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RESEARCH

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Forage offering and seasonal intake comparisons to evaluate European rabbit threat in *Nothofagus* forests of southern Patagonia

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Abstract

Background: The European rabbit (*Oryctolagus cuniculus* L. 1758) was introduced into different regions of the world, generating significant trade-offs that critically impacted native vegetation. Here, we evaluate the rabbit's forage intakes in three vegetation types (forests, shrublands, and grasslands) along the four seasons in a temperate forest landscape in Southern Patagonia and discuss the potential threats over native vegetation. We formulated the following questions: (i) what is the forage offer at each vegetation type? (ii) what is the rabbit's forage intake and how it varied across the seasons along the year? and (iii) which vegetation types and plant life forms were more used according to the rabbit's forage intakes?

Methods: We censused understory vegetation to characterize the forage offer at each vegetation type and determined seasonal dietary intakes using microhistological analysis of pellets. The plant species identified in the field were grouped according to life form classes (tree regeneration, shrubs, forbs, graminoids, orchids, ferns, bryophytes, and hemiparasites). Data were analysed through uni- and multi-variate analyses, determining relationships between forage offer and the rabbit's forage intakes.

Results: Forage intakes revealed changes in plant life form consumption across vegetation types, where intake pressure was considerably different for tree regeneration ($p=0.001$), graminoids ($p=0.001$), and hemiparasites ($p=0.001$). Besides, significant changes in consumption among seasons were detected for shrubs ($p=0.001$), ferns ($p=0.030$), and hemiparasites ($p=0.002$). Although many species play an important role in the rabbit's forage intake networks (e.g., *Chiliotrichum diffusum*, *Holcus lanatus*), the strongest intake linkages were found in exotic grasses (e.g., *Poa pratensis* and *Festuca* sp.), native hemiparasites (e.g., *Misodendrum* sp.), native shrubs (e.g., *Empetrum rubrum*), and native trees (e.g., *Nothofagus* sp.). The summer and autumn seasons presented higher intake compared to the winter and spring seasons. Furthermore, hemiparasites intake (e.g., *Misodendrum* sp.) suggests that rabbits utilize different forage sources depending on the vegetation types.

Conclusions: Rabbits regularly inhabit the forest, even though it is not their preferred vegetation type to live. Rabbit management entails isolating regions that are more favourable to intake and emphasizing the year's season for rabbit control efforts.

Keywords: Forest ecology, *Oryctolagus cuniculus*, Plant–animal interaction, Vegetation type, Herbivory, Habitat use

Background

European rabbit (*Oryctolagus cuniculus* L. 1758) is a keystone-species, which was native to southwestern Europe (Delibes-Mateos et al. 2008; Cortés-Avizanda et al. 2015),

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widely introduced into different regions of the world (Flux and Fullagar 1992; Brown et al. 2020; Seuru et al. 2021). They are monogastric and reproductively efficient herbivores (Chapman and Flux 2008), which usually rest in underground burrows or under dense shrubs to avoid predators (Gálvez Bravo et al. 2009; Kimm et al. 2021). Rabbits often use their latrines as olfactory and visual signals, being a source of territorial information (Ziege et al. 2016; Rouco et al. 2021). The habitat type strongly influences the rabbit's abundance (Cubas et al. 2021). Open fields with short grasses and enough shelter components, such as bushes or trunks, are preferred by rabbits; they also favour flat, low-slope habitats (Parer and Libke 1985; Marques and Mathias 2001). Rabbits' ability to colonize a wide range of habitats is demonstrated by their global distribution (Thompson and King 1994). Despite the rabbit's ecological role in its endemic location (Marín-García and Llobat 2021), in other regions like Oceania and South America, they are considered pests due to their multiple impacts on soil and native vegetation (Eldridge and Myers 2001; Jaksic et al. 2002; Cuevas et al. 2016). The rabbits caused damage to tree regeneration and the root systems of trees (Gowda et al. 2014; Lees and Bell 2008). In fact, rabbits have been listed among the world's 100 most invasive alien species (Lowe et al. 2000), and there is mounting evidence that it is critical to regulating or, if possible, remove them to protect native and endemic plant species (Cubas et al. 2019).

