scientific reports

OPEN

The ecological roles of the European rabbit in the Magellanic/Fuegian ecosystem of southernmost Chile

Francisca Mann-Vollrath[1,2,7], Jennifer Paola Correa-Cuadros[1,2,7]✉, M. Isidora Ávila-Thieme[1,3,4,5], Melanie Duclos[6] & Fabian M. Jaksic[1,2]

The European rabbit has invaded numerous ecosystems worldwide, but rarely steppes. Since its various introduction attempts into the ecosystems of the Magallanes/Fuegian region, the rabbit has become a key player, interacting with species at different trophic levels and generating impacts on ecosystems. To better understand the role of the rabbit in steppe and scrub ecosystems, we characterised the food web in the Magallanes/Fuegian region to understand the identity of their interacting species, the mechanisms and complexities of their interactions to demonstrate that rabbit management may become more complex than just controlling a single species. Based on a bibliographic review and wildlife specialists' opinions, we built the Magellanic/Fuegian food web, evaluated their topological properties and performed a rabbit extinction simulation to assess the possible short-term ecological mechanisms operating in the community. We found that the network had 206 nodes (64% native, 13% exotic, and 22% mixed) and 535 links among nodes. The European rabbit was the most connected node of the food web, had the second largest dietary breadth, and ranked as the seventh prey item with more predators. A rabbit extinction simulation shows a possible release of herbivory pressure on plants, including that on several native plants (e.g., *Gunnera tinctoria*, *Pratia repens*, *Gavilea lutea*, *Tetroncium magellanicus*), and a possible release of competition for some herbivores that share resources with the rabbit (e.g., *Ovis aries*, *Lama guanicoe*, *Bos taurus*). Although rabbit predators have a broad and generalist diet, some such as the native *Galicitis cuja*, could face a 20% reduction in their trophic width and could intensify predation on alternative prey. These results show that the European rabbit is strongly embedded in the Magellanic/Fuegian ecosystem and linked to several native species. Therefore, rabbit management should consider ecosystem approaches accompanied by monitoring programs on native fauna and experimental pilot studies on native flora to conserve the Chilean Patagonia community.

Keywords Chilean Patagonia, Community effects, Conservation, Food web, Magallanes region, *Oryctolagus cuniculus*

The European rabbit (*Oryctolagus cuniculus*) is native to the Iberian Peninsula (and perhaps also northern Africa), which has colonised almost everywhere in the world since the times of the Roman Empire[1,2]. The first record of rabbit introduction to America—specifically to Isabela Island, now Santo Domingo—dates back to November 1493[3]. Although it is currently classified as an endangered species in its native lands[4,5], it has become one of the most damaging invasive species in the world[6]. The first reference to rabbits in central Chile was by Ignacio Molina in 1788[7], but Delibes and Delibes-Mateos[8] provided an earlier date: 1765 in Tierra del Fuego Island, in the extreme south of the continent, now shared by Argentina and Chile. Currently, the rabbit has a

[1]Pontificia Universidad Católica de Chile, Facultad de Ciencias Biológicas, Mención Ecología, Santiago, Chile. [2]Center of Applied Ecology and Sustainability (CAPES), Santiago, Chile. [3]Present address: Escuela de Negocios, Facultad de Ciencias Sociales y Artes, Universidad Mayor, Temuco, Chile. [4]Center for Resilience, Adaptation and Mitigation (CReAM), Universidad Mayor, Temuco, Chile. [5]Instituto Milenio en Socio-Ecología Costera (SECOS), Santiago, Chile. [6]Centro de Investigación para la Sustentabilidad, Universidad Andrés Bello, Santiago, Chile. [7]These authors contributed equally: Francisca Mann-Vollrath and Jennifer Paola Correa-Cuadros. ✉email: jpcorrea4@uc.cl

discontinuous distribution from the Atacama to Los Lagos regions and then to the Magallanes region[7,9–12]. However, some uncommon records of rabbits (sightings) have been reported in the Arica y Parinacota and Tarapacá regions (personal communication).

The Magallanes region extends from the Pacific Ocean (48° 36′ to 56° 30′ S, 66° 25′ to 75° 40′ W) eastwards across the Strait of Magellan and halfway to Tierra del Fuego Island (52°–56° S, 63°–73° W)[13,14]. The introduction of rabbits was attempted several times from 1873–1874 to 1913, but none of these introductions bore fruit, and it was the one of 1936 that generated the rabbit outbreak of 1950–1952[11,12,15]. Once well established, its population grew rapidly due to the rabbits' high reproductive capacity, along with a negligible predation impact by their potential predators because of low population density derived from hunting for their skins[11,12,15,16]. Subsequently, the high rabbit population in the Magallanes region generated an economic income due to commercialisation of their meat and skins[7,17,18], but also had serious consequences for ranchers for their competition for forage with sheep and thus transforming grasslands into wastelands[7,11,12,15]. This led to various control efforts, the most effective being that of 1953, when the myxoma virus was introduced to Tierra del Fuego Island[11,12,15,19], which—although reducing the rabbit population by 99%[11,12,20]—failed to eradicate it. The individuals that survived possibly developed viral resistance[19], and today rabbits are still found in both continental and insular areas of the Magallanes region[11,12].

The rabbit in Chile is considered an invasive species that causes significant damage, generating a loss of 3.25 million US dollars per year[9,21] and numerous ecological effects at the population, community, and ecosystem levels, summarized by Correa-Cuadros et al.[11,12]. The long history of rabbit invasion (since the XVIII century)[7,8] means that it has become an integral part of the Magellanic/Fuegian ecosystem, interacting with species at different trophic levels, simultaneously being prey, herbivore, and competitor[11,12]. Rabbits in continental Magallanes and neighbouring Tierra del Fuego Island consume plant biomass and cause important negative impacts on their abundance[22,23]. They feed on seedlings of various native shrubs and trees (e.g., *Berberis* and *Nothofagus*) and non-native herbs (e.g., *Poa* and *Vicia*), thus affecting their regeneration[22–24]. Plants not consumed by rabbits spread and generate changes in the ecosystem[24,25]. In addition, rabbit burrows increase soil erosion[11,12,26]. Rabbits also have negative impacts on sheep production by consuming the forage available for livestock, thus reducing the output of meat and wool for export[11,12,24,25]. They also compete with native mammals for food and habitat (e.g., *Lama guanicoe, Oligoryzomys longicaudatus*) and favour the population increase of predators and scavengers by being a subsidy of abundant prey[27–29]. Among several other Magellanic/Fuegian predators, the puma (*Puma concolor*), *Lycalopex* foxes, *Leopardus* cats, and birds of prey such as hawks, incorporate rabbits as staple prey to their diet[30,31]. Also, facultative scavenging bird species such as the Buzzard eagle (*Geranoaetus melanoleucus*) and caracaras (*Caracara plancus* and *Milvago chimango*), and strict scavengers such as the Andean condor (*Vultur gryphus*) benefit from rabbit presence[32]. Thus, the rabbit has become a key species (herbivore, competitor, and prey) of the regional food web.

Given the overwhelming evidence of the multiple types of damage generated by invasive species[33], such as the European rabbit[5,11,12], it cannot be overlooked that the rabbit is now functionally integrated into several ecosystems and interacts with multiple species[27–29,34–36]. Therefore, a change in its abundance (e.g., a decrease) can spread through trophic interactions and affect the species with which it interacts both directly and indirectly[37,38], triggering impacts such as release of herbivory for plants, decreased competition for herbivores, or switching prey in predators, among others[28,29,36,37,39–42].

