

COMPARING METHODS FOR ASSESSING HABITAT CONNECTIVITY: A CASE
STUDY OF GÜINAS (LEOPARDUS GUIGNA) IN A FRAGMENTED CHILEAN
LANDSCAPE

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Dedication

This thesis is dedicated to those species about which little is known.

Abstract

Fragmentation creates a matrix which can facilitate or impede connections among patches of habitat. Least-cost path (LCP) and circuit theory (CT) are two methods commonly used to evaluate landscape-level connectivity among patches. Both methods use resistance surfaces that can be generated from Resource Selection Functions (RSF) or the Analytical Hierarchy Process (AHP). Despite the potential conservation implications of connectivity analyses, the methods are rarely compared. I quantified how RSF and AHP resistance surfaces affect estimates of connectivity among protected areas using a South American wild cat, güiña (*Leopardus guigna*), as a case study. I found that 1) path rankings and predicted locations of pinch points depended on the metric and resistance surface used, and 2) LCP is more sensitive to resistance surfaces than CT. These results confirm that connectivity analysis methods should be carefully considered and compared before they are used for conservation decisions.

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Introduction

As a result of both natural and anthropogenic disturbances, the habitat of species may be lost, fragmented or degraded, fundamentally shifting the landscapes on which species exist. This habitat loss causes negative effects in genetic diversity (Klug et al. 2011), species richness (Gurd et al. 2001), and in the distribution and abundance of species (Hargis et al. 1999). Habitat fragments and the intervening landscape matrix can act as facilitators or impeters of animals' movements thus influencing the connectivity between populations (Spear et al. 2010). Small fragments may not be capable of maintaining populations through time, and depending on the size and isolation of fragments in a given area, animals may not be able to move among patches because they perceive the intervening matrix as too dangerous (Tigas et al. 2002).

Habitat modeling has led to the observation that organisms can respond to fragmentation in many different ways (Donovan et al. 1997). For instance, mountain lions (*Puma concolor*) showed a low probability of occurrence in small and isolated fragments (Crooks 2002). Fragmentation also produces behavioral changes in individuals of some species. For example, bobcats (*Lynx rufus*) are less active during the day in fragmented areas compared to non-fragmented areas, which could be a strategy for avoiding human activities because carnivores are more vulnerable than other taxa to conflict with humans (Macdonald & Sillero-Zubiri 2002; Tigas et al. 2002). At the same time, carnivores may increase their activity near habitat edges due to the greater diversity and abundance of potential prey items, such as birds (Vickery et al. 2002) and small mammals (Šálek et al. 2010).

Currently, one of the main conservation priorities is to protect and restore connectivity of broad-scale ecological processes, such as dispersal and gene flow (Crooks & Sanjayan 2006). A major obstacle to achieving this is the difficulty in predicting how animals use heterogeneous habitats that are located between existing parks and reserves, and understanding how conservation or reclamation efforts will affect connectivity between existing, protected populations (McRae & Beier 2007).

One approach to evaluate the impact of habitat fragmentation on particular species is to measure landscape connectivity between spatially distinct populations. Landscape connectivity has been defined by Taylor et al. (1993) as, “the degree to which the landscape facilitates or impedes movement among resource patches”. There are two types of connectivity: structural and functional. Structural connectivity is a description of physical continuity of landcover and only evaluates landscape configuration without considering the behavioral response of the species (Taylor et al. 2006). Functional connectivity, on the other hand, measures how behavioral responses of an individual interact with the landscape elements (e.g., patches and boundaries) to facilitate or impede movement (Tischendorf & Fahrig 2000). In order to evaluate functional connectivity, it is necessary to determine what landscape characteristics the animals respond to, because the way individuals choose their movement paths should be heavily influenced by their resource selection behavior (Beier et al. 2008).

One method that is commonly used to determine functional connectivity is the least-cost path (LCP; Adriaensen et al. 2003). The aim of least-cost modeling is to identify the location of the LCP, which is the pathway (chosen among all possible pathways and assuming that an individual has complete knowledge of the landscape) that

has the minimum cost of traveling between nodes (populations, reserves, etc.; McRae et al. 2008). LCP has been used to identify corridors for species such as California tiger salamanders (*Ambystoma californiense*; Wang et al. 2009), cougars (*Puma concolor*; LaRue & Nielsen 2008), and giant panda (*Ailuropoda melanoleuca*; Li et al. 2010).

Another approach to evaluate landscape connectivity applies circuit theory to ecological systems. This approach uses an analogy between animal movements across a landscape and the flow of current across an electrical circuit where different habitat characteristics act as resistors of different strengths (McRae et al. 2008). A basic measure of connectivity derived from circuit theory is resistance distance (Klein & Randic 1993), which was defined by McRae et al. (2008) as, “the effective resistance between a pair of nodes when all graph edges are replaced by analogous resistors”. The effective resistance between nodes was further defined as, “the resistance of a single resistor that would conduct the same amount of current per unit voltage applied between the nodes as would the circuit itself” (McRae et al. 2008). One feature of resistance distance is that it includes all possible pathways that connect two nodes. As the number of connections between a pair of nodes increases, the resistance distances decreases.

Because circuit theory is based on the assumption of a random walk, it does not presuppose that an individual has complete knowledge of its environment. This technique recognizes crucial corridors or “pinch points”, which are zones with a high probability of use by animals dispersing between nodes and are critical to identify when developing conservation programs (McRae et al. 2008). Thus, this theory can be applied for predicting individual movement, mortality, and dispersal success at finer scales, and patterns of gene flow over large distances (McRae & Beier 2007). This method has been

used in different connectivity studies, such as predicting how mountain lions disperse between private land and protected areas in southern Brazil (Castilho et al. 2011), assessing probability of connectivity among elephant herds (*Loxodonta africana*) in southern Africa (Roever et al. 2013), and identifying landscape characteristics which affect dispersal in tigers (*Panthera tigris*) among protected areas in a human-dominated landscape in Central India (Joshi et al. 2013). Circuit theory appears to be very useful when applied to species where there is little information about their behavior (Crooks 2002; Dickson et al. 2005).

Both LCP and circuit theory require the use of resistance surfaces, which are usually spatially discretized maps (i.e., rasters with a fixed spatial grain) that describe the level to which a given spatial unit obstructs or facilitates connectivity for an individual animal. Resistance surfaces can be developed in a variety of ways, the most common of which is using an expert opinion method such as the Analytical Hierarchy Process (AHP; LaRue & Nielsen 2008; Poor et al. 2012) to identify the relative quality of different cover types in the landscape. Another approach is to use telemetry data to estimate Resource Selection Functions (RSF; Shafer et al. 2012; Roever et al. 2013) to identify multivariate characteristics of the landscape that are attractive to the species in question. Both approaches typically yield a “conductance” map (i.e., higher values are associated with greater probability of selection by the species); however, these can easily be converted to the resistance surfaces required for connectivity analysis.

Despite the variety of approaches that can be used to estimate connectivity, the results are rarely compared among methods (but see St-Louis et al. 2014). Given that connectivity estimates are promoted as metrics to prioritize conservation efforts (e.g., by

ranking pairwise connections to identify areas to either conserve or reclaim; Carroll et al. 2012), the result of using one approach should be qualitatively similar to others. In this study I estimated connectivity among protected areas in southern Chile that support populations of güiña (*Leopardus guigna*), a small felid of conservation concern in South America. I used a variety of approaches to understand how different methods to create resistance surfaces and calculate connectivity affect the rank order of protected area connections. I generated RSF and AHP resistance maps for the study area, and evaluated the degree of connectivity among protected areas generated by both maps using both LCP and resistance distance metrics. Finally, I identified and compared pinch points and current core flow centrality in these resistance maps. With the results obtained from those analyses, I generated three metrics to rank and compare corridor quality by means of the average resistance among protected areas. This study compares approaches that have been commonly used for connectivity analyses in ecology and conservation, and highlights the importance of understanding how the choice of connectivity method and metric can affect the interpretation of results and, in some cases, lead to very different management decisions.

Methods

Study Area

My study area was located in Pucón, Cautín province of the Araucanía region of southern Chile (IX region; Armesto et al. 1998). This is the northern limit of the temperate rainforest (39°15'S), in a pre-Andean zone of the Lake Villarrica catchment. The climate of the region is warm with a dry season lasting less than four months. The

mean annual temperature is 12°C, with a minimum of 8°C and maximum of 15°C on average in the coldest and warmest months, respectively. The annual average rainfall is 2,000 mm concentrated in the winter (Dirección Meteorológica de Chile, 2014).

