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REVIEW

History, control, epidemiology, ecology, and economy of the invasion of European rabbits in Chile: a comparison with Australia

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Abstract We reviewed existing studies on the European rabbit in Chile regarding history, control, epidemiology, ecology, and economic impacts, comparing them with Australia's accumulated knowledge about the same topics. We focused especially on the resulting gaps and challenges to orient efforts toward controlling and managing rabbits in Chile. The European rabbit was first introduced to central Chile in the mid-eighteenth century and was reported as naturalized by 1884. It is among the seven invasive species that most affect Chilean ecosystems and their productive uses. The strongest rabbit impacts have been reported on Chilean islands and in the mainland's sclerophyllous forest biome. Released rabbits colonized both Juan Fernández Archipelago in 1935, becoming a harmful species damaging endemic vegetation and nesting bird populations, and Tierra del Fuego Island in 1936, becoming competitors for forage with sheep. The

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sclerophyllous forest in continental Chile is one of the five Mediterranean ecosystems of the world and one of the 34 critical "hotspots" for conserving the planet's biodiversity. Here, released rabbits and escapees have changed the spatial distribution of native shrubs and herbs, impeding the regeneration of the native matorral. Overall, the impacts of this species during the last 70 years in Chile have been addressed chiefly from a community-ecological perspective, and applied research is lacking for improving public policies and efficient management of this invader. It is urgent to determine the geographical distribution, population size, and drivers of rabbit dynamics to predict their spread and outbreaks. Also, it is necessary to better understand their effects on Chilean natural ecosystems and agroecosystems to assess their economic impacts on biodiversity and production. In addition, it is essential to research pathogens such as Myxoma virus or Lagovirus in Chile, toward determining their prevalence, virulence, and corresponding rabbit immunity, to estimate and potentially harness any contributions such pathogens could make towards controlling populations through biological agents.

Resumen Revisamos los estudios existentes sobre el conejo europeo en Chile en cuanto a historia, control, epidemiología, ecología e impactos económicos, comparándolos con el conocimiento acumulado en Australia sobre los mismos temas. Nos enfocamos especialmente en los vacíos y desafíos resultantes para orientar los esfuerzos hacia el control y manejo de los conejos en Chile. El conejo europeo se introdujo por primera vez en Chile central a mediados del siglo XVIII y se reportó como naturalizado en 1884. Se encuentra entre las siete especies invasoras que más afectan los ecosistemas chilenos y sus usos productivos. Los impactos más fuertes de los conejos se han reportado en islas chilenas y en el bioma del bosque esclerófilo del continente. Los conejos liberados colonizaron tanto el Archipiélago de Juan Fernández en 1935, convirtiéndose en una especie que daña la vegetación endémica y las poblaciones de aves nidificadoras, como en la Isla Tierra del Fuego en 1936, convirtiéndose en competidores de las ovejas por forraje. El bosque esclerófilo de Chile continental es uno de los cinco ecosistemas mediterráneos del mundo y uno de los 34 "hotspots" críticos para la conservación de la biodiversidad del planeta. Aquí, los conejos liberados y escapados han cambiado la distribución espacial de los arbustos y hierbas nativos, impidiendo la regeneración del bosque esclerófilo. En general, los impactos de esta especie durante los últimos 70 años en Chile han sido abordados principalmente desde una perspectiva comunitaria-ecológica, y falta investigación aplicada para mejorar las políticas públicas y el manejo eficiente de este invasor. Es urgente determinar la distribución geográfica, el tamaño de la población y los impulsores de la dinámica del conejo para predecir su propagación y brotes. Además, es necesario comprender mejor los efectos del conejo sobre los ecosistemas naturales y agroecosistemas chilenos para evaluar sus impactos económicos sobre la biodiversidad y la producción agrícola. Además, es fundamental investigar patógenos como el Myxoma o Lagovirus en Chile, para determinar su prevalencia, virulencia y la correspondiente inmunidad en conejos, para aprovechar cualquier contribución que dichos patógenos puedan hacer para controlar poblaciones a través de agentes biológicos.

Keywords *Oryctolagus cuniculus* · Myxomatosis · Myxoma virus · Leporipoxvirus · Rabbit hemorrhagic disease · Calicivirus · Lagovirus · Invasive species · Population dynamics · Epidemics · Viral diseases · Introduction history · Population control · Ecological impacts · Economic impacts

Introduction

The European rabbit (*Oryctolagus cuniculus*) was introduced to central Chile in the mid-eighteenth century and was reported as naturalized by 1884 (Lataste 1892; Jaksic 1998; Jaksic and Castro 2014, 2021). Jaksic (1998) mentioned that rabbits became an agricultural pest in central Chile, being strongly reported as such from 1912 to 1940. Currently, they are considered among the seven invasive species that most affect Chilean ecosystems and primary productivity, generating an estimated loss of 3.25 million USD per year (PNUD 2017a; Araos et al. 2020). The rabbits are nowadays distributed in central and southern Chile from the Atacama Region in the north to the Los Lagos Region in the south and disjointly in Magallanes Region, including Tierra del Fuego Island and adjacent parts of Argentine Patagonia (Jaksic et al. 2002; Camus et al. 2008, 2021; Iriarte 2008). There are also present in Robinson Crusoe

Island, part of the oceanic Juan Fernández Archipelago facing the Valparaíso Region (CONAF 1976, 2009, 2018). Rabbits consume artificial and natural grasslands, shrub shoots, bark of forest and fruiting trees, as well as cacti, tubers, rhizomes, flowers, and –in extreme cases– any vegetable tissue (Simonetti and Fuentes 1982; Simonetti 1989). Thus, rabbits are efficient invaders that colonize many habitats owing to their high reproductive capacity and adaptability to exploit varied resources (Myers and Bults 1977). Females are able to wean six to eight young rabbits (called kittens) per brood and with two to three breeding episodes per year (Myers and Poole 1963; CONAF 1973; Amaya y Bonino 1980; Ferriére et al. 1983). This prolificacy enables a small number of rabbit pairs to colonize a new environment rapidly.

The strongest rabbit impacts have been scientifically reported on Chilean islands and in the mainland's sclerophyllous forest. Rabbits colonized two islands in the Juan Fernández Archipelago in 1935, soon becoming a harmful species that damaged highly endemic vegetation while competing with livestock for forage. On the mainland, the sclerophyllous forest (locally known as matorral) is the most representative ecosystem of central Chile and is considered one of the 34 critical areas for global conservation (hotspots sensu Myers et al. 2000). This ecosystem has been strongly affected by European rabbits because they change the spatial distribution of the native shrubs and herbs, while contributing to the colonization, growth, and success of invasive herbs and grasses, and also forestalling the regeneration of the matorral (Ojeda et al. 2003; Camus et al. 2008, 2014, 2021; PNUD 2017a). The serious impacts of rabbits in Chile have triggered research on their invasion history, ecosystems affected, influence on predator diets, competition with native rodents, consumption of vegetation, dispersion of invasive plants, and more recently, economic valuation of these impacts (Jaksic and Yáñez 1980; Jaksic and Fuentes 1988; Jaksic 1998; Araos et al. 2020). Still, more research is required in key areas of decision-making regarding rabbit management. For instance, on geographical distribution and population size and dynamics of this species. Likewise, it is essential to research the epidemiology of biological agents such as Myxoma or Calicivirus, determining their prevalence, presence, and corresponding resistance, as an alternative to manage the rabbits. This review seeks to gather, analyze, and synthesize updated information on the Chilean rabbit studies in fields such as history, control, epidemiology, ecology, and economy, comparing them with Australia's accumulated knowledge about the same topics. We focused especially on the resulting gaps and challenges to orient efforts toward controlling and managing rabbits in Chile. Indeed, this review identifies which further knowledge is required for rabbit population control, focusing on the gaps and challenges for future studies. We aim to be useful to those interested in managing invasive species and conserving Chile's natural heritage, including not only researchers and managers, but also park rangers, public services, agricultural enterprises, conservation NGOs, and the general public.

European rabbit invasion and control

European rabbits are native to the Iberian Peninsula –including Spain, Portugal, and Gibraltar–, southern France, and northwestern Africa, spanning Morocco and Algeria (Rogers and Myers 1979; Soriguer 1980a; Rogers et al. 1994; Williams et al. 1995; Cooke 1998; Lees and Bell 2008). Introduced from their native lands, rabbits have become an invasive species causing a strong impact on ecosystems and productive systems in Argentina, Australia, Canada, Chile, Colombia, Cuba, Egypt, Germany, Italy, Japan, New Zealand, Poland, Russia, United States, and Uruguay (Mack et al. 2000; Thompson and King 2004). An invasive species is considered as such when accomplishing an expansion and persistence phase, where it increases its density and occupies all the favorable habitats available (Boudouresque et al. 2005). We focus on invasive rabbits in Chile and Australia –which share ecosystems functionally equivalent to those in the Mediterranean basin– to identify similarities and differences in the invasion process and in the effectiveness of Australian control, while learning about their successes and failures as a potential model to apply in Chile.

European rabbits were first brought to Australia by settlers in Tasmania and the Botany Bay area in the late eighteenth century (Peacock and Abbott 2013): 24 rabbits were imported for game purposes, but they escaped their enclosures after a fire (Williams et al. 1995; Mitchell and Balogh 2007). Hunting was then encouraged for commercial purposes, to the extent of exporting 700 million rabbit pelts and 160 million frozen rabbit carcasses solely in 1940 (Williams et al. 1995).