The Magellanic/Fuegian communities face multiple threats due to anthropogenic activities (e.g., hydrocarbon development, grazing pressure, wildfires, and exotic species[23,43,44]), and it thus seems necessary to understand the role that the rabbit plays in the regional ecosystem. One way to study this is through a multi-trophic food web approach[45], which takes a picture of species' positions in different trophic levels across a wide range of direct and indirect interactions and describes trophic relationships and their complexity[46,47]. This community picture of multiple interactions plus node extinction simulations enables the understanding of how a given disturbance (e.g., management or eradication of invasive species) may affect the presence and abundance of each node of the local food web[46,48–52]. Thus, a multi-trophic approach is a complementary and holistic tool to make more informed decisions for developing any management of an invasive species, identifying the non-target species that may be affected, and thereby generating early warnings against unwanted impacts.

Therefore, our objective is to elucidate the extent to which the rabbit is currently embedded into the food web of the Magellanic/Fuegian steppe and scrub ecosystem, with which species it interacts, and hypothesise the possible short-term effects that can be triggered if the rabbit is managed. With this theoretical information, this study seeks to highlight the complexity and potential consequences of rabbit management on the community network and to recommend an ecosystem approach rather than a single-target approach to safeguard against unwanted ecological impacts on other species.

Materials and methods

Study site

The Magallanes region is centred at ca. 53° S and 71° W (ranges 48° 40′–56° 00′ S and 66° 30′–75° 40′ W) and comprises 132,297 km^2 excluding the Antarctic territory[14]. The corresponding adjective is Magellanic[13]. Geographically, there is a west-northerly continental portion, separated from an extensive east-southerly archipelago by the Strait of Magellan. The largest island of that archipelago is Tierra del Fuego Island (Isla Grande de Tierra del Fuego, in Spanish), situated within a polygon ca. 52°–55° S and 65°–72° W. This large island (ca. 48,000 km^2) is split east–west between Argentina and Chile (40:60, respectively) at meridian 68° 34′ W. The corresponding adjective is Fuegian[13]. The surrounding archipelago contains seven medium-sized islands (Hoste, Santa Inés, Navarino, Dawson, Aracena, Clarence, and Staten; ranging from 4100 to 500 km^2 in decreasing sequence), and ca. 3000 smaller islands and islets, most of them located to the southwest of Tierra del Fuego Island (Argentina's Staten Island excepted) and thus are in Chilean territory.

The Magallanes region (Fig. 1) harbours three major climates[53]: temperate cold rainy (mean annual temperature 6 °C and mean annual rainfall 3000 mm), cold steppe (short and cool summers and slightly cold winters, mean annual rainfall of 500 mm), and high ice (mean monthly temperature not higher than 0 °C and annual snowfall 1000–3000 mm). It is divided into three major biomes[54–56]: the Andean-Patagonian forest biome, the Evergreen forest and peat bog biome, and the Patagonian steppe and scrub biome. The first consists of deciduous forests, with woodland physiognomy and a slight herbaceous layer. The lenga (*Nothofagus pumilio*) is the characteristic tree of this biome, together with the canelo (*Drimys winteri*), and the coihue (*Nothofagus betuloides*). The Evergreen forest and peat bog biome, also has a woodland aspect with *Nothofagus* trees and peat bogs of *Sphagnum magellanicum* as representative species. The Patagonian steppe and scrub biome is characterised by low-shrub vegetation, herbs, and grasses. The rabbit is present chiefly in the latter biome[57].

The Magallanes region has ca. 58% of its surface within the Chilean System of Protected Wilderness Areas (SNASPE, in Spanish), because it harbours a high number of unique species[13,14,54]. Among the productive activities of the region are sheep farming (56% of the national total), artisanal and industrial fishing, aquaculture, tourism, and forestry[58]. According to the national inventory of species of the Ministry of the Environment, the region harbours 176 species of animals and 242 species of plants[54,59].

Food web construction

A bibliographic review was carried out through Google Scholar, Scopus, Web of Science, and other search engines for scientific publications or technical reports (but not abstracts), including theses, journal articles, books, and book chapters. Keywords such as south, southern, southernmost, Magallanes, Patagonia, Tierra del Fuego, Chile, diet, species genus (e.g. *Oryctolagus*, *Lama*, *Alopecurus*), species common name (e.g. Rabbit, Guanaco, Mariano),

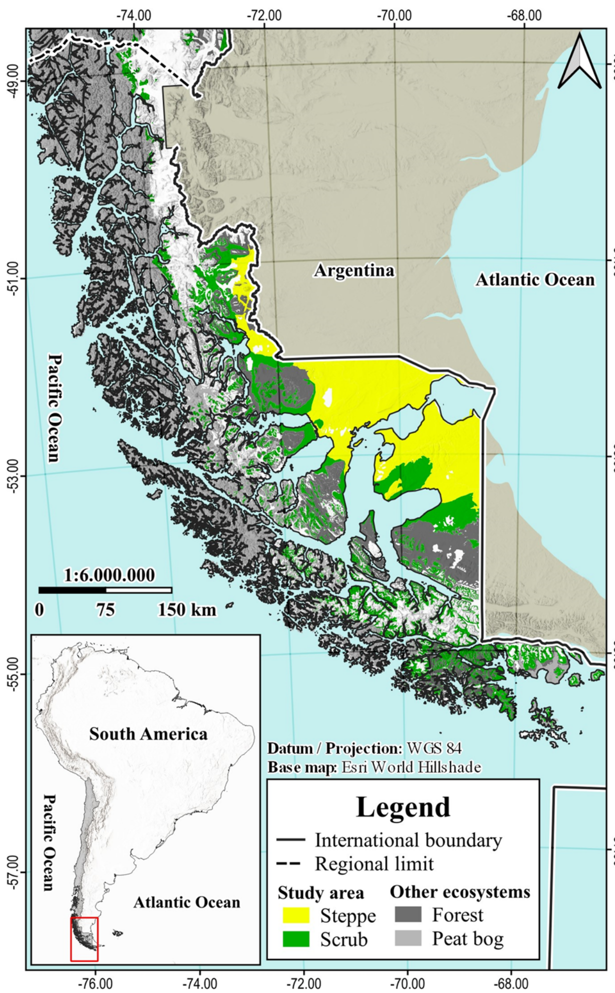

Fig. 1. The Magellanic/Fuegian ecosystems in southernmost Chile. The steppe and scrub biome was the main study area used to build the food web. The whole region has 48 million hectares: the pure steppe has 2.5 million ha and the scrub has 14 million ha (Universal Transversal de Mercator, Datum WGS84, Zone 18S). *We have a copyright holder to publish it under a CC BY open-access license.

species scientific name (e.g. *Oryctolagus cuniculus, Lama guanicoe, Alopecurus magellanicus*) were searched in English and Spanish languages, solely or in combination.

To build a Magellanic/Fuegian food web, literature was first searched based on the diet and trophic relationships of the species directly connected to the rabbit (i.e., carnivores and scavengers that consumed rabbits and those plants that the rabbit consumed). Second, we expanded the network by looking for the predators and prey of each rabbit interaction. Third, the predators and prey of each new species that appeared during the expanding network process were searched for. Fourth, the last step was repeated until no new information could be found (whether they were new species or new trophic interactions). Each new node was searched for its consumers and basal resources (Table 1 Supplementary material) and information was added on diet studies from neighbouring Patagonian regions of Chile and Argentina, which shared similar/same ecosystems and species. Still, Argentinean Patagonia food web construction was excluded because Chile and Argentina differ in policies and regulations (e.g., legal hunting of native carnivores, different policies among provinces, lack of unified control measures against invasive herbivores[36]). Additionally, the two countries have different management practices, and the main focus of this paper is to demonstrate the high integration of rabbits in Chilean ecosystems. The results will be useful for future management actions and national control policies.

