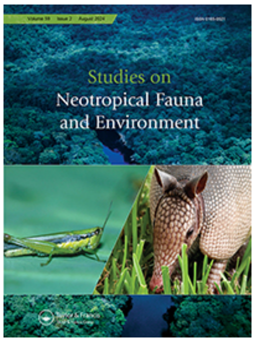

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Diet and foraging role of European hare (*Lepus europaeus*) on two invasive non-native shrubs: *Cytisus scoparius* and *Rosa rubiginosa* in Northwestern Patagonia, Argentina

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ABSTRACT

Browsing by alien vertebrate herbivores can have both positive and negative impacts on plant invasion. We studied the European hare (*Lepus europaeus*) diet and foraging behavior focusing on interactions with two invasive non-native shrub species, *Cytisus scoparius* and *Rosa rubiginosa*. Fecal pellets were used for microhistological analysis of diet and seed identification. Foraging use of both species was evaluated by browsing rankings. The diet consisted of 28 items, predominating native grasses such as *Poa* spp. and *Festuca pallescens*. Among the non-native species, the grasses *Hordeum* spp. leaves and stems of the shrub *C. scoparius*, and seed fragments of *Rumex acetosella*, and rosehip stand out. Fecal pellets contained 431 whole seeds from nine plant species, predominating non-native species. In diet analysis, a portion of damaged rosehip seeds was observed; however, a significant number of viable seeds were previously extracted. This suggests that consumption of *R. rubiginosa* fruits contributes to seed dispersal, facilitating its spread. In contrast, the browsing of *L. europaeus* on the vegetative parts of *C. scoparius* juveniles significantly reduced their cover, which could slow their growth or prevent their spread. These results are an important input for management decisions to prevent or delay the spread of these invasive species.

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Browsing; endozoochory; plant invasion; alien herbivores

Introduction

Native vertebrate herbivores play a crucial role in establishing complex plant–animal interactions, and are important for the diversity, structure, composition, and dynamics of plant communities (Malo & Suárez 1995; Bertiller & Bisigato 1998; Aizen et al. 2002). Invasive mammal species can alter these relationships between native herbivores and vegetation with significant impacts on the biodiversity and even on the economy of an area, affecting human well-being (Pejchar & Mooney 2009; Blackburn et al. 2011). Meta-analyses of field studies have revealed differences in feeding patterns between native and non-native herbivores on native and non-native plant species (Parker et al. 2006). In general, native herbivores consume non-native plants, decreasing their abundance and acting as a biotic resistance to the establishment or spread of non-native plants (Maron & Vilá 2001; Nuñez et al. 2008). Meanwhile, non-native herbivores could have a positive effect on the abundance and richness of non- native plants by consuming native species (Parker et al. 2006; Oduor et al. 2010). This feeding behavior can facilitate the invasion process, through an "invasional meltdown" between the non-native species (Simberloff & Von Holle 1999).

Different scenarios can arise from the interaction between non-native herbivores and plants. The non-native herbivores may disperse non-native plant seeds and promote their germination through endozoochory, facilitating their propagation, as it was observed in various rosehip seed dispersers (Damascos et al. 2005; Martin Albarracín et al. 2018; Dacar et al. 2019; Bobadilla et al. 2020). Alternatively, non-native herbivores may consume fruits of native plants and disperse their seeds, contributing to the recovery or rescue of native biodiversity (Castro et al. 2008; Calvino-Cancela 2011).

In another scenario, several studies showed that non-native herbivores browsing significantly affects seed production, seedling establishment, or plant survival of non- natives, reducing or delaying the invasion process (Williams 1998; Becerra & Bustamante 2009). Studies conducted in New Zealand on European hare

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(*Lepus europaeus*) browsing demonstrated a notable effect on slowing the growth of non-native Scotch broom seedlings, suggesting a potential control mechanism for this invasive species (Williams 1998).

In Patagonia, livestock and invasive alien herbivores, such as European hare, red deer (*Cervus elaphus*), and wild boar (*Sus scrofa*), have detrimental effects on soil structure, decrease plant cover, and limit regeneration of tree native species in temperate forest (Veblen et al. 1992; Vázquez 2002; Sanguinetti et al. 2014; SIB 2019). In Nahuel Huapi National Park, alien mammals and plants reach the highest invasion values among Patagonian protected areas (Merino et al. 2009). Currently, a plan for managing invasive species is actively being implemented, and management actions include initiatives such as establishing controlled hunting seasons in forests of high conservation value to mitigate the impact of red deer (Sanguinetti et al. 2014; SIB).

