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Distribution modelling of the Pudu deer (*Pudu puda*) in southern Chile

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Abstract

The Pudu deer (*Pudu puda*) is endemic to the temperate rainforest of Chile and Argentina and currently faces serious conservation problems related to habitat loss. However, studies undertaken on this species are not sufficient to identify suitable areas for conservation purposes across its distribution range. In order to estimate the current and future distribution of the Pudu deer in southern Chile, we modelled the potential distribution of this species, based on occurrence points taken from seven contiguous provinces of this area using the Maxent modelling method. The Pudu deer distribution covered an estimated area of 17,912 km^2 (24.1% of the area analysed), using a probability of occurrence above 0.529, according to the threshold that maximises the sum of sensitivity and specificity. In contrast to the Andes mountain range, areas with higher probabilities of occurrence were distributed mainly on the eastern and western slopes of the Coastal Mountain Range, where extensive coverage of native forest persists, as occurs in the provinces of Ranco, Osorno and Llanquihue. Projections to 2070, with global warming scenarios of 2.6 and 8.5 rcp, revealed that large areas will conserve their habitability, especially in the Coastal mountain range. Our results reveal that the Coastal mountain range has a high current and future habitability condition for the Pudu deer, a fact which may have conservation implications for this species.

Keywords

conservation, habitability, niche modelling, Pudu deer, temperate rainforest, threatened species

Introduction

The Pudu deer, *Pudu puda* (Molina, 1782), is a cervid endemic to southern South America, characterised by being one of the smallest deer in the world due to its short shoulder height (30–40 cm) and lower body weight (< 15 kg) (Jiménez 2010). This species is distributed in Chile and Argentina from 35°10'S to 46°45'S (Jiménez 2010) and from 39°23' to 42°58'S (Meier and Merino 2007), respectively, occupying an area of 128,278 km^2 according to the International Union for Conservation of Nature (IUCN), mainly located in Chile. The Pudu deer characteristically inhabits the pristine temperate rainforest, particularly in areas of dense understorey growth and native bamboo thickets (Eldridge et al. 1987; Meier and Merino 2007), but can also be found in disturbed and secondary forest habitats (Jiménez 2010). Current conservation status of the Pudu deer is Near Threatened according to the IUCN or Vulnerable, based on the threatened species list of the Chilean Ministry of Environment. This conservation status is related to different threats that appear to have affected the viability of the species. Amongst these, local threats have been identified linked to the expansion of human activities, such as forest loss and fragmentation, predation by domestic dogs, competition with exotic species and poaching activities (Miller et al. 1973; Wemmer et al. 1998; Silva-Rodríguez et al. 2010; Silva-Rodríguez and Sieving 2012; Jiménez and Ramilo 2013). Global warming, as a result of the concentration of greenhouse gases, may constitute another threat that could reduce the future survival prospects of the Pudu deer. It is expected that this factor may affect the habitability conditions of current distribution areas of the species as a consequence of climate change and, therefore, affect its future geographic distribution. This is not an unlikely scenario, since global climate models predict precipitation pattern changes and increased frequency and severity of droughts by the end of the 21st century (IPCC 2014), a process that is expected to impact ecosystem structure and function. In fact, modelling studies have predicted that levels of species loss of all currently-known species will range from 0 to 54%, including an overall extinction risk of 7.9%, as a result of future climate change (Urban 2015).

Although the Pudu deer is under threat, few studies have been carried out on this species and available information is insufficient to clarify its density or identify suitable areas for conservation plans. With regard to density data, available estimations suggest that the Pudu deer population may be fewer than 10,000 individuals across its distribution range (Miller et al. 1973; Wemmer et al. 1998; Jiménez and Ramilo 2013). Another estimation from the IUCN suggests, however, that the Pudu deer population is likely to exceed this figure, based on the assumption of 10% occupancy by this species in the native rainforest. Nonetheless, it should be noted that, to date, no extensive field data-based estimation has been performed to support this. Recent studies on this issue have been performed mostly in small areas of southern Chile, particularly in natural reserves or areas with relatively well-preserved native forests (Delibes-Mateos et al. 2014; Sanino et al. 2016; Zúñiga and Jiménez 2018). Despite this sampling limitation, these studies have contributed important evidence that supports a reduced relative abundance of this species in these areas, since the number of detection events per 100 camera-trap days has been relatively low (0.16−3.4).

Osorno Province (40°13'–41°00'S) is a geographic area located in the northernmost part of the Los Lagos Region. Around 15 native terrestrial mammals have been described in this Province, with the Pudu deer being the only one native deer currently distributed in this area (Iriarte 2010). Large areas of pristine Valdivian temperate rainforest can be found in Osorno Province, mainly in the Coastal and Andes mountain ranges (Miranda et al. 2017). Although previous (Vanoli 1967) and recent (Pavez-Fox and Estay 2016) records support the presence of the Pudu deer in this geographic area, its current distribution and abundance are still unknown, particularly in areas with densely-vegetated forests or associated with different land uses. Since the Pudu deer is characterised by evasive behaviour, cryptic colour, considerable nocturnal activity and also because it inhabits dense forest habitats (Zúñiga and Jiménez 2018), the process of recording field data for the species is a complex task. Reliable data are important for the conservation of the species, for example, to define or potentiate new protected areas, such as national reserves, amongst others. This objective should be addressed as matter of priority, given that, in Chile's current system of protected areas, the most suitable habitat for the Pudu deer is under-represented (about 6%) (Pavez-Fox and Estay 2016), in addition to the increasing degradation of its habitat as a result of native forest loss (Miranda et al. 2017). Another conservation approach that could be implemented in Chile is to maintain viable populations within small areas, as has been suggested by some authors (Shaffer 1987; Simonetti and Mella 1997), given that the Pudu deer presents a restricted home range.

The conservation of the Pudu deer in Chile requires combined efforts in several research areas, such as ecology, genetic structuring of populations and determination of the relative effect of different threats affecting the species in its natural environment. Amongst these issues, a top priority is to determine the current status of populations distributed in areas affected by significant loss or fragmentation of native forest or where it has been replaced by grasslands for agricultural purposes or by exotic forest plantations (Silva-Rodriguez et al. 2011). In the case of Osorno Province, this is a matter of particular concern, given that, between 2006 and 2013, the area planted with exotic tree species increased significantly (+20.6%), a large part of this growth being at the expense of native forest (CONAF-UACh 2014). Given that the habitat of the Pudu deer is closely linked to the native forest, it is important to establish the viability or distribution of populations in those areas of Osorno Province, where original characteristics have been altered due to change of land use as a result of human activity.

