers, 2005). It is believed to become a  
50 significant factor when the amount of suitable habitat in the landscape falls below 10-30%  
51 (Andrén, 1994; Betts et al., 2006), although this threshold might be largely underestimated for  
52 many species (Mönkkönen & Reunanen, 1999). The surrounding matrix, on the other hand, may  
53 either facilitate or hinder patch connectivity by determining the permeability of the landscape to  
54 species movement. While matrix effects are expected to be species-specific (Tischendorf &  
55 Fahrig, 2000; Kindlmann & Burel, 2008), it is recognized that the composition of the matrix  
56 determines its overall permeability to dispersal, with species being more prone to disperse in  
57 matrices that share structural similarities with habitat patches than in highly contrasting matrices  
58 (Ricketts, 2001; Franklin & Lindenmayer, 2009; Watling et al., 2011).

59 Landscapes in water limited environments are characterized by low habitat cover, high  
60 habitat fragmentation, and harsh matrices. In such ecosystems, habitat resources are typically  
61 sparse, naturally patchy, and heterogeneously distributed within an arid / semi-arid matrix (Illius

& O'Connor, 2000; Galvin et al., 2001; Valeix et al., 2010). Connectivity is thus an intrinsic concern for dryland biodiversity (Okin et al., 2015), and is becoming increasingly urgent due to the rapid degradation of water limited ecosystems at a global scale (Hochstrasser et al., 2014). Despite accounting for around 40% of the Earth's land surface area (Niemeijer et al., 2005; Bestelmeyer et al., 2015; Nautiyal, Bhaskar & Khan, 2015; Okin et al., 2015), and harboring high levels of endemism and functional diversity (Al-Eisawi, 2003; Moreira-Muñoz, 2011b; Smith et al., 1997; Wickens, 2013; *www.conservation.org*), drylands have received proportionately little attention in terrestrial ecological studies (Okin et al., 2015). Overland connectivity between populations, in particular, has largely been unexplored.

Chile's Norte Chico (between 27°S and 33°S latitude) is one of the most fragile areas in South America (Downing, 1994). Its characteristic aridity (Sarricolea, Herrera-Ossandon & Meseguer-Ruiz, 2016) makes this region particularly sensitive to climate and land-use changes (Squeo, Arancio & Gutierrez, 2001; Squeo, Arancio & Gutiérrez, 2008a; Fiebig-Wittmaack et al., 2012). Important climatic changes have occurred in the region over the last century, dominated by decreasing trends in precipitation and higher frequencies of drought (Fiebig-Wittmaack et al., 2012), and marked future temperature increases are projected for the periods 2011 to 2030 and 2046 to 2065 (Fiebig-Wittmaack et al., 2012). These climatic changes have resulted in accelerated rates of desertification in the region. This phenomenon is further amplified by human economic activities (i.e. mining, agriculture, livestock production and tourism) and the overexploitation of scarce natural resources such as scrublands and seasonal grasslands for firewood collection and livestock grazing (Campos-Ortega & Jorquera-Jaramillo, 2008; Estevez et al., 2010). Rapid habitat degradation and loss has resulted in many endemic species becoming polarized into small, highly isolated remnant populations. Thus, connectivity between populations may be critical for the persistence of many species of the region. It likely represents an essential component for the conservation of wild large herbivores in particular. Indeed, for



large herbivores, movement between habitat patches is not only necessary to maintain effective population sizes, and thereby their evolutionary potential and long-term survival, but also for individuals to meet their essential needs. Large herbivores in general actually have high requirements in terms of resources (Coughenour, 2008; Ripple et al., 2015), and may thus be unable to survive in small habitat patches (Ripple et al., 2015).

The guanaco, *Lama guanicoe* (Artiodactyla, Camelidae), is an emblematic herbivore indigenous to South America. Anthropogenic habitat disturbance and overhunting during the last century has resulted in its eradication in an estimated 75 % of its original range (Ceballos & Ehrlich, 2002), and it presently occurs in small isolated populations, particularly in the north of its distribution (Marín et al., 2008; Marin et al., 2013), where habitat fragmentation is recognized as the most important threat to this species (IUCN, 2016). In Chile's Norte Chico, *L. guanicoe* is represented by an intermediate-hybrid lineage between the two guanaco sub-species found in Chile: *L. g. cacsilensis* and *L. g. guanicoe* (Marin et al., 2013). The ecology of this lineage is not well known, but there is evidence to suggest that its distribution does not overlap with that of the two guanaco sub-species (González et al., 2013), thus suggesting specific environmental requirements of the hybrid lineage. A unique feature of this lineage is its ability to inhabit coastal environments (González et al., 2013). The long term survival of these coastal populations is tenuous, however, since they likely experience a high degree of isolation. Indeed, local landscape characteristics are likely to restrict dispersal both among coastal populations themselves as well as between the coastal and Andean populations. Human settlements are concentrated along the coast and may thus impede connectivity between coastal populations. In addition, niche modelling at broad geographical scale predicted that coastal and Andean populations were separated by a large area of low habitat suitability acting as a biogeographic barrier (González et al., 2013). In this context, it is critical to better assess the potential connectivity between the guanaco populations of this unique region in Chile, and at a finer spatial scale to better identify

the components of the landscape that limit/facilitate population connectivity and the location of important corridors for local conservation purposes.

In this study, we modelled functional connectivity of *L. guanicoe* populations of Chile's Norte Chico using a resistance-surface-based connectivity modelling approach. To achieve this, we first generated a surface resistance layer by running a regional-scale habitat surface model; and then we mapped functional connectivity using circuit-theoretic connectivity models. The goals of our study were to assess the degree of isolation of coastal and Andean *L. guanicoe* populations, identify habitat patches that most contribute to the network patch connectivity, and evaluate the risk of extinction of the populations.

## MATERIALS AND METHODS

### Study area

The Norte Chico region in Chile is located between 26°S and 32°S. It spans about 115,756 km<sup>2</sup> and encompasses five hydrographic basins (Fig. 1). It is characterized by steep topography with altitude varying from zero to ~5000 masl in only 200 km (Squeo et al., 2008a; Zabala and Trigos, 2009). The climate is predominantly arid, although average temperature, precipitation, and relative humidity vary strongly according to both altitude and latitude (Juliá, Montecinos & Maldonado, 2008). The vegetation is composed of xeric shrublands, woody-stemmed shrubs, spiny scrubs and columnar and spherical cacti patchily distributed within an arid matrix (Novoa, Tracol & López, 2008). Evergreen trees and shrublands dominate slopes, while elevations >2800 masl are dominated by cushion-forming plants, xeric herbs adapted to low temperatures, and high Andean wetland plant species (Squeo et al., 2006; Arancio & Marticorena, 2008b). The region is facing various anthropogenic pressures, including urbanization and mining, and agricultural and livestock activities. The road network includes a coastal highway with four-lanes that crosses the region from North to South and multiple secondary roads.

### 137 *Lama guanicoe* occurrence data

138 We collated occurrence data for the eleven recorded *L. guanicoe* populations in the study area,  
139 comprising three coastal (Pan de Azúcar National Park [1], Llanos de Challe National Park [3]  
140 and Los Choros [6]), two mid-slope (El Calvario stream [7] and Oso Negro sector [4]) and six  
141 high altitude populations (Nevado Tres Cruces National Park [2], El Morro Private Protection  
142 Area [5], Tres Quebradas River Area of high conservation value [8], El Tambo stream [9], Estero  
143 Derecho Private Protection Area & Nature Sanctuary [10], Pelambres Private Area [11]) (Fig. 1).  
144 For populations 3, 6, 7, and 8, we took GPS coordinates of fresh fecal deposits in each season  
145 from years 2012 to 2014. Additionally, we considered geolocation data registered at ten day  
146 intervals between September 2013 and December 2015 for three collared individuals, one in Los  
147 Choros (6) (GPS-GSM Ecotone collars), and two in Tres Quebradas River Area (8) (Argos  
148 satellite telemetry). Finally, we completed our occurrence database by incorporating information  
149 from published sources (González et al., 2013; Bonacic et al., 2014) and observations recorded  
150 by professors of the Department of Biology at the University of La Serena. After eliminating  
151 duplicate occurrence records using ENTools (Warren, Glor & Turelli, 2008; Warren, Glor &  
152 Turelli, 2010), 937 spatially unique records were retained.

