



Invading extreme environments: status of the invasion of the European hare *Lepus europaeus* in the Atacama Desert and the Andean highlands of the Southern Cone of South America

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Abstract The European hare *Lepus europaeus* has been widely distributed throughout the Southern Cone of South America. This geographical area contains extreme climatic environments, which are part of the South American Arid Diagonal. One is the Atacama Desert, known for its extreme aridity, and the other is the Altiplano Plateau, which rises 3700 m.a.s.l. These environments impose serious restrictions on the biota. After intensive sampling in these environments, we concluded that the invasion of this leporid is in a process of geographical expansion. On a macro scale, the presence of hares was correlated with the elevation, mean annual temperature, precipitation in the driest quarter of the year and temperature seasonality. On a local scale, their presence was associated positively with a topographic diversity index and agricultural zones (presence of irrigation canals). High-altitude environments have served as a propagation route for the hare, which has used valleys that descend the western Andean slope to the Pacific Ocean to invade areas in the Atacama Desert, both in Chile and Peru.

Keywords Altiplano · Chile · Distribution · Hare · Invasive species · Maxent

Introduction

In Chile, the Atacama Desert spreads over 1000 km of latitude and represents the southernmost portion of the Pacific coastal desert of South America (Chile and Peru). The desert extends from 5° to 27° S latitude (Arroyo et al. 1988). At altitudes above 2500 m, the Precordillera dominates, a mountainous landscape characterized by scrubland or “tolares”, and at 3700 m.a.s.l. gives way to the Altiplano Plateau, which extends from 15° to 28° S (Gregory-Wodzicki 2000). The Altiplano is shared by Peru, Bolivia, Argentina, and Chile.

Arid conditions have prevailed in this territory since the late Quaternary (Arroyo et al. 1988). From a biotic point of view, the lowest lands (<2500 m) are dependent on the summer precipitation that falls in the highest sectors of the Andes (South American Summer Monsoon), where a tropical bioclimate prevails with rainfall that reaches up to 300 mm/year at 5000 m.a.s.l., dropping to less than 20 mm/year at 2300 m.a.s.l., and at lower altitudes it can be less than 1 mm/year (Houston and Hartley 2003).

The dry conditions in the Atacama Desert impose important restrictions on living beings (adaptations) and have favored the development of endemism (Arroyo et al. 1988). Hence, invading species can

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have a significant impact on these fragile ecosystems. This has been the case of the rapid expansion of the rainbow trout *Oncorhynchus mykiss* (Pallas, 1778) in much of this territory (Lobos et al. 2020), which, for example, threatens fish and amphibians endemic to the area (Vila et al. 2013; Méndez and Correa 2008).

The European hare *Lepus europaeus* (Pallas, 1778) is a lagomorph native to Europe and Eastern Asia, which currently has non-native populations in new areas of Europe, the Australian Continent, and North and South America (Bock 2020). In South America, the hare was introduced in central Argentina (Cañada de Gómez in 1888, Tandil in 1897) and later in the province of Ultima Esperanza in Patagonian Chile (1896 or 1907) (Grigera and Rapoport 1983; Jaksic 2023). In South America, the hare has expanded to a large part of Argentina and Chile and has been recorded in Bolivia, Brazil, Paraguay, Peru, and Uruguay (Bonino et al. 2010). For Chile, until 2008, the Copiapó River was reported as the northern limit of this invasion, which represents a geographical separation between the arid Mediterranean environments and those of the Atacama Desert (Grigera and Rapoport 1983). However, Iriarte (2008) asserts that it would have been present in the high-altitude environments of northern Chile from the 1990s onwards (it is not indicated if there were samplings or it was by interviews), information subsequently used for more regional analyses (Bonino et al. 2010; Jaksic 2023).

Considering the paucity of knowledge regarding the hare invasion in the Atacama Desert and surrounding high-altitude environments, we elaborated an update on the geographical expansion of this invasion and analyzing the environmental factors that may explain the expansion of this leporid in these extreme environments of southern South America.

Methods

Study area

From 2001 to 2023, we conducted opportunistic sampling in northern Chile between the administrative regions of Arica-Parinacota and Atacama, from sea level to 4560 m.a.s.l. (260,324 km²). For this study, we considered the locations at $\leq 2,500$ m.a.s.l. as desert and above that limit as high-altitude environments (Precordillera and Altiplano Plateau). We also

considered some locations immediately south of the Copiapó River (peri-arid Mediterranean biome, the physiognomy of which corresponds to a bush desert) to provide a better geographical context of the invasion area. We survey 134 locations, of which 6.5% corresponds to the region of Arica-Parinacota (nine sampling locations), 16.2% to Tarapacá (21 locations), 48.4% to Antofagasta (54 locations) and 28.9% to Atacama (50 locations) (Appendix 1).

Distribution

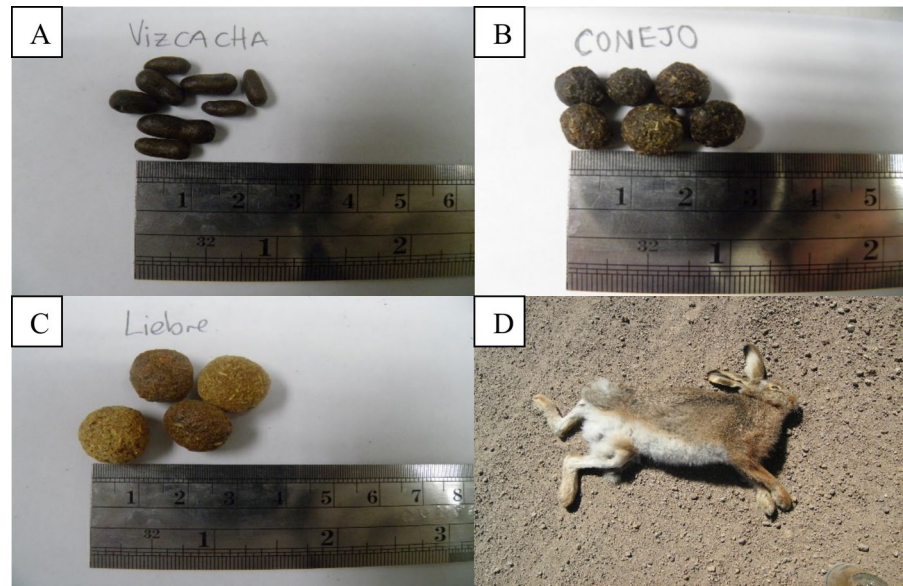
To obtain records, randomly distributed walks were carried out, which covered variable survey ranges and replicates (transects of 500 to 2,000 m long); with the participation of two specialists (Appendix 1). Hare sightings were obtained from feces, the presence of roadkill and direct observations. Additionally, we recorded the presence of *Lagidium viscacia* (Molina, 1782), a native rodent (0.9 to 1.6 k) that lives in rocky places, and of the European rabbit *Oryctolagus cuniculus* (0.9 to 1.8 k) (Linnaeus, 1758) (Fig. 1). The comparison of feces between hares and rabbits shows that the feces of the former are larger, both in length (13.1 ± 1.2 mm, $n=30$ vs. 8.8 ± 0.6 mm, $n=30$; $T=-11.4$, $p<0.01$), width (11.9 ± 1.1 vs. 7.7 ± 0.7 ; $T=-18.1$, $p<0.01$), and height (8.6 ± 0.8 vs. 6.1 ± 0.5 ; $T=-14.1$, $p<0.01$). Hares consistently have light brown feces; rabbits have dark green feces. Hares have feces with thicker fibers; rabbits have feces associated with latrines and holes in the ground (the hare does not make these holes). In terms of shape, hare feces are consistently oval, while in rabbits, they tend to be more rounded.