In this study, we focus on three invasive non-native species of special interest due to their potential ecological relevance: the rosehip shrub (*Rosa rubiginosa*), Scotch broom (*Cytisus scoparius*), and European hare (*L. europaeus*). These non-native shrubs are highly problematic invasive species due to their rapid rate of spread, which alters community structure and negatively affects the biodiversity of native plants. Additionally, these invasive shrubs increase fuel load, alter nutrient cycling, and affect the fire regime in the ecosystem (Damascos & Gallopin 1992; Damascos et al. 2005; Damascos 2008; SIB 2019). The European hare is a generalist, selective, and seed-dispersing herbivore that exploits a wide variety of habitats and adapts its diet to seasonal vegetation changes (Galende & Grigera 1998; Vignolio & Fernandez 2005; Puig et al. 2007, 2014, 2016; Reus et al. 2013; Henríquez et al. 2014; Sokos et al. 2015). Therefore, its plastic feeding provides an opportunity for the dispersal and invasion of non-native plants with fleshy fruits such as rosehip.

Considering that, alien herbivores play an important role in determining the success, failure, or control of invasive plant species, this study evaluates feeding behavior of the European hare on rosehip and Scotch broom, and the potential effects on the propagation or control of these invasive species. A recent study by González (2021) demonstrated that the European hare consumes rosehip fruits, acting as a seed disperser, and strong browsing on vegetative parts of Scotch broom was observed in the field. Based on these observations and previous studies, our objectives were to determine the European hare diet and establish its foraging role, particularly, if there is differential consumption by fruits or vegetative parts of rosehip and Scotch broom. We hypothesize that (1) the European hare is a generalist herbivore that primarily feeds on grasses, (2) the European hare exhibits differential browsing on rosehip fruits, and 3) the European hare exhibits differential browsing on Scotch broom vegetative parts.

Materials and methods

Study area

The study area was located in suburban areas of San Carlos de Bariloche city, surrounding the Nahuel Huapi National Park in Patagonia, Argentina. The climate is humid and temperate, with a strong rainfall gradient from west to east from 4000 mm in the Andes range to 800 mm in the steppe. The highest average annual precipitation occurs mainly during the fall with snowfall during the winter. Temperatures range between 2.81°C in July and 15.15°C in January, with variations according to elevation (Barros et al. 1983). In this region, the Andean Forest is dominated by the native trees coihue (*Nothofagus dombeyi)* and ciprés (*Austrocedrus chilensis)*, with understory of caña colihue (*Chusquea culeou)* and maqui (*Aristotelia maqui*) (Veblen et al. 1992). To the east, the vegetation is a shrubby steppe dominated by grasses such as coirón amargo (*Pappostipa speciosa)*, coirón blanco (*Festuca pallescens)*, coirón poa (*Poa* spp.), and the shrubs neneo (*Mulinum spinosum*) and charcao (*Senecio* spp.) (León et al. 1998). Steppe and forest sites are degraded by anthropogenic use and presence of non-native invasive plant species (e.g. Pinaceae, *Rosa rubiginosa*, *Juniperus communis*, *Cytisus scoparius*).

Non-native mammals in this area included domestic herbivores such as cattle, horses, sheep, red deer, European hares, and wild boars, whereas native herbivores consist only of small rodents (Damascos & Gallopin 1992; Vázquez 2002).

Diet study was carried out during 2019–2020 in austral summer (January) and autumn (May) in sites particularly selected by presence of the invasive shrubs of Scotch broom and rosehip (Figure 1). Three forest sites are located in the Llao Llao Reserve and surroundings: Site 1, 41° 03' S, 71° 33' W (S1); Site 2, 41° 07' S, 71° 27' W (S2); and Site 3, 41° 02' S, 71° 34' W (S3). The steppe sites are located on a peri-urban and rural transition interface that include mosaics of shrub and steppe vegetation: Site 4, 41° 07' S (S4), 71° 13' W; Site 5, 41° 07' S, 71° 11' W (S5); and Site 6, 41° 06' S, 71° 12' W (S6). To study the hare browsing behavior, we selected site 7 (41° 13'S, 71° 41' W) in a transitional environment with both shrubs, although rosehip plants are less prevalent compared to Scotch broom. This site