The landscape is characterized by a matrix of agricultural zones, forest fragments, volcanoes, and lakes and is surrounded by several large areas of contiguous natural forest. My study was focused on the connectivity among three protected areas, Huerquehue National Park (HNP), Villarrica National Park (VNP), and Villarrica National Reserve (VNR), which belong to the Araucarias Biosphere Reserve (Fig. 1). There are two private lands which still contain natural vegetation but I did not include them in my analysis because their permanency is not assured.

Native vegetation in this area is dominated by large deciduous tree species composed primarily of *Nothofagus antarctica*, *Laureliopsis philippiana*, *Saxegothaea conspicua*, *Nothofagus dombeyi*, *Aextoxicon punctatum*, *Nothofagus obliqua*, *Laurelia sempervirens*, *Nothofagus pumilio*, *Gevuina avellana*, and *Eucryphia cordifolia*. In zones > 500 masl *Nothofagus nervosa* and > 800 masl *Araucana araucana* represent the forest (Gajardo 1994; Gedda 2010).

Study Species

The güiña is the smallest wild felid that lives in South America (Nowell & Jackson 1996). This cat inhabits southwest Argentina, and central and southern Chile (Redford & Eisenberg 1992). Güiñas are currently considered Vulnerable with a decreasing population trend by International Union for Conservation of Nature (IUCN; Acosta & Lucherini 2008). Güiñas are threatened by fragmentation and loss of native

forest as natural areas are harvested and subsequently replaced with pine plantations (San Martín & Donoso 1996; Bustamante & Castor 1998; Grez et al. 1998; Acosta 2001). Studies have suggested that güiñas would prefer native forest over other cover types, especially when the forest has dense shrub cover in the understory and is close to watercourses (Sanderson et al. 2002; Acosta-Jamett & Simonetti 2004). In general, güiñas avoid human disturbance (e.g., buildings and roads; Acosta-Jamett & Simonetti 2004).

Data Collection

Between September 2010 and April 2012, five güiñas were captured using Tomahawk® or wooden traps. The güiñas were fitted with Very High Frequency (VHF) radio collars with mortality switches. All capture and handling procedures were conducted under research permit N° 3729, and extension N° 4165 issued by Servicio Agrícola y Ganadero. These procedures were also carried out according to conditions of relevant laws: N° 19.473 of Ley de Caza, N° 868 of Ley de Conservación de la Especies Migratorias de Animales Silvestres, and N° 873 of Convention on International Trade in Endangered Species of Wild Fauna and Flora.

Animal locations were estimated by triangulation from bearings taken at three locations using a Yagi antenna and VHF receiver (Model Sika, Biotrack, UK). To minimize location error, I ensured that the difference among azimuths was $> 60^\circ$ and $< 120^\circ$ (White & Garrot 1990). To reduce location error resulting from movement of the individuals during tracking, all bearings for a given triangulation were collected within a 10-min period. Güiñas were followed for 1-4 hours at different times during day and

night, and their locations were recorded at intervals of 15 min, counted from the first bearing of each 10-min triangulation. Each cat was monitored for at least 15 days a month for the first 3 months after capture. After this time period, each cat was monitored at least 8 days a month.

I used program LOAS 4.0 (Ecological Software Solutions) to estimate point locations from triangulations. Although there were 1153 fixes, only 1113 were used in the analysis because 40 fixes had ellipse areas larger than 8,000 m² (Table 1).

Home ranges were calculated based on 90% Kernel Brownian Bridge with all güiñas locations falling within this kernel, using R statistical software (R Development Core Team 2012) and the “adehabitatHR” package (Calenge 2006; Fig. 2). I added a 100-m buffer to the five individual home ranges, which enabled the detection of habitat that güiñas could reasonably have used (Roever et al. 2013). All spatial data layers were projected to WGS 1984 UTM Zone 19 South and geospatial analysis was conducted with ArcMap 10.1 (ESRI 2013).

Connectivity Analysis

I. Introduction

To conduct the connectivity analysis, I constructed the RSF and AHP models to create conductance surfaces. The RSF model was created using radio telemetry data, distance variables (e.g., distance to roads), and landcover composition within two different buffer sizes. This RSF model was validated to determine its adequacy for predicting selection by güiñas. In the AHP model, I constructed a pairwise comparison matrix and evaluated it in order to determine the consistency of the comparisons. Next, I

converted both conductance layers to resistance surfaces for use in the connectivity analysis: LCP, resistance distance, pinch points and current core flow centrality. From LCP and current maps I generated ratios based on the quality of connections and I compared them. In the pinch point analysis I compared two truncated maps to identify high-priority pinch points. For the current core flow centrality analysis I determined the protected area most important for maintaining connectivity across the study area.

II. Models

A. Resource Selection Function

RSF studies based on radio telemetry data usually use binomial logistic regression for comparing characteristics of used locations to characteristics of available locations (i.e., resource units that were hypothetically accessible to an individual at that time; Manly et al. 2002). In this study, available habitat was randomly sampled within the home ranges of all güiñas at a density of 5 points/ha (Table 1). I created two buffers around each use and available location (100 and 250m radii) to assess how the landscape context could influence habitat use by güiñas (Zuur et al. 2009).

Landcover for the study area was described by a classified shapefile generated from aerial photographs (Fig., 1; Cruz & Dávila Ingenieros Consultores 2007). This classification included 12 land-cover types: native forest, urban/industrial areas, watercourses, shrubland, major road, minor road, lava flow, dumps and rocks, wetland, beach, meadows, plantation, and glaciers/permanent snow. I calculated the proportion of each land-cover type within two buffers (radii of 100 m and 250 m) surrounding all used and available locations. In addition, I computed the distance from each used/available location to the nearest major (paved) and minor (dirt) road, native forest, rural and urban

zones, watercourses and wetlands using Geospatial Modelling Environment 0.7.2.1 (GME; Beyer 2012) and ArcMap 10.1.

I only used variables that have biological significance to güiñas to construct the RSF models. I did not consider three landcover types because they were not available to güiñas: glaciers/permanent snow, beach, and urban/industrial areas. First, as an exploratory analysis, I created RSF models for individual animals in order to evaluate if güiñas had consistent habitat preferences, or if certain individuals preferred different types of habitat. Those results showed that six variables were the most important in determining habitat use by güiñas: native forest in buffers of 100 and 250 m, shrubland in 250-m buffer, and distances to minor roads, watercourses, and rural areas. With those six variables, I constructed models for all animals using conditional logistic regression with the Efron approximation in the “survival” package of R (Therneau 2013). To avoid potential problems with collinearity among predictor variables, variable pairs with a high correlation ($|\text{Spearman's rank correlation}| > 0.6$) were not included in the same model (Fielding & Haworth 1995). Because collinearity is strong when areal statistics are calculated within nested buffers, I computed new variables calculating the difference between the smaller buffer and the larger one (e.g., the area of natural forest in 100 m - the area of natural forest within 250 m). These new variables depicted their initial values relative to the larger buffer (Zuur et al. 2009).

I compared models using Akaike information criterion (AIC) values. This approach penalizes the maximum likelihood for the number of parameters that a model uses, favoring parsimony (Akaike 1973). Due to the relatively small number of cat locations, the AIC values were corrected for small sample size (AIC_c) and were used to

obtain the best supported model by the data (lowest AIC_c value; Burnham & Anderson 2002).

The exponential function of the following equation was utilized in order to determine the coefficients of probability of habitat selection:

$$W(x) = \exp(\beta_1 X_1 + \beta_2 X_2 + \dots + \beta_k X_k),$$

where $W(x)$ is the RSF, and the β values represent the selection strength for each of K covariates in X .

In order to validate the best model, I used k-fold cross-validation and the Spearman's rank correlation coefficient (Boyce et al. 2002). To do this, I created two datasets: one with 20% of the points used by güiñas (randomly selected) and the other with the remaining 80% of the used points and 100% of the available points. Then, I fitted the RSF model to the 80% dataset and I predicted it to the 20% dataset. I identified 10 RSF breakpoints that each hold 10% of each güiña's available points (decile bins), I counted how many used points from a given güiña fell in each bin, and I converted them to proportion of animal's points. This analysis was repeated 100 times and the results were averaged. Known locations falling in higher-ranked RSF bins (i.e., a positive correlation between bin number and count) indicates relatively good model performance (Boyce et al. 2002).

B. Analytical Hierarchy Process

The AHP enables researchers to utilize and benefit from a flexible decision-making approach that is based on pairwise comparison matrices. This method also

provides many potential opportunities that allow an individual or group of researchers to obtain information, insights, and solutions about a specific topic based on their experience. Pairwise comparison evaluates one variable against another using a rank from 1 to 9. A ranking of 1 indicates that parameters are identically important and a ranking of 9 depicts the greatest difference in importance between two variables. From each comparison a weight is generated which is used to rank the variables according to their importance (Saaty 1980).