### 153 Environmental variables

154 Nine environmental variables were considered for the ecological niche models (Table 1), based  
155 on *a priori* expectations of their influence on guanaco populations. All raster maps were prepared  
156 with a ~ 90 m spatial resolution. The landscape variables included characteristics of topography  
157 and vegetation cover. Topographic factors were considered because available evidence indicates  
158 that guanacos tend to prefer mountainous areas with high and medium slopes (Travaini et al.,  
159 2007; Acebes et al., 2010; Pedrana et al., 2010). We derived elevation, slope and aspect layers

from Shuttle Radar Topography Mission digital elevation data (SRTM, Farr et al., 2007), with a spatial resolution of 3 arc-seconds (<http://srtm.csi.cgiar.org>), using Spatial Analyst in ArcGIS 10.2.1 (ESRI, 2014). In addition, we calculated the surface roughness as recommended by Riley (1999) using the Geomorphometry and gradient metrics toolbox version 2.0 (Evans et al., 2014). Since local vegetation plays a determinant role in habitat selection at fine spatial scales by animals (Kotliar & Wiens, 1990; Chetkiewicz, St. Clair & Boyce, 2006), including guanacos (Puig et al., 2008), we derived vegetation cover types from the classification of Chilean vegetation communities (Luebert & Plischoff, 2006). Access to water and statutory protected status are both considered to positively influence *L. guanicoe*'s survival, and layers representing distance to both water sources and protected areas were accordingly generated for use in habitat suitability modelling. Water sources and protected area locations were identified based on the National Wetlands Inventory (Ministerio del Medio Ambiente de Chile (MMA, 2011)), and Coquimbo and Atacama red books (Squeo et al., 2001; Squeo et al., 2008a), respectively. We used distance to both human settlements and roads as proxies for human disturbances. The roads layer was generated based on data from the Ministerio de Obras Públicas de Chile (MOP, 2013). Only paved roads were included. Finally, the distance to human settlements raster was produced based on the Open Street Map database (<https://www.openstreetmap.org>).

### **Habitat suitability modelling and resistance surface**

Habitat suitability was modelled based on a maximum entropy approach using MaxEnt version 3.3.3k (Phillips, Anderson & Schapire, 2006). MaxEnt is a machine-learning method that minimizes the relative entropy between the probability density at the presence sites and the probability density at background locations, the latter representing a random sample of the available environment (Elith et al., 2011). It is widely recognized as the most reliable approach in cases where only presence data are available (Phillips, Anderson & Schapire, 2006; Elith,

Kearney & Phillips, 2010; Yackulic et al., 2013). MaxEnt provides a measure of the probability of habitat suitability, the habitat suitability index (HSI), ranging from 0 to 1. We generated MaxEnt models using a bootstrap approach, where 70% of the occurrence data (i.e. 656 points) were used for training, while the remaining 30% (i.e. 281 points) were used to validate the model. To control for sampling bias, a mask was used to force MaxEnt to pick background information in areas within which the presence data were collected so that all the modelled data (presence and background) contained the same collection bias (Elith et al., 2011). Ten thousand random background locations were selected.

To identify the best solution, MaxEnt uses a regularization multiplier and a set of features (i.e. transformations of the original predictor variables). Because the default settings can generate highly complex models (Kumar, Neven & Yee, 2014a; Kumar, Neven & Yee, 2014b), we first explored different combinations of features and various regularization multiplier values. For the selection of the features, we inspected the species responses (i.e. curves showing the probability of occurrence in relation to each predictor) obtained from various feature combinations. We opted for the linear and product features because their combined use resulted in simpler, more interpretable variable effects. The regularization multiplier is a smoothing parameter designed to reduce model overfitting and complexity (Radosavljevic & Anderson, 2014). To identify the optimal parameter value, we generated models with regularization multipliers varying from one to 20 with increments of one. Based on the Akaike Information Criteria corrected for small sample sizes (AICc), calculated using ENMTools (Warren, Glor & Turelli, 2008; Warren, Glor & Turelli, 2010; Warren & Seifert, 2011), optimal model performance was achieved using a regularization parameter of two. Finally, we reduced the set of environmental variables by excluding those that did not yield better than random predictive ability. This was achieved by running individual models for each variable separately and retaining only those with test area under the curve (AUC) scores of the receiver-operating characteristic (Hanley & McNeil, 1982)

greater than 0.5. AUC scores are used to evaluate model performance, with values of one indicating a perfect fit of the presence data, and values close to 0.5 indicating that the model does not better predict the presence data than random background locations. The collinearity of the remaining variables was then analyzed by calculating Pearson correlations using the “Raster” R-package (Hijmans et al., 2016). In cases where two variables were strongly correlated ( $|r| \geq 0.75$ ), we discarded the variable with the least ecological significance. The final set of environmental variables comprised elevation, distance to wetlands and rivers, vegetation communities, distance to protected areas, distance to urban settlements, and slope.

To construct the habitat suitability model, we ran 20 different bootstrap replicates and used the average results and AUCs. The suitable habitat threshold was defined as the HSI value that maximized the sum of sensitivity (correct predictions of the occurrence) and specificity (correct predictions of the absence), as recommended by Liu, White & Newell (2013). To assess the performance of the model, we tested the significance of the extrinsic omission rate (i.e. the fraction of test localities falling outside the predicted suitable habitat) with a one-tailed binomial test (Phillips, Anderson & Schapire, 2006).

We derived the resistance surface from the habitat suitability scores by inverting and rescaling the HSI values into a continuous scale from one (low resistance / highly suitable for dispersal) to 100 (high resistance / low suitability for dispersal) using a linear scaling function available in ArcGIS 10.2.1 (ESRI, 2014). A barrier layer was then incorporated to generate the final dispersal cost map. We attributed an infinite resistance value to landscape features that we considered to present impenetrable barriers to guanaco movement, including areas of intensive agriculture, towns and cities, mining extraction sites, and large dams; resistance values of 95 and 100 were allocated to unfenced and fenced highways, respectively.

## Modelling landscape connectivity for *L. guanicoe*

We used Circuitscape 4.0 (McRae et al., 2008) to model connectivity and routes of dispersal across the landscape. Circuitscape, based on circuit theory, treats the landscape as a conductance surface, where each pixel represents a resistor with an assigned resistance (or, conversely, conductance) value. Pairwise electrical resistances between locations (McRae, 2006; McRae et al., 2008) are calculated by running a theoretical electrical current between each population pair, with one population being set as the current source and the other as the ground. Contrary to least cost resistance methods, Circuitscape does not assume that animals disperse according to previous knowledge of the surroundings, but is based on random walks (McRae, Shah & Edelman, 2016). It thus links populations through multiple pathways (McRae et al., 2008), such that connectivity between habitat patches increases according to the number of connected pathways, and the effective resistance between two populations is derived from the overall resistance across all pathways. To estimate effective resistance and densities, one ampere of current was injected to the current sources using the resistance surface derived from the habitat suitability model as a conductance surface. A cumulative flow map based on all possible pairs of nodes was constructed displaying the amount of current flowing through each pixel according to the model. A map of maximum current densities between any pair of populations was also generated to identify areas that facilitate the most efficient movement between populations, and to identify pinch points, i.e. areas that are essential for connectivity due to the lack of alternative pathways (i.e. McRae et al., 2008).