In this context, European rabbits are often a hazard to nature conservation (Bergstrom et al. 2009; Bonino and Soriguer 2009). Consequently, applied research for rabbit management frequently targets their control to minimize the species density or try to eradicate them (Angulo and Cooke 2002). For instance, in southern Patagonia (Argentina), exotic rabbits were largely controlled due to their niche competition with livestock and their elevated dispersal rate which indicated a threat of invasion (Galende 2014; de Anquín and Engelhard 2021). Rabbits were controlled using the Myxoma virus in 1954 (Jaksic and Yáñez 1983), and actually, they were restricted to the southwestern area of Tierra del Fuego (i.e. the Myxoma virus was successful in reducing rabbit populations to extremely low levels). Over the past years, the risk of the biological impact of rabbits is still latent in the native forests by consuming understory plants and tree regeneration and requires more knowledge about habitat uses, e.g., impact risks susceptible and low resilience ecosystems. Besides, rabbit's diet can vary through the different vegetation types across the landscape and seasons, e.g., for management and conservation purposes is needed spatial–temporal analyses. In this context, the objective was to evaluate rabbit's forage intakes in three representative vegetation types (*Nothofagus* forests, shrublands, and grasslands) along the four seasons in temperate forest landscapes of Tierra del Fuego in Southern Patagonia (Argentina). These vegetation types were proxies to evaluate if the rabbit's diet exhibits contrasting forage uses that can occur in forested landscapes. We defined the following specific questions: (i) what is the forage offer (assemblage of the species) at each vegetation type? (ii) what is the rabbit's forage intakes and how varied across the seasons along the year? and (iii) which vegetation types and available plant life forms were more used according to the rabbit's forage intakes? We evaluate how is the impact of rabbits over the plant assemblage in the different vegetation types, looking to identify threated life forms or species that could be highly selected as forage.

We hypothesized that the differences between forage intakes of a particular plant species or life form on a particular vegetation type and in their offer in the landscape is a good indicator of preferences/threats or avoidance. For example, if the difference is close to zero, there will not be a preference/threat or avoidance on that species/life forms, therefore rabbits will use vegetation types according to the availability of forage in each one. However, if the difference is negative (less intakes than offer), rabbits avoid it. And finally, if the difference is positive (more intakes than offer), rabbits prefer/threat it. We discuss how these results could help to design better management and conservation strategies for potential menaces to temperate forest landscapes.

Materials and methods

Study area

The study was conducted on a 1000 ha in the southwestern portion of Tierra del Fuego National Park (54°51′02″ S and 68°35′31″ W to 54°51′27″ S and 68°34′12″ W), where *Nothofagus* forests (henceforth forests), shrublands, and grasslands are intermingled across the landscape (Fig. 1). This area was inhabited by wild rabbit populations since 1880 that use all the vegetation types throughout the full year (Jaksic and Yáñez 1983).

Sampling design and data taking

We conducted data collection in the summer of 2013 in three vegetation types (forests, shrublands, and grasslands), selecting four areas as replicas (n total = 12 plots, 5000 m^2 each) by similar physiognomy and relatively homogeneous plant assemblage. According to the rabbit score and population density (Cooke et al. 2008), there were ten or more adult rabbits per hectare in grasslands and shrublands (extremely abundant, pellets and buck-heaps always visible), and one adult rabbit per hectare in forests (scattered pellets and latrines less than 10 m apart). To evaluate forage offer, plant species cover was measured within each plot using a