To create the conductance surface, I developed the pairwise comparison using the results of an extensive literature review and my knowledge about this field in the study area. While creating the pairwise comparison matrix, I only used 10 variables because I assumed that watercourses and glaciers/permanent snow represented complete barriers. After developing this matrix, I used Saaty's consistency ratio (< 0.1 , calculated with the "pmr" package [Lee & Yu 2013] in R) to check for inconsistencies in the assignment of weights (Saaty 1977). Inconsistencies often occur when the associated importance of one variable is not maintained through all pairwise comparisons (Saaty 1977).

III. Resistance Surfaces

A. Resource Selection Function

To extrapolate my RSF model to the landscape, I first converted the study area layer to a raster with a pixel size of 30 x 30 m utilizing ArcMap 10.1. I then constructed a buffer of 15 m around each linear feature because watercourses and roads were represented by lines that were smaller than one pixel; it was necessary to construct these buffers to guarantee that every linear feature had continuity in the raster. Next, I used the package "spatial.tools" (Greenberg 2014) in R to construct two tiff files, which represent

the proportion of landcover within two buffers. The first tiff file represented a 100-m buffer, and the second file depicted a 250-m buffer. Both tiff files included the 12 land covers of the original study area map.

I used the coefficients from the best supported RSF model to create a spatially-explicit RSF map. This process allowed me to calculate the RSF-based conductance map using the following equation:

$$RSF_{cond} = W / \max(W),$$

where $\max(W)$ corresponds to the maximum value of the RSF map. Finally, the resistance layer was created by computing the inverse of the conductance map ($1/RSF_{cond}$).

B. Analytical Hierarchy Process

In order to create the AHP map, I used the raster map of the study area. Once the complete AHP analysis was finished, I reclassified the raster using the weights generated from it and created the conductance map using:

$$AHP_{cond} = AHP / \max(AHP),$$

where $\max(AHP)$ is the maximum AHP weight on the map. As with the RSF-based conductance layer, I calculated the inverse of the AHP conductance ($1/AHP_{cond}$) to obtain the resistance surface.

Calculations to create both resistance surfaces were made using the Raster Calculator in ArcMap 10.1. For easier interpretation of the results, both resistance surfaces were set to have a minimum value of 1.0.

IV. Connectivity Analysis

I used two layers for the conductivity analysis: a) RSF and AHP resistance surfaces with rivers and lakes acting as complete barriers, and, b) a layer of the protected areas which had five patches: three belonging to Villarrica National Reserve, hereafter mentioned as big, medium and small, and the other two representing Huerquehue National Park and Villarrica National Park. Throughout all of the connectivity analyses, I used parks and reserves as source and end nodes for pairwise modeling (McRae & Shah 2011).

A. Least-Cost Path

I used the Linkage Mapper tool of the Linkage Mapper toolkit (McRae & Kavanagh 2011) in ArcMap 10.1 to estimate the least-cost paths among protected areas for both surfaces. Using the results of LCP, I computed two ratios: cost-weighted distance (CWD)/Euclidean distances (ED) and CWD/path length (PL) to compare the differences between RSF and AHP maps. The path ratios calculated between pairs of protected areas were ranked for each resistance map and then compared with a Spearman's rank correlation.

B. Current

The resistance distances between all pairs of nodes were calculated from the cumulative current maps created with the Circuitscape ArcGIS toolbox (McRae 2013). These maps combine all of the current between each pair of core areas into a single layer, with the value of a given cell depicting the total current flowing across it. For this

analysis, I used a cell connection scheme of eight neighbors (i.e., “Queen’s case” neighborhood; McRae & Shah 2011).

I calculated a ratio between resistance distances (RD) and ED which was ranked and compared with the two ratios computed from LCP analysis. I used these three ratios as proxies for corridor quality because they indicate the average resistance among protected areas. Ranking positions ranged from the smallest (1) to the largest (10) average resistance in each corridor, and differences in rankings between methods were compared using Spearman’s rank correlation.

C. Pinch Points

I compared the pinch points (e.g., zones with a high probability of use by animals for moving among core areas [McRae et al. 2008]) delineating the location and areas that were connected in both resistance surfaces. To do this, I utilized the Pinchpoint Mapper tool (McRae 2012a) from the Linkage Mapper toolkit, which calls Circuitscape for the analysis. This tool uses the normalized least-cost corridors generated by the Linkage Mapper tool. Normalization is conducted by subtracting the least-cost corridor for a given pair of cores from all the corridor cells associated to that pair. As grid cells are in cost distance units, they depict the difference in cost between the local corridor and the least-cost path that connects two core areas (WHCWG 2010).

I calculated adjacent pairs of pinch points using a CWD cutoff value, which represents the highest CWD value that restricts the extent of least-cost paths between core areas. If any least-cost distance surpasses that limit, it is deleted (WHCWG 2010). I chose a cutoff value of 1.05 km for both RSF and AHP maps, which corresponds to the

longest distance that a güiña moved in a day in the study area. Doing this, I assessed how much RSF and AHP truncated maps varied in terms of locations of pinch point zones.

D. Current Core Flow Centrality

The current core flow centrality score assesses and identifies which protected areas are critical to maintain connectivity through the network. If the core area that has the largest number of connections in the network is lost, it would increase the distances between protected areas (Brandes 2001). This analysis works by allocating the value of the cost-weighted distance of the least-cost corridor as the resistance of the analogous link that connects two core areas. Then, 1 Amp of current is injected to one node (core area) while the rest of them are set to ground. The analysis is completed when all core areas have been used in this process. This was evaluated with Centrality Mapper (McRae 2012b). This tool is an integral component of the Linkage Mapper toolkit which also uses Circuitscape.

Results

Resource Selection Function

The best population-level RSF model included three land-cover variables and one anthropogenic variable. The model suggested that güiñas select for areas with native forest within a radius of 100 m, for locations close to watercourses and dirt roads, and against areas with a large amount of shrubland within a radius of 250 m. There were two models $< 2 \Delta AIC_c$, but they both had an additional and non-significant parameter (Table 2), suggesting that these were uninformative parameters (Burnham & Anderson 2002). Model validation showed that correlation between frequencies of withheld use data and

bin ranking was positive and strongly significant for güiñas ($r_s = 0.912$, $p < 0.002$; Fig. 3).

Analytical Hierarchy Process

Ranking of the weights from the Analytical Hierarchy Process indicated that the most important habitat component for güiñas was the presence of native forest, followed by shrubland and lava flow, dumps and rocks. Cover types that were ranked with the lowest scores included meadow and three cover types associated with human activity: plantation, major roads, and urban/industrial areas (Table 3). Saaty's consistency ratio was 0.094 (< 0.1) which indicates that there were no inconsistencies in the assignment of weights.

Connectivity Analysis

A. Least-Cost Path

Least-cost paths identified on RSF and AHP maps used similar types of land cover to connect among protected areas; however, an important difference between maps was related to the location of one of their respective LCPs. On the AHP map, the LCP that connects VNP and medium VNR runs very close to an urban/industrial area. In the case of RSF map, the LCP between VNP and HNP crosses through the middle of the protected areas (Fig. 4 and 5).

Within a given map, the ranked path ratios (CWD/ED and CWD/PL) displayed a positive and strong correlation. By contrast, when path ratio rankings were compared between maps, there was no significant correlation (Table 4, 5 and 6a-b).

B. Current

The current map based on the RSF layer (Fig. 6) showed three zones of high concentration of current flow. The largest zone is located on the east side of medium VNR, south of small VNR, south-west and southern portion of HNP. The second area is between the north-west, north and east parts of small VNR and north-west part of big VNR, also covering the northern part of HNP. Lastly, the third zone is situated over the north-east part of VNP and it includes one third of the big VNR, running close to this protected area.

The AHP current map (Fig. 7), in contrast, displayed one large area of high current, which extends south-west of HNP, covering the east portion of medium VNR, surrounding small VNR and finishes in the east part of big VNR. This map also shows a small area of medium to high current flow that expands from the north-east of VNP to approximately one third of big VNR.

When rankings generated from ratios of RD to ED and CWD to ED were compared within the RSF and AHP maps, only the RSF had a positive correlation of ranked path ratios. When comparing the rankings of RD to ED ratios between RSF and AHP maps, I found a strong positive correlation (Table 4, 5 and 6a-b).

C. Pinch Points

Between truncated maps (Fig. 8), there were a total of nine new pinch point areas, of which three were found on the RSF map and six on the AHP map. The biggest difference between both maps was in the location of a pinch point zone which connects VNP and HNP, generated only in the RSF truncated map.

D. Current Core Flow Centrality

My analysis of the RSF and AHP maps showed that big VNR was the most important protected area for maintaining the overall connectivity in the network. Rankings of the remaining areas varied depending on the method (Table 7).