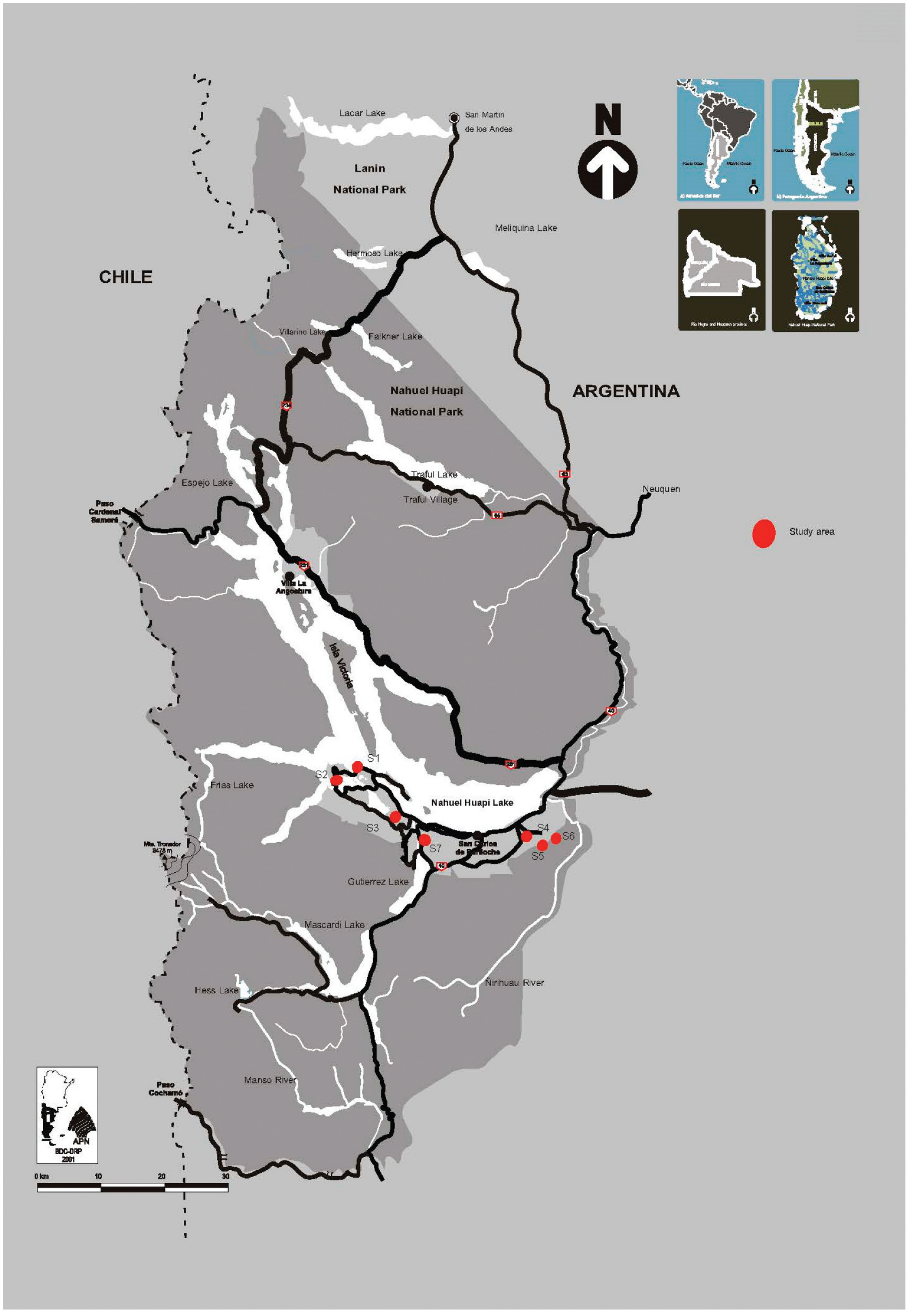

Figure 1. Study area and sampling sites. Forest sites: (S1), (S2), and (S3). Steppe sites: (S4), (S5), and (S6). Transitional site Gutierrez (S7). Modified from division of environmental education map (2013), Nahuel Huapi National Park, APN.

was selected because rosehip plants in advanced stages of invasion form dense shrublands, and the dense understory makes it difficult to visually assess the extent of browsing impact in these environments. Despite these limitations, the site provides browsing data that complements the diet study.

Study species

Rosehip is a non-native invasive shrub of fleshy fruits whose seeds have high viability, longevity, and long latency periods, ensuring a high rate of propagation (Damascos et al. 2005; Martin Albarracín et al. 2018). It especially invades altered environments, such as those disturbed by livestock, fires, and human activities, forming degraded areas and decreasing native plant diversity (Damascos & Gallopin 1992; Damascos et al. 2005). In Patagonia, rosehip seeds are dispersed by domestic cattle (*Bos taurus*), horse (*Equus caballus*) and wild alien herbivores such as silver pheasant (*Lophura nycthemera*), European rabbit (*Oryctolagus cuniculus*), and European hare. In addition, it has been shown that the consumption of its fruits by these herbivores has positive effects on seed germination, which probably favors the propagation of this invasive shrub (Damascos et al. 2005; Martin Albarracín et al. 2018; Dacar et al. 2019; Bobadilla et al. 2020; González 2021).