We used Linkage Mapper Connectivity Analysis Software (available at: [www.circuitscape.org/linkagemapper](http://www.circuitscape.org/linkagemapper)) to build a network of least-cost corridors (McRae & Kavanagh, 2011). The resulting linkage network was then analyzed with the Centrality Mapper module to calculate current flow centrality (CFC) across the networks. CFC is a measure of the amount of dispersal passing through any given link or population as a function of its position in



the network topology, thus allowing the contribution of each population and least-cost path to the linkage network to be assessed.

### **Evaluation of *L. guanicoe* population extinction risk in the study area**

Potential extinction risk of guanaco populations in Chile's Norte Chico was evaluated based on population size estimates, current flow centrality values, and local threats. Population size was estimated using published documentation, mainly from national park censuses and reports from environmental impact studies, or expert opinion. Average values were used in cases where more than one data source was available. We used the current flow centrality values generated for each site in this study. Regarding local threats, each was scaled from 1 (lowest threat) to 10 (highest threat) based on data published by Vargas, Bonacic & Moraga (2016); dog attacks, the most common threat in this region, was allocated a score of 10, illegal hunting and vehicle collisions a score of 5 each, scabies infestation and habitat loss a score of 4 each, and livestock competition a score of 1. Potential extinction risk was evaluated using the formula:  $PER = \text{Log}[(\text{Population size} \times \text{Current flow centrality}) / \text{Sum of Threats}]$ . These values were then ranked from 1 (lower extinction risk) to 5 (higher extinction risk) with  $PER < 2$ : rank 5,  $2 < PER < 2.45$ : rank 4,  $2.45 < PER < 2.9$ : rank 3,  $2.9 < PER < 3.35$ : rank 2, and  $PER > 3.35$ : rank 1.

### **Ethics Statement**

The capture and handling of guanacos for installation of tracking devices were performed according to the highest standards designed to ensure the safety of the animals. Prior approval was obtained from the Chilean authority for wildlife management (Servicio Agrícola y Ganadero – SAG; authorization N°: 3346/2013 and 7899/2014), whose agents have controlled all field manipulations of guanacos to ensure strict compliance with standards and regulations.



## 279 RESULTS

### 280 Habitat suitability model generated by MaxEnt

281 The final model of habitat suitability for *Lama guanicoe* across the study area performed better  
282 than random, with an average training AUC of 0.87 (95% confidence interval: 0.84 - 0.88;  
283 standard error:  $\pm 0.009$ ). Extrinsic omission rate was 0.13 ( $P < 0.01$ ), indicating that the variables  
284 of the pruned model contributed significantly to the habitat suitability predictions. Elevation,  
285 distance to wetlands, and vegetation communities were the most important predictors of habitat  
286 suitability, with a combined contribution of 87.7% to the final MaxEnt model (Table 2). The  
287 occurrence probability response of *L. guanicoe* to each predictor variable varied considerably,  
288 showing a strong negative association with distance to wetlands, distance to protected areas, and  
289 elevation (Fig. 2a,b,f), a positive association with scrubland vegetation communities (Andean  
290 Mediterranean sclerophyll forest, Andean Mediterranean low scrubland of altitude, Coastal  
291 Mediterranean desert scrubland, Fig. 2d), and a weak positive association with slope and distance  
292 to urban settlements (Fig. 2c,e). Overall, our model predicted 29,173 km<sup>2</sup> of suitable habitat  
293 heterogeneously distributed throughout the landscape, equivalent to approximately 25% of the  
294 total study area (Fig. S1B). Medium to high HSI values were found all along the Andes, forming  
295 a continuous stretch of suitable habitat from south to north of the study area up to the Nevado  
296 Tres Cruces National Park (Fig. S1A). By contrast, non-continuous patches of high HSI values  
297 surrounded by extensive zones of unsuitable habitat were predicted along the coast, particularly  
298 in the Limarí, Huasco, and Copiapó basins (Fig. S1A, B).

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

300 The resistance surface derived from the HSI scores showed a gradient of increasing resistance  
301 costs from south to north of the study area, with marked intermediate zones of high resistance  
302 costs within each river basin, being continued north of the Copiapó river basin (Fig. 1). Most of

the areas of lower resistance costs matched with areas of high HSI values (see Fig. 1 and Fig. S1A): they were distributed continuously along high and mid mountains up to the Copiapó river basin, and formed discontinuous patches along the coast separated by the main river basins, except in the Limarí basin. The Copiapó basin also represents the northern limit of the large predicted coastal areas with low habitat resistance, above which only a few discrete low resistance patches were revealed (Fig. 1).

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

The cumulative current density map based on all possible pairwise combinations between the 11 known populations in the study area shows different current density patterns between coastal and mountainous areas. Similar to what was observed in the HSI and habitat resistance maps, highest cumulative current flow occurred within a wide corridor encompassing the mid and high elevation Andean sectors (28°00'02"–30°20'25"S and 69°45'0"–70°26'35"W), which harbor five known guanaco populations (El Morro (5), Calvario (7), Tres Quebradas (8), El Tambo (9) and Estero Derecho (10); Fig. 3). Relatively high cumulative current flow was also found between the populations of Pelambres (11) and Estero Derecho (10) in the south of the study area. By contrast, current flows appeared discontinuous along the coast. Other areas with middle to high movement probabilities were revealed in the center of the study region between and along the transversal Elqui, Huasco and Copiapó valleys, as well as along the highway (Fig. 3). Overall, lowest current flows were found on the northern and southernmost extremities of the study area, including the Pan de Azúcar (1) and Nevado Tres Cruces (2) national parks in the north and the Limarí and Choapa river basins in the south (Fig. 3). Seven pinch-points were identified by our maximum current flow model: one in the high Andes, two in the mid altitudes, three at wildlife crossings located on the highway, and one in the coastal region (Fig. 4).

### Current flow centrality analysis between *L. guanicoe* populations across the study area

Our linkage map revealed a greater density of corridors connecting habitat patches above 600 masl between the Copiapó and Elqui river basins (Fig. 5). Habitat patches of higher centrality score were found in the Oso Negro (4), El Morro (5), Calvario (7), Tres Quebradas (8), El Tambo (9), and Estero Derecho (10) sectors (Table 3), all located at mid or high altitudes. Each of these patches was connected to other geographically close patches by at least two corridors. The northern and southernmost high Andean populations of Nevado Tres Cruces (2) and Pelambres (11), respectively, displayed low current flow centrality scores (Fig. 5, Table 3), only receiving least cost paths of low or medium centrality score. All three coastal populations were associated with relatively low centrality scores (Fig. 5, Table 3). Each was linked to other populations by one to two least resistance routes that crossed the highway, and which, in most cases (four out of five), harbored a pinch point (Fig. 5). No corridors directly linking coastal habitat patches were generated.

### Potential extinction risk of *L. guanicoe* populations across the study area

Based on population size, connectivity (i.e. current flow centrality) and local threats, about half of the known guanaco populations in the study area, mainly in the north, appear to be at significant risk of extinction, with a level  $\geq 3$  (Table 3). The two populations most at risk, characterized by small population size, low connectivity levels, and a high level of threat, are found in the national parks in the north of the study area (i.e. Pan de Azúcar (1) and Nevado Tres Cruces (2); Table 3). By contrast, four of the five least endangered populations, with a risk level ranging from 1 to 2, are located within or near areas of mining activity (i.e. El Morro (5), Calvario (7), Tres Quebradas (8) and Pelambres (11); Table 3). The fifth population with a low risk of extinction, Estero Derecho (10), occurs in a protected area, and although it has a relatively low population size, it shows high connectivity levels and a low level of threat. The remaining

populations, with moderate to high levels of extinction risk, display very low population sizes (Oso Negro (4) and El Tambo (9), two populations also found near sectors of mining activity) or low connectivity levels associated with high threats (Llanos del Challe (3) and Los Choros (6); Table 3). It is also worth noting that the three coastal populations of Pan de Azúcar (1), Llanos del Challe (3) and Los Choros (6) are among the most threatened in the study region.