Discussion

Overall, the two methods used to create resistance surfaces (RSF and AHP) and the two statistics used to quantify connectivity (LCP and circuit theory) generated different path ratio rankings. In spite of the differences, comparing connectivity methods on the same map yielded rankings that were strongly correlated (with the exception of CWD/ED vs RD/ED on the AHP surface). Comparing the same statistics between maps showed low correlation of rankings created by LCP approaches (CWD/PL or CWD/ED); however, circuit theory ratios (RD/ED) yielded very similar rankings. This indicates that LCP approaches are more sensitive to variation in the underlying resistance surface. In general, RSF resistance maps are much more flexible compared to the AHP maps; however, this comes at an increased cost (i.e., tracking animals).

The RSF model I developed showed that there was strong resource selection by the güiña (Figure 3). Results obtained from the best fitting RSF model determined that güiñas select habitat with native forest within a radius of 100 m and avoid zones with shrubland within a radius of 250 m. This is consistent with a previous study that determined that this cat uses almost exclusively native forest (Acosta-Jamett & Simonetti 2004), and with other researches that described this felid as a forest specialist (Dunstone et al. 2002; Sanderson et al. 2002). Two novel findings of this study are that güiñas select

for habitat near watercourses and dirt roads. Acosta-Jamett and Simonetti (2004) also showed this affinity for watercourses, but only in continuous forest. This work expands on that result indicating guiñas also prefer to be near water sources in forest fragments. This preference to use areas near watercourses could be linked with prey's availability (Klar et al. 2008), or they could be used as corridors (Sanderson et al. 2002). The affinity for dirt roads that I identified contrasts with previous work that found that guiñas avoid all roads (Acosta-Jamett & Simonetti 2004). The preference for zones near dirt roads could be an adaptation to the high degree of habitat fragmentation that these animals experience. Given that these roads have low to moderate vehicle traffic they could facilitate the movement of guiñas among forest patches. The use of roads in felids has been described by Trolle and Kery (2005) who found that ocelots (*Leopardus pardalis*) and cougars (*Puma concolor*) prefer to walk on roads rather than on trails.

In general, LCPs calculated on the RSF resistance map tended to be longer than those calculated on the AHP map; the location and shape of routes connecting among nodes also varied substantially between both maps. For example, LCPs computed from the RSF map commonly shared a main route from which arose short paths that connected a pair of nodes, whilst LCPs generated from the AHP map displayed independent routes for connecting nodes.

The current maps based on both RSF and AHP resistance surfaces displayed large differences in current flow allocation. Because the RSF resistance surface was constructed using data from radio telemetry, it integrates landscape features that favor or impede guiña movement through the protected areas. The AHP surface, on the other hand, only evaluates the relative qualities of discrete land-cover types. This contrast

means that RSF maps can be more flexible and (hopefully) yield resistance values closer to the actual preferences of güiñas compared to the coarse approximations of the AHP map. For instance, the RSF map showed large amounts of current flow near watercourses and dirt roads, while the AHP current map did not take proximity to these linear features into account. This is also noted in the zone that is located among medium, small and big VNR and HNP where current flow of the RSF map runs through native forest and near roads, rivers and lake, while in the AHP map it flows mostly across native forest. On the other side, both RSF and AHP current maps shared some areas of high current flow, which almost always occurred in zones where the predominant land cover was native forest.

Based on the results of the comparisons among rankings of ratios within and between RSF and AHP maps, I showed that RSF and AHP maps and all the metrics used to estimate connectivity generated different outcomes. This indicates that more research is needed in selecting the most appropriate method for the analysis of connectivity because choosing the wrong method could yield results that are misleading. For example, because VPN and big VNR are nearly contiguous, the distance computed between them was just one pixel (30m). In the RSF ranking, this connection occupied the last position in the three ratios, whilst in AHP ranking it was first in CWD/ED and CWD/PL ratios and eighth in RD/ED ratio. It is very critical to be aware of this situation because, if it is necessary to allocate resources to maintain connectivity among some areas mainly focusing on the shorter connections, different paths will be chosen depending on the map and metric used.

The discrepancies mentioned before, also are reflected in the differences in the new pinch point areas computed by both RSF and AHP truncated maps. Even though both truncated maps overlap in some areas, they generated pinch point in different zones which could lead to different conservation decisions.

The current core flow centrality scores show that both maps identified the same protected area (big VNR) as the most important area for maintaining connectivity across the study area. Although big VNR does not have the largest area among protected zones, its long shape gives it greater surface area for connections to other nodes. The differences in the ranking of the other protected areas were expected based on the allocation of current flow. For instance, in the RSF map the second most important area was HNP which is located in the center of the high current flow area. A similar situation was observed in the AHP map, where small VNR was determined to be the second most important protected area, and also was situated at the middle of a high current flow area.

One of the reasons that the results from the analysis of the AHP and RSF resistance surfaces differ is that my empirical data on the güiñas resource selection differs somewhat from that reported in the literature. For example, while the literature suggests that güiñas would avoid roads (Acosta-Jamett & Simonetti 2004), my empirical support showed that güiñas actually select for places near to them. Differences between RSF and AHP maps were assessed by Reed (2013), who found that RSFs are more suitable for modeling movement in bobcats at the home range level than AHP surfaces; however, it is critical to note that a poorly constructed RSF model will yield spurious estimates of connectivity.

While RSF methods are powerful because of their ability to incorporate empirical estimates of habitat use for animals in the system of interest, AHP methods can be used in a broader range of scenarios and without detailed empirical work. The AHP map shared some current flow, LCP connection zone and pinch point areas with the RSF map, which makes it useful for preliminary studies, when there is no money to collect data from the field, or when the investigation covers a large area or number of species that would be impractical to sample (Reed 2013). However, aside from those advantages it is important to mention that this method could yield biased assessments of the resistance values due to uncertainty in the expert opinion (Clevenger et al. 2002). Similarly, the RSF approach is not immune to bias because the researcher must choose the variables included in the models. This potential bias could be diminished by exploratory analysis of pilot data and only using biologically relevant variables (Shafer et al. 2012).

The results from my RSF analysis suggest that to maintain connectivity in güiñas among protected areas it is critical to conserve the zone between big VNR and medium VNR, as well the broad area between medium VNR and the south-western portion of HNP. This will ensure the connections among big VNR, HNP and small and medium VNR. Similarly, in order to maintain a connection among small and medium VNR, HNP and VNP two different zones must be maintained: the first located between the south-eastern portion of medium VNR and the north-western portion of VNP, and the second located between north-eastern VNP and southern HNP.

Analysis of the AHP maps yield a slightly different result: to maintain connectivity in güiñas among big VNR, HNP and small and medium VNR, it is necessary to protect the extensive zone of high current flow located from north-west big VNR to

east medium VNR, and the area between east medium VNR and south-western HNP. The AHP maps do not show a specific zone to protect in order to maintain connectivity among small and medium VNR, HNP and VNP.

The implications of the differences in the outcomes obtained from the RSF and AHP maps are that depending on the type of map and metric used, conservation decisions will be different. For example, although both maps shared a zone of high current flow between north-west big VNR and east medium VNR, this area on the AHP map is wider than that on the RSF map. This situation could lead to very different allocations of conservation resources depending on what map (or what statistic) was used in the analysis. Likewise, because the AHP map did not display a high or medium zone of current flow connecting the small and medium VNR, HNP and VNP, a conservation program would not allocate resources to it; however, a study based on the RSF map would protect that area.

In this study I made a comparison among connectivity outcomes generated from RSF and AHP maps. I chose those methods because they have been widely used in connectivity analyses. The results from this study show that there were some similarities and several differences between both maps and connectivity statistics. More research is required to establish which method and metric are more suitable depending on the objectives of a research and the ecology of the study species. For instance, if there is information about the habitat use of a species, I recommend the RSF approach that includes only variables with biological significance; however, if the study includes a large area and there is not enough money for animal tracking, AHP should be used. If the goal of the study is to determine the path with the minimum cost among protected areas,

LCP is more adequate, but if it is important to assess alternative pathways and there is little information about the species, circuit theory should be chosen. This study shows that selection of resistance surfaces and statistics is a critical step in any connectivity analysis. This is also the first analysis of connectivity in güiñas made in this region, and although the number of cats studied was small, it provides initial guidelines to future research and conservation programs focused in maintaining connectivity in this highly fragmented landscape.

Table 1. Summary of collected telemetry data, random points created by individual home ranges, and home range estimation by guñas captured in Pucón, Araucanía region, Chile 2010-2012.