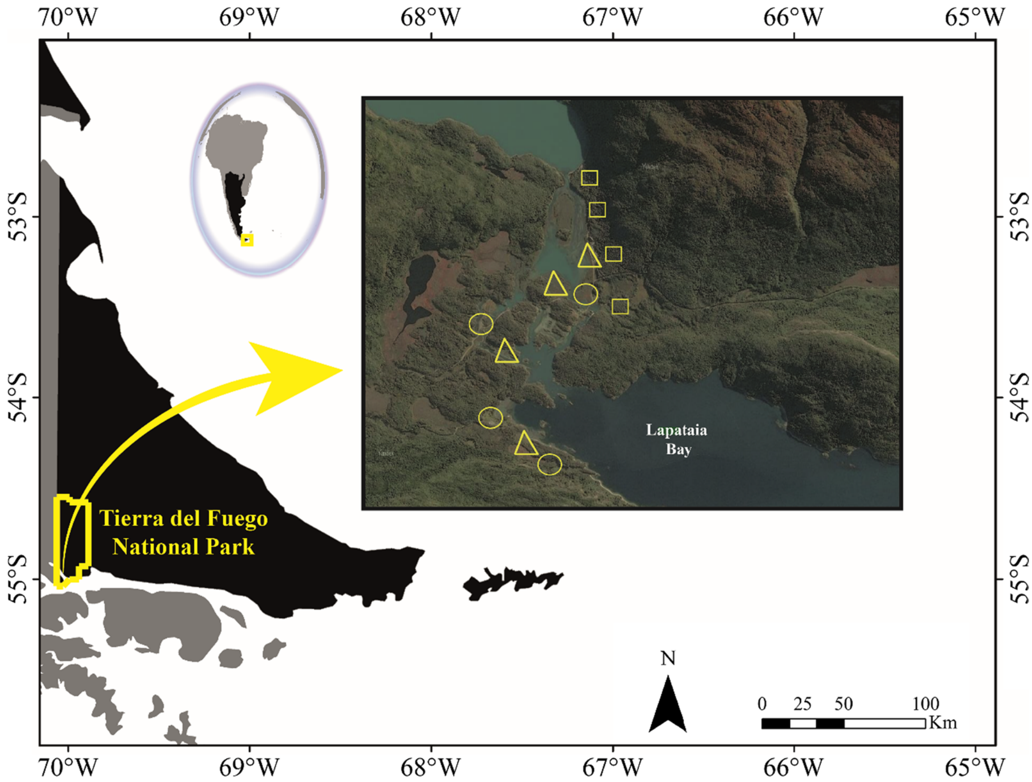

Fig. 1 Location of the study site and plots at the different vegetation types within the Tierra del Fuego National Park. *Nothofagus* forests = squares, shrublands = triangles, grasslands = circles

modified Braun-Blanquet scale (Clarke 1986; Lencinas et al. 2011), as well as woody debris and bare soil covers. Censuses were carried out during middle summer (flowering period) for precise identification of plant species following Moore (1983) and Correa (1969–1998). Then, each plant species was classified according to different life forms: tree regeneration, shrubs, forbs, graminoids, orchids, ferns, bryophytes, and hemiparasites (*Misodendrum* species).

Besides, rabbit fresh pellets were collected randomly from four latrines per site for each season (summer, autumn, spring, and winter) to determine rabbit's forage intakes. The latrines were located next to the burrows that the rabbits had built. In the laboratory, we study the content of rabbit pellets through microhistological analyses. Through these analyses, we determined consumed plant species, which were identified through the recognition of epidermal and non-epidermal tissues following Sparks and Malechek (1968) and Sepúlveda et al. (2004). For this, pellets samples were: (i) dried on a stove at 60ºC until constant weight; (ii) ground with a Willey type mill achieving a particle size of 1 mm; (iii) depigmented with 70º alcohol; (iv) coloured with safranin, and (v) mounted on 24 × 40 mm slides with glycerine gelatine following Williams (1969) and Latour and Sbriller (1981). Five slides were prepared for each mounted sample, and 20 microscopic fields at 100 × magnification were observed. We quantified the occurrence frequency (%) of each identified plant species in each sample to define the composition of the forage intake following Holechek and Gross (1982).