Mathematical modelling of species distributions based on maximum entropy (Phillips et al. 2006) is an interesting tool with several applications in species conservation, especially when information about current and potential habitats is absent (Phillips et al. 2004; Papeş and Gaubert 2007). This method uses the environmental characteristics of areas a species is known to inhabit to estimate the environmental suitability of regions that currently lack record (Anderson et al. 2002). Thus, a predictive model is constructed showing the potential distribution map of the species. Based on this map, it is possible to assess the suitability of sites for conservation purposes (Chefaoui et al. 2005), to predict of geographic ranges of a species (Raxworthy et al. 2003; Anderson and Martínez-Meyer 2004) and identify priority areas for conservation efforts (Peterson et al. 2000), amongst others. Pavez-Fox and Estay (2016) have applied this analysis to model the Pudu deer distribution range in Chile aimed at evaluating the effectiveness of the Chilean National System of Protected Areas to protect the habitat of this deer. Although these authors used several Pudu deer points of occurrence across Chile to model the distribution of this species (in total 73), data density in some geographic areas was low, as was the case for Osorno Province (n < 5). With the exception of the Andes mountain range, this analysis indicated that most areas of the Province presented low suitability for the species, based on the result of a suitability map. Thus, the predicted distribution of the Pudu deer for the Province of Osorno merits further analysis by using a larger dataset in order to confirm the previous modelling.

The objective of this paper was to determine the distribution of the Pudu deer in seven Provinces from southern Chile, including the Osorno Province, by using modelling of species distribution, based on several recent occurrence data. We also modelled the future distribution of the species in the climate change scenario to determine how this phenomenon could affect its potential geographical distribution in the study area. This analysis may provide important clues as to how the species could respond to climate change, for example, in terms of variations in geographic range.

Methods

Study area

The area used for modelling the Pudu deer geographical distribution corresponded to the terrestrial environments between 39° and 44° South latitude of Chile. This geographic area comprises 74,295.5 km^2 and includes, from north to south, the Provinces of Cautín (8,207.6 km^2), Valdivia (9,146.8 km^2), Ranco (9,053.1 km^2), Osorno (9,246.6 km^2), Llanquihue (14,706.8 km^2), Chiloé (8,982.8 km^2) and Palena (14,952 km^2). This region contains a significant remnant of native temperate rainforest that covers a large proportion of each Province, as occurs in Osorno (42.9%), Llanquihue (54.5%), Chiloé (68.3%) and Palena (65.7%) (CONAF-UACh 2014), mostly distributed in the Coastal and Andes mountain ranges (Miranda et al. 2017). Climate in this region is warm-temperate and rainy with a Mediterranean influence and mean annual precipitation and temperature of 2,490 mm and 12.0 °C, respectively (Errazuriz et al. 2000). The Coastal Mountain range located in this area is characterised by an average height of 500 m a.s.l., which tends to gradually decrease towards the south (Ramírez and San Martín 2005; Villagrán and Armesto 2005). Meanwhile, the Andes Mountains present a higher altitude, averaging 1500 m a.s.l., with some elevations above 3000 m a.s.l (Garreaud 2009). Both mountain ranges present a predominance of vegetational formations comprising temperate laurifoliar rainforest, that include the Valdivian, North Patagonian and Subantarctic types (Villagrán and Hinojosa 2005). The temperate rainforest of Chile encompasses the Valdivian Rainforest Ecoregion, which has been listed amongst the most endangered ecoregions of the world and has a critical conservation status (Dinerstein et al. 1995; Olson and Dinerstein 1998; Miranda et al. 2017). In addition, the Valdivian Rainforest Ecosystem is considered a biodiversity hotspot and, therefore, a region of high conservation priority (Ormazabal 1993; Myers et al. 2000; Smith-Ramírez 2004).

Occurrence data

Occurrence records of the Pudu deer were retrieved from several sources, including national park records (Puyehue National Park), incidents of individuals found (alive or injured) in rural areas of the province and reported in the local newspaper supported by photographs (El Diario Austral of Osorno), from records of native fauna rescue operations compiled by the Agricultural and Livestock Inspection Service (Servicio Agrícola y Ganadero (SAG)) Osorno, from direct observation of free-ranging individuals detected by using a camera trap and the naked eye and from indirect signs of the species revealed by footprints (Fig. 1). In total, we considered 88 occurrence points, spanning the period between 2000 and 2019, almost all from the Osorno, Llanquihue, Chiloé and Palena Provinces (Región de Los Lagos) (Fig. 2). This data set also included occurrence points previously reported by Delibes-Mateos et al. (2014) (n = 1) and Pavez-Fox and Estay

Figure 1. Records of occurrence of the Pudu deer in the geographic area studied. Free-ranging individuals registered by using a camera trap at Los Riscos (Coastal mountain range, Purranque district) (**A**), near Hueyusca village (Coastal mountain range, Purranque district) (**B**), injured juvenile individual found in a rural area at Choroy (Coastal mountain range, San Juan de la Costa district) and reported in the local newspaper (**C**) and footprints registered in Puyehue National Park (Andes mountains, Puyehue district) (**D**).