<i>ID</i>	<i>Sex</i>	<i>N total fixes</i>	<i>N fixes used</i>	<i>Period</i>		<i>Home range size (ha)</i>
				<i>monitored (days)</i>	<i>N random points</i>	
F01	Female	272	253	216	2934	586.73
F02	Female	37	36	33	6509	1301.87
F03	Female	169	168	87	3330	665.98
M01	Male	466	455	377	5000	999.92
M02	Male	209	201	91	5526	1105.28
Total		1153	1113	804		

Table 2. Estimated coefficients and standard error for variables, ΔAIC_c corrected for small sample size, model weights and number of parameters of Resource Selection Function models of güiñas in Pucón, Araucanía region, Chile 2010-2012.

<i>Model</i>	<i>Coefficient</i>	<i>se(coefficent)</i>		ΔAIC_c < 2 ^a	w_i^b	K^c
forest_100I ^d	2.97E+00	1.82E-01	***			
shrubland_250 ^e	-6.68E+00	6.43E-01	***	0	0.40	4
dis_minor ^f	-9.78E-04	1.86E-04	***			
dis_water ^g	-2.83E-04	8.19E-05	***			
forest_100I	2.98E+00	1.82E-01	***			
shrubland_250	-6.60E+00	6.43E-01	***	0.58	0.30	5
dis_minor	-1.11E-03	2.18E-04	***			
dis_water	-2.88E-04	8.20E-05	***			
dis_rural ^h	2.14E-04	1.78E-04	---			
forest_250 ⁱ	8.83E-02	1.42E-01	---			
forest_100I	2.94E+00	1.88E-01	***			
shrubland_250	-6.63E+00	6.48E-01	***	1.62	0.18	5
dis_minor	-1.00E-03	1.91E-04	***			
dis_water	-2.83E-04	8.18E-05	***			

^a Difference of Akaike information criteria corrected for small sample size from the top ranked model (AIC_c : 18,360.83).

^b AIC_c model weight.

^c Number of parameters.

^d Native forest within an area of 100m².

^e Shubland within an area of 250m².

^f Distance to minor roads (m).

^g Distance to watercourses (m).

^h Distance to rural places (m).

ⁱ Native forest within an area of 250m².

*** Significant at 0.001.

--- Not significant.

Table 3. Ranking and weights of variables generated from the pairwise comparison matrix in the Analytical Hierarchy Process analysis in Pucón, Araucanía region, Chile 2010-2012.

<i>Variable</i>	<i>Weights</i>	<i>Ranking</i>
Native forest	0.36	1
Shrubland	0.27	2
Lava flow, dumps and rocks ^a	0.11	3
Wetland	0.08	4
Minor road ^b	0.06	5
Beach	0.04	6
Meadows	0.02	7
Plantation	0.02	7
Major road ^b	0.02	7
Urban/industrial areas ^c	0.01	8

^a *Place with few lines of water running down.*

^b *Distance < 250m.*

^c *Distance < 500m.*

Table 4. Summary of the results of least-cost paths and resistance distances generated from the Resource Selection Function resistance surface in Pucón, Araucanía region, Chile 2010-2012. Also, this table shows the ranking of the three ratios which are related to corridor quality.

From core	To core	ED ^a	CWD ^b	LCP ^c length	RD ^d	CWD to path length ratio	CWD to ED ratio	RD to ED ratio ^e	Ranking of ratios		
									CWD to path length	CWD to ED	RD to ED
1	2	4679	36603.70	16229	0.0582	2.26	7.82	12.43	4	7	8
1	3	10744	44135.90	13623	0.0566	3.24	4.11	5.27	7	5	4
1	4	2606	8013.86	3933	0.0138	2.04	3.08	5.31	2	2	5
1	5	19917	132856.78	42004	0.1073	3.16	6.67	5.39	6	6	6
2	3	2700	9410.43	5029	0.0087	1.87	3.49	3.23	1	4	2
2	4	15613	42934.60	19265	0.0762	2.23	2.75	4.88	3	1	3
2	5	18615	160917.30	29538	0.1643	5.45	8.64	8.83	8	8	7
3	4	24103	75132.20	32581	0.0770	2.31	3.12	3.20	5	3	1
3	5	7773	145486.61	21579	0.1606	6.74	18.72	20.66	9	9	9
4	5	30	983.71	30	0.0052	32.79	32.79	174.74	10	10	10

^a Euclidean distance.

^b Cost-weighted distance.

^c Least-cost path.

^d Resistance distances.

^e Values shown were amplified by 10^6 for reducing the number of decimal digits.

Table 5. Summary of the results of least-cost paths and resistance distances generated from the Analytical Hierarchy Process resistance surface in Pucón, Araucanía region, Chile 2010-2012. Also, this table shows the ranking of the three ratios generated from these results.

From core	To core	ED ^a	CWD ^b	LCP ^c length	RD ^d	CWD to path length ratio	CWD to ED ratio	RD to ED ratio ^e	Ranking of ratios		
									CWD to path length	CWD to ED	RD to ED
1	2	4679	16859.80	16494	0.0124	1.02	3.60	2.66	5	10	9
1	3	10744	17914.50	13731	0.0146	1.30	1.67	1.36	7	6	6
1	4	2606	3786.29	3555	0.0028	1.07	1.45	1.07	6	5	4
1	5	19917	35464.60	24882	0.0243	1.43	1.78	1.22	9	8	5
2	3	2700	2886.40	2886	0.0018	1.00	1.07	0.68	1	2	2
2	4	15613	17947.70	17938	0.0108	1.00	1.15	0.69	1	3	3
2	5	18615	31106.40	23055	0.0363	1.35	1.67	1.95	8	6	7
3	4	24103	28327.60	28318	0.0137	1.00	1.18	0.57	1	4	1
3	5	7773	18905.40	10854	0.0382	1.74	2.43	4.91	10	9	10
4	5	30	30.00	30	0.0001	1.00	1.00	2.09	1	1	8

^a Euclidean distance.

^b Cost-weighted distance.

^c Least-cost path.

^d Resistance distances.

^e Values shown were amplified by 10⁶ for reducing the number of decimal digits.

Table 6. Spearman-rank correlations (r_s) among rankings of ratios created from the results of least-cost paths and resistance distances. Correlations were assessed within (a) and between (b) Resource Selection Function and Analytical Hierarchy Process resistance surfaces.

(a)

	<i>Within each map</i>			
	<i>CWD^a to PL^b and CWD to ED^c</i>		<i>CWD to ED and RD^d to ED</i>	
	r_s	p	r_s	P
RSF ^e	0.8182	0.0068	0.8545	0.0035
AHP ^f	0.7777	0.0081	0.5714	0.0844

^a *Cost-weighted distance.*

^b *Path length.*

^c *Euclidean distances.*

^d *Resistance distances.*

^e *Resource Selection Function.*

^f *Analytical Hierarchy Process.*

(b)

<i>Between maps</i>					
<i>CWD^a to PL^b</i>		<i>CWD to ED^c</i>		<i>RD^d to ED</i>	
<i>r_s</i>	<i>p</i>	<i>r_s</i>	<i>p</i>	<i>r_s</i>	<i>p</i>
0.4252	0.2206	0.2918	0.4133	0.9273	0.0001

^a*Cost-weighted distance.*

^b*Path length.*

^c*Euclidean distances.*

^d*Resistance distances.*

Table 7. Current core flow centrality scores generated from Resource Selection Function and Analytical Hierarchy Process resistance surfaces in Pucón, Araucanía region, Chile 2010-2012.

	<i>Current core flow centrality score</i>	
	<i>RSF^a</i>	<i>AHP^b</i>
Huerquehue National Park	5.79	5.35
Villarrica National Reserve (medium)	5.20	5.42
Villarrica National Park	4.69	5.42
Villarrica National Reserve (big)	7.38	7.05
Villarrica National Reserve (small)	5.59	5.45

^a *Resource Selection Function.*

^b *Analytical Hierarchy Process.*

Figure 1. Location of the study area (square) in Pucón, Araucanía region, and its location in the southern Chile (right). This map shows land-cover types, the protected area boundaries, and individual cat locations.