Data analyses

Descriptive statistics of mean percentages and standard deviation (means ± SD) values were used to describe the characteristics of the forage offer at each vegetation type and the rabbit's forage intakes (richness and understory vegetation cover). The average ground cover (%) of the understory was classified by life forms, woody debris, and bare soil, and was compared by one-way ANOVAs, considering vegetation types as the main factor. The rabbit forage intakes (%) classified by life forms were analysed by two-way ANOVAs, considering vegetation types and seasons as the main factors. For all cases, Shapiro–Wilk and Levene methods were used to test normality and homogeneity, respectively. When the assumptions were not met, response variables were log and square-root transformed to normalize their distributions, but non-transformed data are shown. We used Tukey's post hoc test ($p < 0.05$) to evaluate mean differences. Finally, significant interactions were plotted for a better interpretation of the results. These statistical analyses were carried out using Statgraphics software (Statistical Graphics Corp., USA). Besides, we performed a detrended correspondence analysis (DCA) to assess the vegetation types' heterogeneity in the forage offer species composition based on a matrix of 71 species cover (%) of the three studied vegetation types (forests, shrublands, and grasslands). DCA analyses were performed using PC-Ord (McCune and Mefford 1999). Then, we used a chord diagram in R-Studio (https://www.rstudio.com/), created with the Circlize library version 0.4.13 (Gu et al. 2014), to visualize the interrelationships between forage offer and intakes, which were classified by life form at each vegetation type. In addition, we create rabbit intake networks to trace the links between the seasonal species consumed in different vegetation types. We used the Gephi 0.9.2 open access application for this. Among the characteristics of the networks, we considered the size of the network (*n* nodes and *n* links) and the average degree of links to identify species with many or few connections. The distribution algorithm was Force Atlas 2. Finally, plant species/life form and habitat selection were analysed by plotting the weighted average between the proportion of forage offer and intakes by plant species at each vegetation type, expressed as a percentage of the sum of all vegetation type values (Appendices 1 and 2).

Results

Cover vegetation

Within the forage offer, the *Nothofagus* forests had the highest species richness (56 species), followed by grasslands (50 species) and shrublands (43 species). At these three vegetation types, forbs (21.3 ± 2.5), graminoids (15.0 ± 1.7), and shrubs (8.0 ± 1.0) were the life form classes with the highest species richness, while trees, ferns, and orchids were those presented the lowest species richness (< 3 species each). Orchids species (2 species) were only found in the forests, while the other life forms were found in all the vegetation types. Graminoids (53.8 ± 48.1%), forbs (40.1 ± 11.1%), and shrubs (18.7 ± 15.0%) were the life form classes with the higher ground cover within the vegetation types. Graminoid and forb cover was higher in grasslands (99.4% and 51.4%) and shrublands (58.4% and 39.8%), and lower in forests (3.6% and 29.2%). As was expected, shrubs had higher cover in shrublands (34.4%) and forests (16.8%), and lower in grasslands (4.7%). The other life form classes had less than 15% cover. The species with the highest ground cover were *Festuca rubra* (graminoid, 33.5%), *F. magellanica* (graminoid, 26.6%), *Chiliotrichum diffusum* (shrub, 17.9%), *Dactylis glomerata* (graminoid, 16.4%), *F. ovina* (graminoid, 15.9%), and *Agrostis capillaris* (graminoid, 15.9%). Total ground cover showed significant differences among vegetation types (Table 1), with graminoid being higher in grasslands ($p = 0.003$), tree regeneration in forests ($p = 0.011$), and shrubs in shrublands ($p = 0.036$), as expected. In the forests, woody debris ($p < 0.001$) and bare soil ($p = 0.031$) were significantly higher than in other vegetation types, whereas the total vegetation was significantly ($p < 0.001$) higher in shrublands and grasslands.