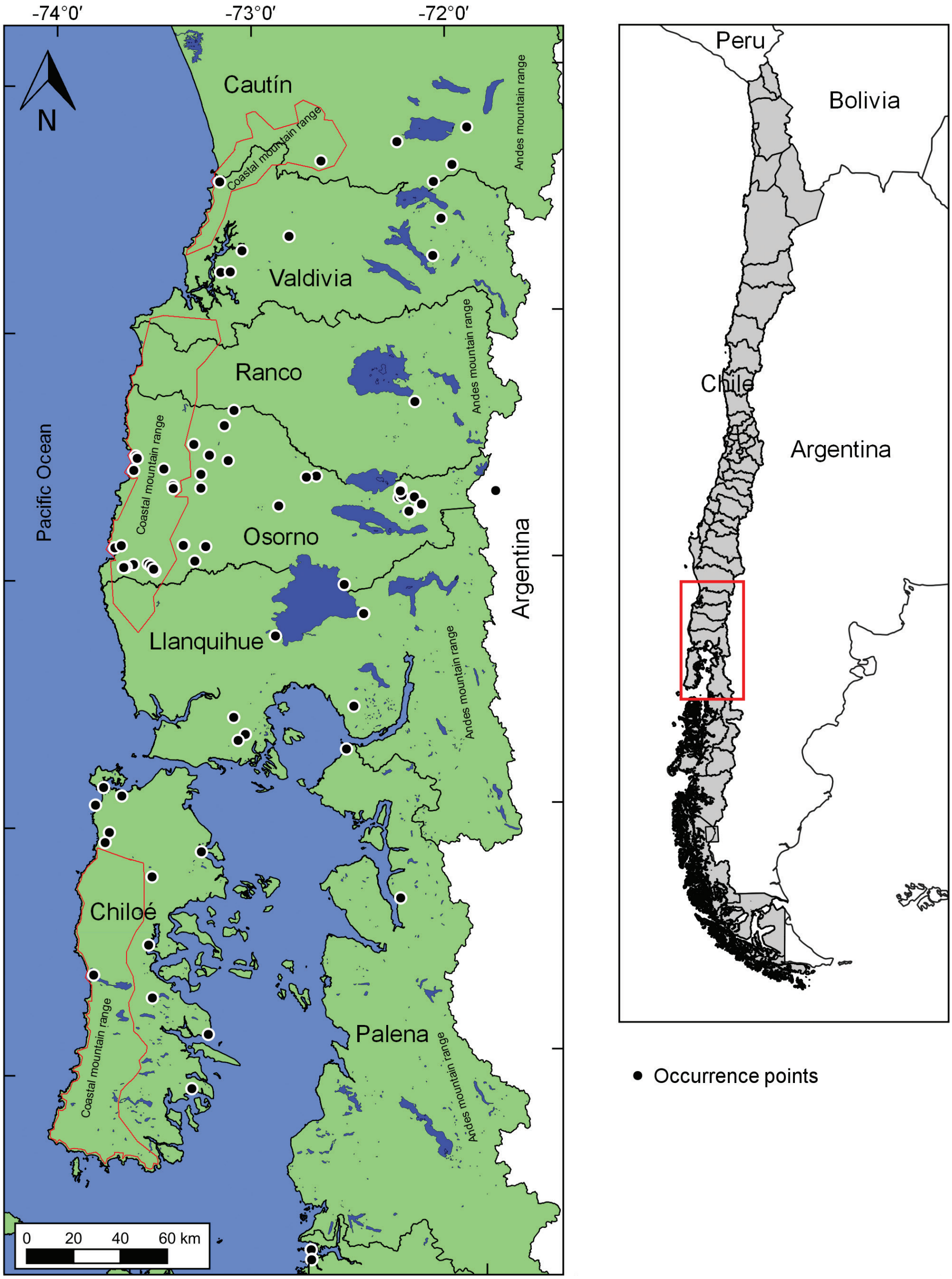

Figure 2. Georeferenced occurrence data of the Pudu deer used for model fitting in southern Chile. Black points indicate occurrence data. Names of each Province are indicated. The polygons with red lines indicate the location of the Coastal mountain range.

(2016) (n = 21), located either within this geographic area or in the nearby northern Provinces of Cautín and Valdivia. Further points located in the adjacent southern Province of Aysén, registered by Sanino et al. (2016) (n = 3), were also included.

Occurrences were georeferenced according to standard procedures whereby coordinates were assigned using Google Earth based on locality names. Details of the occurrence points recorded in this study (n = 63), including locality, coordinates, date, type of evidence and source, can be found in Suppl. material 1: Table S1; while, occurrence points from previous studies (n = 25) are provided in Suppl. material 2: Table S2. The occurrence points covered most of the Pudu's geographical distribution in this area, therefore, capturing almost the full niche of the species to calibrate the model. This aspect is important when modelling the potential future distribution of a species under climate change (Barbet-Massin et al. 2010). In addition, Moran's I index was also calculated to measure the overall spatial autocorrelation of the dataset, based on the estimation of observation independence within a dataset (Moran 1950).

Environmental data

To evaluate the potential geographical distribution of the Pudu deer in the study area and to identify suitable habitats currently occupied by the species, a set of bioclimatic variables from the WorldClim database (http://www.worldclim.org/) were used (Fick and Hijmans 2017). Initially, 19 bioclimatic variables of the Community Climate System Mode (CCSM) climate model (Gent et al. 2011) were considered. To reduce the multicollinearity effect, correlation coefficients were calculated between each pair of variables using the SDM toolbox extension implemented in ARCGIS 10.3 (Brown 2014). In those pairs with a high Pearson correlation value ($r \geq 0.7$), one of the variables was eliminated from the model. Thus, the following bioclimatic variables were selected for analysis: Isothermality (Bio3), Maximum Temperature of Warmest Month (Bio5), Minimum Temperature of Coldest Month (Bio6), Annual Temperature Range (Bio7), Precipitation of Wettest Month (Bio13), Precipitation Seasonality (Coefficient of Variation) (Bio15) and Precipitation of Warmest Quarter (Bio18). All the aforementioned environmental layers have a spatial resolution of 30 seconds of arc (approx.1 km). In addition, land cover and altitude variables obtained from the Diva-Gis database (http://www.diva-gis.org) were included (Hijmans et al. 2001), totalling nine variables for current distribution modelling. Land cover comprises different classes, such as tree cover evergreen and deciduous with broadleaved or mixed leaf type, shrub deciduous cover, herbaceous cover, sparse herbaceous or sparse shrub cover and cultivated and managed areas. Bio5, Bio6, Bio15 and Bio18 variables have previously been used in modelling distribution studies of the Pudu deer (Pavez-Fox and Estay 2016) and other deer species (Pease et al. 2009), since they provide important information that aids accurate determination of deer presence. The graphic results were compared with current land use reported in 2016 for southern Chile by the National Forestry Corporation (CONAF), available in Infraestructura de Datos Geoespaciales (IDE) database of the Ministerio de Bienes Nacionales, Gobierno de Chile (http://www.ide.cl/index.php/flora-y-fauna/item/1513-catastros-de-uso-de-suelo-y-vegetacion). On the other hand, to evaluate how future climate change may affect the potential geographic distribution of the species, the seven bioclimatic variables described above were used, but projected for 2.6 and 8.5 rcp (representative concentration pathways) until the year 2070. These values indicate the increase in heat absorbed by the planet as a result of the concentration of greenhouse gases in each path, measured in Watts per square metre. In this case, 2.6 rcp represents the most optimistic scenario or least climate change (mean temperature rise of 1.0 °C) and 8.5 rcp is the most pessimistic and warmer scenario (mean temperature rise of 2.0 °C) (IPCC 2013; Taylor et al. 2011). Processing of the environmental layers was performed in QGIS 3.22 (QGIS Development Team 2018) and GRASS7 (GRASS Development Team 2016).