They soon spread to most Australian, except the tropics, becoming a harmful species (Cooke and McPhee 2007). The rabbits were initially to be controlled by Red foxes (*Vulpes vulpes*) and Feral cats (*Felis catus*) brought from Europe, together with natural predators and rabbit-proof fences (spanning 1700 km) to keep them out of western Australia. Still, fences and predators did not prevent rabbit dispersal, culminating with infamous outbreaks with an estimated 500 million rabbits at their peak in 1880 (Williams et al. 1995; Richardson 2001; Mitchell and Balogh 2007). Later, the Australian colonial governments endorsed bounty hunting and poisoning to control the rabbit infestation, all these control measures were ineffective at a continental scale (Cox et al. 2013). Then, growing interest developed for using biological control from self-disseminating pathogens. In the early 1950s, Australian government authorities started releasing the insect transmitted Myxoma virus as a potential agent to controlling rabbits (Kerr 2012). The Myxomatosis spread strategy was efficient, suppressing rabbits for several decades, but rabbit numbers increased again due to the rapid development of host genetic resistance to the virus (Voigt 1987; Cox et al. 2013; Alves et al. 2019). Thus, *Lagovirus*-caused Rabbit Hemorrhagic Disease Virus (RHDV) was released in 1996, again substantially reducing rabbit populations across the entire continent. A second strain of RHDV was released in 2017 to boost the effects of rabbit biocontrol (Strive and Cox 2019). Currently, Australian researchers are improving existing tools and investigating new ones, including potential additional pathogens (Cooke 1998, 2007; Sharp and Bowman 2004).

In Chile, Juan Ignacio Molina first described the presence of European rabbits by the mid-eighteenth century (Camus et al. 2008), but they apparently became naturalized only by 1884 (Lataste 1892; Camus et al. 2008, 2014, 2021). By the 1920s rabbits were seen as an opportunity for Chilean economic development based on their pelt, fur, and meat. Raising hutches in central Chile led to rabbits being released or escaping into natural environments, contributing to their dispersal and transformation into a harmful species. The rabbit invasion in central Chile meant significant damage to forest plantations, agricultural crops, and livestock pastures (Jaksic and Fuentes 1988; Jaksic 1998; Camus et al. 2008). Even so, the Chilean Directorate of Fishing and Hunting in 1949 allowed the introduction of rabbits to southern islands with the purpose to creating a source of local wealth (Camus et al. 2008), with rabbits then rapidly spreading from central to southern Chile (Jaksic and Castro 2014, 2021). Towards the beginning of the 1970s, rabbits occupied approximately 3 million hectares and with densities between 1 and 10 rabbits/ha (CONAF 1974). Chile has adopted conventional hunting, trapping, fumigants, and anticoagulant baits to control feral rabbits. Still, these have little effect on their abundance most of the time (Jaksic and Fuentes 1988, 1991; Camus et al. 2008, 2014, 2021). Hunting is done by firearms such as shotguns and rifles, trained dogs, cage traps, and wire ties in farms, pastures, and forest plantations (Arentsen 1954; CONAF 1976). In addition, anticoagulant baits are used –e.g., Brodifacoum, which prevents blood clotting and kills rabbits from internal bleeding– but require a careful application due to their impact on other wildlife species (Arentsen 1954; Ojeda et al. 2003). Also, different fumigants are applied into burrows, which must be subsequently sealed to achieve the desired effect (Sáiz et al. 1982). Rabbit control in forest plantations was usually carried out with sodium monofluoroacetate but the risks associated with this chemical led to its prohibition starting in 1988. Since then, rabbits are controlled chiefly with Brodifacoum (Rodríguez 1988).

European rabbits were first introduced to Tierra del Fuego Island ca. 1880 by Thomas Bridges, who settled in its Argentine part north of the Beagle Channel, from which they were translocated to smaller neighboring islands (Bridges 1949; Amaya and Bonino 1981), followed by a release of two pairs of rabbits set free in 1936 at Punta Santa María close to the Chilean city of Porvenir (Arentsen 1953, 1954; Jaksic and Yáñez 1983; Jaksic 1998; Jaksic et al. 2002). The descendants of the latter came to be considered harmful in the early 1950s when an estimated 30–35 million rabbits overgrazed the pastures used for sheep ranching (Jaksic and Yáñez 1983; Cattan and Valderas 1987; Camus et al. 2008). During that period, there were several attempts to control rabbits (Arentsen 1953; Mann 1981; Ferriére et al. 1983; Jaksic and Yáñez 1983). First it was the introduction in 1951 of 24 young foxes (*Lycalopex griseus*) of both sexes from continental Magallanes and perhaps adjacent Argentinian Tierra del Fuego (Pine et al. 1979), which were released at Onaisín (65 km ESE of Porvenir). This fox was brought because its island congener (*Lycalopex culpaeus*) was already scarce due to hunting for export of pelts (Jaksic and Yáñez 1983; Iriarte and Jaksic 1986; Iriarte et al. 1997). Then, sheep ranchers tried to control rabbits through direct hunting, trapping, and poisoning with cyanide gas (Jaksic and Yáñez 1983; Jaksic 1998; Etchegaray 2005). But none of these methods proved effective. Finally, in 1954 sheep ranchers brought the Myxoma virus, under the authorization of the Ministry of Agriculture and implemented by the Department of Livestock and Animal Health of Magallanes Region (Arentsen 1954; Camus et al. 2008). Myxomatosis caused a significant reduction of rabbit abundance, which ceased to be a problem for ranchers. The transmission of the disease was possible through direct contact among rabbits due to their high density, without the aid of biological vectors (Arentsen 1954; CONAF 1974; Jaksic and Yáñez 1983).

The Juan Fernández Archipelago is composed of Robinson Crusoe, Alejandro Selkirk, and Santa Clara islands. UNESCO labelled this oceanic archipelago as a World Biosphere Reserve in 1977, recognizing it as an ecosystem with a high level of plant endemism (CONAF 1976, 2009). European rabbits were introduced to Robinson Crusoe Island in 1935, and 40 years later they were considered a harmful species because of their contributing to decreased vegetation cover, extinction of native species, and increased soil erosion (Kahler 1953; Brescia 1979; Camus et al. 2008). In this island, the rabbit population almost doubled over four years of sampling, from 24,275 rabbits in 1998 to 40,266 in 2002 (CONAF 2014), and currently their abundance may be higher (J. L. Cabello, pers. comm.). Rabbits continue to be challenging to control due to the complex topography of the island, making it difficult to implement conventional methods (anticoagulants, fumigants, hunting, trapping). In addition, the use of anticoagulant baits could affect other species of local fauna by their consuming dead rabbits. In Santa Clara Island, southwest of Robinson Crusoe, and with only 221 hectares (Sáiz et al. 1982), the rabbits competed with sheep for the available vegetation, which by the end of the 1970s led the settler community to request the intervention of authorities (Ojeda et al. 2003). In 1981, the National Forestry Corporation –CONAF in Spanish– implemented a control program through lasso leghold traps to permanently remove rabbits but did not affect their population (Mann 1981; Ojeda and Sáiz 2001). In 2003, CONAF implemented an integrated control system to eradicate the rabbits, thus enabling a recovery of degraded soils and stabilization of dunes. The control consisted of using a fumigant inside the caves –Aluminum phosphide– and an anticoagulant bait –Bromadiolone and Brodifacoum– (CONAF 2009). Also, hunting by humans and predation by natural enemies (*Falco sparverius fernandensis* and *Asio flammeus suinda*) was encouraged (Gálvez and Ojeda 2002). The rabbits on Santa Clara Island were finally extirpated and natural regeneration of the vegetation has developed (Ojeda et al. 2003; CONAF 2009). Alejandro Selkirk Island has never had an invasion of rabbits.

Pingüino de Humboldt National Reserve (Atacama and Coquimbo Regions) comprises three landbridge islands: Chañaral, Choros, and Damas. The largest number of species of flora with a worrying conservation status have been recorded on the Choros and Chañaral islands due to the herbivory pressure by rabbit population on them (CONAF 2013). The rabbits there overgrazed a wide variety of native plants, eroded the soil by their surface and burrowing activities, and took over the nesting burrows of Humboldt's Penguin (*Spheniscus humboldti*) and Diving Petrel (*Pelecanoides garnotii*) (CONAF 2013, PNUD 2017b). According to the International Union for the Conservation of Nature, IUCN, these two species are vulnerable and near threatened respectively. The intrusion of rabbits into the burrows of the Diving Petrel caused the adults to abandon the nest, risking the interruption of parental care of eggs or young (CONAF 2013, PNUD 2017b). The Humboldt's Penguin was more indirectly affected because the consumption of cacti by rabbits interfered with their nesting under them, thus reducing their population density (CONAF 2003, 2013). Integrated rabbit control and eradication procedures were implemented on Chañaral and Choros islands in 2013 and 2017, respectively, using mechanical and chemical methods to reduce the rabbit population, resulting in the reappearance of absent species and the regeneration of vegetation cover (CONAF 2013; PNUD 2017a). There are no rabbits on Damas Island.

In summary, the European rabbit invasion process in Chile and Australia was similar in that they were intentionally introduced for economic purposes such as meat, pelt, and fur supply, including sport hunting and pets. Rabbits were released or escaped from captivity and successfully colonized their new environments, becoming a harmful species on account of their high numbers and negative effects on artificial and natural ecosystems. The major difference between Australia and Chile rests on the management of rabbits. Australia began to control the rabbits with viral diseases after realizing that conventional trapping, hunting, or poisoning were inefficient at the landscape scale. Their management was successful as insect vectors were available to aid the transmission of these viruses. Although high mortality rates of rabbits were achieved in Chile following the release of the Myxoma virus, its application was not carried out most effectively because no insect vectors were introduced that would maintain the cycle of infection in rabbits throughout time. The Chilean government did not investigate if vectors were present on Tierra del Fuego Island, and did not introduce them, and even today there is no exact records of where myxomatosis or other viruses are present, or of their efficacy on culling rabbit populations. Rabbit eradication has been achieved only in a few Chilean islands or islets by implementing a combination of conventional methods. This old-time recipe does not seem to work on the mainland, thus requiring another type of control such as biological (viral) agents, a matter which must be urgently investigated.