For a regional context, we performed a search for georeferenced information at <https://esa.journals.onlinelibrary.wiley.com/doi/full/https://doi.org/10.1002/ecy.3155>, which provides access to a database with distribution records of invading mammals present in South America, for countries with which Chile shares the Atacama Desert and high altitude environments.

Environmental factors related to the presence of hares

First, we performed a niche modeling, including records obtained in our study area (62 records) and a general background review for the two biomes (96 bibliographic records spaced by at least “1000” m

Fig. 1 Differentiation of feces of micromammals present in the study area. A Vizcacha *Lagidium viscacia* native rodent, B European rabbit *Oryctolagus cuniculus*, and C European hare *lepus europaeus*. In D, a record of a roadkill hare in Surire, Altiplano in Arica-Parinacota



between them to reduce spatial autocorrelation). We used 19 environmental predictor variables and an elevation layer (Giovanelli et al. 2008), all with a 30 arc-second resolution (available at <http://www.worldclim.org>). Additionally, we incorporated a layer based on the NDVI normalized difference vegetation index (use for quantifying the health and density of vegetation) and a human impact index (Sanderson et al. 2002), which were aligned and transformed to the previously indicated resolution. To select the most representative variables, we used a principal component analysis (PCA), where the first two axes quantified 97% of the variability, and then we reduced the redundancy between two variables by eliminating those that were highly correlated (Pearson correlation > 0.6). We used the version MAXENT 3.4.3 to model the ecological niche of the species (Phillips et al. 2006). To develop the model, we randomly selected 75% of the occurrence points and used the remaining 25% to validate the model. We evaluated the model performance using the Receiver Operating Characteristics Curve (ROC), which results by plotting the sensitivity values (the fraction of the true positives, against 1 minus the fraction of false positives, or specificity) for all the thresholds of the model. Herein, we applied the minimum training presence threshold; areas above this value are considered suitable. The area under the curve (AUC) of the ROC measures the ability of a model to discriminate between sites

where a given species is present and sites where it is absent. Values of the AUC equal to or less than 0.5 account for models with predictive discrimination abilities no better than random, equivalent to 1 account for models with perfect predictive power. Then, we used MAXENT models to identify the importance of each independent variable in explaining species distribution through a jackknife analysis (Phillips et al. 2006).

Second, to determine the factors explaining the presence/absence of the species at a local scale, we defined buffer areas of 500, 1000 and 5000 m around each location ($n = 134$); these spatial scales have been shown to be sensitive to explored land cover variables in hares, according to what was proposed by Caravaggi et al. (2015). We measure 8 topographical, ecological, and anthropic variables (Lobos et al. 2013; see Table 1); where an exploratory data analysis using Pearson's correlation coefficients did not detect high correlations between the covariates (> 0.6). To explore which variables were correlated with the presence of *L. europaeus*, we constructed generalized linear models with a binomial distribution (multiple logistic regressions). The presence/absence data for the species was utilized as a response variable of the topographic, ecological, and anthropic variables. We used a stepwise backward selection approach to find the best model and applied Akaike's Information Criterion for model selection. To develop the model, we used the R package.

Table 1 Topographic, ecological, and anthropic variables used in this study

Variables	Attributes
<i>Topographic</i>	
Elevation (ELE)	Central coordinates of each site, expressed in m.a.s.l., recorded in the field with GPS
Density of watercourses (DWC)	Sum of the length of watercourses (m) within each site, divided by the area of its polygon (km ²). Maps are available at http:// www.ide.cl
Topography diversity index (TDI)	Variety of topo-climate niches. Available at http://developers.google.com/earth-engine/datasets/catalog/CSP_ERGo_1_0_Global_SRTM_topoDiversity
<i>Ecological</i>	
NDVI	Based on the normalized difference vegetation index (NDVI). Maps are available at http:// www.ide.cl
<i>Anthropic</i>	
Road density (RD)	Sum of the length of roads (m) within each site divided by the area of the polygon (km ²). Maps available at http:// www.ide.cl
Density of irrigation canals (DIC)	Length of canals (m) at a site divided by the area of the polygon (km ²). Maps available at http:// www.ide.cl
Distance to a populated area (DPA)	Distance (m) to the closest populated area. Maps available at http:// www.ide.cl
Human impact index (HII)	Mean value of human influence index by Sanderson et al. (2002) for each site

Results

Distribution

The hare was recorded in 62 locations of a total of 134 (46.3%); with 43 records through feces, 15 from direct sighting and four from roadkill (Appendix 1). From south to north (Fig. 2), the region of Atacama contained the greatest level of invasion with 42 locations with presence (84%), in the region of Antofagasta 10 sites showed the presence of hares (18.5%), the region of Tarapacá had four locations with presence (19%) and in the region of Arica- Parinacota there was a record of hare in six locations (66.7%). In the desert biome, there were records of hares in 46.9% of the locations, while in high-altitude environments it was 45.7%. With respect to high-altitude environments, the records at the highest altitude were in Caspiche (site 96, 4560 m.a.s.l.) and Maricunga (S95, 4546 m.a.s.l.). The review for the countries bordering Chile (Fig. 2) shows little georeferenced information reported in scientific publications; however, the presence of the hare in all the countries that share these environments is noted. The desert and high-altitude environments in southern Peru shows an important occurrence of the hare.

On the other hand, associated with the presence of the hare, we had records of the rabbit *O. cuniculus*, but only in the Atacama region, at sites mainly

associated with the periarid Mediterranean region between 0 to 863 m.a.s.l. The presence of the native rodent *L. viscacia* was associated with the presence of hares at 24 locations, most over 2800 m.a.s.l.