Additionally, to verify the bibliographic register, to confirm predator–prey relationships, and to estimate missing trophic links, we consulted with wildlife specialists, managers and field technicians from CONAF-Magallanes (National Forestry Corporation) and SAG-Magallanes (Agricultural and Livestock Service). Simultaneously, the list of species was compared with the National Species Inventory (https://especies.mma.gob.cl/CNMWeb/Web/WebCiudadana/Default.aspx)[59], where searched information data to species for which had not found diet.

During the bibliographic search, we observed that diet analyses had different taxonomic resolutions of prey, generating shortcomings in constructing the trophic network. For example, some publications reported predators that consumed "passerines" versus those identifying passerine species (e.g., *Zonotrichia capensis*). In this case, it is not advisable to consider these prey as two different nodes because a given species also belongs to the passerine category. Thus, we decided that if > 50% of predator diets reported only the clustered node (e.g., passerines), such bundled nodes would be used, removing species-specific nodes. This way, any predator that consumed a given passerine species would be connected to the bundled node and not to separate specific nodes. In the contrary case, some consumers were reported to used one or more species of *Nothofagus (N. antarctica, N. obliqua, N. pumilio,* or *N. nitida*), while others were reported to consume only the cluster node (*Nothofagus* spp.). In this case, we assumed that the latter could consume either species. Finally, another criterion we used to build the food web was that those species with predators but without prey were designated as basal (i.e., within the primary producers level in the food web), and they included species without dietary data as well as insectivorous birds and insects, either because we could not find studies or because they were not specific enough (e.g., they consumed "seeds").

Food web analysis

Through a list of interactions between species, we constructed a binary adjacency matrix using the Network 3D program[60,61], where 0 is absence and 1 is the presence of trophic interactions. We analysed the structural attributes of the network, including species richness (S), number of links (L), connectance ($C = L/S^2$), generality SD (standard deviation of generality; generality of a node is the number of species consumed as normalised by L/S), and vulnerability SD (standard deviation of vulnerability; vulnerability of a node is the number of species consumed as normalised by L/S)[46,62,63]). In turn, we classified the nodes as either native, exotic, or mixed nodes, the latter representing some Orders, Families and Genera that have native and exotic representatives (*e.g.,* the node *Agrostis* spp. contains native *Agrostis glabra* and introduced *Agrostis capillaris*). We performed this classification to better understand the relationship between rabbits as invasive species and their nodes, and how their interactions and the management of rabbits could structure or modify the food web/community. To quantify how embedded the rabbits were into the food web, we calculated each node's connectivity, number of predators, and number of prey, and ranked the rabbit position.

Rabbit extinction simulation

We carried out a simulation of rabbit extinction to evaluate the ecological mechanisms involved (e.g., release from predation, reduction of trophic niche) that could trigger short-term responses in the ecosystem, using the Network Extinction package[52] and graph[64] in R[65]. For this, we removed from the network the node belonging to the rabbit, and quantified the percentage of prey lost to predators (reduction of trophic niche) and the percentage of predators that lost prey (release from predation/herbivory) in the food web.

Results

The Magellanic/Fuegian steppe and scrub food web resulted in a network with 206 nodes and 535 trophic interactions (Links, L) and a connectance of 0.013 (Fig. 2). In the network trophic levels, 82% were primary producers (plants and basal species—see Methodology), 10% intermediate species (carnivores, herbivores, and omnivores), and 8% corresponded to top predators (carnivores and scavengers). The food web was made up of 132 native nodes (64%), 29 exotic (13%), and 45 (22%) mixed—native and exotic representatives—(Table 1 Supplementary material, Fig. 2). The link density (L/S) was equal to three, representing the number of interactions per node. The network had a vulnerability SD = 1.4 and a generality SD = 2.9, which implies that it was more homogeneous in terms of vulnerability than in generality, having nodes with very wide dietary breadth (e.g., guanaco, *Lama guanicoe,* with 47 consumed items/nodes, or sheep, *Ovis aries,* with 40) versus others with much narrower dietary breadth (e.g., quique, *Galictis cuja,* with five prey items).

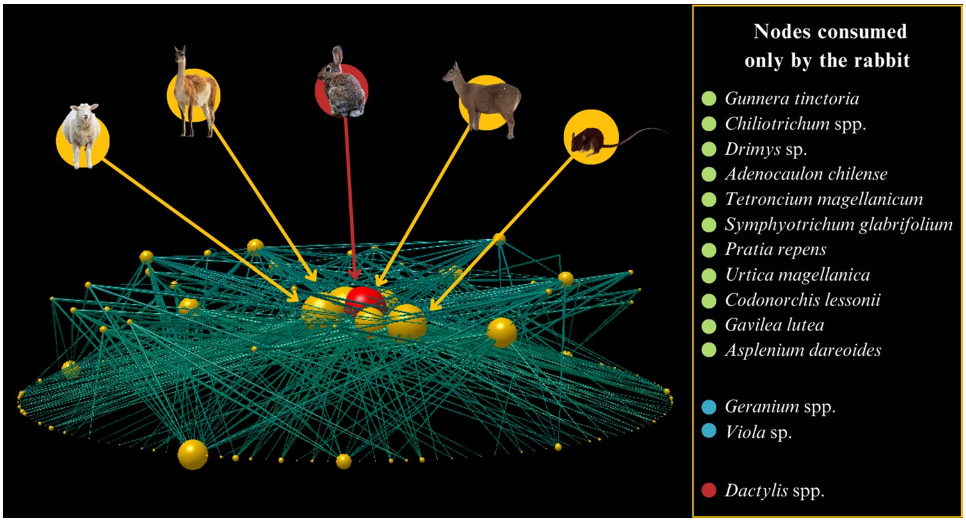

Fig. 2. Food web of the European rabbit *Oryctolagus cuniculus* in the Magellanic/Fuegian steppe and scrub. Each circle represents a node (species), and each line represents a link (trophic interaction). The size of each node represents the number of trophic interactions associated with it: larger sphere size indicates more trophic interactions. Species inside the yellow box represent plants consumed exclusively by rabbits, where the green colour indicates a native species, blue a mixed-origin species, and red an exotic species. *We have a copyright holder to publish it under a CC BY open-access license.

The European rabbit was the most connected species in the network (connectance = 10.8), which means the rabbit node had the most trophic interactions (56 links, 10% direct interactions within the food web). At the same time, it was the second in generality (16.9) after the guanaco *Lama guanicoe* (18.1). The other species in sequence of connectivity after European rabbits were: *Lama guanicoe* (native herbivore; connectance = 10.2; 53 links), *Ovis aries* (domesticated herbivore; connectance = 9.6; 50 links), *Oligoryzomys longicaudatus* (native herbivore; connectance = 8.5; 44 links), and *Hippocamelus bisulcus* (native herbivore; connectance = 7.9; 41 links) (Fig. 2). These five species accounted for half of the links in the entire network (45%, 244 out of 535).