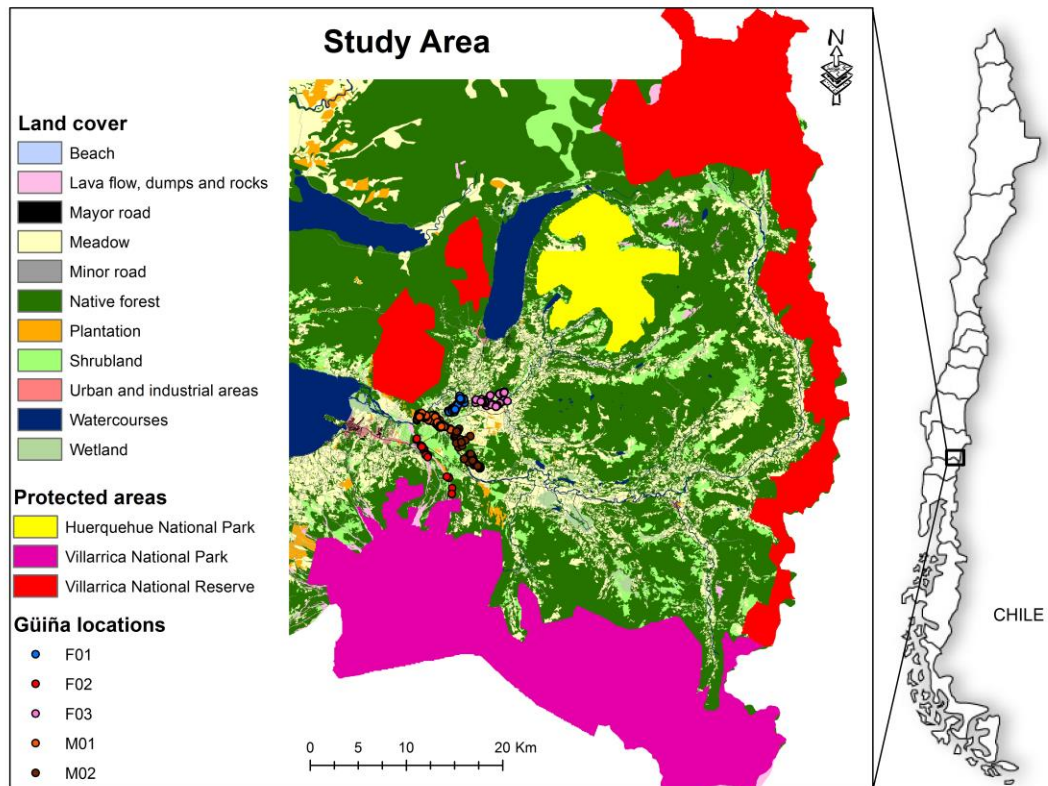


Figure 2. Home ranges based on 90% Kernel Brownian Bridge calculated for the five guñas; areas ranged from 587 - 1302 ha.

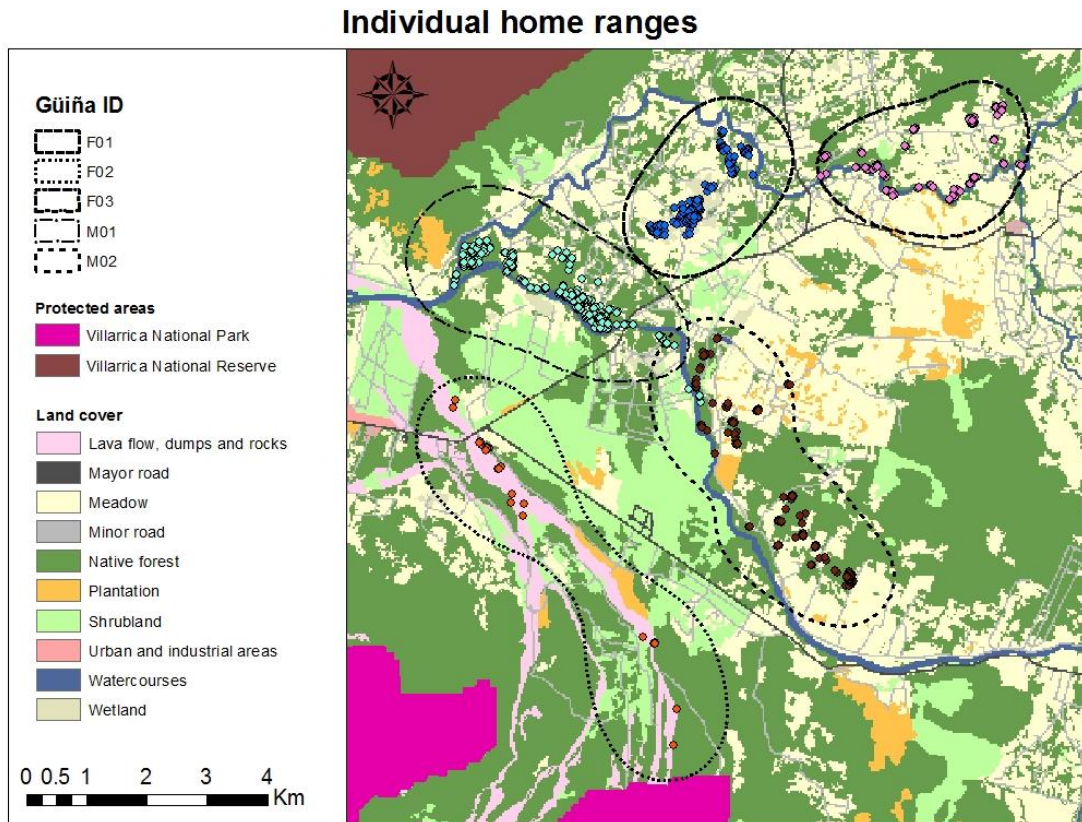


Figure 3. Proportion of points of categories (bins) of RSF scores withholding 20% of used points by güiñas and utilizing 100% of random points in Pucón, Araucanía region, Chile 2010-2012. This figure also shows boxplots of each category.

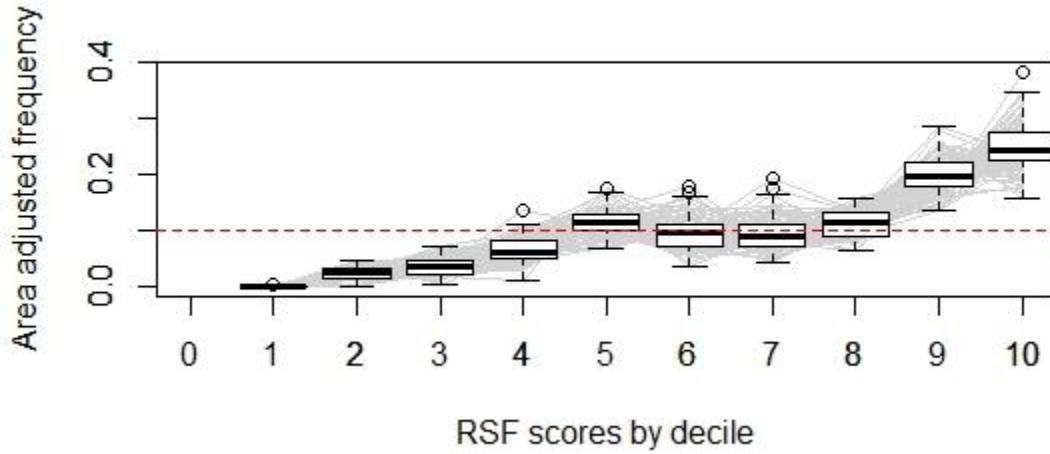


Figure 4. Least-cost paths generated from Resource Selection Function resistance surface among protected areas in Pucón, Araucanía region, Chile 2010-2012. This map shows 10 LCPs calculated by means of Linkage Mapper tool.