Environmental factors related to the presence of the hare

For niche modeling, we considered 6 minimally correlated variables (Table 2). The jackknife analysis shows that the main variables contributing to the model were altitude, mean annual temperature, precipitation in the driest quarter of the year, and temperature seasonality. The model performed properly well (AUC=0.96). To discriminate between sustainable and unsustainable areas, we use the lowest prediction for a place in the presence of the species as the minimum threshold of presence. In this sense, some invaded locations have a low predictive value of 0.075 (Fig. 3).

On a local scale, the logistic regression models show that the presence/absence of hares was influenced significantly and positively by the topography diversity index at all scales and by density of irrigation canals in the model with a 5 km buffer (Tables 3 and 4). There were no significant effects of the rest of the variables and R^2 were < 0.3.

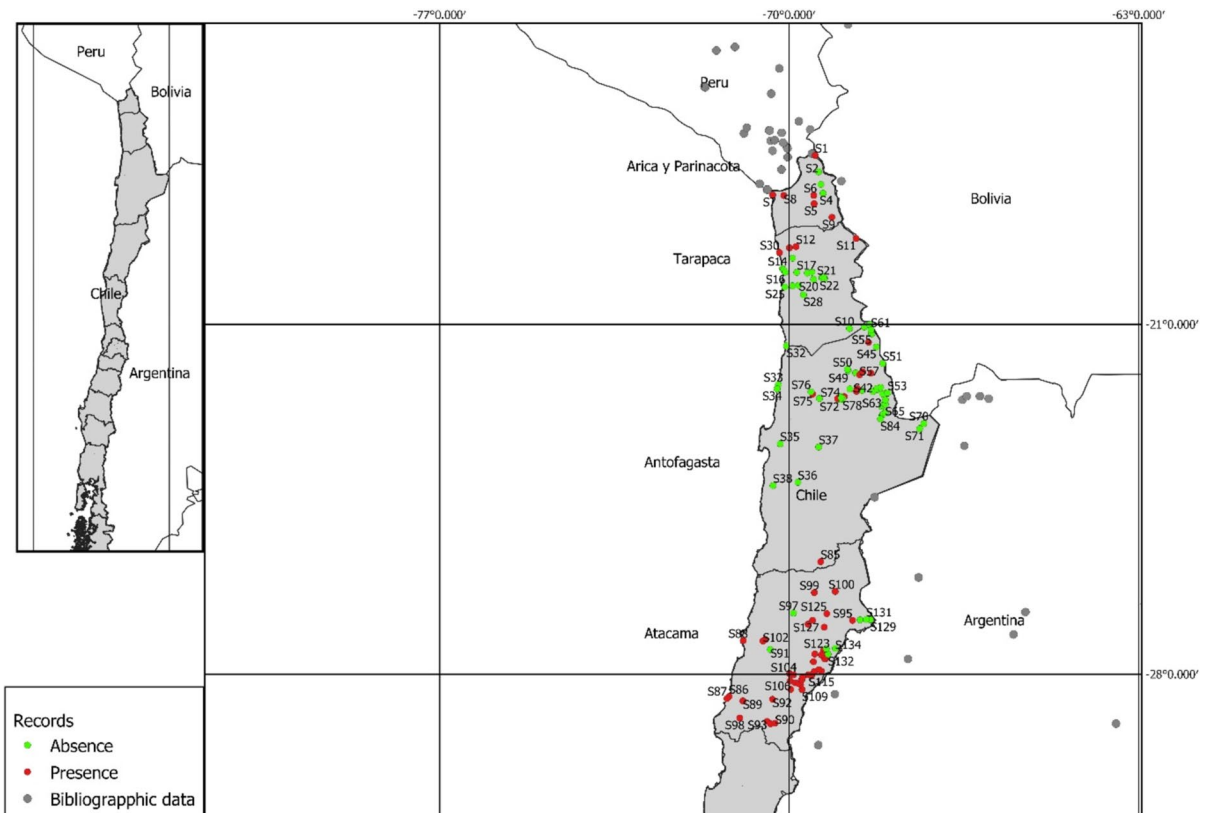


Fig. 2 Distribution of *Lepus europaeus* in the Atacama Desert and the Andean highlands of the Southern Cone of South America

Table 2 Variables that contained the most useful information according to the jackknife test for niche model of *Lepus europaeus* habitat suitability

Variables	Percentage contribution of variables
Elevation	33.7
Annual mean temperature	30.4
Precipitation of Driest Quarter	14.8
Temperature Seasonality	10.9
Precipitation of Warmest Quarter	7.7
Human Index Impact	2.6

Discussion

Until the 2000s, the presence of the hare in high-altitude environments and the Atacama Desert had not been reported formally in the scientific literature, although its presence was reported in the Chilean Altiplano by 1990 (Iriarte 2008) and in the coastal and high-altitude environments of Peru

between 1995 and 1998 (Zeballos et al. 2012). In the latter country, it is considered to have spread from the department of Tarija in Bolivia, on the border with Argentina (Cossíos 2004); however, it has also been suggested that it could have been from the Chilean coast, which would explain the early records in Tacna (Zeballos et al. 2012). Subsequent regional reviews (Bonino et al. 2010; Jakšić 2023) have suggested a continuous distribution in the Southern Cone. In this study, we observed that the high-altitude environments associated with the South American Arid Diagonal (with low rainfall, open environments, and the presence of scrub and grasslands) that extend in a NW–SE direction (Abraham et al. 2020) have been widely occupied by hares, favoring their dispersion towards the north of the continent and semiarid areas of central-eastern South America (Chaco and Cerrado domains) (Fig. 3). In the case of the Atacama Desert, its extreme aridity has hindered the establishment of the hare, so it is restricted to some oases, valleys