DCA identified the main species related to each vegetation type (total variance = 0.995; axis 1 with an eigenvalue of 0.342, and axis 2 with an eigenvalue of 0.385), where plant species assemblage greatly differed among treatments. Most of the plants are related to one specific vegetation type (Fig. 2), while some groups of plants shared the habitat between two groups (forests and shrublands, and shrublands and grasslands). Few plants presented a generalist behaviour, presenting the same cover and occurrence in all the vegetation types, e.g., *Urtica magellanica*, *Bromus unioloides*, *Cotula scariosa*, *Acaena magellanica*, *Poa pratensis* (exotic), as well as the bryophytes as a whole group.

Pellets of rabbit analysis in the laboratory

Overall (in all seasons), the life forms that were highly taken in were graminoids (50.4 ± 16.0), shrubs (15.3 ± 0.2), and forbs (14.5 ± 2.3). The least consumed forms were ferns, orchids, and bryophytes (less than 3%). As was expected, tree regeneration

Table 1 ANOVAs of ground cover (%) for different vegetation types, where plants were discriminated by life forms

Ground cover types	Forests	Shrublands	Grasslands	*F (p)*
Tree regeneration	2.1 b	0.1 a	0.1 a	7.66 (0.011)
Shrubs	12.5 ab	23.8 b	4.5 a	4.93 (0.036)
Forbs	18.0	23.8	26.6	3.45 (0.077)
Graminoids	3.0 a	40.5 b	59.5 b	12.27 (0.003)
Orchids	2.3	0.0	0.0	–
Ferns	6.6	4.5	0.6	1.15 (0.358)
Bryophytes	7.5	4.5	3.8	1.37 (0.301)
Total vegetation	51.9 a	97.3 b	95.0 b	14.79 (0.001)
Woody debris	11.3 b	0.5 a	0.0 a	66.86 (< 0.001)
Bare soil	36.8 b	2.3 a	5.0 a	14.77 (0.031)

Different letters in each row indicate significant differences between vegetation types (Tukey test at $p < 0.05$)

F (p) = Fisher test and significance between brackets. Different letters in each row indicate significant differences between vegetation types (Tukey test at $p < 0.05$). Data of shrubs were square-root transformed, but not transformed data are shown