## DISCUSSION

### Habitat suitability of *Lama guanicoe* in Chile's Norte Chico

In this study, we identified connectivity pathways for *L. guanicoe* in a region of Chile characterized by small and fragmented populations (Marín et al., 2013). To achieve this goal, we first developed a regional scale habitat suitability model. Consistent with González et al. (2013), we identified areas of suitable habitat along both the coastline as well as the Andes. Overall, predicted habitat suitability comprises an area of 29.173 km<sup>2</sup>, which slightly exceeds the prediction of González et al. (2013) for the same region (i.e. 23.481 km<sup>2</sup>). Differences in the resolution of the models may explain the observed discrepancy. Because González et al. (2013) aimed to evaluate habitat suitability across the entire *L. guanicoe* distribution range in Chile, they used data layers of a much lower resolution (3 x 3 km) than ours (90 x 90 m). Models built over large areas are expected to have weak local predictive power due to regional niche variation (Osborne & Suárez-Seoane, 2002; Murphy & Lovett-Doust, 2007), and higher resolution models are therefore better suited for regional scale applications (Carroll, McRae & Brookes, 2012) as was the case here.

We found that resource factors most strongly influenced *L. guanicoe* distribution in Chile's Norte Chico, followed by elevation and then disturbance factors. Vegetation and distance to water resources accounted for 72% of the predictive ability of the Maxent model; these variables constrained *L. guanicoe*'s presence to seven of the 33 vegetation communities of the

study area (Luebert & Plischoff, 2006), and to areas located less than 5 km from water resources. The spatial arrangement of the resource factors resulted in a heterogeneous distribution of habitat categorized as suitable. The largest sector occurred in the foothills of the mid and high elevation areas (2000 – 4500 masl), where four of the influential vegetation communities (Andean Mediterranean sclerophyll forest of *K. angustifolia* and *G. trinervis*, Mediterranean pastureland of *N. spathulatus* and *M. spathulata*, Andean tropical Mediterranean underbrush *A. subterranea* and *A. echinus*, Andean Mediterranean underbrush *Laretia acaulis* and *Berberis empetrifolia*) are developing, and where numerous Andean wetlands are present (Squeo, Arancio & Gutierrez, 2001; Squeo et al., 2006; Squeo et al., 2008b). High Andean wetlands may not only provide water supply for *L. guanicoe*, but also fulfill various other needs such as food and shelter (Torres, 1992). The other three influential vegetation communities (Coastal desert's Mediterranean thicket of *O. gigantea* and *E. breviflora*, Coastal desert's Mediterranean thicket *H. stenophyllum*, Mediterranean desert scrubland of interior *H. stenophyllum* and *F. thurifera*) are restrained to coastal areas, and in a section excluding the southernmost and northernmost regions. In the coastal areas, water resources are sparse and scattered, resulting in large stretches of unsuitable habitat along the coast.

Elevation accounted for 16% of the model's predictive ability, with occurrence probabilities gradually declining with increases in elevation. However, even at the highest elevations, the HSI values did not fall below the habitat suitability threshold. This finding is consistent with literature reports of physiological and physical adaptations of guanacos to high altitude (Wilson, 1989; Starck & Wang, 2005). Compared to resource factors and elevation, disturbance factors only moderately influenced *L. guanicoe* distribution. Distance to wetlands and distance to protected areas accounted for a combined 10.6% of the predictive ability of the model; as anticipated, proximity to protected areas demonstrated a positive effect on occurrence probability, while proximity to human settlements had the opposite effect. While none of the

distance to human settlements was associated with HSI corresponding to unsuitable habitat, the fact that adverse effects were detected suggests that the current growth in urbanization in the region (INE, 2012) may become a serious threat for *L. guanicoe* in the near future.

#### **Landscape connectivity, local extinction risks and conservation priorities**

Our study contributes important knowledge for the conservation of *L. guanicoe* in Chile's Norte Chico. 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 range 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 Moro) in particular demonstrated a 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 Andean region. As a result, most of the population groups in this region probably face relatively low extinction risks, despite the threats posed by illegal hunting, livestock competition, and habitat loss due to mining. Of the Andean populations, only the two located at El Tambo and Nevado Tres Cruces National Park were identified as being associated with high local extinction risk. In both cases, population sizes were small (i.e.  $N < 70$ ), a situation that decreased resilience to local threats. The Nevado Tres Cruces National Park population appeared to be at particular risk given its higher degree of isolation. It is well recognized that small isolated populations are more sensitive to the consequences of environmental, demographic and genetic stochastic factors, putting their survival at risk over time (Frankham, Briscoe & Ballou, 2002). Given the relatively high threat posed by the mining industry to high-altitude

ecosystems in this region (Squeo et al., 2006; Troncoso et al., 2017), these results suggest that *L. guanicoe* populations can persist in the Andean region of Chile's Norte Chico only if connectivity is maintained among these existing populations. This implies that this should be a key criterion in environmental impact assessments and mitigation programs implemented in terms of environmental Chilean law (Supreme Decree No. 40, 2012 of the Environment Ministry) (Ambiente, 2013) in development proposals potentially affecting *L. guanicoe*.

Connectivity patterns along the coast contrasted strongly with those observed in the Andes. The coastal landscape was essentially dominated by low to medium current areas. Low current areas can either reveal barriers to movement or very large corridors (Cushman, Chase & Griffin, 2010). In the present case, they occurred in high-resistance areas (i.e. low quality habitat), indicating that individual movement among coastal populations is unlikely, probably due to the influence of urbanization and intensive agriculture over the past 50 years, particularly along the Huasco river watershed (Novoa & López, 2001). As a result, coastal populations were predicted to only connect to medium and high altitude populations, forcing animal movement throughout the four-lane highway that extends latitudinally over the study area. This finding raises concerns about the actual effectiveness of these pathways. Indeed, highways are expected to be important dispersal barriers for *L. guanicoe*, resulting in mortalities due to vehicle collisions or animals becoming trapped in barbed wire fences bordering the highway (Vanak, Thaker & Slotow, 2010). In a recent study, vehicle collisions were recognized as the third largest cause of guanaco mortality in northern Chile (Vargas, Bonacic & Moraga, 2016). This suggests that effective connectivity between coastal and inland populations might be limited. In fact, we identified several pinch points along the highway coincident with locations of wildlife underpasses. Two of them were located in the pathways linking Llanos del Challe to Oso Negro and Los Choros to El Cavario, which demonstrates that animal movement between these populations is highly dependent on the effectiveness of wildlife crossings. To date, it is unknown



if guanacos utilize these structures effectively. This should be a topic of future research, particularly since evidence suggests that ungulates tend to demonstrate a preference for utilizing overpasses rather than underpasses (Simpson et al., 2016). Overall, our results revealed precarious connectivity among the coastal populations: either they were linked to other populations through low centrality pathways, as was the case between Pan de Azúcar and Nevado Tres Cruces national parks, or connectivity was jeopardized by pinch points that, if transformed into barriers, would result in complete isolation of the populations. It is thus likely that the coastal populations are functionally isolated, a situation that would endanger their long-term persistence. Actions to protect or restore their connectivity might thus be crucial for the conservation of the remnant coastal populations of *L. guanicoe*.

Other areas that should be prioritized are those playing a key role in the connectivity network. Our model recognized El Morro and Calvario patches as the most important habitat patches for overall connectivity, facilitating individuals' dispersal between several pairs of known populations. If these resource patches were to be lost, it would result in considerable increases in the distance and/or transit times between populations (Carroll, McRae & Brookes, 2012). While our analyses suggest that *L. guanicoe* populations in these two sectors are not at high extinction risk, future regional planning should consider maintaining their integrity for the long-term persistence of this emblematic species in this region of Chile.