European rabbit viral diseases

This section focuses on Myxomatosis and Rabbit Hemorrhagic Disease, the major viral diseases with clinical significance affecting European rabbits. We compare the Myxoma infection in Australia and Tierra del Fuego Island (Chile), focusing on Australian efforts to control the rabbit and the gaps and challenges detected in Chile.

Myxomatosis is a disease caused by the Myxoma virus, which is a poxvirus in the genus *Leporipoxvirus*. Myxoma is a linear double-stranded DNA virus (Bertagnoli and Marchandeau 2015). The natural hosts are the tapeti rabbit (*Sylvilagus brasiliensis*) in South and Central America and the brush rabbit (*Sylvilagus bachmani*) in North America. Myxoma causes only a mild disease in the natural hosts (*Sylvilagus* spp.) but is severe and usually fatal in European rabbits (*Oryctolagus cuniculus*) (Fenner and Marshall 1957; Soriguer 1980b). Myxomatosis has two forms of expression: A nodular or myxomatous and a respiratory or amyxomatous form (Dunsmore et al. 1971). The first one, which is more common, is characterized by skin lesions in conjunction with respiratory infections (Fenner and Ratcliffe 1965). Symptomatology is characterized by subcutaneous masses (myxomas), swollen and oedema in the eyelids, face or genitals. The nodular form also causes fever, lethargy, depression, anorexia, hypothermia, and purulent blepharoconjunctivitis (Hurst 1937; Brun et al. 1981; Kerr 2012; Kerr and Donnelly 2013). In late infections or in recovering rabbits, the surface of cutaneous lesions may be hemorrhagic, black, or scabbing (Fenner and Marshall 1954). Normally, rabbit death occurs from 8 to 15 days after the infection (Best et al. 2000). Myxoma does not discriminate age or sex in the rabbit population, but very young rabbits are more susceptible. Passively transmitted maternal antibodies may protect newborn rabbits (OIE 2018). The second –amyxomatous– form of the disease is clinically milder and generally nonlethal, with a predominance of respiratory signs and fever, displaying clear or purulent nasal discharge (Bertagnoli and Marchandeau 2015).

Myxoma transmission occurs mainly by bloodsucking insects, which infect rabbits through intradermal injection (Calvete 1999). Vectors are mosquitoes (*Anopheles annulipes, Culex annulirostris, Culex irritans*) and fleas (*Ctenocephalides canis, Ctenocephalides felis*, *Pulex irritans*, *Spilopsyllus cuniculi*) (Calvete 1999; Cox et al. 2013; Kerr and Donnelly 2013). The virus particles remain in the insect mouthparts protected by proteins from the myxomatous exudates (Joubert et al. 1972; Williams and Parer 1972). Mosquitos and fleas can also act as reservoirs for the virus for a long time (Joubert et al. 1972; Fullagar 1977). Fleas perform their reservoir role more effectively than mosquitoes due to their greater resistance to a wider range of temperatures and lack of food, especially under stable humidity and temperature conditions (Chapple and Lewis 1965). Hence, weather can influence the performance of Myxoma strains and their virulence because high temperatures in summer can dampen the effect of the disease (Calvete 1999; Aparicio et al. 2006). The highest mortality corresponds to summer epizootics followed by those in autumn and spring (Arthur and Louzis 1988; Ross et al. 1989; Rogers et al. 1994). Although Myxomatosis during winter is less prevalent, attenuated strains can improve their transmission capacity

(Sobey et al. 1983). Transmission by direct contact between infected rabbits is possible through the contact of ocular, nasal, semen, or genital secretions and from areas of eroded skin, or through fomites (Ross et al. 1989; Cox et al. 2013; OIE 2018). Rabbits that are infected but have not yet developed the disease can act as early carriers due to the high viremia and the appearance of the first myxomas (Kerr and Donnelly 2013). Transmission of the amyxomatous form occurs through respiratory and conjunctival secretions via direct contact (Marlier et al. 2000; Kerr and Donnelly 2013).

The Rabbit Hemorrhagic Disease is caused by a positive strand RNA virus of the family Caliciviridae, genus *Lagovirus* (Abrantes et al. 2012; Kerr and Donnelly 2013). The Calicivirus was described in China as an acute, fatal, and highly contagious hepatitis characterized by high morbidity and mortality in rabbits (Liu et al. 1984; Chen 1986; Xu and Chen 1988). RHDV causes pulmonary oedema, fever, listlessness, anorexia, blood clots in heart, lungs and kidneys, liver necrosis, and splenomegaly (Xu et al. 1988; Cooke 2002; Turon et al. 2003). Some individuals present seizures and nervous disorders, lateral recumbency, coma, and convulsions (Chen 1986; Xu and Chen 1988). Further, pathological lesions include circulatory disorders such as hemorrhage, and a frothy discharge from the nostrils or reproductive organs (Xu et al. 1985; Rosell et al. 1989; Teifke et al. 2002; Servicio Agrícola y Ganadero SAG 2020). Nevertheless, most rabbits do not show clinical abnormalities prior to death as the course of the disease is extremely rapid, 12 to 36 h after the onset of fever (Morisse 1989; Fuller et al. 1993; Henning et al. 2005; Abrantes et al. 2012). RHDV transmission is by direct contact through oral, conjunctival, and intranasal exposure (Capucci et al. 1991; Guelfi et al. 1993; Lenghaus et al. 1994). Further, the transmission is possible via fomites, including carcasses, contaminated environments, or flies feeding on carcasses (Morisse et al. 1991; Huang 1991; Lenghaus 1993). Calicivirus is robust and persists for prolonged periods in the environment (McColl et al. 2002; Henning et al. 2005; Cooke 2016). Likewise, some spread involving biting insects such as mosquitoes (*Culex annulirostris*) and fleas (*Spilopsyllus cuniculi, Xenopsylla cunicularis*) is feasible, based on laboratory experiments (Lenghaus et al. 1994; McColl et al. 2002; Kerr et al. 2015; Jernelov 2017). Carrion-feeding flies (*Caliphora* spp.) and bushflies (*Musca vetussima*) that feed on rabbit carcasses have been shown to play an important role as mechanical vectors of RHDV (Schwensow et al. 2014; Hall et al. 2019). Rabbits of all ages are susceptible to infection, but young rabbits (< 4–8 weeks) rarely develop a lethal disease due to reasons that remain understood (Xu 1991; Cooke 2007; Kerr and Donnelly 2013; Neave et al. 2018; SAG 2020). The epizootics of RHDV usually begin in autumn and winter, with most cases occurring in the colder months because the virus does not survive at high temperatures (Xu et al. 1985; Calvete 1999; Cooke 2007).

Myxoma virus was brought to Australia from the South American tapeti rabbit (*Sylvilagus brasiliensis*) and released in 1950 as a biological control against European rabbits (Fenner and Fantini 1999; Angulo 2003). Myxomatosis spread in a few months and produced a mortality rate higher than 99% (Fenner and Ross 1994; Rogers et al. 1994). The success in Myxoma transmission was further boosted by releasing the flea *Spilopsyllus cuniculi* in the early 1970s, as well as the arid-adapted rabbit flea *Xenopsylla cunicularis* in the mid-1990s (Williams and Parer 1972; Parer 1977; Kerr et al. 2012). Notwithstanding, through time Myxoma strains evolved towards less virulent phenotypes as rabbits began to develop genetic resistance and increased their populations again (Sobey et al. 1973, 1977; Shepherd 1980; Fenner and Fantini 1999; Terauds et al. 2014). Subsequently, researchers attempted to introduce a new more virulent strain of Myxoma, but it failed and was not established in the field (Cooke 1983; Kerr 2012). Decades later, another virus –specific for European rabbits– was brought to Australia: The Rabbit Hemorrhagic Disease Virus (RHDV), initially confined in the laboratory, escaped from field trials at Wardang Island off the coast of South Australia and spread throughout the continent in late 1995 (Cooke 2002, 2007; Fenner 2010). Like Myxoma virus, RHDV was highly successful with an immediate and devastating impact on rabbit populations (Bowen and Read 1998; Mutze et al. 1998; Saunders et al. 1999). Nonetheless, recent studies show that rabbits are beginning to develop resistance and are again starting to increase (Nystrom et al. 2011; Elsworth et al. 2012), although a reduction in virulence has not been observed for RHDV (Elsworth et al. 2014). Researchers have been looking for new virulent strains or new diseases to continue controlling rabbits (Cooke 2007, 2016; Fenner 2010; Cox et al. 2013; Jenckel et al. 2021). In 2015, a new RHDV arrived at the Australian continent. This new virus, termed RHDV2, was first described in Europe in 2010 (Dalton et al. 2009; Le-Gall Recule et al. 2013). It causes a disease similar to RHDV but with some important differences: It can fatally infect rabbits at a very young age (Hall et al. 2021) and can overcome immunity to the original RHDV (Calvete et al. 2018). Unlike RHDV, which is strictly species specific and only infects European rabbits, RHDV2 has been shown to infect a series of hare and cottontail species (Neimanis et al. 2018; Mohamed et al. 2021). Following its introduction to Australia via uncertain routes, RHDV2 reduced resident wild rabbit populations by an average of 60% (Ramsey et al. 2020).

In Chile, rabbit viral diseases are notably less studied than in Australia. The Myxoma virus was released to control rabbits in Tierra del Fuego Island in 1953, to stall the serious rabbit impact on livestock forage (Arentsen 1953, 1954). This campaign began in 1953 with laboratory tests, and one year later, the Myxoma virus was released but without introducing its vectors (mosquitos and fleas) (Jaksic and Yáñez 1983; Jaksic 1998; Camus et al. 2008, 2014, 2021). The Myxoma transmission then occurred by direct contact from rabbit to rabbit, taking advantage of their high density (Amaya and Bonino 1981; Mann 1981). Although this biological control was successful in decreasing rabbit numbers and economic losses, rabbits persisted for decades, although not with the same ecological and economic impacts as before (CONAF 1973, 1974). Rabbit ectoparasites in continental Chile are four species of mites: *Sarcoptes scabiei* var. *cuniculi*, *Psoroptes equi* var. *cuniculi*, *Notoedres cati* var. cuniculi and *Cheyletiella parasitovorax*, whereas in the Juan Fernandez archipelago rabbits present some degree of infestation by the ectoparasites *Cheyletiella parasitovorax*, *Haemodipsus* sp. and *Lystrophorus* sp. (Acevedo 1990b). Still, none of these has been tested as myxoma vectors.