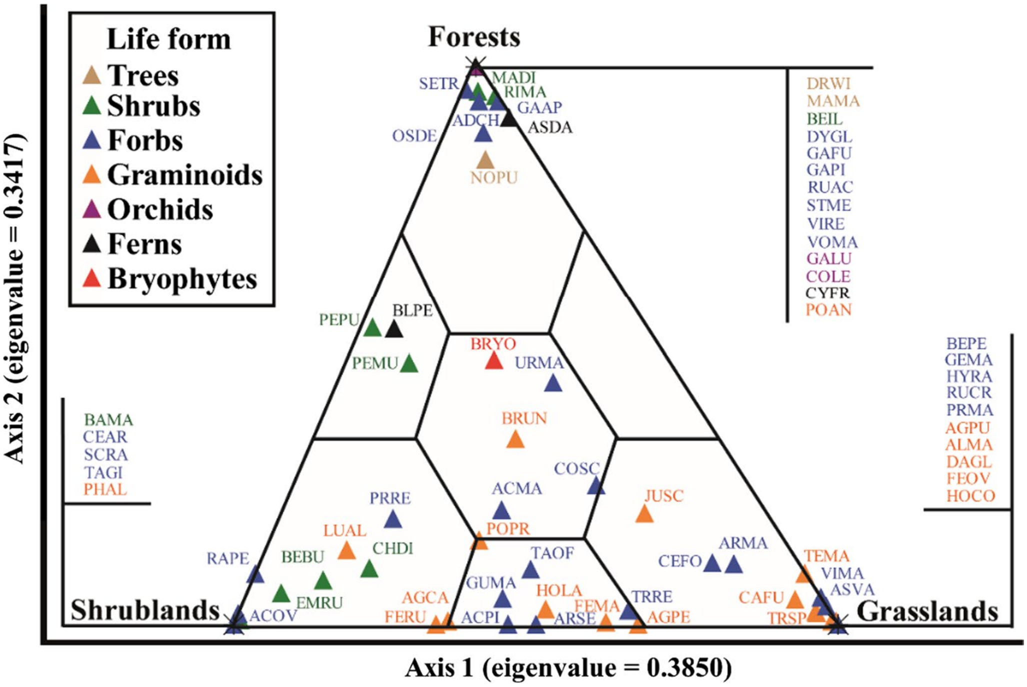

Fig. 2 Detrended correspondence analysis (DCA) to show forage offer by vegetation type, based on the cover (%). Plant species are classified by life forms, and codes are shown in Appendix 1. BRYO corresponded to Bryophytes (as a one whole group)

and hemiparasites were mostly consumed in the forests (>15% compared to the other vegetation types). The dominant species consumed by the rabbit were: *Poa pratensis* (graminoid, exotic) (50.4 ± 2.3%), *Festuca* sp. (graminoid) (36.2 ± 6.6%), *Misodendron* sp. (hemiparasite) (18.1 ± 5.1%), *Holcus lanatus* (graminoid) (17.1 ± 1.2%), *Empetrum rubrum* (shrub) (16.0 ± 2.3%), *Blechnum penna-marina* (fern) (16.0 ± 0.6%), *Berberis* sp. (shrub) (15.7 ± 1.8%), and *Nothofagus* sp. (tree) (12.2 ± 4.0%). The forage intakes showed differences in the consumption of the plant life forms among the different vegetation types (Table 2), e.g., consumption of tree regeneration ($p < 0.001$) and hemiparasites ($p < 0.001$) were significantly higher in forests, while consumption of graminoids ($p < 0.001$) were significantly higher in grasslands and shrublands. When plant life forms were analysed among seasons, we found significant differences for shrubs ($p < 0.001$), ferns ($p = 0.030$) and hemiparasites ($p = 0.002$), where those groups were greatly consumed during winter and spring. Significant interactions were found for shrubs ($p = 0.019$). The interaction in shrubs was mainly explained by the differences in the consumption in grassland among seasons, where winter and spring were higher than in forests, while shrublands presented intermediate values (Fig. 3).

Different vegetation types have different degrees of rabbit forage intake networks, with some exotic species being more connected than natives (Fig. 4). In the winter, there were fewer plant species (41 species), but in the spring, there were 42 species, 44 species in summer (peak of species), and 42 species in the autumn. This result was similar to what happened with linkages and average degree (the average number of links connecting to a species), revealing that the complexity of intake interactions decreases when the vegetation structure shifts from forest to shrubland and grassland. Although many of the species play an important role in the rabbit intake networks (e.g., *Chiliotrichum diffusum*-CHDI, *Holcus lanatus*-HOLA, *Pernettya* sp.-PESP, *Berberis* sp.-BESP), the strongest intake linkages were found in the exotic grass *Poa pratensis* (POPR) (in all types of vegetation throughout the four seasons) and *Festuca* sp. (FESP), native hemiparasite *Misodendrum* sp. (MISP) (mainly in forests in winter, spring, and autumn), native shrub *Empetrum rubrum* (EMRU) (mainly in shrubs and grasslands in spring, summer, and autumn), and native tree *Nothofagus* sp. (NOPU) (in the forest during autumn). It is remarkable that, in the autumn season, the POPR, the MISP, and the NOPU had a predominant role in the intake of the rabbit in the forest (average degree = 40). It may indicate

Table 2 Average rabbit forage intakes by plant life form (%), two-way ANOVA and Tukey test results, at each studied vegetation type and along the four seasons of the year