## CONCLUSIONS

In this study, we used a resistance-surface-based connectivity modelling approach to investigate functional connectivity of *L. guanicoe* in Chile's Norte Chico. Our results demonstrate that functional connectivity is an issue of concern in this region, and provide pertinent information for the conservation of this species. Indeed, we found that isolation may jeopardize the viability of the three coastal populations, which are the last remaining in Chile. Very few of the connectivity



pathways may in fact facilitate access to these populations, and the effectiveness of these routes needs to be investigated, since their functionality appears to be wholly dependent on wildlife crossing structures that may or may not be appropriate for *L. guanicoe*. Our results were rather comforting for most Andean populations, for which we predicted high connectivity levels; and two populations in particular were found to play a central role in the connectivity network. Collectively, these results indicate that future conservation and management plans involving *L. guanicoe* in the Norte Chico region should adopt a landscape strategy designed to conserve functional connectivity between coastal and Andean populations, as well as protect habitat patches that likely function as stepping stones within the connectivity network.

## ACKNOWLEDGEMENTS

We thank the staff of the National Forestry Corporation (CONAF - Atacama), the Community of Los Choros, the Environmental Department of Nevada Mining Company for their assistance in the field, the team of veterinarians of Fauna Australis laboratory (PUC Chile) for their invaluable support and medical veterinary assistance in field, the assistance from Juan Serratos in GIS data processing and analysis, and the professors of the Department of Biology at the University of La Serena A. Cortés and R. Osorio by their contributions. We are also thankful to Craig Weideman for revising the English.

## FUNDING

This study was supported by a grant from the Institute of Ecology and Biodiversity (IEB) of Chile and the South America-Barrick Gold Corporation.

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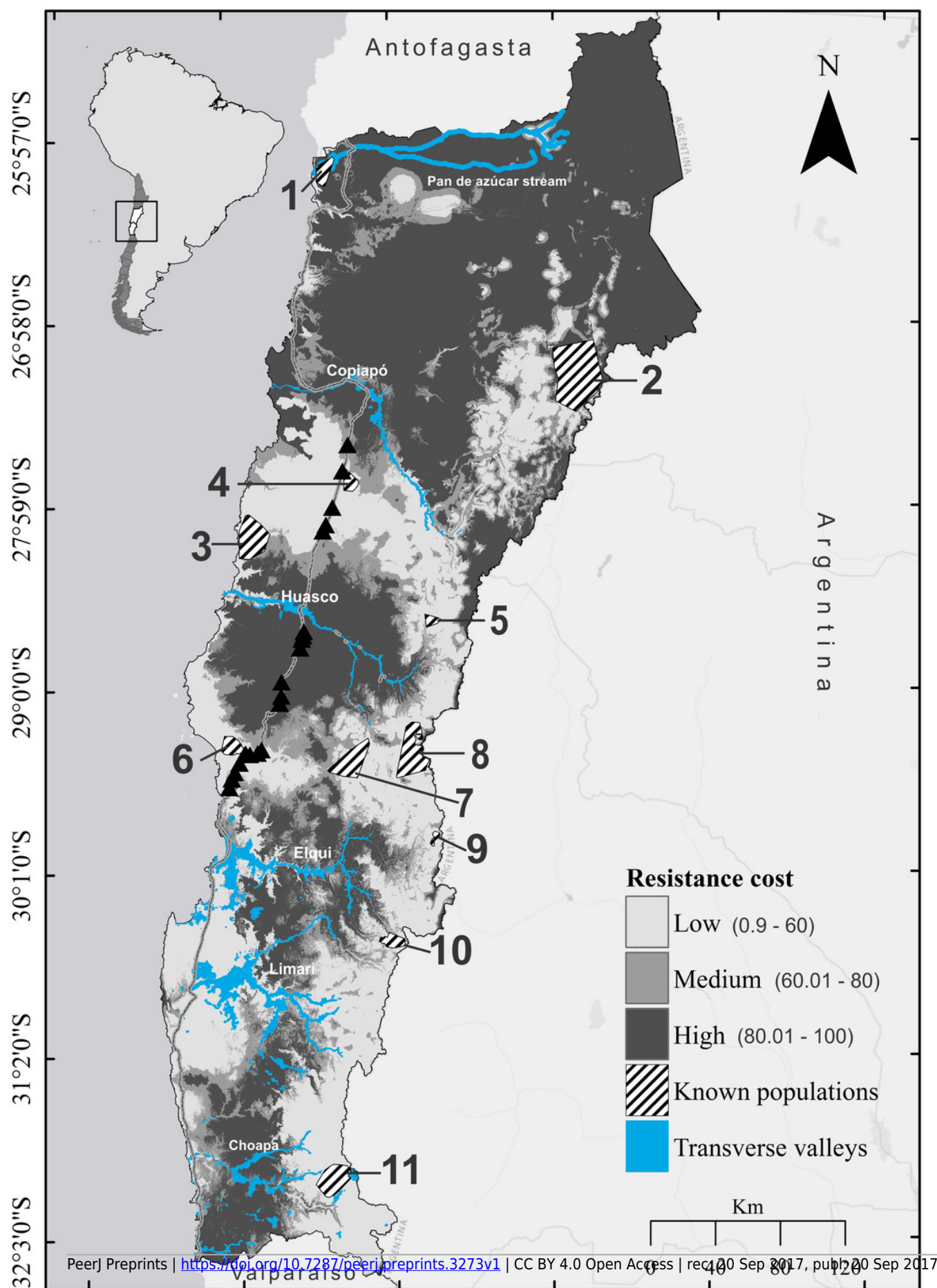
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# Figure 1

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

Resistance values were estimated by inverting and rescaling the HSI values, generated by habitat suitability modelling 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 with known 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.