Myxoma virus has not been studied in any other part of Chile. According to SAG, Myxomatosis is present in Chile from the Coquimbo to the Biobío Regions, causing recurrent outbreaks over time, being a disease that is mandatory to notify (Table 1) (MINAGRI 2015; SAG 2019). Indeed, there were press reports in 2013 about Myxomatosis cases in the Biobío Region, commented together with their consequences for the carnivore assemblage that preys on rabbits (BiobíoChile, Soychile, and UdeC media in 2013). Also, the peri-urban area of Santiago in Metropolitan Region, showed evidence of Myxomatosis with high rabbit mortality in 2016 (MINAGRI 2015; ATM and CODELCO 2018; Pavez 2020). And finally, Lago Peñuelas National Reserve in Valparaiso Region, had a large Myxomatosis outbreak: This episode lasted about three months and began in spring of 2016 until summer of 2017 (CONAF park rangers, pers. comm.). Up to now, there is still a lack of standardized Myxoma records regarding their territorial distribution and size of the cases in Chile. SAG has not reported presence of RHDV in the country.

Table 1 Number of cases of Myxomatosis in European rabbits in Chile. Information obtained by Transparency Law from the Agricultural and Livestock Service (SAG 2019)

Year	Coquimbo Region	Metropolitan Region	O'Higgins Region	Biobío Region	Total cases
2014	0	2	0	0	2
2015	0	107	0	1	108
2016	1	2	0	0	3
2017	0	3	11	0	14
2018	41	0	0	0	41

Regions are ordered from northern to southern locations, from left to right.

In summary, viral diseases were similarly applied in Chile and Australia in the 1950s to control the impact of rabbits. The Australian methodology was more effective by stocking and releasing vectors to aid the spread of the disease. Mosquitoes were responsible for the initial spread in 1952, and endemic ticks and fleas were not as widespread. In Chile, no vectors were introduced, and few have been described to be endemic. In addition, Australia kept a tight lid on the rabbit infestation over time, monitoring rabbit numbers as well as virus-host coevolution and rabbit resistance, later introducing a new virus (RHDV) to prevent rabbit densities from building up again. When controlling rabbits in Tierra del Fuego Island, Chile did not consider that rabbits would eventually generate resistance to Myxoma; the situation of the virus in the country still being unstudied. This highlights the necessity of viral diseases research in Chile including outbreaks, territorial distribution, seasons, environmental conditions, rabbit susceptibility, prevalence, mortality, morbidity, resistance, and Myxoma strains present in the country. It is fundamental to examine unpublished reports on Myxomatosis distribution, or even RHDV, to provide a strong basis for making future management decisions and gauge their potential as future biological control agents in continental Chile or on islands such as Robinson Crusoe. Finally, it is crucial to understand the relationships between rabbit population dynamics, Myxomatosis prevalence, and their local vectors (mosquitos and fleas). Myxomatosis outbreaks usually are synchronized with rabbit population cycles, with viral diseases spreading more efficiently when higher contact rates occur (Keer and Donnelly 2013; Abarca et al. 2016; Cooke 2016). Most of this information is missing in Chile.

European rabbit ecological impacts

This section focusses on European rabbit characteristics that result in environmental impacts, in Australia and Chile. Also, about the importance of understanding the population dynamics of this species to manage it efficiently, recognizing which drivers affect their fluctuations.

The European rabbit ecology has been well studied throughout history because they are native to the western Mediterranean basin and have become a troublesome invasive species elsewhere since the sixteenth century if not before (Soriguer 1979; Flux and Fullagar 1992; Flux 1994; Rogers et al. 1994; Long 2003). Literally thousands of reports have described its distribution, behavior, feeding, reproduction, physiology, mortality, population dynamics, factors affecting their densities, habitats occupied, and their place in food webs (Soriguer 1979; Thompson and King 2004; Lees and Bell 2008). Rabbits inhabit open grassland, savanna, shrub-steppe, and even dense vegetation such as scrub, bracken, fallen timber, and rock outcrops (Cook 2007; Jernelov 2017). They feed on artificial and natural grasslands, shrubs, fruit trees, cacti, tubers, rhizomes, flowers, and in extreme cases any plant with some water and nutrients, considerably affecting vegetation cover (Myers and Poole 1963; Thompson and King 2004). The wide distribution of the rabbit around the world, as native or invasive, is attributed to their high population growth rate and reproductive capacity, with a gestation of only 30 days and the female's ability to go into estrous cycle while nursing her young (Gálvez-Bravo 2011). The number of litters per year is two to six, with up to seven offspring each (Wood 1980; Wheeler and King 1985; Myers et al. 1994). Usually, the breeding season is between spring and summer, and the increase phase is from summer to autumn (Soriguer 1979, 1980a, 1981; Gibb 1990; Villafuerte and Delibes-Mateo 2007). The female is receptive throughout the year (but in Australia it depends on the availability of green forage), and juveniles leave their burrows by three weeks of age and reach sexual maturity between four to nine months old (Soriguer 1981; Myers et al. 1994; Angulo 2003).

Rabbits are widely distributed in varied Australian landscapes, including urban and coastal areas (Jernelov 2017). They prefer well-drained and deep sandy soils, low vegetation, scrub, blackberry bushes or fallen logs for shelter, and localities with intermediate rainfall and uncommon droughts (Williams et al. 1995). They occasionally do well in hot arid zones, even though physiologically they are not well adapted to dry conditions (Myers and Parker 1975; Cooke 2007; Jernelov 2017). They occur in short grass areas such as semi-arid or heavily grazed pastures, currently inhabiting 4 million km^2 of Australia, mostly south of the Tropic of Capricorn and in environments ranging from sub-alpine sites to stony deserts and from subtropical grasslands to wet coastal plains (Cooke 2007). Where present, certain native tree and shrub seedlings are selectively grazed by rabbits (Bird et al. 2012), preventing their regeneration and leading to high ecological impacts even at very low rabbit densities. A recent study lists rabbits as one of Australia's most damaging invasive species (Bradshaw et al. 2021).

Rabbits are present in Chile from the southern fringe of the Atacama Region in the north (M. Duclos, pers. obs.) to the Los Lagos Region in the south and then reappear in the Magallanes Region (Jaksic et al. 2002; Iriarte 2008). There are discrepancies regarding their presence in the Antofagasta, Atacama, and Aysén Regions (Jaksic et al. 2002; Bonino and Soriguer 2004; Iriarte 2008; CONAF 2014). In Magallanes Region, although rabbits were nearly exterminated in Tierra del Fuego Island in the 1950s (Jaksic and Yáñez 1983; Camus et al. 2008, 2014, 2021), there are still surviving populations in Chile's Yendegaia Bay (Bonino and Gader 1987) and

Argentina's Ushuaia and Parque Nacional Tierra del Fuego (A. Schiavini, pers. comm., May 2020). They also occur in higher densities on the Magallanes mainland, north of Punta Arenas and up to the limit with Argentina (G. Flores, pers. obs.; D. R. Martínez, pers. comm.; December 2021). Nonetheless, the information on the distribution and abundance of rabbits in Chile is very general, and greater precision would be valuable. Rabbits in central Chile use the open spaces within shrubland areas, modifying the landscape according to their needs (Simonetti 1983, 1989). They prefer to eat native perennial herbs over Eurasian-origin grasses, removing unprotected herbs and shrub seedlings, thus forestalling their reproduction (Jaksic and Fuentes 1980; Jaksic and Soriguer 1981; Simonetti and Fuentes 1983; Fuentes et al. 1983). Consequently, rabbits restrict native herbs to areas under bushes, while spaces between shrubs are occupied by introduced grasses (Keely and Johnson 1977; Fuentes and Simonetti 1982; Figueroa et al. 2004).

The population dynamics of rabbits depend on endogenous factors such as density-dependence, cyclicity, growth rate, reproduction, and physiology, which allows them to respond to environmental changes and adjust their abundance (Wells et al. 2016). They also depend on exogenous drivers such as weather conditions (precipitation, humidity, evaporation, and temperature) (Gilbert et al. 1987), vegetation cover (Hayward 1961; Rogers and Myers 1979; Wallage-Drees 1983; Martins et al. 2003), soil conditions for digging burrows, plant protective cover –specifically of shrubs– (Poole 1960; Cooke 1977; Jaksic et al. 1979a, b; Simonetti and Fuentes 1982; Parer and Libke 1985; Moreno et al. 1996), predators and diseases, among others (Pech and Hood 1998; Mutze et al. 2002, 2010; Mellin et al. 2016; Lurgi et al. 2018; Brown et al. 2020). Nevertheless, all authors concur that some drivers influence more than others the rabbit density depending on the site (Cooke 2007; Roy-Dufresne et al. 2019; Brown et al. 2020).