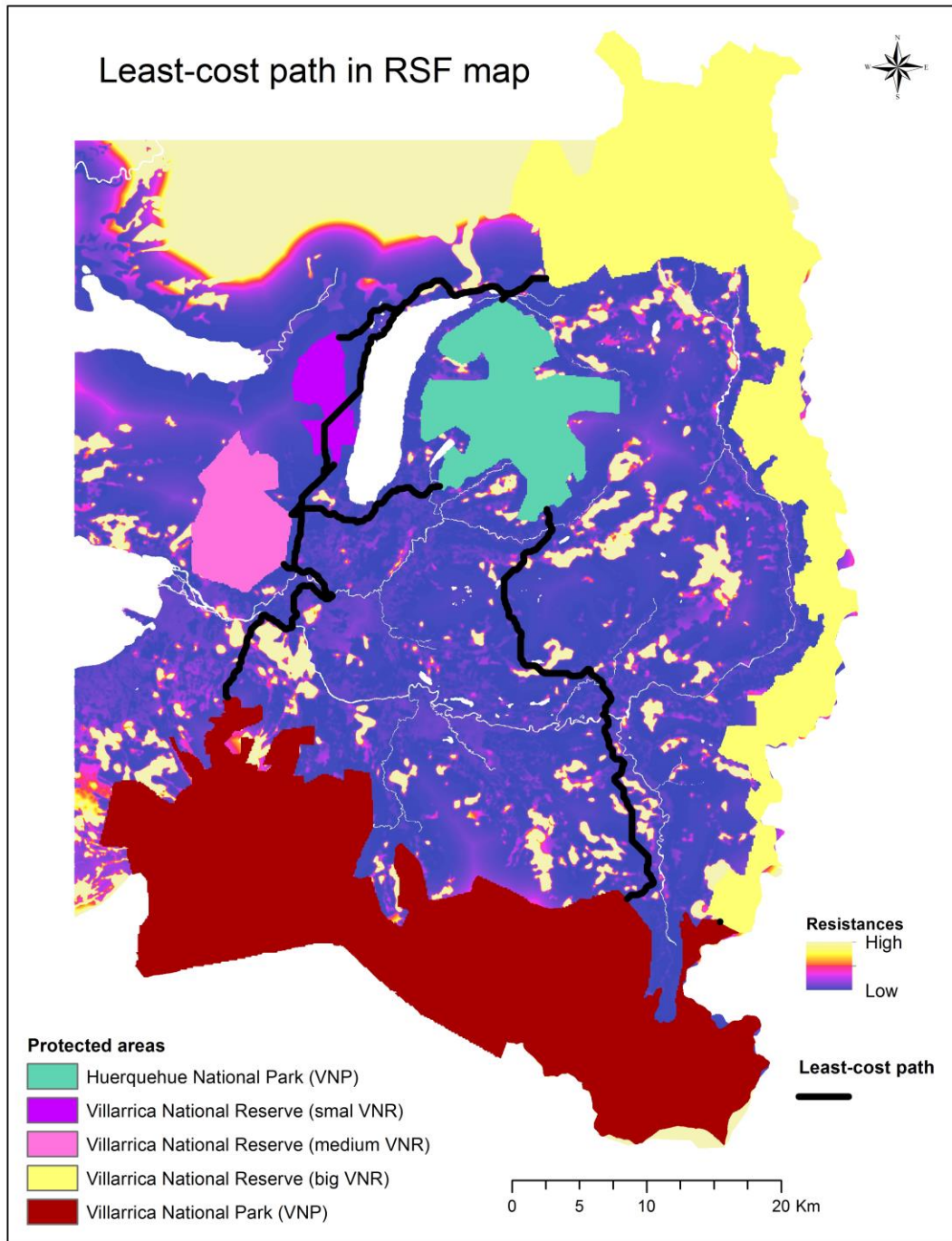


Figure 5. Least-cost paths generated from Analytical Hierarchy Process resistance surface among protected areas in Pucón, Araucanía region, Chile 2010-2012. This map shows 10 LCPs calculated by means of Linkage Mapper tool.

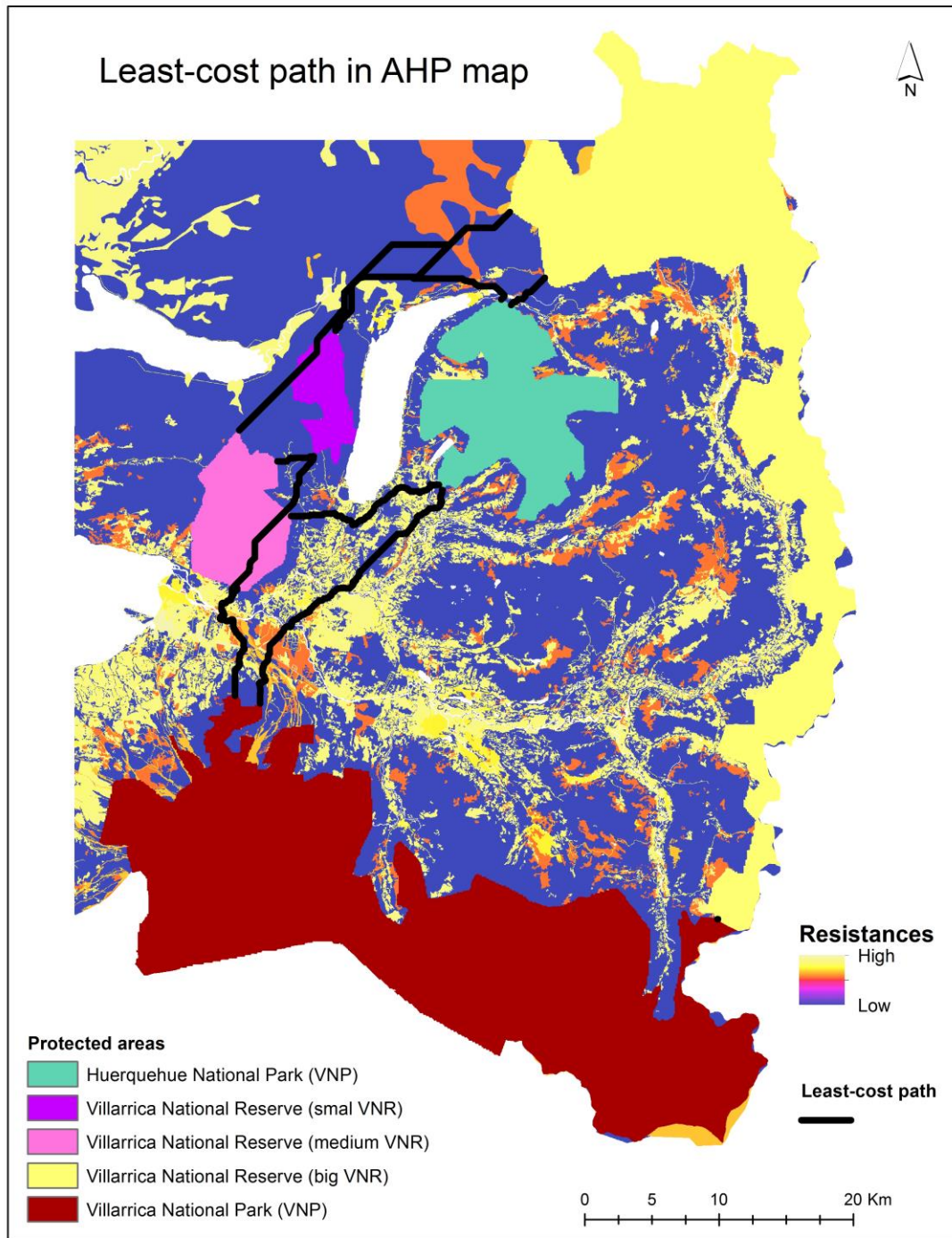


Figure 6. Cumulative current map generated from Resource Selection Function resistance surface in Pucón, Araucanía region, Chile 2010-2012. This map shows a large zone of high current flow located on the east side of medium VNR, south of small VNR, south-west and southern portion of HNP.