The rabbit was preyed on by 12 species, of which 11 were native and one was an exotic invasive (*Neogale vison*) (Fig. 3A). Among predators/scavengers with the broadest dietary breadth were *Vultur gryphus*, *Lycalopex griseus*, and *Neogale vison*. Rabbit predators with the narrowest dietary breadth were *Galicitis cuja*, *Leopardus pajeros, L. geoffroyi,* and *Lyncodon patagonicus*.

The Magellanic/Fuegian food web focused on predator–prey trophic relationships. Nevertheless, it also displays the rabbit's potential competitors for resources (Fig. 3B). Rabbits consumed 14 species exclusively, most of which were native (78%). The remaining plants they consumed (30 species) were shared with other herbivores, 40% native and 60% exotic, including *Lama guanicoe, Ovis aries,* and *Bos taurus,* which shared 19–22 plants with rabbits, followed by *Hippocamelus bisulcus* (sharing 12 species), *Oligoryzomys longicaudatus* (11 species), *Sus scrofa* (4 species), *Lepus europaeus* (3 species), *Zaedyus pichy* (1 species), and *Chaetophractus villosus* (1 species). The percentages of native, exotic, and mixed-origin nodes of the species consumed by rabbits were 59%, 14%, and 27%, respectively.

When removing the rabbit node from the food web through a rabbit extinction simulation (Fig. 4A), 11 plant nodes lost from 10 to 20% of their consumers, 12 plants lost from 20 to 30%, one plant lost 30–40%, and six plants lost 40–50% of their consumers. Also, 14 plant nodes lost 100% of their consumers—meaning predation release—(*Gunnera tinctoria, Chiliotrichum* spp., *Drimys* sp., *Adenocaulon chilense, Tetroncium magellanicum, Symphyotrichum glabrifolium, Pratia repens, Urtica magellanica, Codonorchis lessonii, Gavilea lutea, Asplenium dareoides, Geranium* spp., *Viola* sp., and *Dactylis* spp.), among which 78% were native species.

Most rabbit predators were not greatly affected by rabbit removal because they did not lose more than 20% of their prey (Fig. 4B). Only one species, *Galictis cuja*, lost 20% of its prey (trophic decrease). Therefore, the main ecological mechanism triggered by the removal of the rabbit node was the release of pressure on plants from its herbivory.

Discussion

Historically, biological invasions due to human actions have resulted in new environments and community structures worldwide[66,67]. Further, invasive species that have naturalised in their new environment have become adapted to the trophic network, interacting with many species at different trophic levels[28]. Although the ecological effects of these species are generally negative, it is relevant to increase knowledge about their role in food webs, about their impacts/effects on an ecosystem, and about the possible consequences for the local community[29,68]. European rabbits can modify and impact the structure of food webs, and can even destabilise them[27,36,69], as has been evidenced throughout the world[5,28,41,70–72]. The Magellanic/Fuegian steppe and scrub food web showed the rabbits' key role as a consumer of native and exotic plants, a competitor for other herbivores, and a prey for various native and exotic predators and scavengers. This study shows that the rabbit has integrated deeply

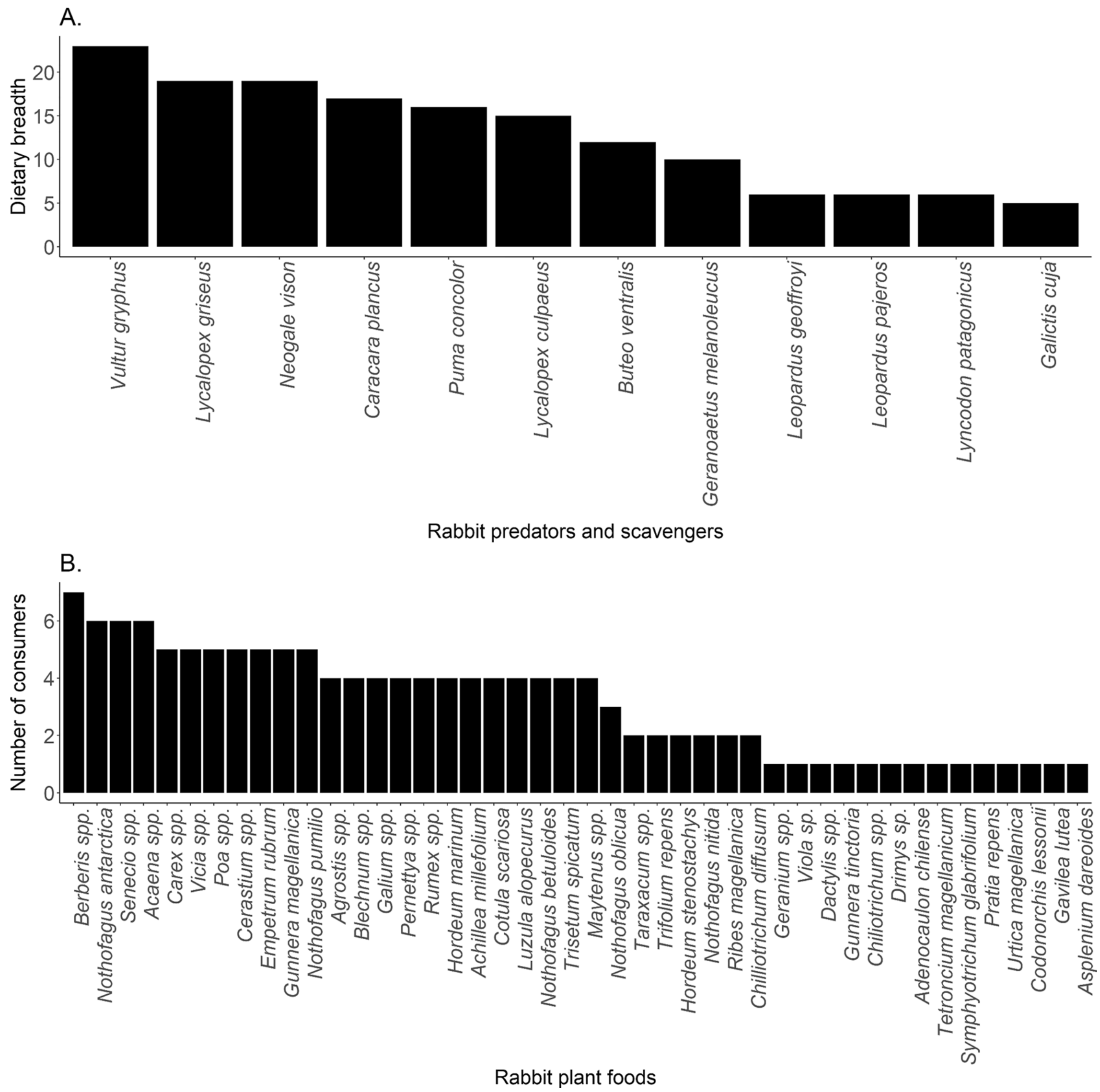

Fig. 3. The relative importance of the European rabbit *Oryctolagus cuniculus* in the Magellanic/Fuegian steppe and scrub of southernmost Chile. (**A**) Dietary breadth of rabbit predators in decreasing order. (**B**) Resources used by rabbits in decreasing order. *We have a copyright holder to publish it under a CC BY open-access license.

into the Magellanic/Fuegian steppe and scrub food web and highlights the importance of studying the possible short-term impacts of their control.