Rabbit distribution and abundance depend highly on weather conditions, food supply, shelter availability, and predator pressure (Rodríguez 1988; Calvete 1999; Lombardi et al. 2003). First, weather –apart from providing rainfall and adequate temperature conditions—may ameliorate other limiting resources for rabbits –food or shelter– allowing escape from predators (Berryman et al. 1984; Berryman 1999a, b). Secondly, plant food supply is an important requirement for rabbit reproduction and population growth because it contributes to an early breeding and prolonged reproductive season (Delibes and Calderón 1979; Wood 1980; Gilbert et al. 1987; Wallage-Drees and Michielsen 1989; Martins et al. 2003). Rabbits consume a variety of plants, including roots, crops, pastures, herbs and grasses, shrubs, and young trees (Williams and Moore 1989; Mutze et al. 2008; Mellin et al. 2016). The supply of nutrient-rich forage precipitated by rainfall can positively influence ovulation, gestation, and lactation (Seif and Pederson 1978; French and Schultz 1984). Frequently, rabbit reproduction is in synchrony with plant growth, where both the reproductive rate and offspring production increase (Cooke and McPhee 2007). For example, rabbit populations start increasing when the first rains fall, and the vegetation cover re-emerges after a period of drought (Delibes and Calderón 1979; Wood 1980; Wheeler and King 1985). Thirdly, shelter is essential for rabbit reproduction and protection against predators and climatically adverse conditions (Rogers and Myers 1979; Parer and Libke 1985; Parer et al. 1987). Thus, the availability of burrows is a relevant resource for rabbits because they are social mammals that form large groups of related individuals that rest underground (King et al. 1984; Parer and Libke 1985). Warren destruction thus greatly reduces rabbit populations (Cooke 1982; Kolb 1994). Rabbits can excavate complex tunnels systems ranging from three to 45 m long and diameters of 15 cm, with chambers for nesting or feeding up to 30 or 60 cm tall; they can dig up to two meters deep in adequate soil (Briceño 2019). Rabbits prefer to build burrows in deep and permeable soils to insulate themselves from heat in arid regions (Hayward 1961; Cooke 1982). They can tolerate a loss of up to 50% of their weight in water during prolonged periods of drought (Rodríguez 1988; Kolb 1991; Cooke and McPhee 2007). Favorable environmental conditions, including rains or humidity, influence soil conditions and soften hard surfaces (Trout and Smith 1995). Rabbits can then dig easily, lowering predation risk and increasing rabbit reproduction (Gilbert et al. 1987; Bell and Webb 1991; Knoepp et al. 2000; Martins et al. 2003; Fordham et al. 2012; Mellin et al. 2016). Finally, predators can and sometimes do regulate rabbit local abundance, by preventing a given population to increase (Newsome et al. 1989). Still, rabbits do not have specialized predators and are thus threatened by generalist predators (King and Wheeler 1985; Villafuerte 1994; Hanski et al. 2001; Sinclair 2003). Many authors point out that such predators can keep rabbits at low densities only when the rabbit population has been previously affected by droughts, heavy snowfalls, or diseases (Hansson 1971, 1979, 1987; Calvete 1999). Usually, predators cannot control rabbits at high densities because predation pressure becomes saturated, that is, rabbit population growth rate is higher than predation rate (Myers and Poole 1963; Myers 1964; Myers and Parker 1975; Cooke 2007). Additionally, generalist predators can switch easily between rabbits and abundant alternative prey, contributing to relaxing the already weak predator control on rabbits (Jaksic and Ostfeld 1983; Newsome et al. 1989; Trout and Tittensor 1989). In this context, research shows that in Australia large rabbit populations have sustained very high populations of introduced mesopredatores such as Feral cats (*Felis catus*) and Red foxes (*Vulpes vulpes*) and the sustained reduction of rabbit numbers by RHDV has led to long term reduction of these predators and consequently the rebound of several threatened native mammalian species (Pedler et al. 2016).

In Australia, rabbits occur across the mainland (Stodart and Parer 1988) and appear well adapted to a broad range of environmental conditions (Cooke et al. 2018). Brown et al. (2020) assessed long-term data of rabbits and high-resolution environmental variables to identify the main population drivers: They depend on interannual temperature (increasing the probability of detection), precipitation, pasture availability, and possibly the prevalence of RCV-A1, a non-pathogenic endemic virus similar to RHDV that can provide partial immunity to the lethal biocontrol virus. Rabbits in cooler, wetter areas tend to be more abundant due to higher food availability and seem more resistant to infection with lethal RHDV (Brown et al. 2020). The effects of pasture availability and water content combined with cooler temperatures and regular seasonal rainfall apparently drive the high rabbit abundances found along the southern coastline (Gilbert et al. 1987; Cooke 2012). Also, the effects of the RCV-A1 virus and its prevalence are positively correlated with high rabbit densities, because that virus provides partial protection from lethal RHDV (Strive et al. 2013; Liu et al. 2014; Cooke et al. 2018). These studies highlight the complex interactions between rabbit populations, weather conditions, disease vectors, and epizootics (Cooke 1983; Liu et al. 2014), showcasing that long-term analysis of invasive species provides an important opportunity to manage rabbits by understanding their fluctuations to predict spatially explicit abundance patterns. This type of assessment is required to identify where and under which environmental conditions rabbits attain high and stable abundances due to population recruitment and resistance to population perturbations (Baker and Bode 2016; Lurgi et al. 2016; Brown et al. 2020).

In their native Europe, rabbit populations depend highly on food and shelter availability, and they are strongly affected by predator activity (Lombardi et al. 2003; Lurgi et al. 2018). In Australia, rainfall promotes plant growth thus providing food for rabbits to grow, find a mate, and reproduce, especially in winter at the start of the breeding season (Williams et al. 1995; Cooke 2011). There, rain also produces moister soil conditions, becoming more favorable for rabbits to dig their burrows, and diminishes evaporation that prevents soil compaction (Newsome 1966; Kolb 1994). Rabbits in Australia are preyed on by Dingoes (*Canis familiaris dingo*), Red foxes (*Vulpes vulpes*), Feral cats (*Felis catus*), Wedgetail eagles (*Aquila audax*), Little eagles (*Hieraaetus morphnoides*), Brown goshawks (*Accipiter fasciatus)*, Brown falcons (*Falco berigora*), and Goannas (*Varanus* spp.) (Parer 1977; Baker-Gabb 1984; Ridpath and Brooker 1986; Newsome et al. 1989). Cats tend to eat younger –and foxes older– rabbits, and both carnivores can maintain rabbit populations at low densities, especially when long hot summers have caused rabbit population declines due to lack of food (Newsome et al. 1989; Newsome 1990). Still, these two predators are also invasive species and usually are targets of control themselves, which enables rabbit numbers to increase quickly (Newsome et al. 1989; Sinclair 1996). The regulation of rabbits by predators is weak at densities below eight to 15 rabbits/km^2, when predators turn to feed on alternative prey, and rabbit populations escape from their hunting pressure (Trout and Tittensor 1989; Newsome 1990).

In Chile, rabbits and their negative impacts have stimulated research since the late 1970s, to learn about the native and alien plants consumed and dispersed by them, the ecosystems where they live, their competition with native mammals and livestock, their influence on the diet of native predators, among

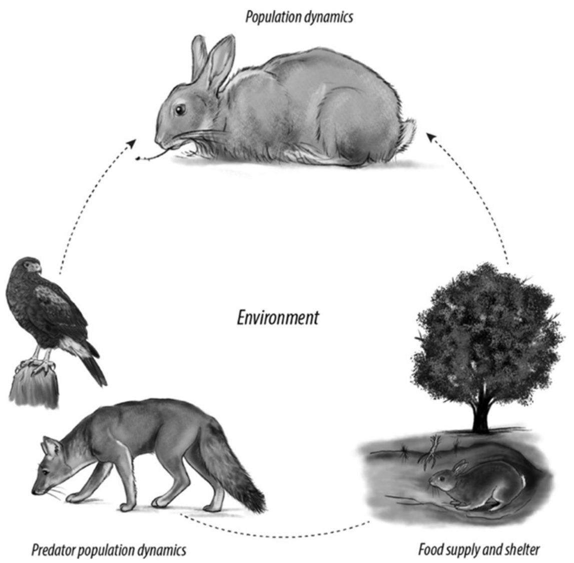

Fig. 1 Simplified network of drivers that influence European rabbit populations in Chile. A Chilean hawk (*Parabuteo unicinctus*) and a Culpeo fox (*Lycalopex culpaeus*) are portrayed as typical predators. Authors' design

others (Jaksic et al. 1979a, b; Jaksic and Yáñez 1980; Jaksic and Fuentes 1988, 1991; Jaksic 1998; Ojeda et al. 2003; Camus et al. 2008, 2014, 2021; PNUD 2017a). Notably absent is research on the population dynamics of rabbits, despite being essential to understand their fluctuations, and the factors that trigger outbreaks (Fig. 1). With regard to predators in Chile, they have been reported to be inefficient regulators of rabbit populations (Jaksic et al. 1979a, 1979b; Jaksic and Yáñez 1980; Jaksic and Soriguer 1981; Jaksic and Ostfeld 1983), but those conclusions currently seem dated and require re-examination with more powerful analytical tools. More quantitative information is needed to complete the population dynamic motion picture of rabbits in Chile. For example, on climatic and soil data, primary production, breeding season, litter size, diseases, and trophic interactions where the rabbit is involved, both with competitors and predators. Also, it is necessary to know the quality and quantity of vegetation consumed by rabbits in different regions of Chile to identify the most vulnerable ecosystems. Remote sensing with normalized vegetation index (NDVI) could be used to determine vegetation cover change and use this information in population dynamic models to analyze the influence of food resources on rabbits and vice versa (Newsome 1966; Wood 1980; Burrell et al. 2017).