Scotch broom is an invader shrub in many regions worldwide, where it causes significant damage to native plant biodiversity and economic losses (Williams 1981; Bossard & Rejmanek 1994). This shrub establishes itself particularly in disturbed areas, such as those that are logged, grazed, or burned, as well as on margins of roads (Bossard & Rejmanek 1994; Simberloff et al. 2003). Ants, wild boars, horses, and sheep facilitate the dispersal of the Scotch broom (Bossard 1990; Manzano et al. 2005), although in Argentina there is no record of dispersal by animals.

The European hare exploits a wide variety of habitats and its browsing affects vegetation structure, eliminates seedlings, and is capable of dispersing seeds of non-native and native species (e.g. Homolka 1982; Rose & Platt 1992; Izhaki & Ne'eman 1997; Williams 1998; Reichlin et al. 2006; Green et al. 2013; Sokos et al. 2015). Herbivory pressure on native forests, damage to horticulture and forestry, and potential competition with livestock and native fauna are among the main negative ecological effects of this invasive herbivore (Bonino 2009; Galende & Raffaele 2013; Barbar & Lambertucci 2018; Jaksic 2023).

Fecal collection

To determine the European hare diet and identify seeds composition in both steppe and forest environments, we conducted sampling during two specific periods to detect the presence of fruits from Scotch broom (January–February) and rosehip (April–May). Fecal pellets were collected and grouped by site into forest and steppe categories for subsequent diet analysis. At each study site, an approximate area of 150×10 m, 20 fresh fecal groups of different sizes were randomly collected in order to maximize the probability of sampling different individuals. Each fecal sample group consisted of at least five closely associated fecal granules. In total, 240 groups of fecal pellets (20 samples $\times$ 6 sites $\times$ 2 sampling dates) were collected.

Diet analysis

To determine the composition of the European hare's diet, we utilized fresh fecal pellets, which were analyzed using micro-histological techniques enabling the identification of the epidermis of leaves, stems, and seed teguments (Sparks & Malechek 1968). In a previous study, whole seeds of rosehip and scotch broom were manually separated from these same hare feces for seed germination testing (González 2021). Therefore, in this study, microscopically identified seed fragments correspond to seeds damaged during the digestive process, while in feces whole seeds were recorded separately in the seed category.

To conduct the diet analysis, we grouped 20 individual fecal samples collected during each sampling period to create three composite samples per site, each composed of 100 g of fecal material. This method allowed us to analyze representative samples that reflect the dietary composition of European hare across different environments. The use of composite samples in our study was informed by previous research demonstrating that this approach yields comparable results to averaging individual samples (Borrelli et al. 2004). While the use of composite samples may result in loss of variability among individual samples, it is a cost-effective and efficient method for diet analysis, providing similar and reliable insights.

Fecal pellets and reference plants collected in the field were dried at 60°C and then ground to a size of 1 mm. The material was depigmented with 90% alcohol, cleared with sodium hypochlorite, and colored with safranin. Finally, the samples were mounted with glycerin jelly for microscopic observation. To recognize microscopic plant fragments, for each fecal sample, five slides were made and 20 microscopic fields were systematically examined on each slide (Holechek & Gross 1982). Plant tissues were identified by comparison to reference epidermal tissues of leaves, fruits, and flowers from our microhistological laboratory (CRUB-UNCO).

For each fecal sample, 100 microscopic fields were observed using a microscope with a magnification of 100X (Holechek & Gross 1982). In total, 1800 microscopic fields were observed (3 samples × 100 fields × 6 sites). Plant fragments and shrub seeds were identified to the species level whenever possible, and these dietary items were classified by their epidermal characteristics into functional groups of vegetation (shrubs, herbs, grasses, and trees). We also collected those plant species missing from our laboratory collection, and we prepared the reference slides of epidermal tissues of leaves, fruits, and stems.

Rosehip and Scotch broom browsing

To estimate the effects of European hare browsing on rosehip and Scotch broom species at site seven (S7), we established two transects, each measuring 1000 × 2 m, at the roadside. The European hare is the only medium-sized herbivore in the area, thus we considered browsing on vegetative parts of plants with branch tips cut at a 45° angle as characteristic signs of hare browsing. Degree of browsing of these species was visually estimated through the cover of plants affected using the browse index (BI). The browsing ranks (BI) assume the following values: (0) the species is not browsed, (1) light (browsed 25% of the total plant), (2) moderate (50% browsed), and (3) heavily browsed (>50% browsed). The BI index = Σ total browsing ranks (BI) (modified from Galende & Raffaele 2013, based on; Wardle et al. 1971).

To assess whether there was selective browsing according to plant development stage, we measured the height of each individual and categorized them as either young (<1.5 m height) or mature (>1.5 m height) (Williams 1981; Damascos 2008).