Primary producers had the most nodes compared to other trophic levels in the network, where most were native species. The importance of plant ecological roles is evident through the consumption by the species most connected to the food web, which are all herbivores (e.g., rabbits—*Oryctolagus cuniculus*-, guanaco—*Lama guanicoe*, sheep—*Ovis aries*, long-tailed mouse—*Oligoryzomys longicaudatus*, huemul—*Hippocamelus bisulcus*), highlighting the relevance of conserving plants for the community against threats such as invasive species[37]. The rabbit consumed 36% of the plant species in the Magellanic/Fuegian food web, among which more than half were native, which highlights its potential impact on the conservation of the magellanic flora.

As medium-sized abundant herbivores, rabbits have the potential to alter many ecological processes[29,36], strongly affecting primary producers through massive consumption, and by creating strong interaction links through feeding or competition with other herbivores[28,29,40,73]. Therefore, rabbit management could relieve herbivory pressure on plants—as observed in the rabbit extinction simulation (see "Results")—likely increasing their biomass and controlling the dispersal of exotic species that alter the composition and structure of the ecosystem[74,75]. This lagomorph consumed 36% of the plants in the network, where 14 species were consumed only by rabbits (e.g., *Gunnera tinctoria*, *Urtica magellanica*, *Tetroncium magellanicum*, and *Codonorchis lessoni*). In this case, rabbit control could directly benefit the growth and abundance of these plants, thus becoming a food resource available for other native nodes that could replace the ecological functions of the rabbit and conserve important plants in the steppe and scrub ecosystems, such as *T. magellanicum,* which is a monotypic species of evolutionary significance[76], or *C. lessonii*, which is endemic and the only representative of the subfamily

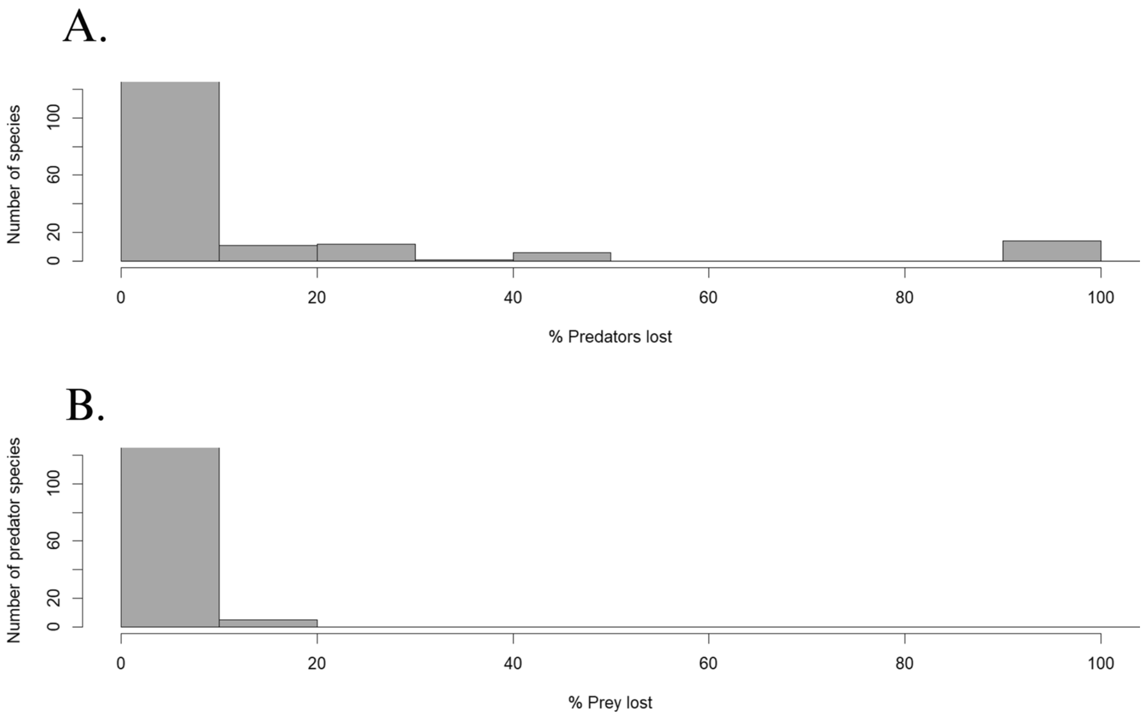

Fig. 4. Rabbit extinction simulation in the Magellanic/Fuegian steppe and scrub food web. (**A**) Number of prey species that lose a certain percentage of predators by removing the rabbit from the network. (**B**) Number of predator species that lose a certain percentage of their prey by eliminating the rabbit. *We have a copyright holder to publish it under a CC BY open-access license.

Codonorchideae in Chile[77]. Further, several studies have shown a positive impact on plant biomass after removing invasive species, including species reappearance[37,40,78]. Still, in the Magellanic/Fuegian steppe and scrub ecosystems, the impact generated by the rabbit may extend beyond native to exotic plants, where the possible effects of a reduction in rabbit density are unknown and need to be evaluated[37,38]. A potential impact could be an uncontrolled increase in exotic plants that are consumed only by rabbits (e.g., *Dactylis* spp.), thus becoming detrimental to the ecosystem—perhaps this genus should be monitored under experimental pilots without the presence of the rabbit to evaluate the possible mechanism that may be unchained. Notice that rabbits consumed exotic species such as *Poa* spp. and *Taraxacum* spp., which are highly effective colonisers although not dispersed by rabbits because they are anemochorous[79]. Therefore, rabbit control would not necessarily affect their dispersal.

The majority of plants that rabbits consumed were shared with a variety of herbivores, such as guanaco (*Lama guanicoe*, 22 shared nodes), sheep (*Ovis aries*, 21 shared nodes), and cattle (*Bos taurus*, 19 shared nodes), which could suggest competition for food[80–82], thus affecting both native species and livestock. For instance, *Empetrum rubrum, Senecio* spp., *Acaena* spp., and *Rumex* spp. are not only part of the diet of rabbits, but also of native species with conservation importance, such as the huemul[83] and the guanaco[84]. These plants are also economically valuable for livestock (sheep and cattle), an important productive system in the Magallanes region. Additionally, species of the *Nothofagus* genus have high ecosystem value by hosting diverse species and playing a key role in livestock grazing[85]. The Magallanes region has seen a decrease in the number of cattle in the last 17 years: 11% reduction in bovines (140 thousand to 120), 35% (10 thousand to 6) in horses, and 37% (2.2 million to 1.4) in sheep[86]. A decrease in the carrying capacity of the fields for sheep production has been attributed to the rabbit herbivory in Isla Grande de Tierra del Fuego during the 1950s[87]. Furthermore, because of carnivore-livestock conflicts, especially with the puma[88], there has been a conversion from medium-sized (sheep) to large-sized livestock (cattle). In this sense, any management aimed at controlling rabbits would contribute to the recovery of soils and basal resources, benefiting other native prey species[41], and increasing the availability of pastures for sustainable livestock management through regenerative grazing[89–91].