Rabbits in Chile interfere with the structure, composition, and functioning of ecosystems, affecting their services, benefits, and the well-being of other users (PNUD 2017a). They modify the shrub spatial distribution and their survival rate, leading some species to local extinction, preventing the normal renewal of the native shrubland and its successional process. They shift the composition of shrubs toward those less palatable while broadening their distance to each other (Fuentes and Simonetti 1982; Fuentes et al. 1983; Simonetti and Fuentes 1983; Jaksic and Fuentes 1988, 1991; Fernández and Sáiz 2007; Camus et al. 2008, 2014, 2021; Castro et al. 2008). Rabbits specifically harm the regeneration of the endemic palm (*Jubaea chilensis*) (Fleury et al. 2015), the shrub *Cryptocarya alba* (Benedetti 2012), and the perennial herb *Convolvulus chilensis* (Suárez et al. 2004). They contribute to disperse invasive plants such as the poppy (*Papaver somniferum*) (Cuevas and van Leersum 2001; Constible et al. 2005; Fernández and Sáiz 2007). Rabbits were introduced to Robinson Crusoe Island in 1935 (Jaksic 1998; Cuevas and van Leersum 2001). This island contains a most interesting biodiversity worldwide, comprising 131 endemic species (62% of the vascular native flora of Chile), 12 endemic genera, and one endemic family (Matthei et al. 1993; Marticorena et al. 1998; Stuessy et al. 1998; Myers et al. 2000; MMA 2014) and rabbits have reduced the vegetation cover by direct consumption, threatening this unique flora. Besides, rabbit activity on the island causes an ecosystem transformation into an arid terrain –desertification– due to the absence of trees to retain the humidity, giving rise to droughts, and accelerating erosion (Acevedo 1990a; CR^2 2015; CONAF 2016) with 40% of soils already affected severely (Cuevas and van Leersum 2001; CONAF 2016).

Rabbits in Chile are preyed upon by native carnivores such as foxes (*Lycalopex culpaeus* and *L. griseus*), cats (*Puma concolor*, *Leopardus guigna,* and *L. colocolo*), skunks (*Conepatus chinga* and *C. humboldtii*), and grisons (*Galictis cuja*) and by alien carnivores such as mink (*Neovison vison*). Also, by kestrels, eagles, and hawks (*Falco sparverius*, *Geranoaetus melanoleucus*, *G. polysoma,* and *Parabuteo unicinctus,* respectively), and by owls (*Tyto alba, Athene cunicularia,* and *Bubo magellanicus*) (Jaksic and Fuentes 1988, 1991). Still, they do not seem able to keep rabbits in check because they consume easier to handle prey (Jaksic and Soriguer 1981; Jaksic and Ostfeld 1983). Predators ate rabbits in small proportion, according to studies conducted in the late 1970s to late 1980s (Yáñez and Jaksic 1978; Jaksic et al. 1980; Schlatter et al. 1980; Jaksic and Soriguer 1981; Jaksic and Ostfeld 1983; Jiménez and Jaksic 1989, 1990, 1991). The surprisingly low predation upon rabbits was attributed to native predators not yet having learned to hunt for this recently introduced prey (Jaksic et al. 1979a, 1979b; Jaksic and Yáñez 1980; Jaksic and Fuentes 1988, 1991). These authors put forth that those local predators were used to the simple escape behavior of their native prey –which dash straight to the nearest shelter—and not to the escape strategy of rabbits that includes zigzag runs, leaps, and back-tracks (see review in Jaksic 1986). Alternatively, the same predators consumed a high proportion of native rodents that nonetheless had remarkably stable abundance (Jaksic and Soriguer 1981; Fuentes and Simonetti 1982). Interestingly, from the late 1980s onward a sustained increase in the consumption of rabbits has been observed among the eagle *Geranoaetus melanoleucus,* the hawk *Parabuteo unicinctus*, and the fox *Lycalopex culpaeus* (Simonetti 1986; Iriarte et al. 1989; Pavez et al. 1992, 2010; Rubio et al. 2013). For instance, at the same study site to the east of Santiago city, fox diet had 20% rabbit numerical representation in 1976 (Jaksic et al. 1980), 37% in 1983 (Simonetti 1986), and 48% in 1984 (Iriarte et al. 1989). This increased rabbit intake paralleled the concomitant decrease in the consumption of the native Degu rat (*Octodon degus*), which gradually declined over the last decades due to loss of shrub cover, fragmentation and deterioration of its habitat, soil degradation by erosion and compaction, competition for food with rabbits, and increased human and dog presence (Pavez et al. 2010; see Dukes and Mooney 2004 for a similar case in California). Regulation of rabbit populations by predation in Chile may be similarly ineffective as in Australia, probably because the respective predators are generalists, saturate their functional response at high rabbit density, and display switching between alternative prey (Myers and Poole 1963; Myers 1964; Jaksic and Soriguer 1981; Jaksic and Ostfeld 1983; Berryman 1999a, ba, 1999a, b b; Hanski et al. 2001; Sinclair 2003). Thus, it is possible that predators in Chile can help keep rabbits at low density only if droughts or other limiting conditions (weather, food, parasites, diseases) reduce their population size first.

In summary, the ecology of the European rabbit in Chile and Australia appears to be closely similar. The differences observed are based on dissimilar efforts at monitoring populations and environmental drivers; Australia having a long history of tracking throughout its territory, with robust data on weather, soil, plant conditions, and on predator functional and numerical responses that allow construction of population-based and spatially explicit models to understand the impact of this invasive species in the local interactions network. In contrast, Chile has yet to start monitoring rabbit populations and identify the main drivers that influence their dynamics over the short and long terms.

European rabbit economic impacts

Australia is among of the largest food producers globally with the greatest direct exploitation of agriculture based on grazing lands (Chen et al. 2018; Kucukvar et al. 2019). Rabbits have been considered the main harmful species for agriculture, causing significant losses in the sheep, beef, and wool industry due to their voracious herbivory and high reproductive rate (Croft et al. 2002; Cooke et al. 2013). They generate a strong tension on the pasture composition and compete for forage chiefly with cattle and sheep, resulting in a reduction in the volume and quality of wool, increasing the associated cost of animal feed, decreasing livestock reproduction, and causing weight loss (Croft et al. 2002; Vere et al. 2004; Cooke et al. 2013). For example, sheep in areas without rabbits have on average 7.23 kg greater live weight and produce 21% more greasy wool per year in comparison with sheep that competed with rabbits numbering 72/ha, while limiting the ability of sheep and cattle to survive and recover from drought, common in semiarid ecosystems (Williams et al. 1995). In addition, forestry, tree plantations, and vegetable crops suffer browsing damage by rabbits, causing declines of native flora, and facilitating the invasion of exotic plant species (Mitchell and Balogh 2007). For instance, rabbits threaten the survival of more than 300 Australian native flora and fauna species, of which 24 are critically endangered, such as the Pygmy possum, Orange-bellied parrot, and Ballerina orchid

(Gibb and Williams 1994; Williams et al. 1995; Gong et al. 2009). Rabbits cause losses for the agricultural industry valued at AUD $206 million yearly by competing with cattle and sheep for food, while contributing to soil erosion, damaging crops, and destabilizing the land, potentially leading to livestock injury (Vere et al. 2004; Bradshaw et al. 2021).

Detailed knowledge of rabbit distribution and abundance in Australia have allowed to estimate their impact on sheep and cattle production, by calculating the equivalence of the competitive interference of food relative intake due to access to resources (Vere et al. 2004; Cooke et al. 2013). Researchers have weighed the rabbit effect on the supply function (equilibria market and expenditure-profit curve shifts), calculating the economic damage by the variation in meat and wool supply and prices (Vere et al. 2004; Gong et al. 2009; Cooke et al. 2013; McLeod 2016). The rabbit represents 36% (AUD 216.63 million) of the total impact of invasive species damage to the Australian economy, becoming the invasive species with the most significant economic impact in the country (Gong et al. 2009; McLeod 2016). Relative rabbit and sheep intake ratio/ha is 16:1, causing a decrease of 14% on beef and sheep meat production, and of 15% in the wool industry (Gong et al. 2009; Vere et al. 2004), reducing by 60% the forage available to domestic cattle and sheep (Cooke et al. 2013; McLeod 2016). Currently, agriculture losses amount to over AUD 2 billion per year, but before introducing the Myxoma virus, rabbits caused losses for AUD 600 million (Bomford and Hart 2002). Rabbit economic impact is proportional to their abundance and thus introduction of Myxomatosis in 1950 and RHDV in 1995 (Cooke 2007; Cooke et al. 2013) meant that these viruses combined reduced financial losses by 75 to 95%, estimated at AUD 53 billion from 1950 to 1995 and at AUD 17 billion since 1995 (Cooke et al. 2013). Rabbit control increased production of wool and meat by 26% during that period but their populations began to rise again as they developed resistance (Cooke et al. 2013). The investment in additional control measures was reduced and meant a change in the cost–benefit frontier, increasing the total costs to maintain and optimize the financial returns of this productive sector (Waithman 1979; McLeod 2016). RHDV was applied in 1995, which achieved 80% reduction of rabbits, and the increase in production meant a profit of AUD 600 million yearly (Gong et al. 2009). Cooke et al. (2013) estimated that pooled Myxoma and RHDV introduction meant a benefit of about AUD 70 billion for the meat and wool industry (ACIL 1996). Economic valuation of rabbit damages has used data collected from the wool, sheep and beef meat, and grain markets to calculate changes in the total surplus (consumer and producer surplus and the producers' net income) (Vere et al. 2004; Gong et al. 2009; Cooke et al. 2013; McLeod 2016). Thus, the economic impact has been estimated through the avoidable or induced costs, evaluating the observed changes in the producers' income using the cost–benefit frontier model (Cooke et al. 2010, 2013). Likewise, variations in social welfare have been estimated by weighting changes in total surplus, using models that assume fixed prices of a product in the face of supply changes, limiting itself to evaluating producers' surplus (Vere et al. 2004). Other researchers have reconstructed the supply and demand functions of the market by weighting the producer surplus, where the differential between market price, cost of production, and consumer surplus is between the willingness to pay and the market price (Gong et al. 2009). This output is useful to evaluate the change due to rabbit impact, using estimates of elasticities such as the variation of supply and demand in price changes (Vere et al. 2004; McLeod 2016). For example, the cost–benefit ratio for Australian agriculture of using rabbit poisoning (with sodium fluoroacetate) caused an 83% decrease of rabbits in New South Wales –saving AUD 1.2 million/year– and 24–73% of those in South Australia –saving AUD 0.56 million yearly (Saunders et al. 2002). In addition, the wool industry had losses of AUD 130 million per year owing to rabbits before the release of RHDV. Afterward, agricultural production increased by AUD 600 million annually, involving AUD 300 million from the wool sector, AUD 150 million from meat cattle, AUD 80 million from crops, and AUD 70 million from sheep meat (Vere et al. 2004; Gong et al. 2009). Recent estimates have valued the cumulative benefit of Myxomatosis and RHDV to Australian pastoral industries at about AUD 96 billion over the last 60 years (Vere et al. 2004; Gong et al. 2009). Although these biological control agents have provided ongoing rabbit control for over 60 years with little cost, they have not eliminated the root problem. The overall loss caused by rabbits to agriculture and horticulture in Australia is estimated to be about AUD 206 million per year (Gong et al. 2009). Finally, the economic value of environmental benefits owing to rabbit control has not been calculated, nor that of suppressing Feral cats (*Felis catus*) or Red foxes (*Vulpes vulpes*) (Read and Bowen 2001; Holden and Mutze 2002), or that of recovering native flora and fauna (Mutze 2016; Pedler et al. 2016).