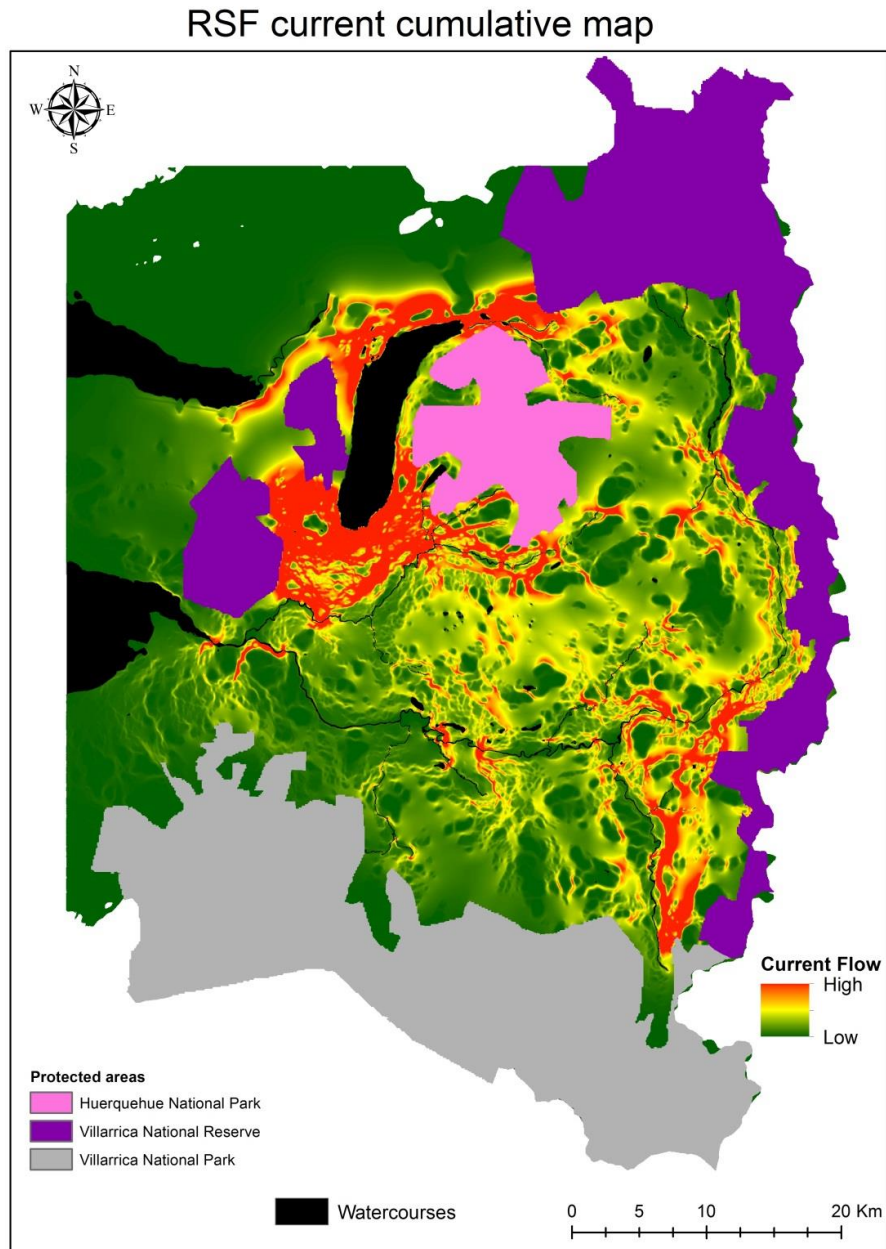


Figure 7. Cumulative current map generated from Analytical Hierarchy Process resistance surface in Pucón, Araucanía region, Chile 2010-2012. This map shows a large zone of high current flow which extends south-west of HNP, covering the east portion of medium VNR, surrounding small VNR and finishes in the east part of big VNR.

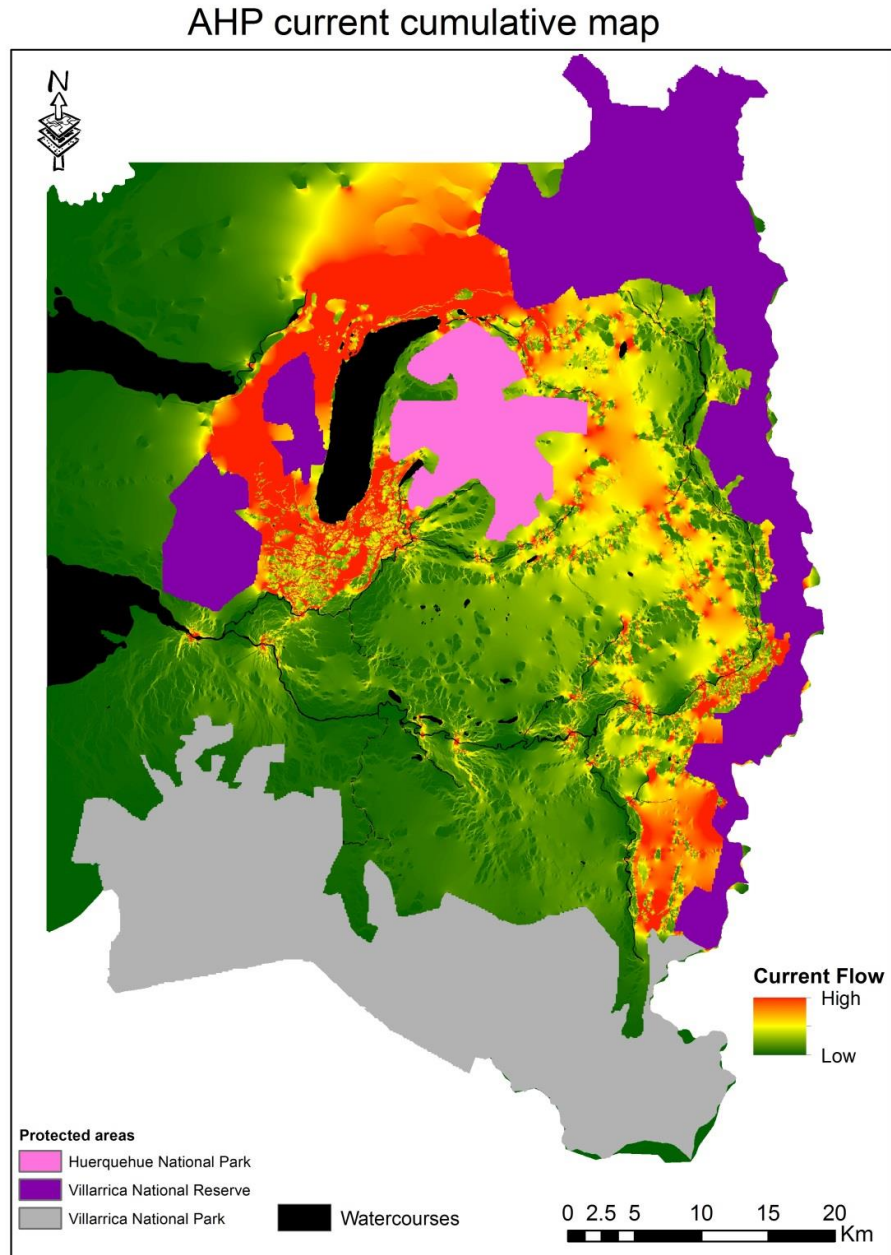
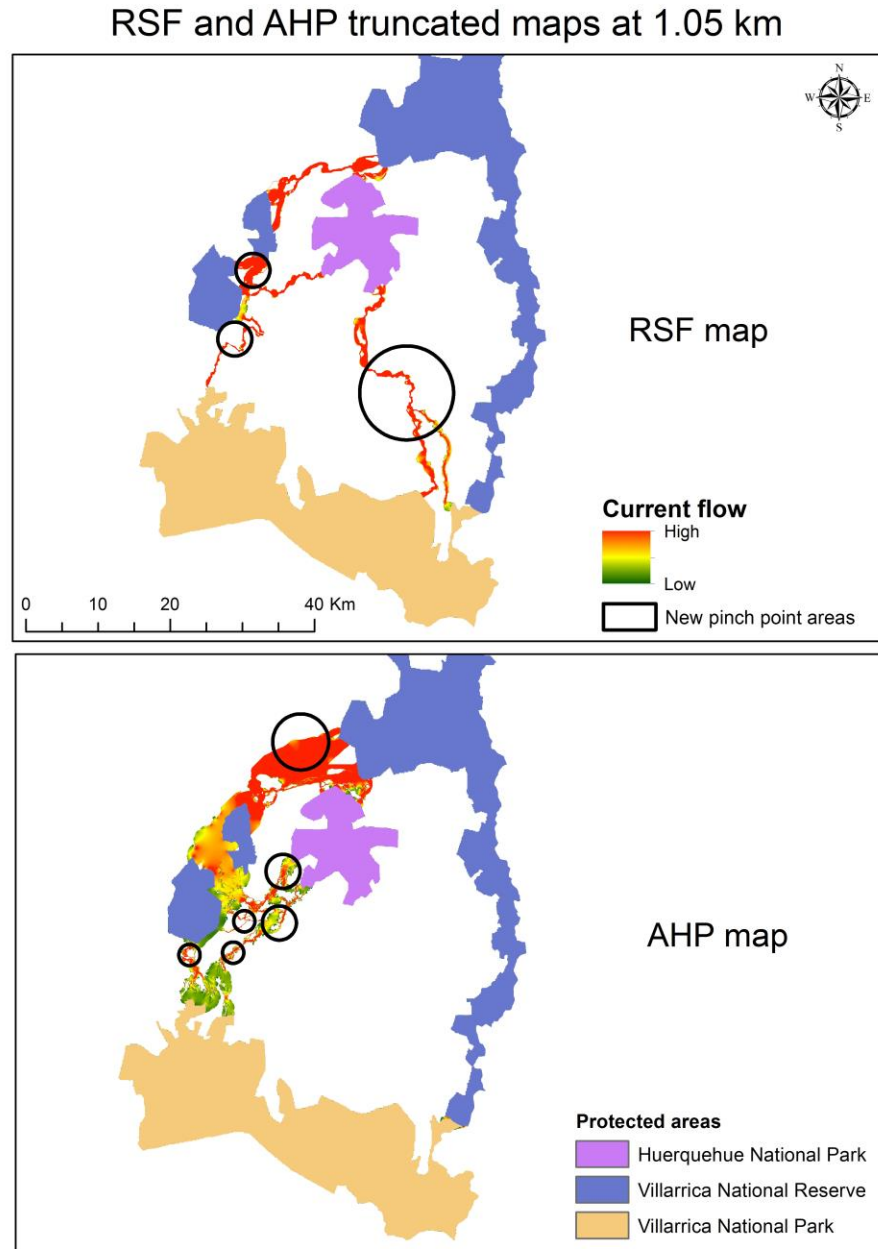


Figure 8. Pinch point areas calculated from Resource Selection Function and Analytical Hierarchy Process truncated maps in Pucón, Araucanía region, Chile 2010-2012. There were a total of nine new pinch point areas between maps, of which three were supplemented by RSF and six by AHP.



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