High rabbit abundance has resulted in them becoming the primary prey for some predators, even enabling the rise of a rabbit-eating guild[36]. The European rabbit is now considered the main prey of many native predators in invaded regions and has been generating a dietary shift among them, channelling most of the biomass input to their diets, generating strong interaction links, and affecting the food web configuration and stability[11,12,27–29,34–36,41,42,92]. Here, the rabbit is now common prey for carnivores, scavengers, and omnivores—mainly native to the Magallanes region, where most have a prey range of 10–20 species, being considered generalists. Rabbit population must be managed in Chilean Patagonia. Still, this requires consideration of possible flow-on effects to top- and meso-predator diets and potential secondary impacts on prey due to predators switching their feeding behaviour[37,38,40]. The predators' short-term response to a shortage in their rabbit prey may be to adjust their attack rates on native prey, altering the food web and making it necessary to monitor key and at-risk species (e.g., *Galictis cuja*—see Results)[29,41]. Speculatively, perhaps regional predators would direct higher pressure on another abundant invader, the European hare (*Lepus europaeus*), which would not be unwelcome news[93]. A plausible scenario for generalist predators, recognizing their plastic feeding behaviours, is to adapt to the availability of resources and shift their diets, weakening other links as a consequence of establishing a strong link with rabbits[28,80].

Our study shows that the network approach can provide a powerful tool for elucidating potential ecosystem-wide effects of European rabbits and hypothesising the consequences of management interventions. Rabbit control is more complex than just controlling a single species. It needs to carry out fauna monitoring and flora experiments to evaluate the effects on the network. Still, two limitations of our approach should be highlighted: (a) Missing links in the predator–prey or herbivore-plant interactions which are not considered because of a lack of information on them. These could affect estimates of niche breadth and of predation or herbivory pressure. (b) Variable diet records, with widely different sampling intensities in diet studies. Better sampled diets are more trustworthy than others based on a small sample. For future work we propose: (a) To collect information on the frequency of feeding interactions and—if possible—the amount of food consumed. (b) To estimate the total amount of biomass coming from the prey or plants and going to the consumers, to better capture the functional status of a species in a food web, (c) To carry out bioenergetic mathematical models to quantify the strength of the interactions considering the flow of nutrients or energy across the food web.

Data availability

The datasets generated and analysed during the current study are available in the [Magellanic_food_web] repository, [https://github.com/IsidoraAvilaThieme].

Received: 25 September 2023; Accepted: 19 August 2024
Published online: 23 August 2024

References

1. Lever, C. *Naturalized Mammals of the World* (Longman, 1985).
2. Long, J. Introduced mammals of the world: Their history. *Distribution Influence.* https://doi.org/10.1071/9780643090156 (2003).
3. Rabadá, J. C. Los primeros conejos llegaron a América iniciado noviembre de 1493. *Información Veterinaria* **9**, 21–24 (2008).
4. Smith, A. & Boyer, A. *Oryctolagus cuniculus (Europe Assessment)*. (2007).
5. Lees, A. & Bell, D. A conservation paradox for the 21st century: The European wild rabbit *Oryctolagus cuniculus*, an invasive alien and an endangered native species. *Mammal Rev.* **38**, 304–320 (2008).
6. Lowe, S., Browne, M., Boudjelas, S. & De Poorter, M. 100 of the world's worst invasive alien species: A selection from the global invasive species database. *Published by The Invasive Species Specialist Group (ISSG) a specialist group of the Species Survival Commission (SSC) of the World Conservation Union (IUCN), 12pp. First published as special lift-out in Aliens* **12**, (2000).
7. Camus, P., Castro, S. & Jaksic, F. E. conejo europeo en Chile: Historia de una Invasión Biológica. *Historia (Santiago)* **41**, 305–339 (2008).
8. Delibes, R. & Delibes-Mateos, M. Linking historical ecology and invasion biology: Some lessons from European rabbit introductions into the new world before the nineteenth century. *Biol. Invasions.* https://doi.org/10.1007/s10530-015 (2015).
9. PNUD, Programa de las Naciones Unidas para el Desarrollo. *Valoración Económica Del Impacto de Siete Especies Exóticas Invasoras Sobre Los Sectores Productivos y La Biodiversidad En Chile*. (Ministerio del medioambiente, Santiago, 2017).
10. Jaksic, F. M., Iriarte, J. A. & Jiménez, J. E. The raptors of Torres del Paine National Park, Chile: Biodiversity and conservation. *Rev. Chil. Hist. Nat.* **75**, 449–461 (2002).
11. Correa-Cuadros, P. *et al.* History, control, epidemiology, ecology, and economy of the invasion of European rabbits in Chile: A comparison with Australia. *Biol. Invasions* **25**, 309–338 (2022).
12. Correa-Cuadros, P. *et al. Invasion Del Conejo Europeo En Chile-European Rabbit Invasion in Chile*. (2023).
13. Molina, W. Identidad regional en Magallanes, sus expresiones simbólicas y territoriales. *Magallania (Punta Arenas)* **39**, 59–69 (2011).
14. ODEPA, Oficina de Estudios y Políticas Agrarias. *Informativo Regional Magallanes y La Antártica Chilena*. (Ministerio del medioambiente, 2021).
15. Arentsen, P. Control biológico del conejo: difusión del virus mixomatosis cuniculus, por contagio directo, en la Isla Grande de Tierra del Fuego. (1954).
16. Pisano, E. L. Estepa patagónica como recurso pastoril en Aysén y Magallanes. *Ambiente y Desarrollo* **1**, 45–49 (1985).
17. Iriarte, A., Feinsinger, P. & Jaksic, F. Trends in wildlife use and trade in Chile. *Biol. Cons.* **81**, 9–20 (1997).
18. Iriarte, A. & Jaksic, F. The fur trade in Chile: An overview of seventy-five years of export data (1910–1984). *Biol. Cons.* **38**, 243–253 (1986).
19. Berrios Etchegaray, P. Virus como control biológico del conejo silvestre europeo (*Oryctolagus cuniculus*). *TecnoVet* **11**, 15–20 (2016).
20. Jaksic, F. & Yáñez, J. Rabbit and fox introductions in Tierra del Fuego: History and assessment of the attempts at biological control of the rabbit infestation. *Biol. Cons.* **26**, 367–374 (1983).
21. MMA, Ministry of the Environment. El Problema de las Especies Exóticas Invasoras en Chile. (2017).
22. Amaya, J. & Bonino, N. El conejo silvestre Europeo (*Oryctolagus cuniculus*) en Tierra del Fuego. *IDIA (Buenos Aires)* 388. 14–33 (1981).
23. Huertas Herrera, A., Toro Manríquez, M., Laura, B., Lencinas, M. & Martínez Pastur, G. J. Forage offering and seasonal intake comparisons to evaluate European rabbit threat in Nothofagus forests of southern Patagonia. *Ecol. Process.* **11**, 1–14 (2022).
24. Bonino, N. & Soriguer, R. The invasion of Argentina by the European wild rabbit *Oryctolagus cuniculus*. *Mammal Rev.* **39**, 159–166 (2009).
25. Bonino, N. Interacción trófica entre el conejo silvestre europeo y el ganado doméstico en el noroeste de la Patagonia Argentina. *Ecol. Aust.* **16**, 135–142 (2006).
26. Silva, C. A. & Saavedra, B. Knowing for controlling: Ecological effects of invasive vertebrates in Tierra del Fuego. *Rev. Chil. Hist. Nat.* **81**, 123–136 (2008).
27. Lambertucci, S. A. *et al.* Spatial and temporal patterns in the diet of the Andean condor: Ecological replacement of native fauna by exotic species. *Anim. Conserv.* **12**, 338–345 (2009).
28. Barbar, F., Hiraldo, F. & Lambertucci, S. Medium-sized exotic prey create novel food webs: The case of predators and scavengers consuming lagomorphs. *PeerJ* **4**, 1–15 (2016).
29. Barbar, F. & Lambertucci, S. The roles of leporid species that have been translocated: A review of their ecosystem effects as native and exotic species. *Mammal Rev*. **48**, 245–260 (2018).