Modelling and statistical methods

To build geographical distribution models of the species under current and future environmental conditions, we used the MAXENT v.3.2.0 programme (Phillips 2017). The model was adjusted using 10,000 iterations, variable response curves, logistic output, generation of replicas with the bootstrap method and a regularisation multiplier value equal to 2. However, to maximise model fitting, we undertook tests under a range of regularisation coefficient values to choose the optimal value of this parameter, aimed at reducing overfitting (Merow et al. 2013). During this modelling process, the best model was evaluated by cross-validation using the Area Under Curve of test data, prior to splitting presence locations into training and test data. The logistic model output gives an estimate between 0 and 1 of probability of presence (Pearson et al. 2007). The relative importance of each variable to the model was estimated using the contribution percentage and the jackknife method. Each model (current, rcp 2.6 and rcp 8.5) was replicated 10 times, using a data ratio of 20% for training and 80% for evaluation, using a bootstrap framework (Hijmans 2012). Maxent models were evaluated using the Area Under Curve (AUC). The AUC measures the ability (probability) of the Maxent model to discriminate between presence sites and background sites (Phillips et al. 2006), thus, this parameter is useful to evaluate the geographical distribution of the species. Values of AUC range between 0 and 1.0, with values greater than 0.9 considered as an optimal threshold for species area predictions (Peterson et al. 2011). Pearson product-moment linear correlations were carried out to assess the relationship between the most important bioclimatic variables in the model and the probabilities of occurrence of the Pudu deer in the study area.

Post-processing

The fitted model, trained in the study area, was later projected to the terrestrial environments of provinces from southern Chile included between 39° and 44° south latitude, to estimate distribution of the species. The original map was converted to a binary map (0 = not suitable, 1 = suitable), applying a threshold, based on maximising the sum of sensitivity and specificity (SSS) (Liu et al. 2013). This method is recommended for threshold selection when only presence data are available, since it performs better than other threshold criteria (Liu et al. 2013).

Results

Current geographical distribution

Our dataset does not show significant ($P > 0.05$) spatial autocorrelation according to Moran's I index, either at the longitudinal ($I = 0.7790$, $P = 0.0845$) or latitudinal ($I = 0.0465$, $P = 0.8978$) geographic coordinates. Therefore, this result indicates that, in both cases, the occurrence points are randomly distributed. The best fitting model has a gain in AUC training of 0.910, an AUC of 0.908 and a standard deviation of 0.037. The evaluation value of AUC above 0.9 indicates that the model has a high ability to discriminate between sites with species presence versus sites where species is absent (background sites). Based on the seven WorldClim bioclimatic variables, in addition to the variables of land cover and altitude, the Maxent model predicts that the Pudu deer probabilities of occurrence in the study area varied between 0.0 and 0.9 (Table 1) and are shown in red scale in Fig. 3A. The Pudu deer distribution predicted by Maxent modelling covered an estimated area of 17,912 km^2 (24.1% of the area analysed), based on a probability of occurrence above 0.529, according to the threshold that maximises SSS (Table 1). These areas are highlighted in grey in the binary map (Fig. 3C). It can be observed that these areas are distributed mainly in the western sector of the Provinces of Valdivia, Ranco, Osorno and Llanquihue, on the eastern and western slopes of the Coastal mountain range, overlapping with sectors that currently contain extensive areas of native forest (Fig. 3B). There is also a high degree of overlap with extensive areas of either exotic tree plantations or mixed forest coverage (native and exotic). Furthermore, Ranco, Osorno and Llanquihue Provinces have areas with higher occurrence probability in the western slope of the Andes Mountain range. In the case of Chiloé and Palena Provinces, these higher occurrence areas are located in the northern part of the Province and in coastal areas, respectively. In addition, the SSS threshold value indicates that Osorno, Chiloé, Llanquihue and Ranco Provinces contain a large percentage of its total area, with higher occurrence probability of the Pudu deer, with 58.3%, 39.1%, 26.3% and 23.4%, respectively (Fig. 4). The environmental variables that most affect the current geographical distribution of the Pudu deer are Bio13 (relative contribution of 40.9%), Bio15 (34.5%) and Bio6 (11.2%) (Table 2). On the contrary, land cover and altitude variables combined contribute less than 4% of the model. A similar trend is observed for Bio13, Bio15 and Bio6 variables after jackknife analysis for model training gain reach a total maximum gain of 1.41, with variables Bio13 and Bio6 alone showing highest gains. When these variables are omitted, training gains are lowest, thus, revealing its importance in the model, i.e. the other variables provide scarce information (Table 2). The correlation analysis of variables that most affect the current geographical distribution of the Pudu deer and the probabilities of occurrence of the species in the study area indicates a strong significant positive association for Bio13 ($r = 0.654$, $df = 332991$, $P < 0.0001$), Bio15 ($r = 0.377$, $df = 332991$, $P < 0.0001$) and Bio6 ($r = 0.606$, $df = 332991$, $P < 0.0001$) variables.

Table 1. Occurrence probabilities and projected area for the current distribution of the Pudu deer in southern Chile.