Data analysis

We calculated the percentage frequency for each dietary item and functional group (shrubs, trees, grasses, and herbs) per site. The diet contribution of each item was expressed as total mean (± SE). Differences in diet proportions between functional groups (shrubs, trees, grasses, and herbs) were detected using Kruskal-Wallis and subsequent Tukey's multiple comparison test (Zar 1995). Differences in consumption of functional groups and the main dietary species (>4%) between steppe and forest were detected by the Mann Whitney test. Differences in browsing degree between juvenile and mature plants were detected by chi-square test.

Results

Diet composition

The European hare's diet composition determined in six sites of steppe and forest areas was constituted of 28 food items, with a predominance of non-native plants (Table 1).

The diverse diet includes a range of food items highlighting grasses as *Poa* spp., and leaves and stems of *C. scoparius* shrub (Table 1. Figure 2). Other important dietary components included grasses such as *Hordeum* spp. and *Festuca pallescens*, with *Rumex acetosella* being the most consumed herb (Figure 2).

The European hare exhibited differential browsing behavior, showing high consumption of stems and leaves of *C. scoparius*. However, reproductive parts of this shrub, such as seed teguments, were represented in very low proportions in the diet (Table 1). The identified seed fragments correspond to those that were damaged during the digestive process, since the whole seeds were extracted from these samples for germination tests. Seed fragments of 10 species represented 23% of diet, predominating non-native species such as *R. acetosella* and rosehip (Table 1).

The European hare exhibited significant differences in the consumption of plant groups, with higher frequencies of grasses compared to shrubs and herbs (Kruskal–Wallis test: H (2, 18) = 11.94, $p = 0.002$).

Between the steppe and forest sites there were no differences in the consumption of grasses (Mann–Whitney Z = −0.65, $p = 0.82$), shrubs (Z = 0.21, $p = 0.51$), and herbs (Z = 1.09, $p = 0.27$). In both environments, the contribution of main dietary items (>4%) was similar: *F. pallescens* (Z = −1.09, p = 0.27), *Hordeum* spp. (Z = −1.52, p = 0.12), *C. scoparius* (Z = −1.21, $p = 0.82$), *R. rubiginosa* (Z = 1.52. p = 0.12), *R. acetosella* (Z = 1.52. $p = 0.12$), *Poa* spp. (Z = 1.52, p = 0.12), and *Bromus* spp. (Z = −0.21, p = 0.82). Only *Pappostipa* spp. was significantly most consumed in steppe sites (Z = 1.96. p = 0.04), while *Chusquea culeou*, a typical forest species, was a dietary item in this environment (Figure 2).

Whole seed composition in feces

We identified 431 whole seeds in hare feces, of which corresponded 355 to herbs and 76 to shrubs (Table 1). Non-native seeds of *R. acetocella* and *Juniperus* sp.

Table 1. Diet composition of the European hare in forest and steppe sites based on analysis of 240 fecal pellet groups. Dietary items correspond to fragments of vegetative parts and seeds. Values are expressed as percentage frequency, mean, standard error (SE). Whole seeds correspond to extracted from feces. (*) indicates non-native species. (N/E) items not evaluated. Values of rosehip and raspberry seeds (#) are data from González (2021).