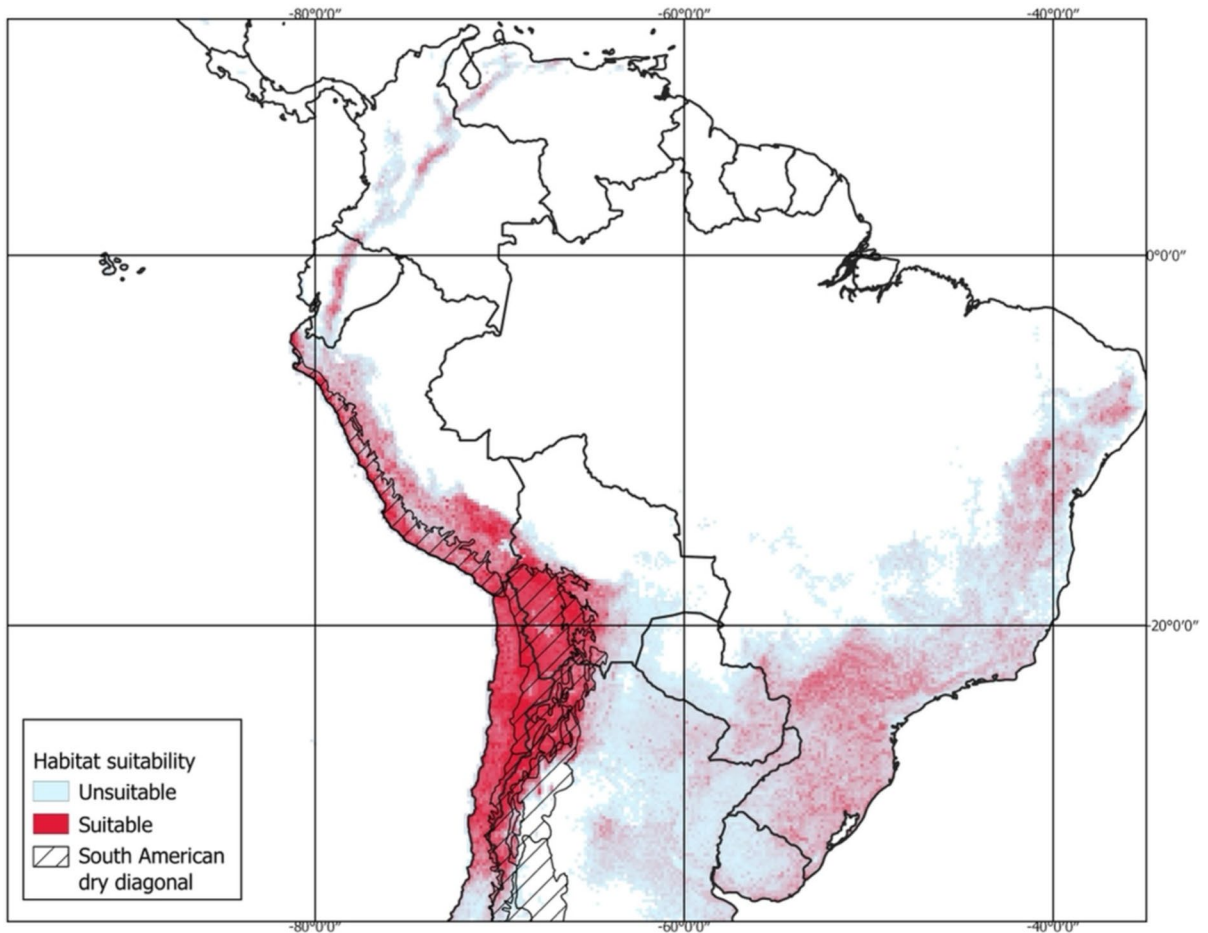


Fig. 3 Niche model for the invasion of *Lepus europaeus* is based on records from the Atacama Desert and the Andean highlands of the Southern Cone of South America. Red and blue colors represent suitable and unsuitable areas, based

on the minimum threshold of presence value (probability of occurrence ≥ 0.075). Diagonal arid according to Abraham et al. (2020)

with vegetation, and in the surroundings of cities such as Arica in Chile and Tacna in Peru, where agriculture is developed. The invasion of the Andean highlands has enabled dispersion flows through valleys that extend in an E-W direction, which have watercourses (vegetation) that drain towards the Pacific, in the Atacama Desert, like the valleys of the Copiapó River (Atacama region), Loa River (Antofagasta), Tana River (Tarapacá), and Lluta—Camarones (Arica and Parinacota). In these geographical regions, the hare is in an expansion process, thus, for example, in locations in the basin of the Loa River in the Antofagasta region (San Pedro River 1 S67, San Pedro River 2 S58, Chiu Chiu S60, Lasana S41, Yalquincha S59, Loa

River in South Coya S75), their presence was not recorded until at least 2020, a situation that changed by 2023, with a clear expansion from Bolivia.

When considering the area invaded by this species, niche modeling shows that the main factor related to its presence corresponds to the elevation (associated with the presence of scrub and grasslands). Second, there is the average annual temperature, which is low (11.9 ± 7 °C). Third, there is the precipitation of the driest quarter of the year (mean = 49.6 mm; minimum = 0 maximum = 353 mm); in this biogeographical region, rains are concentrated in summer season associated with the South American Monsoon, a precipitation event highly variable between years and locations (Houston and Hartley 2003). In its natural

Table 3 Comparison of generalized linear models for the evaluation of the determining factors of the presence/absence of *Lepus europaeus* in Chile’s area of invasion.

Models with buffer of 0.5 km		
Variables	AIC	R ²
TDI + ELE	123.7	0.17
DPA + TDI + ELE	125.0	0.18
DPA + TDI + ELE + NDVI	126.1	0.19
DPA + DWC + TDI + ELE + NDVI	127.6	0.19
DPA + DWC + RD + TDI + ELE + NDVI	129.6	0.19
DPA + DWC + RD + HII + TDI + ELE + NDVI	131.6	0.19
DPA + DIC + DWC + RD + HII + TDI + ELE + NDVI	133.6	0.19
Models with buffer of 1 km		
Variables	AIC	R ²
TDI + DIC	161.4	0.16
TDI + DIC + RD	162.3	0.17
TDI + DIC + RD + ELE	163.0	0.17
DPA + TDI + DIC + RD + ELE	163.8	0.15
DPA + TDI + DIC + DWC + RD + ELE	164.7	0.19
DPA + TDI + DIC + DWC + RD + ELE + NDVI	166.6	0.19
DPA + HII + TDI + DIC + DWC + RD + ELE + NDVI	168.2	0.19
Models with buffer of 5 km		
Variables	AIC	R ²
DIC + TDI + ELE	139.6	0.27
DIC + RD + TDI + ELE	140.0	0.28
DIC + TDI	141.3	0.25
DPA + DIC + RD + TDI + ELE	141.9	0.28
DPA + DIC + RD + TDI + ELE + NDVI	143.8	0.28
DPA + DIC + DWC + RD + TDI + ELE + NDVI	145.8	0.28
DPA + DIC + DWC + RD + HII + TDI + ELE + NDVI	147.6	0.28

The models with the lowest Akaike information criterion (AIC) were chosen as the best and are shown in bold. R² coefficient of determination. Abbreviations in Table 1

distribution range, mountainous environments usually are addressed as non-favorable for the hare, probably due the climatic conditions that are less benign to it, unlike the lowlands (Naldi et al. 2020). We believe that it is still premature to establish the geographical area that the hare will occupy, given that it is still in a process of expansion; nevertheless, the projection of the model reinforces that the South American Arid Diagonal (Andes Mountain range) has been a suitable environment for the species. Zeballos et al. (2012) indicate that the species should reach up to the northern limit of Perú; in our case, with records from a larger area, there is a probability that it will extend even further north following the Andes mountain range (Ecuador, Colombia, Venezuela) and that its presence will be consolidated throughout the southern Altiplano and other arid environments in South America.