2°14'0"W 71°13'0"W 70°12'0"W 69°11'0"W 68°10'0"W 67°9'0"W



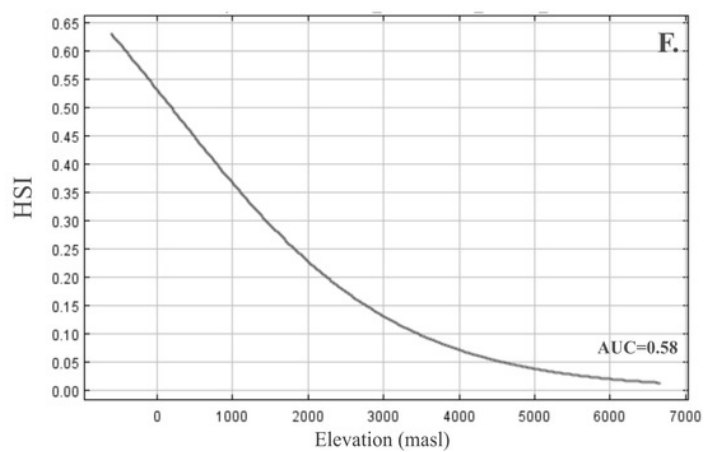
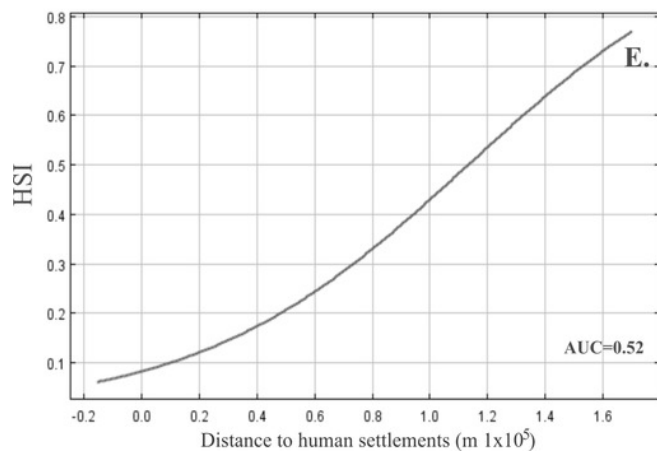
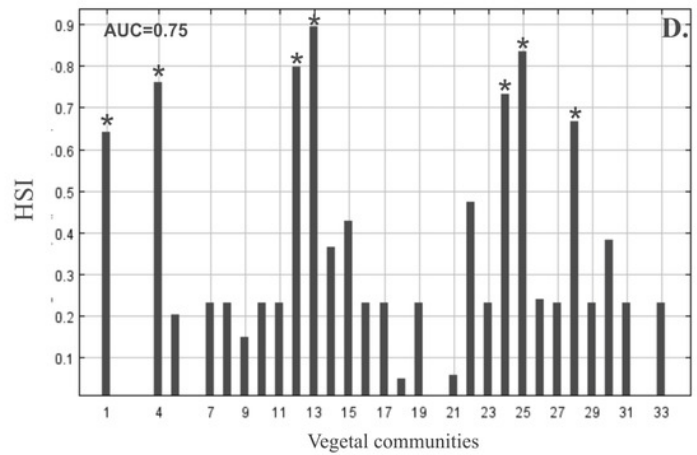
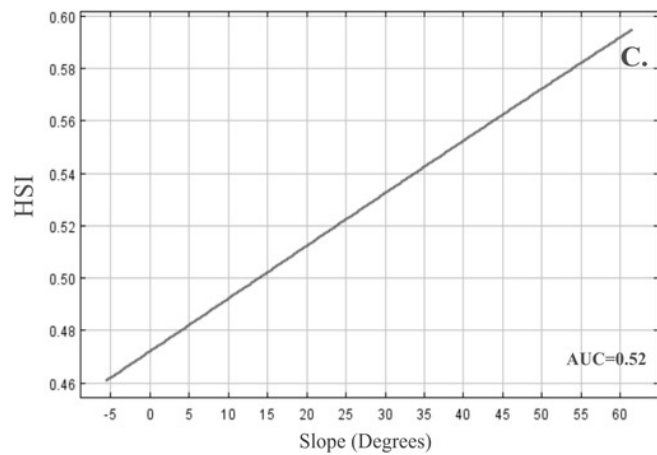
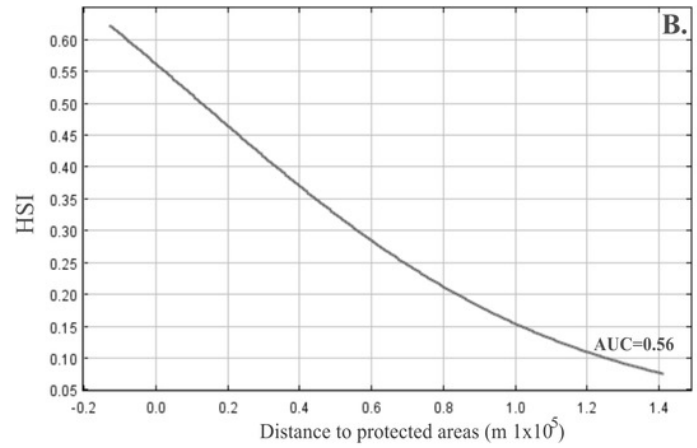
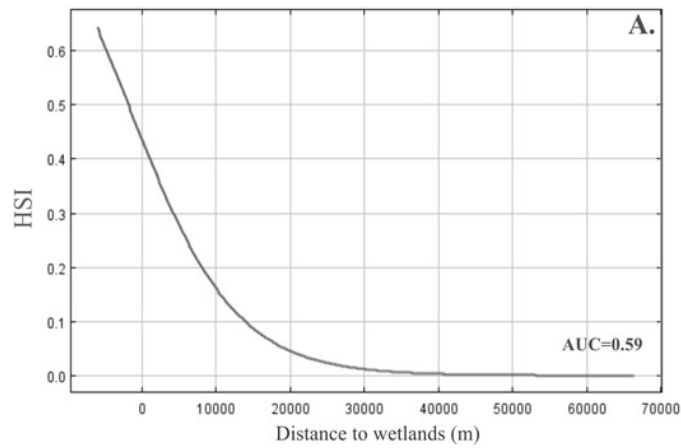


## Figure 2

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

Marginal response curves generated independently 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 vegetal communities (D), each of them being described in Table S1. The predictive power of the variables, reported within the plot area in each case, is given by a Jackknife test of variable importance using AUC on test data for each individual environmental variable retained in the MaxEnt model.



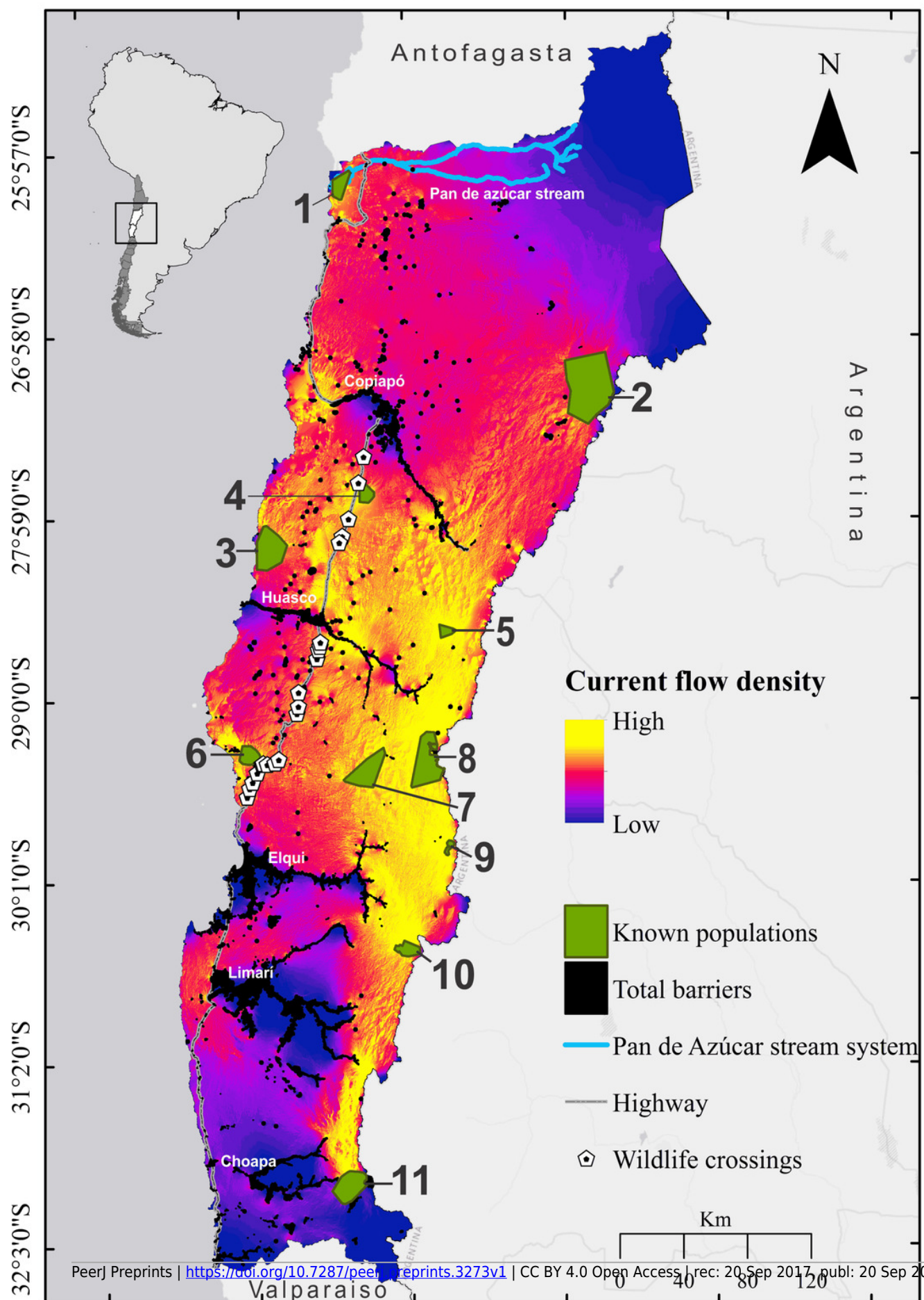


# Figure 3

Cumulative current flow density map for the guanaco *Lama guanicoe* across the study region.