From 1910 to 1984 Chile exported more than 4 million rabbit pelts to the world, representing almost 73% of Chilean wildlife exports of that period (Iriarte and Jaksic 1986; Jaksic and Fuentes 1988). From 1987 to 1993, 1.25 million rabbit pelts were legally exported from Magallanes Region alone (Iriarte et al. 1997). No further information on rabbit trade has been published since. During the 1960-1970s, the Chilean government promoted the consumption of rabbits through a comprehensive management plan, controlling populations and promoting exploitation, but this initiative failed to become established and industrialized (CONAF 1974). No further initiatives have been implemented since. Rabbits have positively impacted the market economy as a commercial resource that has provided employment and income in rural areas, as well as supplying meat, fur, and pelts (Iriarte and Jaksic 1986; Iriarte et al. 1997; Camus et al. 2008, 2014, 2021). For example, rabbit consumption represents a food subsidy equivalent to 11% of the annual family income (Isla and Katunaric 2006), improving food security and access to animal protein with great nutritional value at low cost in rural

Table 2 European rabbit impacts on productive systems and on ecosystem services in Chile, highlighting gaps of economic knowledge

Area	Impact	Sign	Description	Knowledge gap
Productive system	Agricultural crops	(–)	Consumption of seedlings of grape and fruit trees	Quantify rabbit densities, identify damage to crops, costs of management, economic thresholds, and losses
	Forest plantations	(–)	Consumption of pine and eucalyptus seedlings	Quantify rabbit densities, identify damages to plantations, costs of management, economic threshold, and losses
	Livestock raising	(–)	Competition for forage with cattle and sheep	Evaluate interspecific competition and determine the meat, milk, and wool production losses
	Fishing	(–)	Burrowing activities cause landslides to sea	Evaluate erosion impact and silting on harvest of sea resources
	Island tourism	(–)	Consumption of endemic flora and affectation of sightseeing	Determine vegetation consumption rates and their visual impact
Ecosystem service	Primary production	(–)	Loss of regeneration of forests, shrublands and grasslands	Determine vegetation consumption rates and their effects on regeneration
	Predation	(+)	Contribution to diet of native predators	Analyze consumption rate of rabbits by native predators, evaluate the importance of rabbits in local food webs
	Erosion	(–)	Soil erosion by overgrazing and burrow excavation	Quantify erosion due to feeding and burrowing activities of rabbits and their desertification effects
	Invasive dispersion	(–)	Dispersal of invasive plant species	Assess the dispersal rate of invasive plants and their impact on regeneration of forests, shrublands, and grasslands
	Competition	(–)	Competition for food with native mammals	Analyze competitive rates of rabbits with native mammals, evaluate their importance in local food webs
	Native dispersion	(+)	Dispersal of native plant species	Assess the dispersal rate of native plants and their impact on regeneration of forests, shrublands, and grasslands
	Game production	(+)	Supplementation of meat and pelts for rural families	Quantify rabbit densities, hunting pressure, costs, and economic returns

communities of Tregualemu, Maule Region (CONAF 1974; Risam et al. 2005; Krupova et al. 2020). Still, rabbits have demonstrated their destructive potential in natural and anthropic ecosystems, damaging agricultural crops and forestry plantations, and impacting on livestock activities (Ferriére et al. 1983; Ojeda et al. 2003; Camus et al. 2008, 2014, 2021).

Rabbits affect Chilean ecosystems not only ecologically but also economically, generating losses in productive systems and biodiversity services. They cause economic losses in agriculture, livestock, forestry, and potentially tourism (Table 2) impacting on large-scale and small-scale practices, generating production loss, and reducing food quality and human income (Ojeda et al. 2003; Camus et al. 2008, 2014, 2021; PNUD 2017a; Cerda et al. 2020). Rabbit impact on subsistence agriculture has not been measured so far in Chile, while that on industrial agriculture has been claimed to cause an external cost by operations to control rabbits, thus reducing profits in the wine industry. Still, cost indicators for protection against rabbits are currently unreported. Sheep production was reduced by 1,898,593 kg of wool, and meat by 1,947,776 kg in Tierra del Fuego over the period 1953–1954 (Arentsen 1954; Briceño 2019). Amaya and Bonino (1981) and Bonino (2006) calculated that 12 to 16 rabbits equate the feeding of one sheep. Further, rabbit voracity generates intense stress on the production and composition of pastures, decreasing their productivity and species diversity (Simonetti 1983; Gader 1986; Bonino 1995, 2006; Bonino and Soriguer 2009; Pavez et al. 2010). Still, there are no economic estimates regarding the losses or costs in meat or milk production by interference of livestock from rabbits. They are also known to cause extensive losses in forestry due to their browsing seedlings, preventing establishment, growth, and regeneration of exotic pines and eucalyptus. Such economic costs involve the loss of planting (587,931 ha lost from 2006 to 2014), replanting costs (USD 17.96/ha), and delayed exploitation of the stands affected (Rodríguez 1988; Acuña and Drake 2003; CONAF 2014). The main commercial seedlings affected by rabbit consumption are those of Monterrey pine (*Pino radiata*), *Atriplex* spp., *Eucalyptus* spp., and fruiting trees (Rodríguez and Trevizan 1984; Rodríguez 1988). The damages observed consist of cutting the apical bud of newly planted trees and browsing of bark at their base (Camus et al. 2014), producing lateral growth that disables the tree commercially, preventing its development, and producing a nascent and small growth resulting from the regrowth of lateral buds, eventually generating their death (Gader 1986; Rodriguez 1988). Plantations endure damage during the first two to three years of implantation until the seedling has grown to about 50 to 60 cm and its apical tips are out of the reach of rabbits. The cost of tree planting programs is often increased because of the need to erect tree guards. The maximum consumption of seedlings is usually observed during the winter, due to the scarcity of other vegetation to rabbits (Bonino 1994; Bonino and Soriguer 2009).

The negative rabbit impacts have long been noted in production systems and natural ecosystems of Chile, but there are significant information gaps to assess rabbit effects economically and to determine their magnitude (PNUD 2017a). It is always a challenge to quantify and economically evaluate the direct and indirect impacts of a species on fixed and non-use goods, but a major economic valuation of rabbit impacts in Chile was performed by PNUD (2017a) and later published by Araos et al. (2020). The annual loss possible to value from rabbits is calculated at USD 2,982,998 on biodiversity and USD 266,339 on productive systems, basically forest and fruit plantations (PNUD 2017a). Thus, Chile has an annual loss of USD 3,249,337 attributed to rabbits, where most of the cost (90%) is from the non-use values (culture, heritage, and existence benefits) due to a high percentage of endemism and unique landscapes on islands or forests (PNUD 2017a). Chilean government has spent at least USD 1,465,754 to eradicate rabbits from Chañaral and Choros islands (PNUD 2017a). Therefore, to fully understand the rabbit impact on the well-being of Chilean society it is necessary to advance in studies that aim at directly assessing the perception of different sectors and interest groups about the potential rabbit damage on the Chilean ecosystems (Van de Wouw et al. 2011; Gutiérrez 2015). PNUD (2017a) used the total economic impact assessment methodology (VET) to integrate and account for the rabbit impacts on goods and services. They presented a value linked to their use, provision, and regulation with those that do not have an associated market, whose value carried out a weighting of the rabbit damage to the well-being of Chilean society based on information collected (PNUD 2017a; Araos et al. 2020). Secondary sources estimated the rabbit impacts on the provisioning of ecosystem services by weighting restoration and prevention costs in forest and fruit plantations (PNUD 2017a; Albarracín et al. 2018; Araos et al. 2020), pointing out that the calculated values represent underestimates due to insufficient information on private investments to prevent damage to wine plantations, which are highly relevant within the national agricultural sector (PNUD 2017a). Estimates of consumer goods and services affected by rabbits for the Chilean economy were ca. USD 266,000 annually (PNUD 2017a). The forestry sector generated USD 5.27 billion in exports during 2016 (INFOR 2017), while the fruit sector including cherry, orange, walnut, and lemon generated USD 1.27 billion (ODEPA 2021b). The differences between the income of the affected industries and the weighted expenses attributable to rabbit action (10^4 magnitude orders) allow to suppose that at present, the impact on these economic sectors is negligible (PNUD 2017a). Nevertheless, the total income of a given industry is not distributed equitably among the different producers, and there will be differences in terms of investment capacity in prevention and control strategies. Rabbit impact on the agricultural sector is surely unevenly distributed in Chile, having a greater effect on the surplus of small producers and on subsistence activity. These estimates must be interpreted carefully, being taken as a minimum platform to assess the economic impact caused by rabbits (PNUD 2017a).