At a more local level, hare (presence/absence) was positively associated with spatial heterogeneity (terrain slopes, undulations and humidity), which is a proxy for habitat quality and a comprehensive reflection of ecological suitability within a geographic region at all spatial scales (topographic diversity index). Instead, hare had a positive association with the density of irrigation canals (associated with agricultural development in this arid geographical area) only at the landscape (i.e. 5 km) scale. Other variables were not significant in our analysis, although the presence of valleys with river-related vegetation has facilitated their dissemination to the lowest areas of the western slope of the Pacific (Cossíos 2004).

In its natural habitat, the hare is considered a species that prefers open environments and where the anthropic transformation of the landscape would favor its dispersion. The same pattern (fields,

Table 4 The best models determining factors of the presence/absence of *Lepus europaeus* in Chile’s area of invasion at 0.5, 1 and 5 km buffer.

Variables	Model to 0.5 km			Model to 1 km			Model to 5 km		
	B	Z	p	B	Z	p	B	Z	p
Intercept	-0.85	-1.5	0.13	-1.8	-4.6	<0.01	-20.9	-3.6	<0.01
Topographic diversity index	34.06	4.3	<0.01	3.13	4.5	<0.01	39.1	4.6	<0.01
Elevation	-0.01	-1.8	0.08				-0.01	-0.7	0.49
Density of irrigation canals				0.01	1.8	0.06	0.02	2.8	<0.01

B is the coefficient of multiple regression, Z is the Z-test value, and p is the probability under the null hypothesis. Values in bold indicate significance

sugarcane plantations, and managed forests) that has been reported in its rapid expansion towards the southeast of Brazil (Pasqualotto et al. 2020). The presence of the hare in these extreme environments of South America is remarkable, considering that other invasive mammal species, such as rodents of the genera *Mus* and *Rattus*, have been unsuccessful in these settings (Lobos et al. 2005), always being recorded in association with a human presence. On the other hand, a second invasive leporid, the European rabbit *O. cuniculus*, has thus far failed to expand into these environments, only managing to invade as far as the Copiapó river basin, which separates the arid Mediterranean environments from the desert (Di Castri 1968). Although the feces of both species have similarities, it is possible to discriminate them according to morphological (size, shape, color, fiber thickness) and behavioral aspects (rabbits have feces associated with latrines and holes in the ground, and forms large social groups); this is reinforced by direct observations of these animals in the geographic areas of this study.

In terms of conservation, the expansion of the hare could be detrimental to the flora (interfering with the structure and composition of the vegetation) and create competition with native herbivores (Jaksic 2023 for a review). In this second case, we can mention the Vizcacha, a native rodent that lives in the rocky areas (inland cliff, mountain peak) of most of our study area between 700 and 5100 m.a.s.l. (Bernal 2016) and the *Chinchilla chinchilla* (Lichtenstein, 1829), an endangered species distributed between 3,000 and 6,000 m.a.s.l., with populations showing a serious decline (Roach and Kennerley 2016). The rapid advance of the hare in

this geographical area should be a matter of concern due to the high levels of endemism and threat of the biota that inhabit these extreme environments.

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Author contributions GL conceived the idea; NR and GL collected most data; NR organized the dataset and analyses; GL created the figures; GL wrote the first draft.

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Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

Ethics approval All research pertaining to this article did not require any ethics committee approval.

Appendix 1

Locations (sites) surveyed in this study. Regions: 1= Tarapacá, 2= Antofagasta, 3= Atacama; 15 Arica-Parinacota. Coordinates in UTM and Datum WGS 84. Records: 0= absence, 1= presence. No records (nr).

Localities	Sites	REGIONS	Coordinates		Elevation (masl)	Transsect number	<i>L. europaeus</i>	Type of register			Hare records		O. cuniculus	<i>L. viscacia</i>	
			East	North				Feces	Direct	Roadkill	2001–2008	2009–2015			2016–2023
Pisagua	S30	1	374815	7837038	70	3	1	1	0	0	nr	1	1	0	0
Tana 2	S13	1	395722	7847509	922	2	1	1	0	0	nr	1	nr	0	0
Tana 1	S12	1	409440	7850004	1132	3	1	1	0	0	nr	1	nr	0	0
Colchane	S11	1	535883	7868539	3727	1	1	0	0	1	0	0	1	0	1
Río Loa en Coya Sur	S75	2	445519	7523202	1208	2	1	1	0	0	0	0	1	0	0
Río San Salvador	S79	2	496819	7513640	1900	3	1	1	0	0	0	0	1	0	0
Ojos de Opache	S73	2	497788	7513253	1957	5	1	1	0	0	0	0	1	0	0
Yalquincha	S59	2	510799	7517614	2340	2	1	1	0	0	0	0	1	0	0
Chiu Chiu	S60	2	535860	7529549	2534	3	1	1	0	0	0	0	1	0	0
Lasana, Río Loa	S41	2	537657	7535350	2591	1	1	0	0	1	0	0	1	0	0
Camino a Ollague	S57	2	542379	7566362	3073	1	1	0	1	0	0	0	1	0	0
Río San Pedro 1	S67	2	548658	7573422	3285	3	1	1	0	0	0	0	1	0	1
Salar de Cárcote	S43	2	561125	7638464	3690	3	1	1	0	0	0	0	1	0	1
Río San Pedro 2	S58	2	565953	7569936	3757	2	1	1	0	0	0	0	1	0	1
Desembocadura Río Huasco	S86	3	284323	6851650	0	3	1	1	0	0	1	1	1	1	0
Huasco sur	S87	3	280244	6847034	50	3	1	1	0	0	1	1	nr	1	0
Río Copiapó	S88	3	310000	6976000	50	1	1	0	1	0	1	1	1	1	0
Serranía Poblete	S102	3	349104	6975677	233	1	1	0	1	0	1	nr	nr	1	0
Maitencillo	S89	3	311563	6842337	263	3	1	1	0	0	1	nr	nr	0	0
Piedra Colgada 1	S101	3	353894	6979282	265	1	1	0	0	1	1	1	nr	1	0
Tranque Lautaro	S103	3	402709	6904097	748	2	1	1	0	0	1	nr	nr	0	0