	Steppe			Forest					
Dietary items	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Mean	SE	N Seeds
Grasses	48.3	47.2	45.3	44	52.5	78	52	5.3	N/E
Poa spp.	14.1	26	21.9	15.6	2.4	2.3	14	4.01	N/E
Pappostipa spp.	7.3	4.4	11	1.7	0.4	2.3	4.52	1.64	N/E
Festuca pallescens	0.3	4.9	7.8	1	17.8	40.6	12.0	6.27	N/E
Bromus spp*	8.6	5.7	0.6	5	9	5.3	5.69	1.23	N/E
Hordeum spp*	17.7	6.3	4	20.1	13.9	18.4	13.4	2.76	N/E
*Holcus lanatus**	0.4	0	0	0	0.1	1.5	0.35	0.24	N/E
Chusquea culeou	0	0	0	0.6	9	8.3	2.9	1.8	N/E
Shrubs	21.7	19	38.3	26.3	32.5	14.9	25.4	3.36	2072
Mulinum spinosum seeds	0.7	0.5	0.5	0.7	1.8	0.2	0.74	0.23	3
Rosa rubiginosa fruits*	2.2	5.6	14.6	0.6	2.4	1.5	4.4	2.13	1185#
*Cytisus scoparius**	18.1	9.4	13.3	17.1	13.6	10.2	13.6	1.43	0
*Cytisus scoparius seeds**	0	0.8	0.3	0	0	0.1	0.21	0.13	0
Ephedra spp. seeds	0	0	0	4.4	6.6	1.5	2.09	1.14	12
Discaria spp.	0.6	0.7	7.8	0	0.3	0	1.6	1.26	0
Juniperus communis seeds*	0	0	0	0.3	0	0.2	0.08	0.05	3
Berberis microphylla seeds	0.1	0.3	0.3	3.3	3.4	1.1	1.41	0.62	53
Embotrium coccineum seeds	0	0	0	0	0.3	0	0.05	0.05	5
Senecio spp.	0	1.8	1.5	0	0	0	0.55	0.35	0
Rubus idaeus seeds*	0	0	0	0	4.1	0	0.68	0.68	344#
Herbs	31.8	33.7	10.1	21.5	13.4	4.9	19.2	4.69	355
Eryngium paniculatum	1.1	4.1	1.4	0	0.4	0	1.2	0.63	0
Rumex acetosella seeds*	23.1	19.7	4.8	11.5	4.2	2.1	10.9	3.59	322
Mutisia spp. seeds	1.2	8.6	0.6	1.7	2.1	0.6	2.5	1.25	12
*Plantago lanceolata**	2.6	0.3	0.3	1.4	0.4	1.5	1.09	0.38	0
Hypochaeris chilensis	3.5	0.8	0.9	5.4	6.3	0.8	2.9	1.02	0
*Cerastium arvense**	0.3	0.1	2.1	0.9	0	0	0.6	0.34	0
Junellia patagonica	0	0.1	0	0	0	0	0.02	0.02	0
Trifolium spp.*	0	0	0	0.6	0	0	0.09	0.09	0
Fragaria chiloensis	0	0	0	0	0	0	0	0	21
Trees	0	0	1.8	0	0	0.4	0.09	0.06	0
Maytenus boaria	0	0	0.2	0	0	0.4	0.3	0.28	0
Pinus spp.*	0	0	1.7	0	0	0	1.42	0.65	0
Not identified	1.0	1.0	4.3	2.0	2.0	2.2	2.05	0.29	0

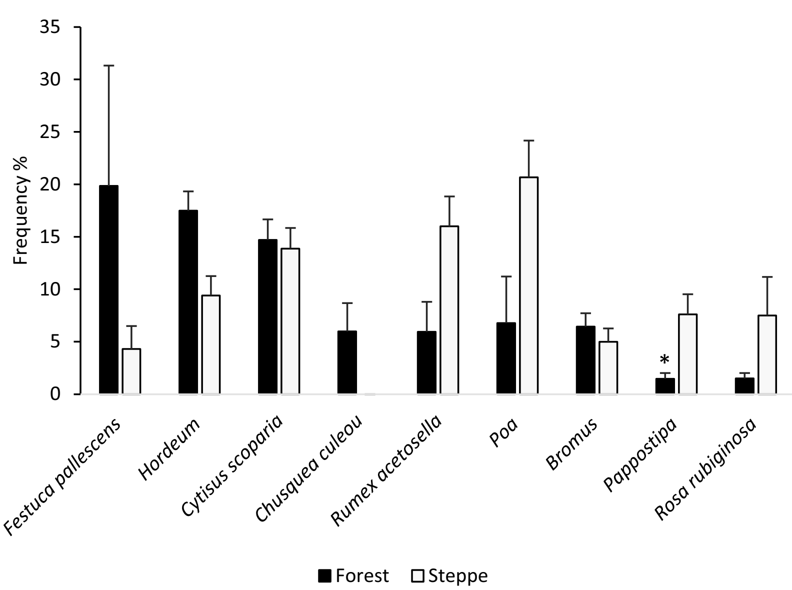

Figure 2. Main components (>4%) of the European hare diet in six forest and steppe sites based on analysis of 240 fecal pellet groups. Mean and standard error (SE) (*) indicates significant differences.

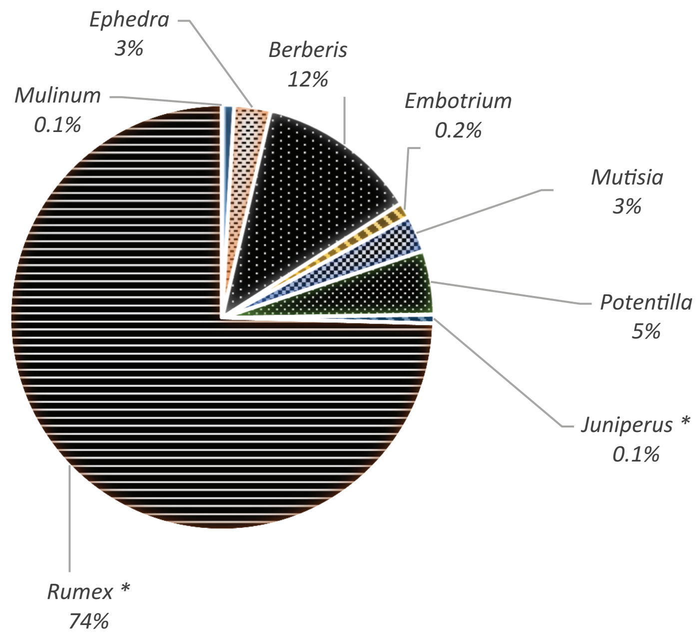

Figure 3. Contribution of whole native and non-native seeds (*) present in 240 pellet groups of European hare in forest and steppe areas ($n = 431$).

represented 75% of the total seeds identified, while seeds of native species were in low proportions (Table 1, Figure 3). Whole seeds of *C. scoparius* and *R. rubiginosa* were not registered in these feces, because they were previously extracted (González 2021)(Table 1, Figure 3).