Occurrence probabilities	Projected area (km^2)	Contribution (%)
0.0–0.1	6,401.0	8.6
0.1–0.2	5,438.3	7.3
0.2–0.3	8,652.6	11.6
0.3–0.4	13,628.9	18.3
0.4–0.5	17,545.7	23.6
0.5–0.6	13,676.0	18.4
0.6–0.7	7,056.0	9.5
0.7–0.8	17,14.4	2.3
0.8–0.9	182.6	0.2
0.9–1.0	0.0	0.0
Total	74,295.5	100
SSS threshold	17,912.0	24.1

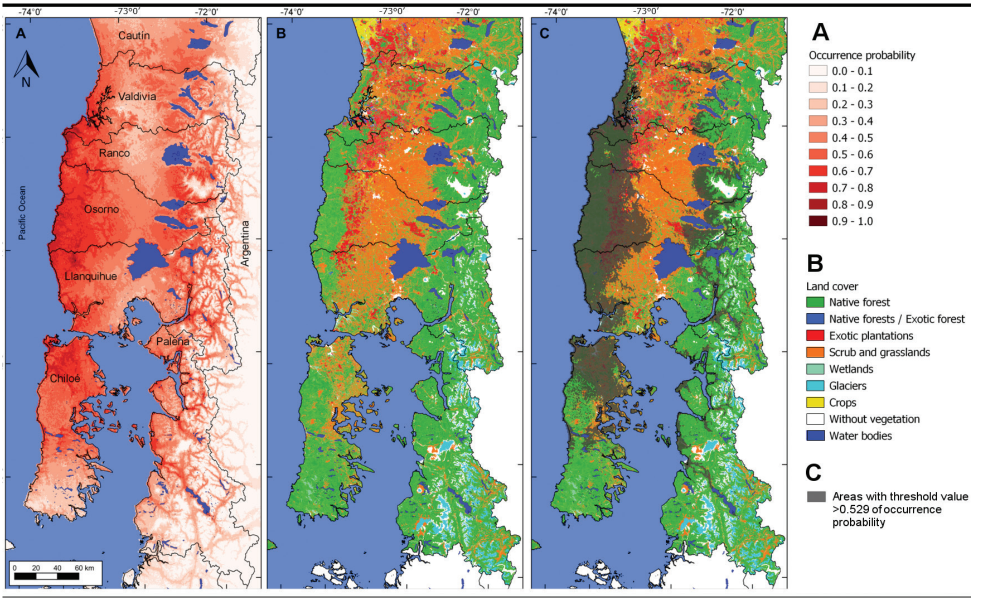

Figure 3. Projection of the fitted geographical distribution model of the Pudu deer in southern Chile. Projection under the current conditions (**A**), land use in the study area (**B**) and overlapping of suitable areas (grey areas) according to the SSS threshold value (> 0.529 of occurrence probability) on land use (**C**). In (**A**), red variations represent the predicted probability of suitable habitat conditions for the species.

Future geographical distribution

Since no projection data were available for land cover and altitude variable provided a limited contribution to the model, we excluded these variables when estimating the future geographical distribution of the Pudu deer. Thus, using the seven bioclimatic variables of WorldClim, Maxent predicts that the species currently develops over an area of 34,124.4 km^2 (SSS threshold value > 0.443), in environments whose habitat probabilities

Table 2. Estimates of relative contributions of the environmental variables to the Maxent model for the current geographical distribution of the Pudu deer in southern Chile.

Variable	Relative Contribution (%)	Permutation importance (%)	Jackknife of regularised training gain	
			With only variable	Without variable
Bio13	40.9	15.3	0.54	1.05
Bio15	34.5	11.0	0.37	1.00
Bio6	11.2	43.3	0.50	1.05
Bio18	4.0	14.2	0.51	1.08
Altitude	3.4	6.2	0.27	1.07
Bio3	2.8	7.4	0.18	1.03
Bio5	2.8	1.4	0.19	1.07
Land cover	0.5	1.3	0.02	1.08
Bio7	0	0	0.10	1.08

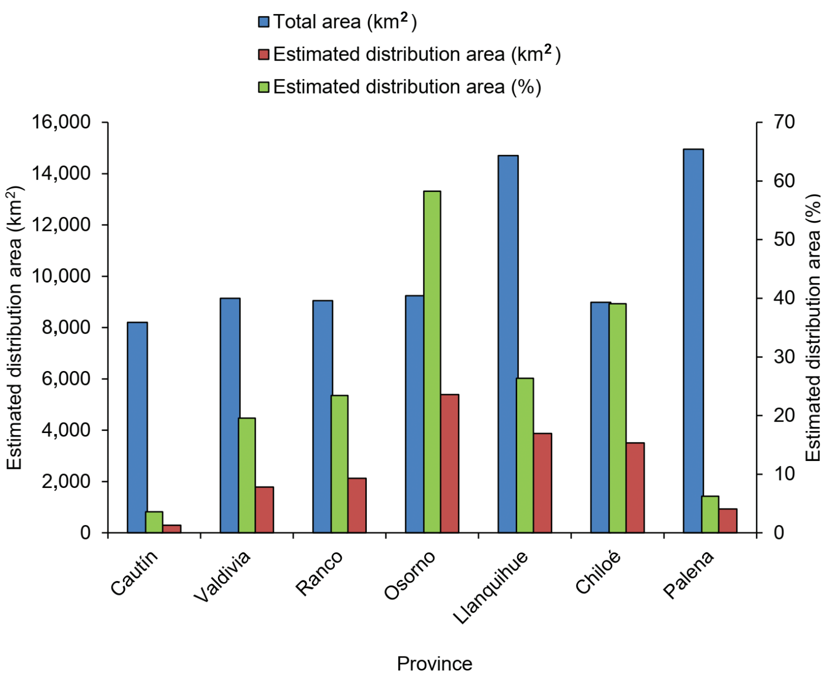

Figure 4. Bar chart representing the size of estimated current Pudu deer distribution areas in different Provinces of southern Chile. The estimated distribution area was determined as the areas with high probability of occurrence (> 0.529), based on the threshold that maximises the sum of sensitivity and specificity. Total areas of each Province and size of estimated distribution areas (km^2) are shown. Percentage of estimated distribution area with respect to total area of the Province is also indicated.

of occurrence fluctuated between 0.0 and 0.9 (Table 3 and Fig. 5). For projections to 2070 with global warming scenarios of 2.6 and 8.5 rcp, the geographical distribution area comprises 35,717.8 km^2 (SSS threshold value > 0.435) and 20,056.3 km^2 (SSS threshold value > 0.540), respectively. Thus, there is a slight increase of 4.7% for 2.6 rcp, but a strong reduction of 41.2% for 8.5 rcp, with respect to the prediction of the model for current geographical distribution (Table 3). In addition, the predictions suggest that, in the

Table 3. Probability ranges of occurrence of the Pudu deer in southern Chile for current conditions and projections for 2070 in two global warming scenarios.