Australian researchers have estimated the investment in control technologies by the wool industry in the context of an integrated competitive market, translated into losses of surplus for the remaining producers, using values of the elasticities, price, equilibrium quantity, and change in supply proportional to the rabbit impact (Vere et al. 2004; Gong et al. 2009). This approximation could be useful to disaggregate the rabbit impact among the different agricultural producers in Chile, requiring a sufficiently extensive availability of information from the respective markets to reconstruct the supply functions for the other producer groups. Unfortunately, there is insufficient data to make these estimates. An alternative could be to evaluate the differential rabbit impact among the producers through contingent valuation methods by direct surveys of willingness to pay (WTP) to avoid the adverse effects that rabbits cause on production. The weighting of rabbit impact is related to the degree of disruption or benefit it generates on ecosystem services, depending on preferences and people's perceptions according to their socioeconomic level, occupation, degree of education, moral values, environmental awareness, consumer preferences, location, and regulatory policies (Costanza et al. 1997; MEA 2005; Albarracín et al. 2018; Dara 2019). On the other hand, livestock production in Chile was not analyzed in the PNUD (2017a) report, even though this activity is considered worldwide as one of the industries that experiences the highest imposition of costs and loss of profits due to rabbits (Gong et al. 2009; Cooke et al. 2013; McLeod 2016). Rabbit impact on the beef, sheep, and wool production in Australia amounts to about AUD 217 million (McLeod 2016). Likewise, in Argentina, the dietary overlap between rabbits and sheep and cattle has been observed, indicating trophic interference for food resources, which could have negative consequences on the sectoral productivity (Bonino 2006; Bobadilla 2021). In Chile, although the livestock activity does not generate similar returns to that of Australia or Argentina, the raising of cattle constitutes 14% of the country's meat production in terms of weight, which is destined for domestic consumption (ODEPA 2021a). Therefore, although rabbits may impact the Chilean livestock industry, the absence of quantitative information on cattle/rabbit interference and its influence on the productivity of meat and other derivatives, constitutes a major gap of knowledge in the country.

In summary, the financial assessment carried out by PNUD (2017a) highlights the need to gain clarity regarding the economic magnitude of rabbit damages in Chile and to develop quantitative information for guiding management, control, and mitigation policies (Albarracín et al. 2018). There is little quantifiable data to allow weighing in economic terms the costs and benefits of rabbit activities on production systems and ecosystem services. Even though the Chilean government has developed several programs for the control and eradication of rabbits on islands, there is scarce information to perform economic valuation of the rabbit problem, thus limiting the ability to adopt targeted policies for comprehensive management, considering both the costs and benefits (CONAF 1974; Cerda et al. 2020; Araos et al. 2020). Therefore, it is imperative to quantify the different economic indicators of direct effects on livestock, soil erosion, dispersion of invasive plants, damage in the regeneration of the sclerophyllous forest, and indirect effects on fisheries (Table 2).

Prospects for further research and concluding remarks

The phylogeographic patterns of population differentiation and territorial expansion of the European rabbit in Chile remain largely unknown. The two major rabbit releases in the country (in 1884 to the Talca piedmont and in 1936 to Tierra del Fuego Island, Camus et al. 2021) were for economic purposes. It is unclear if these releases involved the same domestic stocks. Thus, it is necessary to assess the genetic structure of wild and domestic rabbit populations in Chile. This requires investigating their genetic relationships (variability, polymorphisms, differentiation), reconstructing their geographic expansion, and comparing the genetics of naturalized populations in Chile with those in Spain and France, which were all colonized by the subspecies *Oryctolagus cuniculus cuniculus*, from which all domestic breeds are exclusively derived. Chilean populations are likely of domestic origin, but this should be confirmed through rabbit mitochondrial DNA (mtDNA) analysis of liver, kidney, or fecal samples (Monnerot et al. 1994). We propose that such study should be started on wild populations in central Chile and in the Magallanes Region, to determine the alleles present focusing on mtDNA variation and immunoglobulin polymorphism (van der Loo et al. 1991). Also, it is necessary to address the epidemiology of viral diseases among rabbit populations, with the prospect of their future biological control in Chile. Three fundamental steps should be taken. First, to analyze the rabbit population in areas with a record of Myxomatosis cases, for example, Lago Peñuelas (Valparaíso Region) or Los Angeles (Biobío Region). We propose to capture rabbits by trapping or hunting every two months to understand the cycle of Myxomatosis in these populations. The rabbits collected should be necropsied to take samples (skin and eyelids with myxomas, liver, duodenum, or blood) to analyze by qPCR (time real polymerase chain reaction) and determine if Myxoma is present and which are its strains for future isolation. In the 1950s, viral control of rabbits in Tierra del Fuego Island did not consider the eventual resistance to Myxoma. Therefore, is relevant to analyze the current Myxomatosis status in the Magallanes Region (screening Tierra del Fuego Island, Punta Arenas, and Puerto Natales). It should be determined not only which Myxoma strains are present, but rabbit resistance to it (antibodies analysis), prevalence of the viral disease on rabbit populations, and sites with Myxomatosis outbreaks. The methodological design could be that proposed above, adding blood sampling to obtain the serum for antibodies tests. Finally, it is relevant to identify the main insect vectors (mosquitoes or fleas) involved in the Myxoma transmission cycle, monitoring with light or Malaise traps near rabbit burrows and directly on rabbits, using a comb.

It is necessary to understand rabbit population cycles, factors affecting them, and their underlying mechanisms, to predict rabbit outbreaks and collapses, and to efficiently control their populations. Long time-series (ideally with 15 years of data), are indispensable to achieve this approach, involving rabbit population numbers, climatic variables (precipitation, humidity, temperature, evaporation), vegetation cover, soil characteristics, and competitor/predator abundances. Building such datasets is important to test whether the population dynamics of rabbits is mainly due to the influence of climatic factors or to the escape of predators. We recommended applying seasonal autoregressive and annual models (Merritt et al. 2001; Berryman 1999a) to identify which are the endogenous factors (specific to the rabbit population) from those exogenous ones (climate, competitors, predators). Seasonal models evaluate the outbreak phase (breeding season until the peak) and the collapse phase (peak until the bottom abundance) to identify the factors that explain rabbit dynamics. This model also allows the inclusion of density-dependence feedback, testing the effects of previous abundances (Hansen et al. 1999). Complementarily, annual models (Royama 1992) enable an understanding of the exogenous factors through a vertical effect (exogenous factor effect on rabbit growth rate) and a lateral effect (exogenous factor effect on rabbit carrying capacity). Both models (seasonal/annual) can determine the influence of endogenous and exogenous factors on the rate of change to predict population abundance through a simulation-based approach, using fitted models and cross-validation that check the accuracy of the selected model (Turchin 2003).

On the other hand, trophic webs of multiple species models provide tools to understand better and thus predict the complex effects of an invasive species and the impact of its control or elimination on ecosystems (Buenavista & Palomares 2018). In an invasive species management scenario, it is relevant to study the rabbit effect on other mammals that compete for space and resources and the diet shifts of predators that currently prey on rabbits. Building and studying the rabbit food web helps understanding their interactions and feedbacks in a network filled with other species. Thus, literature and empirical data on the diets of diverse species are imperative to build that food web and understand the relevance of rabbits and the possible community responses if rabbits are controlled or eradicated. We hypothesize that the European rabbit has increased their interspecific interactions in the food web along all Chile. Therefore, we predict that the European rabbit interacts directly and indirectly with many native and non-native species and that their populations benefit predators, deplete vegetation cover, and outcompete other mammals.

According to PNUD (2017a), 90% of the rabbit impact in Chile is concentrated on damage to biodiversity, including endemic fauna and flora. No current data enable to ponder, in monetary terms, the effect of rabbits on cultural and heritage ecosystem services. Still, contingent market methodology (Willingness to pay WTP, Willingness to accept WTA) allows the weighting of non-use values associated with the community's perceptions of natural assets. These approaches could be useful in the central zone of Chile, where human communities somehow benefit from rabbit production. Here, there are ecosystems with a significant degree of species endemism affected by rabbits (e.g., sclerophyllous forest), which requires generating knowledge of public utility for biodiversity management before the emergence of potential conservation issues. Comparing the current costs imposed by rabbits on the agricultural-forestry sector with the income received from exports, indicate that the damage caused by this invasive species does not seem significant in relative terms. Nonetheless, it is important to note that income within the sector is unevenly distributed, so that it cannot be ruled out that rabbits affect small-scale and subsistence farming. Therefore, we propose to focus on small producers for future rabbit impact studies. Given the limited availability of information, we think it is necessary to carry out full-fledged fieldwork. Finally, from a worldwide perspective, the greatest negative impact of the European rabbit on production systems occurs in the livestock sector, mainly in cattle and sheep breeding. Despite this, no studies have assessed this activity's damage caused by rabbits in Chile. Magallanes Region is the country's area with greater production and export of sheep meat and wool, and has several localities (Peninsula Antonio Varas, Puerto Natales, Punta Arenas) with high potential for such future studies, because they have both wild and domestic rabbit populations that negatively affect feeding livestock pastures.

This review ponders what is known about the European rabbit as an invader in Chile and, reflecting on the Australian experience, puts forth what new knowledge is needed to manage this species efficiently. The serious negative impacts caused by European rabbits during the last 150 years in Chile have been addressed chiefly from a community-ecological perspective with some theoretical bias. Applied research is lacking for improving public policies and efficient management of this invader. It now becomes urgent to determine the geographical distribution, population size, and drivers of rabbit dynamics to predict their spread and outbreaks toward carrying out efficient control. Also, it is necessary to understand their impacts on Chilean productive systems and natural ecosystems to value them economically. In addition, it is essential to research the presence of pathogens such as Myxoma or Calicivirus in Chile, determining their distribution, prevalence and possibly virulence. Long-term monitoring of rabbits is critical to assess their impact on economic activities, and time-series studies should identify the key factors that determine population dynamics in different ecosystems.

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Declarations

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