Rosehip and Scotch broom browsing

The European hare browsed plants of Scotch broom and rosehip. The greatest impact was recorded in the Scotch broom plants ($n = 132$), of which 98% presented a strong browsing effect on the leaves and stems (Browse Index (BI) = 372). The Scotch broom juvenile individuals <1.5 m tall were significantly browsed, (91%) ($X^2 = 86.4$, df = 1, $p < 0.001$) and exhibited high values of browse index (BI = 3) whit a reduction in cover >50% ($X^2 = 193$, df = 2, $p < 0.001$) (Figure 4) (see Online Resource, ESM1a, b). Mature Scotch broom plants (9%) exhibited low BI values (BI = 1 and BI = 2) with a reduction in cover between 25% and 50%.

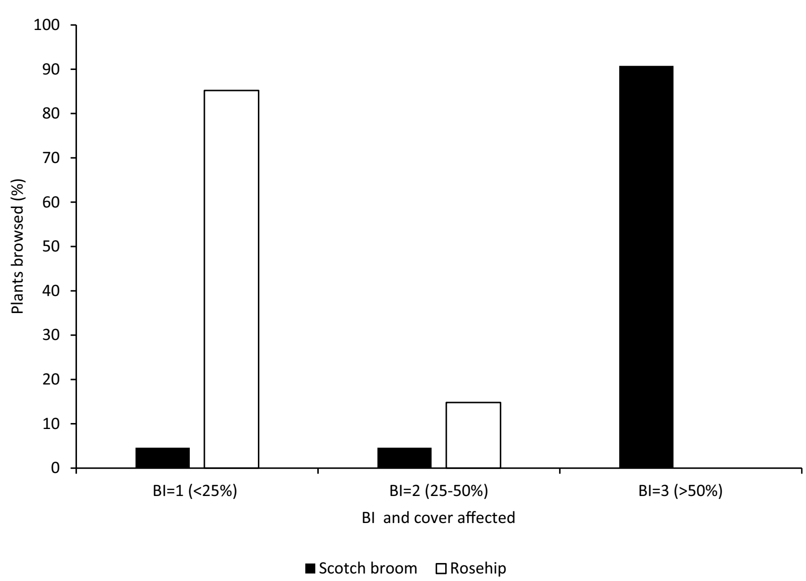

Figure 4. Browsing percentage of scotch broom and rosehip plants and plant cover affected by European hare browsing. Browse index (BI).

Rosehip plants were recorded in lower numbers compared to scotch broom ($n = 27$) and 96% of the individuals showed signs of browsing at the tips of the stems, at low levels (BI = 31). Juvenile individuals <1.5 m tall (85%) were the most browsed ($X^2 = 13.37$, df = 1 $p < 0.001$) and browsing intensity values (BI) were relatively low, resulting in a rosehip cover reduction of less than 25%. Browsed mature plants (15%) showed higher degree of browsing (BI = 2) and cover was reduced between 25% and 50% (Figure 4).

Discussion

Diet

In the steppe and forest areas of northwestern Patagonia, the European hare exhibits a feeding behavior typical of a generalist herbivore, differentially browsing rosehip fruits and the vegetative parts of Scotch broom, two invasive shrubs in the region. The diet consists of leaves, stems, and fruits from a variety of food items, including grasses, shrubs, trees, and herbs, with non-native species predominating.

The feeding behavior of *L. europaeus* is characterized by a diet primarily based on grasses, with main items including *Poa* spp., *Hordeum* spp., *Festuca pallescens*, accompanied by important contributions of *C. scoparius* shrub, and Rumex *acetosella* herb. Despite the differences in vegetation composition of steppe and forest (León et al. 1998), the consumption of functional groups and main dietary items was similar, with the only exception *Pappostipa* spp., which was consumed significantly more in steppe sites where it is a dominant species.

The generalist and plastic feeding behaviors of hares, exhibiting variations across habitats, has been documented in various regions. Studies conducted along an Andean altitudinal gradient encompassing the Puna, Cardonal, and Monte phytogeographic provinces have demonstrated this adaptable feeding behavior (Reus et al. 2013; Puig et al. 2016; Jaksic 2023). Similarly, plastic behavior has been observed in studies conducted in Patagonia (Galende & Grigera 1998; Puig et al. 2007; Galende & Raffaele 2013).