Localities	Sites	REGIONS	Coordinates		Elevation (masl)	Transsect number	<i>L. euro-paeus</i>	Type of register			Hare records		O. cuniculus	<i>L. viscacia</i>	
			East	North				Feces	Direct	Roadkill	2001–2008	2009–2015			2016–2023
Junta Río Manflas y Copiapó	S104	3	403946	6901921	1161	2	1	1	0	0	1	nr	nr	0	0
Río Jorquera	S107	3	409933	6901230	1325	3	1	1	0	0	1	nr	nr	0	0
Pinte	S90	3	375260	6793580	1450	3	1	1	0	0	1	nr	nr	0	0
Río Manflas 1	S105	3	403705	6887270	1470	1	1	0	1	0	1	nr	nr	0	0
Río Montosa 1	S108	3	413679	6883657	1662	3	1	1	0	0	1	nr	nr	0	0
San Felix	S93	3	359658	6797500	1945	3	1	1	0	0	1	1	1	0	0
Río Ramadillas	S113	3	426618	6890214	2092	3	1	1	0	0	1	1	nr	0	0
Quebrada San Andrés 1	S126	3	438469	7013830	2398	3	1	1	0	0	1	nr	nr	0	0
Río de la Sal	S99	3	450570	7083927	2532	1	1	0	1	0	1	1	1	0	0
Quebrada San Andrés 2	S127	3	447357	7022428	2668	1	1	0	1	0	1	nr	nr	0	0
Río Montosa 2	S109	3	427305	6868848	2800	1	1	0	1	0	1	nr	nr	0	0
Río Turbio 2	S120	3	449300	6930640	2814	1	1	0	1	0	1	nr	nr	0	0
La Pepa	S128	3	470496	7007483	3327	3	1	1	0	0	1	1	nr	0	0
Quebrada las Guanacas	S124	3	465004	6945674	3586	3	1	1	0	0	1	nr	nr	0	0
Vega Pircas Coloradas	S116	3	445457	6899132	3700	3	1	1	0	0	1	nr	nr	0	0
Mina Refugio	S123	3	469050	6955485	3900	1	1	0	1	0	1	1	nr	0	0
Mina La Coipa	S125	3	475585	7037305	4180	3	1	1	0	0	1	1	nr	0	0
La Japonesa, Vallénar	S98	3	305912	6804264	863	1	1	0	1	0	1	1	nr	1	1
Relincho	S92	3	369598	6846650	1622	4	1	1	0	0	1	nr	nr	0	1
Río Pulido 1	S111	3	420438	6882338	2013	1	1	1	0	0	1	nr	nr	0	1
Río El Potro	S110	3	424384	6879332	2014	3	1	1	0	0	1	nr	nr	0	1
Río Pulido 2	S112	3	426249	6889941	2095	1	1	1	0	0	1	nr	nr	0	1
Río Pulido 3	S114	3	428157	6895891	2353	1	1	1	0	0	1	nr	nr	0	1

Localities	Sites	REGIONS	Coordinates		Elevation (masl)	Transsect number	<i>L. europaeus</i>	Type of register			Hare records		O. cuniculus	<i>L. viscacia</i>	
			East	North				Feces	Direct	Roadkill	2001–2008	2009–2015			2016–2023
Agua de la Piedra, Jun-cal	S85	3	463085	7152475	2858	3	1	1	0	0	1	nr	nr	0	1
Río Manflas 2	S106	3	405083	6868962	2890	3	1	1	0	0	1	nr	nr	0	1
Río Figueroa	S121	3	451928	6947724	2904	3	1	1	0	0	1	nr	nr	0	1
La Hoyada	S94	3	366233	6792210	2906	3	1	1	0	0	1	nr	nr	0	1
Río Piracas Coloradas I	S115	3	440111	6901588	2999	3	1	1	0	0	1	nr	nr	0	1
Río Turbio 1	S119	3	460512	6913042	3159	3	1	1	0	0	1	nr	nr	0	1
Río Cachitos	S117	3	451259	6908684	3278	1	1	0	1	0	1	nr	nr	0	1
Río de la Gal-lina	S118	3	465366	6909647	3289	3	1	1	0	0	1	nr	nr	0	1
Salar de Ped-ernales	S100	3	492326	7086496	3467	3	1	1	0	0	1	1	1	0	1
Caspiche	S122	3	471030	6937429	4300	4	1	1	0	0	1	nr	nr	0	1
Maricunga	S95	3	526647	7022289	4546	1	1	0	1	0	1	1	1	0	1
Caspiche	S96	3	473133	6937345	4560	1	1	0	1	0	1	nr	nr	0	1
Desemboca-dura Río Luta	S7	15	359662	7964412	17	2	1	1	0	0	nr	1	1	0	0
Poconchile	S8	15	382955	7963233	411	3	1	1	0	0	nr	1	1	0	0
Tignamar	S5	15	447296	7945437	3204	3	1	0	1	0	nr	1	1	0	0
Chapiquina	S6	15	446395	7963953	3470	1	1	0	1	0	nr	1	1	0	0
Visviri	S1	15	449274	8052431	4090	1	1	0	0	1	0	1	1	0	1
Surire	S9	15	484884	7915436	4303	3	1	1	0	0	0	0	0	0	1
Caleta Buena	S14	1	381501	7801270	3	3	0	0	0	0	0	0	0	0	0
Alto Hospicio	S25	1	386604	7760420	538	3	0	0	0	0	0	0	0	0	0
Camino a caleta Buena 1	S16	1	387198	7793457	648	3	0	0	0	0	0	0	0	0	0
Camino a caleta Buena 2	S15	1	383609	7798691	732	3	0	0	0	0	0	0	0	0	0

Localities	Sites	REGIONS	Coordinates		Elevation (masl)	Transsect number	<i>L. euro-paeus</i>	Type of register			Hare records		O. cuniculus	<i>L. viscacia</i>
			East	North				Feces	Direct	Roadkill	2001–2008	2009–2015		
Pampa del Tamarugal 1	S28	1	425641	7743352	1001	1	0	0	0	0	0	0	0	0
Pozo Almonte 1	S26	1	402571	7763295	1029	1	0	0	0	0	0	0	0	0
Pozo Almonte 2	S27	1	415429	7764334	1051	1	0	0	0	0	0	0	0	0
Pampa del Tamarugal 2	S29	1	402313	7824398	1120	1	0	0	0	0	0	0	0	0
Camino a caleta Buena 3	S17	1	411339	7793160	1148	3	0	0	0	0	0	0	0	0
Huara	S18	1	433402	7791747	1174	3	0	0	0	0	0	0	0	0
Camino a Mamña	S20	1	446616	7777778	1304	3	0	0	0	0	0	0	0	0
Quebrada de Tarapaca	S19	1	443273	7793545	1321	3	0	0	0	0	0	0	0	0
Quebrada Quipisca	S21	1	464076	7781813	1903	3	0	0	0	0	0	0	0	0
Cerro Colorado 1	S23	1	464674	7780657	2134	1	0	0	0	0	0	0	0	0
Cerro Colorado 2	S24	1	467868	7782532	2311	1	0	0	0	0	0	0	0	0
Cerro Colorado 3	S22	1	469601	7779821	2348	1	0	0	0	0	0	0	0	0
Yuruguaico	S10	1	521701	7668824	4150	3	0	0	0	0	0	0	0	1
Desembocadura Río Loa	S32	2	390753	7630074	12	2	0	0	0	0	0	0	0	0
Punta Atalía	S34	2	372144	7534590	20	3	0	0	0	0	0	0	0	0
Caleta Viuda	S33	2	374547	7544225	131	4	0	0	0	0	0	0	0	0
Mejillones	S31	2	597805	7525713	150	3	0	0	0	0	0	0	0	0
Antofagasta norte	S35	2	379538	7413513	1015	3	0	0	0	0	0	0	0	0
Aguas blancas	S36	2	416271	7328381	1030	3	0	0	0	0	0	0	0	0