30. Jaksic, F., Yáñez, J. & Rau, J. Trophic relations of the southernmost populations of Dusicyon in Chile. *J. Mammal.* **64**, 693 (1983).
31. Zurita Redón, C., Soto, N. & Jaksic, F. Historical ecology and current abundance of the translocated Chilla or Grey fox *Lycalopex griseus* on the large Tierra del Fuego Island shared by Argentina and Chile. *Aust. Ecol*. 1–17 (2023).
32. Duclos, M. *et al.* Latitudinal patterns in the diet of Andean condor (*Vultur gryphus*) in Chile: Contrasting environments influencing feeding behavior. *Sci. Total Environ.* **741**, 140220 (2020).
33. Simberloff, D. *Invasive Species: What Everyone Needs to Know* (Oxford University Press, 2013).
34. Olsen, J., Cooke, B., Trost, S. & Judge, D. Is wedge-tailed eagle, *Aquila audax*, survival and breeding success closely linked to the abundance of European rabbits, *Oryctolagus cuniculus*?. *Wildl. Res.* **41**, 95–105 (2014).
35. Fleming, P. A. *et al.* Distinctive diets of eutherian predators in Australia. *R. Soc. Open Sci.* **9**, 220792 (2022).
36. Barbar, F. & Lambertucci, S. A. Invasive herbivores shape food web structure: European rabbit and hare acting as primary prey are conservation challenges. *Biol. Conserv.* **281**, 110016 (2023).
37. Zavaleta, E. S., Hobbs, R. J. & Mooney, H. A. Viewing invasive species removal in a whole-ecosystem context. *Trends Ecol. Evolut.* **16**, 454–459 (2001).
38. Thompson, E., Driscoll, D., Venn, S., Geary, W. & Ritchie, E. Interspecific variation in the diet of a native apex predator and invasive mesopredator in an alpine ecosystem. *Aust. Ecol.* **47**, 1260–1270 (2022).
39. Donlan, C. J., Tershy, B. R. & Croll, D. A. Islands and introduced herbivores: Conservation action as ecosystem experimentation. *J. Appl. Ecol.* **39**, 235–246 (2002).
40. Lurgi, M., Ritchie, E. & Fordham, D. Eradicating abundant invasive prey could cause unexpected and varied biodiversity outcomes: The importance of multispecies interactions. *J. Appl. Ecol*. **55**, 2396–2407 (2018).
41. Barbar, F. & Lambertucci, S. Introduced lagomorph produce stronger potential apparent competition in invaded communities than any other species in a similar but native food web. *Biol. Invasions* **21**, 3735–3740 (2019).
42. Gübelin, P. *et al.* European rabbit invasion in a semi-arid ecosystem of Chile: How relevant is its role in food webs?. *Life* **2023**, 1–20 (2023).
43. Inostroza, L., König, H. & Zasada, I. Last of the wild revisited. Assessing spatial patterns of human impact on landscapes of Southern Patagonia, Chile. *Regional Environ. Change* **16**, 2071–2085 (2016).
44. Radic, S., Corti, P., Muñoz-Arriagada, R., Butorovic, N. & Sánchez-Jardón, L. Steppe ecosystems in Chilean Patagonia: Distribution, climate, biodiversity, and threats to their sustainable management. 175–202 (2024). https://doi.org/10.1007/978-3-031-39408-9_7.
45. Blanchard, G. & Munoz, F. Revisiting extinction debt through the lens of multitrophic networks and meta-ecosystems. *Oikos* **2023**, e09435 (2023).
46. Dunne, J. A. Food webs. in *Encyclopedia of Complexity and Systems Science* (ed. Meyers, R. A.) 3661–3682 (Springer, New York, 2009). https://doi.org/10.1007/978-0-387-30440-3_216.
47. Pimm, S. L., Lawton, J. H. & Cohen, J. E. Food web patterns and their consequences. *Nature* **350**, 669–674 (1991).
48. Abrams, P. A., Menge, B. A., Mittelbach, G. G., Spiller, D. A. & Yodzis, P. The role of indirect effects in food webs. in *Food Webs: Integration of Patterns & Dynamics* (eds. Polis, G. A. & Winemiller, K. O.) 371–395 (Springer US, 1996). https://doi.org/10.1007/978-1-4615-7007-3_36.
49. Yodzis, P. The indeterminacy of ecological interactions as perceived through perturbation experiments. *Ecology* **69**, 508–515 (1988).
50. Dunne, J. A., Williams, R. J. & Martinez, N. D. Network structure and biodiversity loss in food webs: Robustness increases with connectance. *Ecol. Lett.* **5**, 558–567 (2002).
51. Smith-Ramesh, L. M., Moore, A. C. & Schmitz, O. J. Global synthesis suggests that food web connectance correlates to invasion resistance. *Glob. Change Biol.* **23**, 465–473 (2016).
52. Ávila-Thieme, M. *et al.* NetworkExtinction: An R package to simulate extinction propagation and rewiring potential in ecological networks. *Methods Ecol. Evolut*. **14**, 1952–1966 (2023).
53. Xercavins, A. Notas sobre el clima de Magallanes (Chile). *Revista Geografia* **18**, 95–110 (1984).
54. Salinas, P. R. *Diagnóstico Del Estado y Tendencia de La Biodiversidad: Región de Magallanes y de La Antártica Chilena.* (2016).
55. CONAF. CONAF—Corporación Nacional Forestal. Chile. http://www.conaf.cl/parques-nacionales/ (2019).
56. Sánchez, A. & Morales, R. *Las Regiones de Chile: Espacio Físico y Humano-Económico* (Universitaria, 1993).
57. Venegas, C. & Siefeld, W. *Catálogo de Los Vertebrados de La Región de Magallanes y Antártica Chilena*. (Universidad de Magallanes, 1998).
58. ODEPA, Oficina de Estudios y Políticas Agrarias. *Región de Magallanes y de la Antártica Chilena Información regional 2019 Actualización marzo de 2019*. (2019).
59. Vera, J. Magallanes: Economic and demographic dynamics 1960–2006: Special development laws; what to do and what to avoid. *Magallania (Punta Arenas)* **36**, 63–78 (2008).
60. Montoya, J. M., Pimm, S. L. & Solé, R. V. Ecological networks and their fragility. *Nature* **442**, 259–264 (2006).
61. Yoon, I. *et al. title>Webs on the Web (WOW): 3D Visualization of Ecological Networks on the WWW for Collaborative Research and Education*. *Electronic Imaging, Visualization and Data Analysis* vol. 5295 (2004).
62. MMA. Inventario nacional de especies. *Ministry of the Environment* http://especies.mma.gob.cl/CNMWeb/Web/WebCiudadana/Default.aspx (2020).
63. Dunne, J., Williams, R. & Martinez, N. Food-web structure and network theory: The role of connectance and size. Proc Natl Acad Sci USA 99: 12917–12922. in *Proceedings of the National Academy of Sciences of the United States of America* **99**, 12917–22 (2002).
64. Williams, R. Network 3D: Visualizing and modelling food webs and other complex networks. *Microsoft Research, Cambridge, UK* http://research.microsoft.com/en-us/um/cambridge/groups/science/tools/network3d/network3d.htm (2010).
65. R Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/. (2020).
66. Everett, R. Patterns of pathways of biological invasions. *Trends Ecol. Evolut.* **15**, 177–178 (2000).
67. Jaksic, F. & Castro, S. *Biological Invasions in the South American Anthropocene: Global Causes and Local Impacts. Springer Nature, Cham, Switzerland, Xix + 346 pp.* 47 (2021). https://doi.org/10.1007/978-3-030-56379-0_2.
68. Camus, P., Castro, S. & Jaksic, F. European rabbit (*Oryctolagus cuniculus* L.) in Chile: The human dimension behind a biological invasion. In book Biological invasions in the South American Anthropocene: Global causes and local impacts. in 171–185 (2021). https://doi.org/10.1007/978-3-030-56379-0_8.
69. Novaro, A., Funes, M. & Walker, S. Ecological extinction of native prey of a carnivore assemblage in Argentine Patagonia. *Biol. Conserv*. **92**, 25–33 (2000).
70. Green, R. E. & Griffiths, G. H. Use of preferred nesting habitat by stone curlews *Burhinus oedicnemus* in relation to vegetation structure. *J. Zoologys.* **233**, 457–471 (1994).
71. Bowden, C. G. R. Selection of foraging habitat by woodlarks (*Lullula arborea*) nesting in pine plantations. *J. Appl. Ecol.* **27**, 410–419 (1990).
72. Baker-Gabb, D. J. The breeding ecology of twelve species of diurnal raptor in northwestern Victoria. *Aust. Wildlife Res.* **11**, 145–160 (1984).
73. Dawson, T. & Ellis, B. Diets of mammalian herbivores in Australian arid, hilly shrublands: Seasonal effects on overlap between euros (hill kangaroos), sheep and feral goats, and on dietary niche breadths and electivities. *J. Arid Environ.* **34**, 491–506 (1996).
74. Marchant, R., Kefford, B. J., Houghton, M., Wasley, J. & King, C. K. Slow recovery of stream invertebrates on subantarctic Macquarie Island after eradication of introduced rabbits and regrowth of vegetation. *Mar. Freshwater Res.* **74**, 1171–1177 (2023).