Occurrence probabilities	Current potential distribution (km²)	2.6 rcp scenario		8.5 rcp scenario	
		km²	Reduction (%)	km²	Reduction (%)
0.0–0.1	6,900.7	6,346.1	-8.0	6,596.0	-4.4
0.1–0.2	6,273.2	5,269.9	-16.0	5,921.6	-5.6
0.2–0.3	9,043.1	8,351.5	-7.6	8,874.2	-1.9
0.3–0.4	11,776.0	13,073.4	+11.0	13,227.3	+12.3
0.4–0.5	15,874.9	16,063.0	+1.2	12,622.2	-20.5
0.5–0.6	14,521.2	15,389.5	+6.0	16,397.3	+12.9
0.6–0.7	7,271.4	7,076.3	-2.7	7,905.3	+8.7
0.7–0.8	2,348.5	2,391.0	+1.8	2,384.0	+1.5
0.8–0.9	286.5	334.4	+16.7	367.5	+28.3
0.9–1.0	0.0	0.0	–	0.0	–
Total	74,295.4	74,295.0	0.0	74,295.4	0.0
SSS threshold	34,124,4	35,717.8	+4.7	20,056.3	-41.2

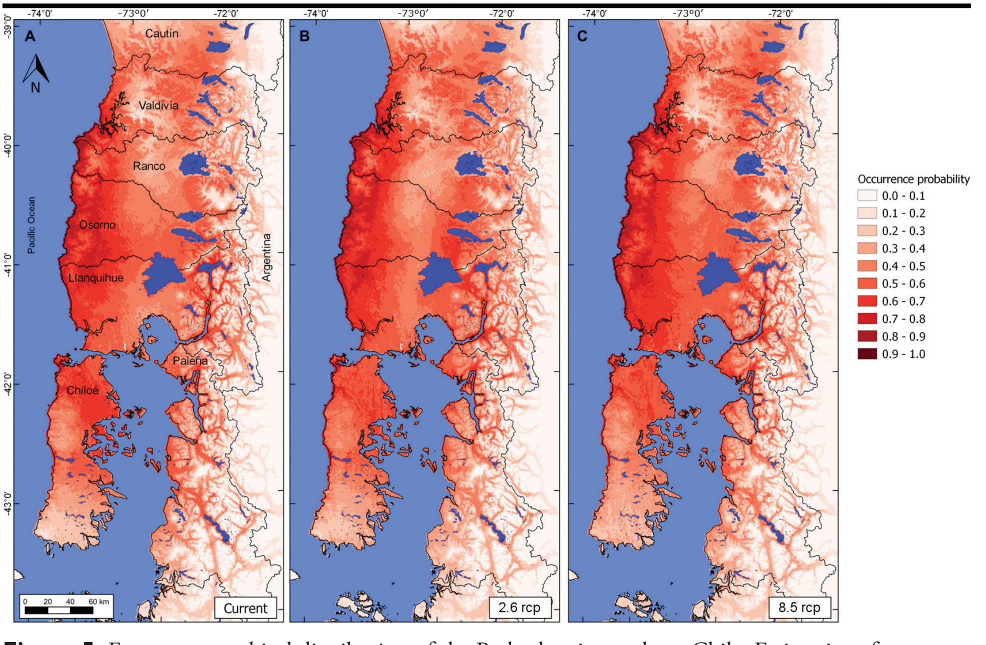

Figure 5. Future geographical distribution of the Pudu deer in southern Chile. Estimations for current conditions (**A**) and for projections to 2070 under 2.6 rcp (**B**) and 8.5 rcp (**C**). Red variations represent the predicted probability of suitable habitat conditions for the species.

future, areas with good habitability conditions will tend to increase. Thus, for example, under scenarios of 2.6 and 8.5 rcp and considering the highest probability of occurrence range from 0.8 to 0.9, there is an increase in area of 16.7% and 28.3% with respect to the 286.5 km^2 obtained in a similar probability of occurrence range with the current geographic distribution (Table 3). In addition, in both scenarios and taking into account the SSS threshold value, good habitability conditions currently observed in the west of Ranco, Osorno and Llanquihue Provinces and in the northern sector of the Province of Chiloé, will be maintained in the future (Fig. 6). These areas also coincide with sectors

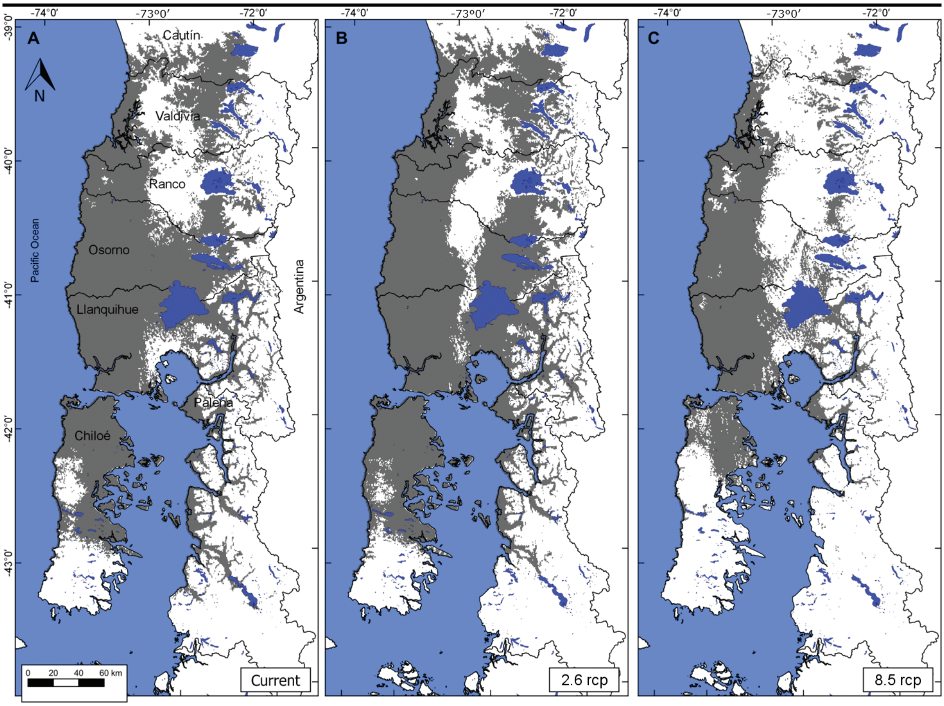

Figure 6. Binary maps showing future geographical distribution of the Pudu deer in southern Chile. Estimations for current conditions (**A**) and for projections to 2070 under 2.6 rcp (**B**) and 8.5 rcp (**C**). Grey areas represent the predicted probability of suitable habitat conditions for the species based on the SSS threshold value. SSS threshold values were as follows: > 0.443 for current scenario, > 0.435 for 2.6 rcp and > 0.540 for 8.5 rcp.