Current flows represent passage probabilities calculated between all pairs of habitat patches with known populations by injecting one Ampere of current. Habitat patches corresponding to the known guanaco populations are numbered as in Figure 1.

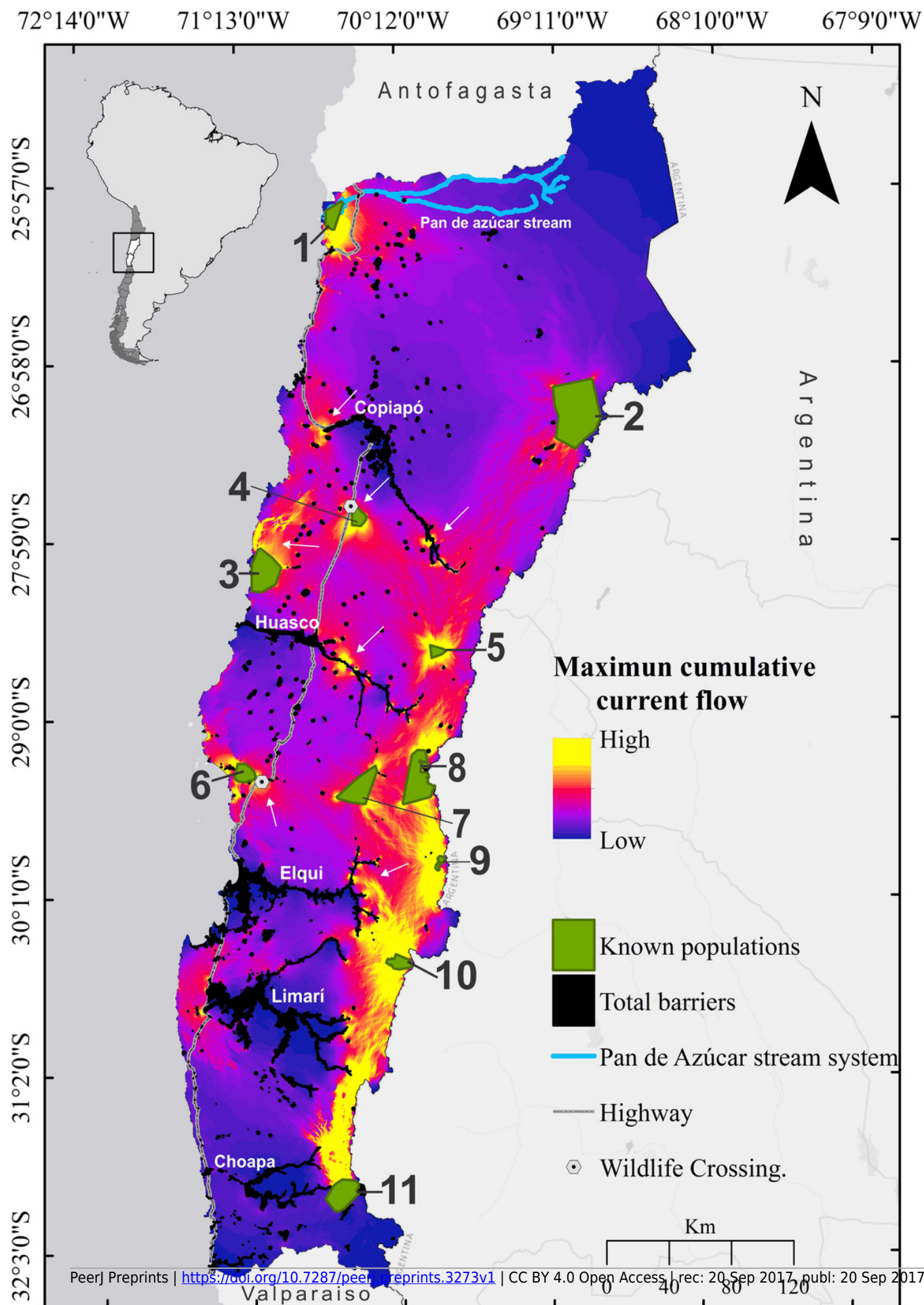
72°14'0"W 71°13'0"W 70°12'0"W 69°11'0"W 68°10'0"W 67°9'0"W



# Figure 4

Maximum cumulative current flow map generated by Circuistcape for the guanaco *Lama guanicoe* across the study region.

White arrows indicate locations identified as pinch points. Habitat patches corresponding to the known guanaco populations are numbered as in Figure 1.