Localities	Sites	REGIONS	Coordinates		Elevation (masl)	Transsect number	<i>L. europaeus</i>	Type of register			Hare records		O. cuniculus	<i>L. viscacia</i>
			East	North				Feces	Direct	Roadkill	2001–2008	2009–2015		
Baquadano	S37	2	458284	7406842	1100	3	0	0	0	0	0	0	0	0
Antofagasta sur	S38	2	365653	7320730	1100	2	0	0	0	0	0	0	0	0
Río Loa en María Elena	S76	2	441887	7528241	1181	3	0	0	0	0	0	0	0	0
Río Loa medio	S77	2	459508	7513695	1317	3	0	0	0	0	0	0	0	0
Laguna Los Patos	S72	2	500470	7511186	2113	3	0	0	0	0	0	0	0	0
Río Loa Cascadas	S74	2	502147	7511299	2164	3	0	0	0	0	0	0	0	0
Río Loa en Calama	S46	2	503792	7511166	2194	3	0	0	0	0	0	0	0	0
Río Salvador	S47	2	505314	7518695	2231	3	0	0	0	0	0	0	0	0
Vertiente Licantatay	S80	2	504225	7515140	2235	1	0	0	0	0	0	0	0	0
Río Loa en Calama 2	S78	2	507371	7514011	2261	3	0	0	0	0	0	0	0	0
Vilama en salar de Atacama	S84	2	585002	7468188	2501	3	0	0	0	0	0	0	0	0
Chuquicamata	S39	2	522326	7534980	2573	3	0	0	0	0	0	0	0	0
Río Salado 1	S40	2	547793	7531501	2576	1	0	0	0	0	0	0	0	0
Río Salado 2	S66	2	578007	7535990	3085	1	0	0	0	0	0	0	0	0
Camino a Caspana	S42	2	569959	7528820	3128	1	0	0	0	0	0	0	0	0
Río Caspana 1	S62	2	578871	7533415	3174	3	0	0	0	0	0	0	0	0
Quebrada Potrero	S52	2	534316	7570381	3238	3	0	0	0	0	0	0	0	0
Tocorpuri	S69	2	595585	7510306	3271	3	0	0	0	0	0	0	0	0
Toconce	S68	2	585961	7538003	3280	3	0	0	0	0	0	0	0	0
Salar de Ascotán	S45	2	577430	7627803	3742	11	0	0	0	0	0	0	0	0
Río Caspana 2	S48	2	589551	7523578	3803	3	0	0	0	0	0	0	0	0
Aguas Calientes 1	S71	2	665173	7446282	4245	3	0	0	0	0	0	0	0	0

Localities	Sites	REGIONS	Coordinates		Elevation (masl)	Transsect number	<i>L. euro-paeus</i>	Type of register			Hare records		O. cuniculus	<i>L. viscacia</i>
			East	North				Feces	Direct	Roadkill	2001–2008	2009–2015		
Vilama 3	S81	2	588595	7476413	2742	1	0	0	0	0	0	0	0	1
Vilama 4	S82	2	590162	7478312	2845	1	0	0	0	0	0	0	0	1
Vilama 5	S83	2	594997	7481747	3178	1	0	0	0	0	0	0	0	1
Rio Grande sitio 1	S63	2	587812	7495410	3342	1	0	0	0	0	0	0	0	1
Rio Grande sitio 2	S64	2	589584	7498029	3475	1	0	0	0	0	0	0	0	1
Salard de Alconcha	S44	2	552463	7672244	3700	5	0	0	0	0	0	0	0	1
Río Machuca	S65	2	595199	7500834	3996	3	0	0	0	0	0	0	0	1
La Cantina	S49	2	518853	7575021	4000	3	0	0	0	0	0	0	0	1
Amincha	S56	2	567590	7656708	4000	3	0	0	0	0	0	0	0	1
Coska	S61	2	566514	7665935	4001	3	0	0	0	0	0	0	0	1
Quebrada Las Llaletas	S50	2	517217	7578428	4086	3	0	0	0	0	0	0	0	1
Quebrada La Perdiz	S51	2	590560	7591168	4100	3	0	0	0	0	0	0	0	1
Puquios	S54	2	563678	7677695	4100	3	0	0	0	0	0	0	0	1
Quebrada del Inca	S55	2	567070	7659619	4110	3	0	0	0	0	0	0	0	1
Vega El Tatio	S53	2	599985	7525797	4305	3	0	0	0	0	0	0	0	1
Vega de Tara	S70	2	673992	7457338	4326	3	0	0	0	0	0	0	0	1
Candelaria	S91	3	364080	6956968	1500	3	0	0	0	0	0	0	0	0
Inca de Oro	S97	3	409240	7038515	1661	3	0	0	0	0	0	0	0	0
Laguna Verde 3	S131	3	553961	7024369	4363	3	0	0	0	0	0	0	0	0
Laguna Verde 2	S130	3	541764	7023518	4463	3	0	0	0	0	0	0	0	0
Laguna Verde 1	S129	3	562206	7023815	4485	3	0	0	0	0	0	0	0	0
Laguna Negro Francisco 2	S133	3	474700	6959480	4180	3	0	0	0	0	0	0	0	1
Laguna Negro Francisco 1	S132	3	478408	6947500	4263	3	0	0	0	0	0	0	0	1

Localities	Sites	REGIONS	Coordinates		Elevation (masl)	Transsect number	<i>L. europaeus</i>	Type of register			Hare records		O. cuniculus	<i>L. viscacia</i>
			East	North				Feces	Direct	Roadkill	2001–2008	2009–2015		
Laguna Negro Francisco 3	S134	3	492566	6960113	4309	3	0	0	0	0	0	0	0	1
Camino a Colpitas	S2	15	456544	8016048	4180	2	0	0	0	0	0	0	0	1
Camino a Sutire	S4	15	466089	7968613	4340	2	0	0	0	0	0	0	0	1
Camino a Chungará	S3	15	461406	7988335	4412	2	0	0	0	0	0	0	0	1

References

Abraham EM, Rodríguez MD, Rubio MC, Guida-Johnson B, Gomez L, Rubio C (2020) Disentangling the concept of “South American Arid Diagonal.” *J Arid Environ.* <https://doi.org/10.1016/j.jaridenv.2019.104089>

Arroyo MTK, Squeo F, Armesto JJ, Villagrán C (1988) Effects of aridity on plant diversity on the northern Chilean Andes: Results of a natural experiment. *Ann Missouri Bot Gard* 75:55–78. <https://doi.org/10.2307/2399466>

Bernal N (2016) *Lagidium viscacia*. The IUCN Red List of Threatened Species 2016: e.T11148A22190789. <https://doi.org/10.2305/IUCN.UK.2016-2.RLTS.T11148A22190789.en>. Accessed on 15 September 2023.