75. Ross, N. *Rabbit Impacts on Ground Layer Plant Communities in Arid Rangelands*. (2023).
76. Von Mering, S. Tetroncium and its only species, *T. magellanicum* (Juncaginaceae): Distribution, ecology and lectotypification. *Willdenowia* **43**, 13–24 (2013).
77. Novoa, P., Espejo, J., Alarcon, D., Cisternas, M. & Domínguez, E. *Guía de Campo de Las Orquídeas Chilenas*. (CORMA, 2015).
78. Glen, A. S. *et al.* Eradicating multiple invasive species on inhabited islands: The next big step in island restoration?. *Biol. Invasions* **15**, 2589–2603 (2013).
79. Vidal, O. *et al.* Plantas invasoras en el Parque Nacional Torres del Paine (Magallanes, Chile): Estado del arte, distribución post-fuego e implicancias en restauración ecológica. *Anales del Instituto de la Patagonia* **43**, 75–96 (2015).
80. Jaksic, F. M. Vertebrate invaders and their ecological impacts in Chile. *Biodiversity Conserv.* **7**, 1427–1445 (1998).
81. Baldi, R., Albon, S. & Elston, D. Guanacos and sheep: Evidence for continuing competition in arid Patagonia. *Oecologia* **129**, 561–570 (2001).
82. Pontigo, F., Radic, S., Moraga, C. A., Pulido, R. & Corti, P. Midsummer trophic overlap between guanaco and sheep in Patagonian Rangelands. *Rangeland Ecol. Manag.* **73**, 394–402 (2020).
83. Vila, A. R., Borrelli, L. & Aprile, G. Summer diet of huemul, *Hippocamelus bisulcus*, in Río de las Vueltas valey, Argentina. **39**, 113–117 (2011).
84. Muñoz, A. & Simonetti, J. A. Diet of guanaco in sheep-free rangeland in Tierra del Fuego. *Chile. Cien. Inv. Agric.* **40**, 185–191 (2013).
85. Alonso, M., Balocchi, O. & Schmidt Alcoholado, A. Caracterización de la estrata herbácea en praderas y bosques de ñirre (*Nothofagus antarctica*) en la Patagonia sur de Chile. *C&I Forestal* **22**, 43–52 (2016).
86. INE. *Censo Agropecuario*. https://www.ine.gob.cl/estadisticas/economia/agricultura-agroindustria-y-pesca/censos-agropecuarios (2021).
87. Vázquez, D. Multiple effects of introduced mammalian herbivores in a temperate forest. *Biol. Invasions* **4**, 175–191 (2002).
88. Llanos, R., Andrade, A. & Travaini, A. Puma and livestock in central Patagonia (Argentina): From ranchers' perceptions to predator management. *Human Dimensions Wildlife* **25**, 1–16 (2019).
89. Jaksic, F. & Fuentes, E. El conejo español: ¿Un convidado de piedra? En libro Ecología del paisaje en Chile central: Estudios sobre sus espacios montañosos. in 88–101 (1988).
90. Croft, J. D., Fleming, P. J. S. & van de Ven, R. The impact of rabbits on a grazing system in eastern New South Wales. 1. Ground cover and pastures. *Aust. J. Exp. Agric.* **42**, 909–916 (2002).
91. Larraín, R., Mansky, V., Mayol, M. & Melo, Ó. *Cambios Económicos y Productivos de La Ganadería Regenerativa En Chile*. (2022).
92. Palacios, R., Walker, S. & Novaro, A. Differences in diet and trophic interactions of Patagonian carnivores between areas with mostly native or exotic prey. *Mammalian Biol. Zeitschrift für Säugetierkunde* **77**, 183–189 (2012).
93. Jaksic, F. M. Historical ecology and current status of the European hare Lepus europaeus in South America: A new species in new countries. *Stud. Neotropical Fauna Environ.* **1**, 28. https://doi.org/10.1080/01650521.2023.2217064 (2023).

Acknowledgements
We are grateful to the Center of Applied Ecology and Sustainability (CAPES) for the opportunity to carry out this research and to ANID PIA/BASAL FB0002 for funding it. JP Correa-Cuadros is grateful to FONDECYT 3220027 and MI Ávila-Thieme FONDECYT 3220110. Also, to the Corporación Nacional Forestal (CONAF; more specifically CONAF-Magallanes and their park rangers), to the Servicio Agrícola y Ganadero (SAG; more specifically SAG-Magallanes), and especially to Nicolás Soto, for support in the food web data input. We thank Megan McFarland for kindly checking the English version of the manuscript.

Author contributions
F Mann-Vollrath and JP Correa-Cuadros contributed equally to this work and shared the first-co authorship. F Mann-Vollrath, JP Correa-Cuadros, and MI Ávila-Thieme designed the study and analysed the data. F Mann-Vollrath, JP Correa-Cuadros, MI Ávila-Thieme, M Duclos, and FM. Jaksic co-wrote the text. JP Correa-Cuadros and FM Jaksic drafted the final version of the manuscript.

Funding
We are grateful to ANID PIA/BASAL FB0002 for funding this research. JPC acknowledges the support of FONDECYT 3220027 and MIAT FONDECYT 3220110.

Competing interests
The authors declare no competing interests.

Additional information
Supplementary Information The online version contains supplementary material available at https://doi.org/10.1038/s41598-024-70511-6.

Correspondence and requests for materials should be addressed to J.P.C.-C.