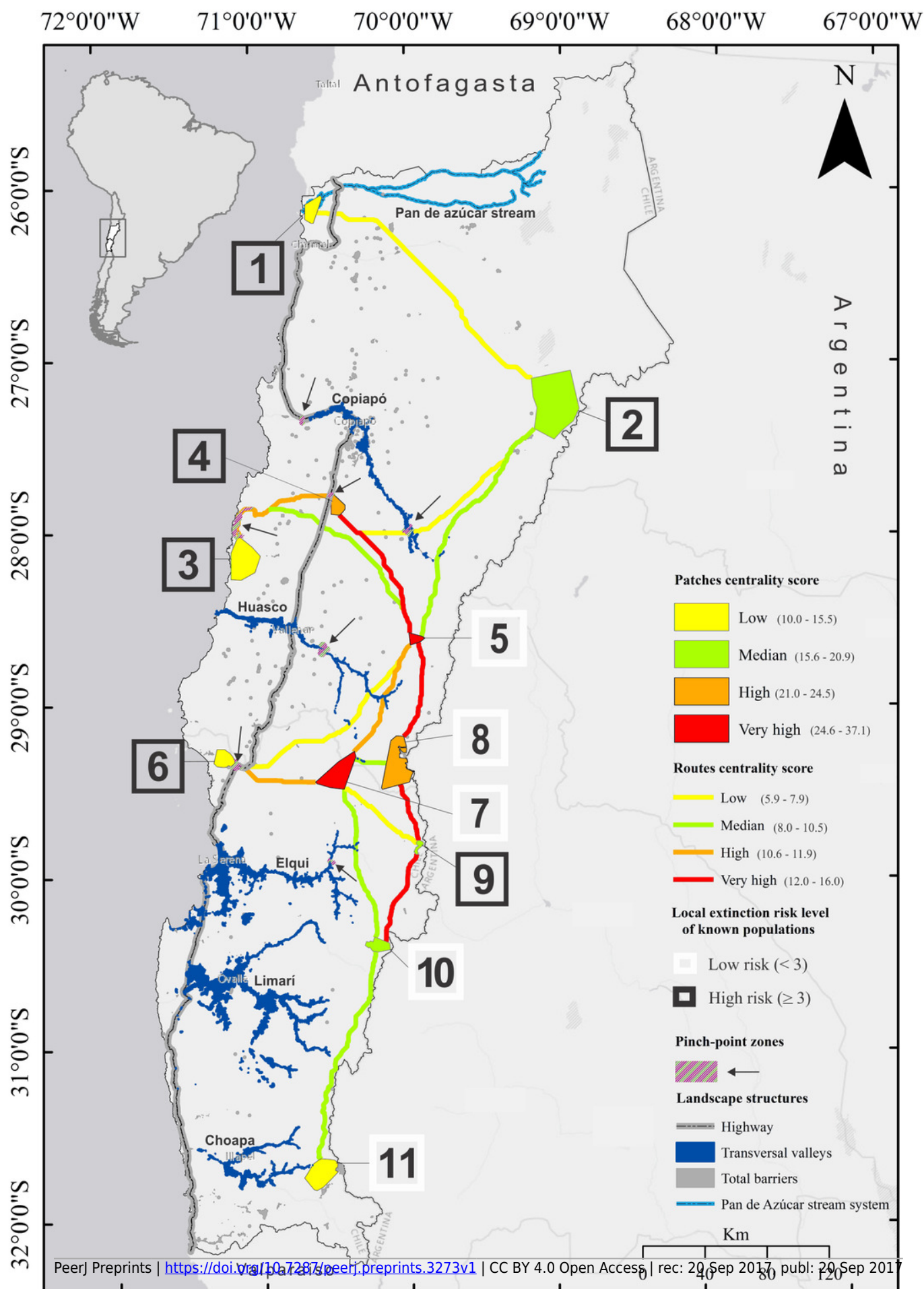




# Figure 5

Linkage network map of the known *Lama guanicoe* populations in the study area produced with the Linkage Mapper Connectivity Analysis software.

Transverse river valleys are represented on the map. Habitat patches corresponding to the known guanaco populations are numbered as in Figure 1.



# **Table 1** (on next page)

Environmental variables used for habitat suitability modeling with MaxEnt



**Table 1.** Environmental variables used for habitat suitability modeling with MaxEnt

| GIS Data sources         |   |  |  |                |
|--------------------------|---|--|--|----------------|
| Data                     | Name  | Data type  | Source   | Date           |
| Digital Terrain Model    | Shuttle Radar Topography Mission (SRTM)   | 90m Raster   | United States Geological Survey (USGS) (Farr et al., 2007) | 2000           |
| Roads                    | Red vial: polilínea de los caminos de Chile   | Vector   | (MOP, 2013)  | 2013           |
| Water Bodies             | Inventario Nacional de Humedales  | Vector   | (MMA, 2011)  | 2011           |
| Land Uses                | Open Street Map   | Vector   | Open Street Map  | 2013           |
| Vegetation               | Pisos Bioclimáticos   | Vector   | (Luebert & Plischoff, 2006)                                | 2006           |
| Communities              |   |  |  |                |
| Protected areas          | Libro rojo de la flora nativa y de los sitios prioritarios para su conservación; Región de Atacama y Región de Coquimbo | Vector   | (Squeo et al., 2001)<br>(Squeo et al., 2008a)              | 2001,<br>2008a |
| GIS Products             |   |  |  |                |
| GIS data layer           | Description   | Original data source   |  |                |
| Elevation                | Altitude above sea level  | SRTM (90 m)  |  |                |
| Roughness                | Surface roughness   | SRTM (90 m)  |  |                |
| Aspect                   | Slope direction.  | SRTM (90 m)  |  |                |
| Slope                    | Rate of maximum change in z-values  | SRTM (90 m)  |  |                |
| Distance to urban areas  | Euclidean distance to nearest urban area  | (Open Street Map, 2013)  |  |                |
| Distance to water bodies | Euclidean distance to nearest water bodies  | (MMA, 2011)  |  |                |
| Distance to roads        | Euclidean distance to nearest paved roads   | (MOP, 2013)  |  |                |
| Vegetal communities      | Main vegetal communities described in the study region  | Pisos bioclimáticos (Luebert & Plischoff, 2006)  |  |                |
| Protected areas          | Protected areas along the Coquimbo and Atacama regions  | Libro rojo de la flora nativa y de los sitios prioritarios para su conservación; Región de Atacama y Región de Coquimbo, (Squeo et al., 2001; Squeo et al., 2008a) |  |                |

## Table 2 (on next page)

Relative contribution of the environmental variables to the final habitat suitability model produced by MaxEnt

**Table 2.** Relative contribution of the environmental variables to the final habitat suitability model produced by MaxEnt

| <b>Environmental variable</b>   | <b>Contribution (%)</b> |
|---------------------------------|-------------------------|
| 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                     |

### Table 3 (on next page)

Extinction risk level of the known *Lama guanicoe* populations based on potential populations size, local threats and connectivity extent approximated by current flow centrality values.

1: Lower risk – 5: Higher risk

**Table 3.** Extinction risk level of the known *Lama guanicoe* populations in the study area based on potential populations size, local threats and connectivity extent approximated by current flow centrality values. 1: Lower risk – 5: Higher risk.

| ID | Habitat patch name               | Estimated population size | Protection status   | Local threats   | Current flow centrality | Local extinction risk | References   |
|----|----------------------------------|---------------------------|---|---|-------------------------|-----------------------|--|
| 1  | Pan de Azúcar National Park      | 120                       | National park   | Illegal Hunting/ Dog attacks                                | 11.8                    | 5                     | Census of Pan de Azúcar National park. Historical average from 2000-2015. Professional reports, (CONAF, 2015).   |
| 2  | Nevado Tres Cruces National Park | 80                        | National Park   | Illegal Hunting/ Dog attacks/ Disease by scabies            | 15.9                    | 5                     | Census of Nevado Tres cruces National park. Historical average from 2000-2016. Professional reports, (CONAF, 2016).  |
| 3  | Llanos de Challe National Park   | 900                       | National Park   | Illegal Hunting/dog attacks/ Vehicle collisions             | 15.2                    | 3                     | Census of Llanos de Challe National park. Historical average from 2000-2014. Professional reports, (CONAF, 2014).  |
| 4  | Oso Negro sector                 | 70                        | Flowering desert priority site                              | Illegal Hunting/ Vehicle collisions                         | 23.7                    | 4                     | Reports from Environmental Impact Study, Oso Negro Mining Company, (SEIA, 2012).   |
| 5  | El Morro                         | 200                       | Private Protected Area                                      | Illegal Hunting/ Habitat loss                               | 37.1                    | 2                     | Reports from Environmental Impact Study, El Morro Mining Company, (SEIA, 2011).  |
| 6  | Los Choros                       | 300                       | Unprotected area  | Dog attacks/ Vehicle collisions/ Competition with livestock | 13.6                    | 4                     | Yearly Census of Guanacos. Andes Iron 2012 – 2013, (SEIA, 2013).   |
| 7  | Calvario stream                  | 200                       | Unprotected area  | Illegal Hunting/ Competition with livestock                 | 29.3                    | 2                     | Pascua-Lama Mining Project, Biodiversity Report 2012. Unpublished data: Seasonal census 2012-2014; (Cortés & Zepeda, 2012).                                    |
| 8  | Tres Quebradas River             | 500                       | High Conservation Value Area                                | Illegal Hunting/ Habitat loss                               | 24.2                    | 2                     | Pascua-Lama Mining Project, Biodiversity Report 2012. Unpublished data: Seasonal census 2012-2014; (Cortés & Zepeda, 2012)                                     |
| 9  | El Tambo stream                  | 50                        | High Conservation Value Area                                | Illegal Hunting   | 20.5                    | 4                     | Opinion of Expert (Cortes A., Osorio R., Universidad de La Serena, Pers. Com.). Reports from Environmental Impact Study, El Tambo Mining Company (SEIA, 1994). |
| 10 | Estero Derecho nature sanctuary  | 100                       | Private Protected Area & Nature Sanctuary                   | Competition with livestock                                  | 20.9                    | 2                     | Plan de Manejo de Estero Derecho, (APP-SN, 2017).  |
| 11 | Pelambres Area                   | 1300                      | Unprotected area / Private area of Pelambres Mining Company | Habitat loss  | 10                      | 1                     | González & Acebes (2016)   |