Bock A (2020) *Lepus europaeus* (Lagomorpha: Leporidae). *Mamm Species* 52(997):125–142. <https://doi.org/10.1093/mspecies/sea010>

Bonino N, Cossíos D, Menegheti J (2010) Dispersal of the European hare *Lepus europaeus* in South America. *Folia Zool* 59(1):9–15. <https://doi.org/10.25225/fozo.v59.i1.a3.2010>

Caravaggi A, Montgomery WI, Reid N (2015) Range expansion and comparative use of insular congeneric lagomorphs: invasive European hares *Lepus europaeus* and Irish hares *Lepus timidus hibernicus*. *Biol Invasions* 17:687–698. <https://doi.org/10.1007/s10530-014-0759-1>

Di Castri F (1968) Equisse écologique du Chili. *Biologie de l’Amérique australe*. En: Debouteville CI & Rapaport (eds) Editions du centre national de la Recherche Scientifique. Paris, IV: 7–52.

Cossíos D (2004) La liebre europea *Lepus europaeus* (Mammalia, Leporidae) especie invasora en el sur de Perú. *Rev Peru Biol* 11(2):209–212. <https://doi.org/10.15381/rpb.v11i2.2458>

Giovanelli JGR, Haddad CFB, Alexandrino J (2008) Predicting the potential distribution of the alien invasive American bullfrog (*Lithobates catesbeianus*) in Brazil. *Biol Invasions* 10:585–590. <https://doi.org/10.1007/s10530-007-9154-5>

Gregory-Wodzicki K (2000) Uplift of the Central and Northern Andes: a review. *GSA Bull* 112:1091–1105. [https://doi.org/10.1130/0016-7606\(2000\)1122.0.CO;2](https://doi.org/10.1130/0016-7606(2000)1122.0.CO;2)

Grigera DE, Rappoport EH (1983) Status and distribution of the European hare in South America *J Mammal* 64(1):163–166. <https://doi.org/10.2307/1380771>

Houston J, Hartley AJ (2003) The central Andean west-slope rainshadow and its potential contribution to the origin of hyperaridity in the Atacama Desert. *Int J Climatol* 23(12):1453–1464. <https://doi.org/10.1002/joc.938>

Iriarte JA (2008) *Mamíferos de Chile*. Lynx Ediciones, Barcelona, p 521

Jaksic FM (2023) Historical ecology and current status of the European hare *Lepus europaeus* in South America: a new species in new countries. *Stud Neotrop Fauna Environ.* <https://doi.org/10.1080/01650521.2023.2217064>

Lobos G, Ferrer M, Palma RE (2005) Presencia de los géneros invasores *Mus* y *Rattus* en áreas naturales de Chile: un riesgo ambiental y epidemiológico. *Rev Chil Hist Nat* 78(1):113–124. <https://doi.org/10.4067/S0716-078X2005000100008>

- Lobos G, Cattán P, Estades C, Jaksic FM (2013) Invasive African clawed frog *Xenopus laevis* in southern South America: key factors and predictions. *Stud Neotrop Fauna E*. <https://doi.org/10.1080/01650521.2012.746050>
- Lobos G, Saez P, Villablanca R, Prado M, Cruz-Jofré F, Fibla P, Méndez MA (2020) Invasion of salmonids in the Puna and Southern Chilean Altiplano: patterns and threats to the biodiversity. *BioInvasions Rec* 9(4):853–864. <https://doi.org/10.3391/bir.2020.9.4.19>
- Méndez M, Correa C (2008) Diversidad de especies: Anfibios. In: Comisión Nacional del Medio Ambiente (ed), Biodiversidad de Chile, Patrimonio y Desafíos. Ocho Libros Editores, Santiago de Chile, pp 284–289
- Naldi L, Ilaria G, Ferretti M, Zaccaroni M (2020) Density estimates and habitat preferences of the European hare (*Lepus europaeus*) on mountainous areas in Italy. *Mammal Study* 45(2):1–9. <https://doi.org/10.3106/ms2019-0057>
- Pasqualotto N, Boscolo D, Vesiani NF, Paolino RM, Rodrigues TF, Krepšči VG, Chiarello AG (2020) Niche opportunity created by land cover change is driving the European hare invasion in the Neotropics. *Biol Invasions*. <https://doi.org/10.1007/s10530-020-02353-y>
- Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. *Ecol Modell* 190:231–259. <https://doi.org/10.1016/j.ecolmodel.2005.03.026>
- Roach N, Kennerley R. (2016) *Chinchilla chinchilla*. The IUCN Red List of Threatened Species 2016: e.T4651A22191157. <https://doi.org/10.2305/IUCN.UK.2016-2.RLTS.T4651A22191157.en>. Accessed on 15 September 2023.
- Sanderson EW, Jaiteh M, Levy MA, Redford KN, Wanneb AV, Woolmer G (2002) The human footprint and the last of the wild. *Bioscience* 52:891–904. [https://doi.org/10.1641/0006-3568\(2002\)052\[0891:THFATL\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2002)052[0891:THFATL]2.0.CO;2)
- Vila I, Morales P, Scott S, Poulin E, Véliz D, Harrod C, Méndez MA (2013) Phylogenetic and phylogeographic analysis of the genus *Orestias* (Teleostei: Cyprinodontidae) in the southern Chilean Altiplano: the relevance of ancient and recent divergence processes in speciation. *J Fish Biol* 82:927–943. <https://doi.org/10.1111/jfb.12031>
- Zeballos H, Medina C, Pino K, Mejía-Ríos A, Pari A (2012) La liebre europea *Lepus europaeus* (Lagomorpha: Leporidae) una especie invasora en el Perú. *Rev Peru Biol* 19(3):267–273. <https://doi.org/10.15381/rpb.v19i3.1120>

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