Hare diets exhibit diversity ranging from shrub-based at higher altitudes to grasses at lower altitudes, and this variation is determined by differences in availability, phenology, and plant toxins, as discussed in several studies carried out in Argentina (Galende & Grigera 1998; Puig et al. 2007; Galende & Raffaele 2013; Reus et al. 2013).

For the first time, high proportions of Scotch broom leaves and stems and the presence of rosehip fruits were detected as key components of the hare's diet. The relevant consumption of rosehip fruits was evidenced in the numerous seed fragments in the diet and in the whole seeds extracted in the feces (González 2021). These fruits have high nutritional value and are the only fleshy fruits available during the Patagonian winter (Damascos et al. 2005). Therefore, the invasive shrub rosehip provides an extra food resource for hares that consume the fruits and subsequently disperse its seeds, establishing a mutualistic relationship. In Patagonia, both native and non-native herbivores also consume this food resource, contributing to the dispersal and propagation of rosehip (Damascos et al. 2005; Martin Albarracín et al. 2018; González 2021).

The incorporation of seasonal rosehip fruits into the European hare's summer–autumn diet is similar to observations in the northern hemisphere, where hares adapt their diet to different environments and seasonal conditions (Homolka 1982; Reichlin et al. 2006; Sokos et al. 2015). For example, in Mediterranean ecosystems, when forage quality declines, this herbivore incorporates seeds, fruits, and grapes, which contribute in high proportions to its diet (Sokos et al. 2015).

Whole seed present in feces

The European hare disperses whole seeds of both native and non-native species through their feces. Among the non-native seeds that predominate, particularly those of the herb *R. acetosella* and the shrub *J. communis*, while native seeds, such as *Berberis microphylla* and *Mutisia* sp. are found in low quantities. Despite the high proportion of vegetative parts, the seed fragments of *C. scoparius* recorded in the diet were very scarce. This result confirms a differential browsing behavior by hares, which avoids consuming the seeds of this shrub, as observed in a previous study by González (2021).

Other herbivores showed a similar feeding behavior on this species, tending to avoid consuming certain part plants due to the presence of alkaloids, whose concentrations increase at maturity, and are located mainly in seeds, pods, and roots (Bossard 1990; Bossard & Rejmanek 1994; Gresser et al. 1996).

The ability of hares to disperse viable seeds of both non-native and native plants was observed in regions of Israel and Australia, suggesting they could facilitate their propagation (Izhaki & Ne'eman 1997; Green et al. 2013). However, many seeds undergo varying degrees of damage during the digestive process (Shupp et al. 1997).

In Argentina, several studies recognize that *L. europaeus* is an endozoochoric disperser of both non-native and native seeds (Vignolio & Fernandez 2005; Henríquez et al. 2014; González 2021). Regarding rosehip seeds, in the hare's diet we observed a high proportion of seed fragments, which were damaged in the digestive process. Despite this damage, González (2021) recorded a high number of viable rosehip seeds in these fecal samples after ingestion, along with a positive effect on germination. This interaction, primarily among alien species, provides evidence consistent with the invasive meltdown hypothesis (Simberloff and Von Holle), suggesting that the European hare could play a significant role in the dispersal and potential establishment of the invasive *R. rubiginosa* in the area.

Rosehip and Scotch broom browsing

The European hare exhibits strong browsing on Scotch broom, displaying differential browsing that mainly affects stems and leaves of young plants, resulting in a substantial reduction in Scotch broom plant cover. In contrast, browsing on rosehip plants is limited to fruits, and the intensity is relatively low compared to Scotch broom. Studies conducted in New Zealand have shown both positive and negative effects of *Lepus* spp. browsing. They negatively affect the recovery of native species in areas of high conservation value (Rose & Platt 1992; Wong & Hickling 1999). Conversely, the effect of European hare browsing on seedlings of non-native Scotch broom contributes to slowing the spread of this invasive shrub (Williams 1998).

In summary, European hares may play an important role in the native ecosystems of the Andean-Patagonian region. They actively consume fruits and disperse seeds of the invasive non-native rosehip, facilitating its propagation. Additionally, the differential browsing of European hare on Scotch broom juveniles affected their growth, which can potentially stop, delay, or prevent the invasion by this shrub species. These initial results highlight novel interactions between this alien mammal and two invasive alien plants and provide valuable input for generating management actions and control plans, particularly in the protected natural areas of Patagonia.

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Author contribution

All authors contributed to the conception and design of the study. Gladys Galende and Tomas González carried out the preparation of the material, data collection, and analysis.

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Data availability statement

Data will be available for any person interested.

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