Table 4. Relative contribution of the environmental variables used to model the future geographical distribution of the Pudu deer in southern Chile.

Variable	Future 2070 with 2.6 rcp				Future 2070 with 8.5 rcp			
	Relative Contribution (%)	Permutation importance (%)	Jackknife of regularised training gain		Relative Contribution (%)	Permutation importance (%)	Jackknife of regularised training gain	
			With only variable	Without variable			With only variable	Without variable
Bio13	50.5	48.9	0.59	1.02	47.5	24.6	0.54	1.03
Bio15	28.1	4.7	0.31	1.03	26.3	5.1	0.26	1.02
Bio6	13.2	25.1	0.51	1.02	15.5	42.8	0.53	1.01
Bio3	3.3	7.1	0.11	1.02	6.3	17.3	0.12	0.98
Bio5	2.9	4.6	0.12	1.02	3.8	8.5	0.12	0.99
Bio7	1.2	0.8	0.10	1.07	0	0	0.12	1.04
Bio18	0.9	8.8	0.51	1.04	0.6	1.7	0.47	1.04

where native forest prevails. In contrast, towards the western sectors of the Andes mountain range (i.e. east of the Provinces), habitats for this species will present a low probability of occurrence. In order of importance, the variables that contribute most to the geographic distribution model for a scenario of 2.6 rcp are Bio13 (relative contribution of 50.5%), Bio15 (28.1%) and Bio6 (13.2%). The same variables contribute to the 8.5 rcp scenario as follows: Bio13 (47.5%), Bio15 (26.3%) and Bio6 (15.5%) (Table 4). The results of the jackknife analysis on the training gain of the model for these variables reach a total maximum value of 1.41 and 1.33 for the scenarios of 2.6 rcp and 8.5 rcp, respectively. In both scenarios, the environmental variables with highest gains are Bio13 and Bio6, which therefore, appear to contribute the most useful information by themselves. When they are omitted, a great decrease in the total gain of the models occurs (Table 4).

Discussion

Our prediction of the current geographical distribution of the Pudu deer was consistent with the habitat hypothesis proposed for the species in southern Chile by Pavez-Fox and Estay (2016). However, our results differed in terms of habitability probabilities, given that these were higher in certain geographical areas compared to those reported by previous authors. For example, we observed that, between 40°00' and 41°30' South (approx.) (i.e. at the latitudinal section of Ranco, Osorno and Llanquihue Provinces), the eastern and western slopes of the Coastal mountain range show high habitability conditions for the species (occurrence between 0.5 and 0.9). This high probability may be related to the fact that extensive native forest coverage still exists in this mountain range. In the same latitudinal section, but circumscribed to the Andes mountain range, we obtained areas mainly with low to medium-level probability of occurrence (from 0.2 to 0.5), both in the precordilleran and higher altitude sectors. On the contrary, Pavez-Fox and Estay (2016) found low or medium habitability categories for the Pudu deer in similar areas of the Coastal mountain range, while the central valleys, along with the western and eastern slopes of the Andes mountain range, presented better environmental conditions for the species. We estimate that these discrepancies may be related to the inherent variables used in both studies, such as sampling effort, number of records of the species, amplitude of the geographical area analysed and selection of environmental variables. Regarding sampling effort, since data came from different sources, it is possible that observers' bias may have occurred, affecting the occurrence points in the dataset. However, this effect is likely to have been minimal since records were obtained from public (e.g. Agricultural and Livestock Inspection Service) and private (e.g. Puyehue National Park) agencies with a wide experience in the conservation of native fauna. These institutions maintain reliable records of this type of fauna, both regarding species identification and the date and place where sighted. Moreover, to avoid species misidentification from other sources (e.g. El Diario Austral of Osorno), occurrence records were only considered positive when photographs or videos of the species were available. Other records included in the dataset are very accurate, since they were compiled either directly by us, using camera-trap and footprints or from literature (Delibes-Mateos et al. 2014; Pavez-Fox and Estay 2016; Sanino et al. 2016). Future actions aimed at compiling Pudu deer occurrence points in an online public database, curated by experts, should benefit geographical distribution studies of this cervid in Chile.

The potential distribution model shows that the areas with the best habitability conditions were located in the western Provinces of Ranco, Osorno and Llanquihue, overlapping with areas where the vegetation formations of the Valdivian Laurifolio Forest and Evergreen Forest of the Coastal Range predominate (Luebert and Pliscoff 2006). These native forest formations have been of great interest in terms of conservation efforts due to their status as a biodiversity hotspot and high level of endemism (Myers et al. 2000; Nahuelhual et al. 2007). However, despite their importance for the conservation of biodiversity in southern Chile, these forest formations have been exposed to a rapid rate of destruction and degradation due to anthropogenic causes (Myers et al. 2000; Echeverria et al. 2006, 2007). In fact, according to a study of historical reconstruction of vegetational cover and land use carried out by Lara et al. (2012), the loss of native forest, considering all vegetation formations registered in the regions of Los Ríos and Los Lagos, would be a consequence of its gradual replacement by grasslands and bushes (25% and 27%, respectively). This phenomenon would be more accentuated in the central valleys, located between the Andean and Coastal mountain ranges (Miranda et al. 2017). However, given that the eastern and the western slopes of the Coastal mountain range exhibit a lower degree of anthropic intervention, even though it is adjacent to valleys where there is greater agricultural and forestry activity, this geographical area, as identified in this paper, represents an ideal area for conservation of the Pudu deer. In fact, most of the records used in the modelling carried out in this study were taken from this area, which reflects its importance as an appropriate habitat for the survival of the species.

The AUC value above 0.9 suggests that our model describes the current potential of the Pudu deer distribution with a high degree of precision. Amongst the variables that mainly influenced probability of occurrence of the Pudu deer were precipitation of wettest month (Bio13), seasonality of precipitation (Bio15) and minimum temperature of coldest month (Bio6), which together contributed to 86.6% of the model. In contrast, Pavez-Fox and Estay (2016) reported that the most important variables in their prediction were seasonality in temperature (Bio4) and range of daytime temperatures (Bio7). This difference between the bioclimatic variables identified by both studies may be related to the size of the geographic area used in modelling. In our case, the area was smaller than that used by Pavez-Fox and Estay (2016), given that they analysed a geographic area spanning from 36° to 43° South latitude of Chile, including an adjacent area from Argentina and, therefore, lower environmental variability is to be expected. In addition, these authors used environmental variables obtained from modelling studies of other cervid species, whereas in our analysis, the environmental variables selected were those that presented low levels of collinearity in the study area. The considerable importance of the Bio13, Bio15 and Bio6 bioclimatic variables in our model could be related to some biological characteristics of the Pudu deer, such as habitat use and temperature tolerance. For example, wettest month precipitation could be related to vegetation availability throughout the year, since precipitation modulates the soil moisture and, therefore, the understorey growth in the temperate rainforest. Since this resource is used by the Pudu deer for feeding, cover and for escaping from threats (Jiménez 2010), the presence of temperate rainforest with a well-developed understorey throughout the year would enhance the Pudu deer abundance. In fact, Simonetti and Mella (1997) observed that stands with well-developed undergrowth in exotic plantations from central Chile, are important for Pudu deer abundance and that other medium-sized mammals. In the case of coldest month minimum temperature, this variable indicates that low temperature is relevant to the probability of occurrence of the Pudu deer. In fact, a medium-high positive correlation was found amongst both variables. This result suggests that this cervid is better adapted to low, rather than high, temperatures. Pavez-Fox and Estay (2016) obtained a similar result, where mean diurnal temperate range was negatively related to habitat suitability, i.e. this species would be intolerant to sudden changes in temperature throughout the day. Moreover, this result also concurs with data on the Pudu deer activity pattern, since minimal activity occurred in the daytime, when temperatures are higher than other periods of the day, such as dawn, dusk and night (Eldridge et al. 1987, Zúñiga and Jiménez 2018).

The evaluated climate change scenarios suggest that, in the future, Pudu deer would be prone to maintain their presence in large areas where habitability conditions are currently appropriate. However, as has been reported in other studies (e.g. Ortíz-Yusty et al. 2014; Holloway et al. 2016; Bruneel et al. 2018), this trend should be considered with caution, because Maxent modelling only relates records of the species with environmental variables, but not with other variables that may also have an impact on the distribution of species, such as geographical barriers, ecological interactions or particular requirements (Guisan and Zimmermann 2000; Soberon and Peterson 2005). Taking these restrictions into account, distribution models, projected for global warming increases of 2.6 and 8.5 rcp, indicate that most habitability areas will be conserved to the west of Ranco, Osorno and Llanquihue Provinces and in the northern sector of the Chiloé Province, with probabilities of occurrence greater than 0.5. This scenario will be more evident in the Coastal mountain range. In contrast, by 2070, several areas in the western slopes of the Andes Mountain range, that currently represent suitable habitats for the species, are expected to decrease. This process would lead to loss native forest quality as a result of environmental homogenisation. This homogenisation could be the result of the increase in variables, such as minimum temperature of the coldest month (Bio 6) and the decrease in precipitation of the wettest month (Bio13). It should be noted that the negative effects of temperature increase in models of potential distribution have been reported for other cervids, such as the Himalayan Musk Deer (*Moschus leucogaster*) and the Alpine Musk Deer (*Moschus chrysogaster*) (Khadka and James 2017; Lamsal et al. 2018). This effect is considered to be due the fact that temperature increase can negatively influence the quality and productivity of vegetation that maintains equilibrium in terrestrial ecosystems (Klein et al. 2007). In addition to the combined effect of these environmental variables on the future distribution of the Pudu deer, we must consider the process of native forest loss occurring in the southern-central Chile due to anthropogenic activities, given that this variable plays a key role in the conservation of the species (Silva-Rodríguez et al. 2011). It has been suggested that the net loss of native forest was lower in recent years compared to the 1970−1990 period (Smith-Ramírez 2004; Miranda et al. 2017). However, this process is likely to continue in the future due to the persistence of factors that are difficult to control, such as forest fires (González et al. 2011), continuous and unregulated felling of forests (Donoso et al. 2014), increase in the use of native trees as firewood for domestic and industrial heating (Gómez-Lobo 2005; Marín et al. 2011) and land use change (Lara et al. 2012). In this sense, conservation of the Pudu deer depends largely on the adoption of stricter regulations than those currently in existence in order to avoid future native forest degradation (Miranda et al. 2017), especially in those areas where habitability conditions for the species are optimal. This issue is especially important in areas where future distribution of the Pudu deer is projected, as is the case in western sectors of the Ranco, Osorno and Llanquihue Provinces, that include the Coastal range and to the north of the Province of Chiloé. Unfortunately, forest fragmentation in this geographic area is expected to continue in the future, based on the extrapolation to 2020 of the current deforestation rate recorded from 1976 to 1999 (Echeverria et al. 2008). Thus, this forest fragmentation process may constitute a major concern and could have potentially detrimental consequences for Pudu deer conservation under global climate change.

Conclusions

In contrast to the Andes mountain range, Maxent modelling predicted high probabilities of occurrence for the Pudu deer on the eastern and western slopes of the Coastal mountain range, located to the west of the Ranco, Osorno and Llanquihue Provinces, where extensive coverage of native forest persists, in addition to the northern sector part of the Province of Chiloé. In projections to 2070, with global warming scenarios of 2.6 and 8.5 rcp, this geographic area could conserve its habitability conditions that are currently appropriate for the species. Our prediction of potential Pudu deer geographical distribution is similar to the habitat identified for this species in southern Chile in a previous study. Since the Pudu deer is classified as Vulnerable in Chile, with a declining population size due to several factors, the distribution study performed here provides important data to identify specific geographic areas to develop conservation plans for this species. This is an important goal for the long-term conservation of the species.

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Supplementary material 1

Table S1

Authors: Nelson Colihueque, Aldo Arriagada, Andrea Fuentes

Data type: species data

Explanation note: Details of the occurrence points of the Pudu deer (*Pudu puda*) from southern Chile, including locality, coordinate, date, type of evidence and source.

Link: https://doi.org/10.3897/natureconservation.41.53748.suppl1

Supplementary material 2

Table S2

Authors: Nelson Colihueque, Aldo Arriagada, Andrea Fuentes

Data type: species data

Explanation note: Details of the occurrence points of the Pudu deer (*Pudu puda*) from southern Chile obtained from previous studies, including locality, coordinate, date and source.

Link: https://doi.org/10.3897/natureconservation.41.53748.suppl2