Factors	Tree regeneration	Shrubs	Forbs	Graminoids	Orchids	Ferns	Bryophytes	Hemiparasites
A: Vegetation types								
Forests	15.9 b	15.1	17.2	32.1 a	0.1	5.8	1.9	11.9 b
Shrublands	3.4 a	15.5	13.6	57.4 b	0.0	5.5	1.2	3.5 a
Grasslands	1.9 a	15.5	12.8	61.8 b	0.0	4.7	0.5	2.7 a
F *(p)*	39.26 (< 0.001)	0.03 (0.967)	1.97 (0.153)	19.03 (< 0.001)	–	0.40 (0.674)	2.78 (0.080)	22.51 (< 0.001)
B: Season								
Winter	7.9	18.3 b	14.6	44.2	0.0	6.8 b	0.9	7.3 ab
Spring	6.5	19.3 b	11.9	44.6	0.1	7.5 b	1.8	8.4 b
Summer	5.8	10.4 a	16.5	58.8	0.1	3.3 a	0.9	4.3 a
Autumn	8.2	13.3 a	15.1	54.1	0.1	3.8 a	1.2	4.1 a
F *(p)*	0.67 (0.578)	10.85 (< 0.001)	0.96 (0.421)	2.87 (0.050)	–	3.33 (0.030)	0.67 (0.580)	6.65 (0.002)
Interactions								
F *(p)*	0.20 (0.975)	2.95 (0.019)	0.92 (0.490)	0.20 (0.973)	1.16 (0.348)	0.58 (0.743)	1.00 (0.444)	1.98 (0.397)

Different letters in each row indicate significant differences between vegetation types (Tukey test at $p < 0.05$)

F (p) = Fisher test and significance between brackets. Different letters in each column indicate significant differences between the levels (Tukey's test at $p < 0.05$). The data of hemiparasites were log-transformed to accomplish ANOVA assumptions, but not transformed data are shown

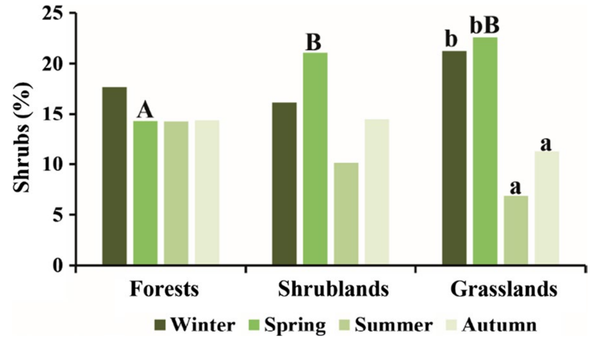

Fig. 3 Interactions corresponding to the life form of shrubs in Table 2. Tukey's test revealed significant differences between letters at $p < 0.05$. For comparisons between vegetation types (forest, shrubland, grassland), lower case letters were utilized, whereas capital letters were used for comparisons between seasons (winter, spring, summer, autumn)

that the rabbit in the forest requires more effort to look for forage, even if it concentrates on specific species (e.g., POPR, NOSP, and MISP).

Chord diagrams showed the comparison between the forage offer in the different vegetation types and the composition of the rabbit's forage intake (Fig. 5). The relationships showed a differential use of the different plant life forms according to the occurrence in the different vegetation types. The rabbit intakes included all life form classes, from orchids to the graminoids, but graminoids were the main life form ingested in the three types of vegetation. However, rabbits got a diverse intake of the different classes of life forms, which was more varied in the forests and shrublands than in the grassland. Chord diagrams showed that the rabbits preferred graminoids and forbs over the other components, however, they consumed the other groups according to their availability in the different environments, e.g., graminoids are scarce in the *Nothofagus* forests, which were supplanted by other groups (shrubs, regeneration trees, and bryophytes). However, in overall analyses, we can see that forbs, bryophytes, and orchids life forms were avoided as forage intakes in all vegetation types compared to the occurrence in the natural areas (Fig. 6). In forests and shrublands, rabbits preferred tree regeneration and graminoids. In grasslands, contrary to our expectations, the rabbits prefer shrubs; while the graminoid offer and intakes are nearly identical, indicating that this forage was consumed when it is available.

Discussion

European rabbits' forage intakes exhibit contrasting forage uses in the studied vegetation types in southern Patagonia. Based on the understory plant communities available in the studied area, there is a different forage offer for consumption, and many plants are specific

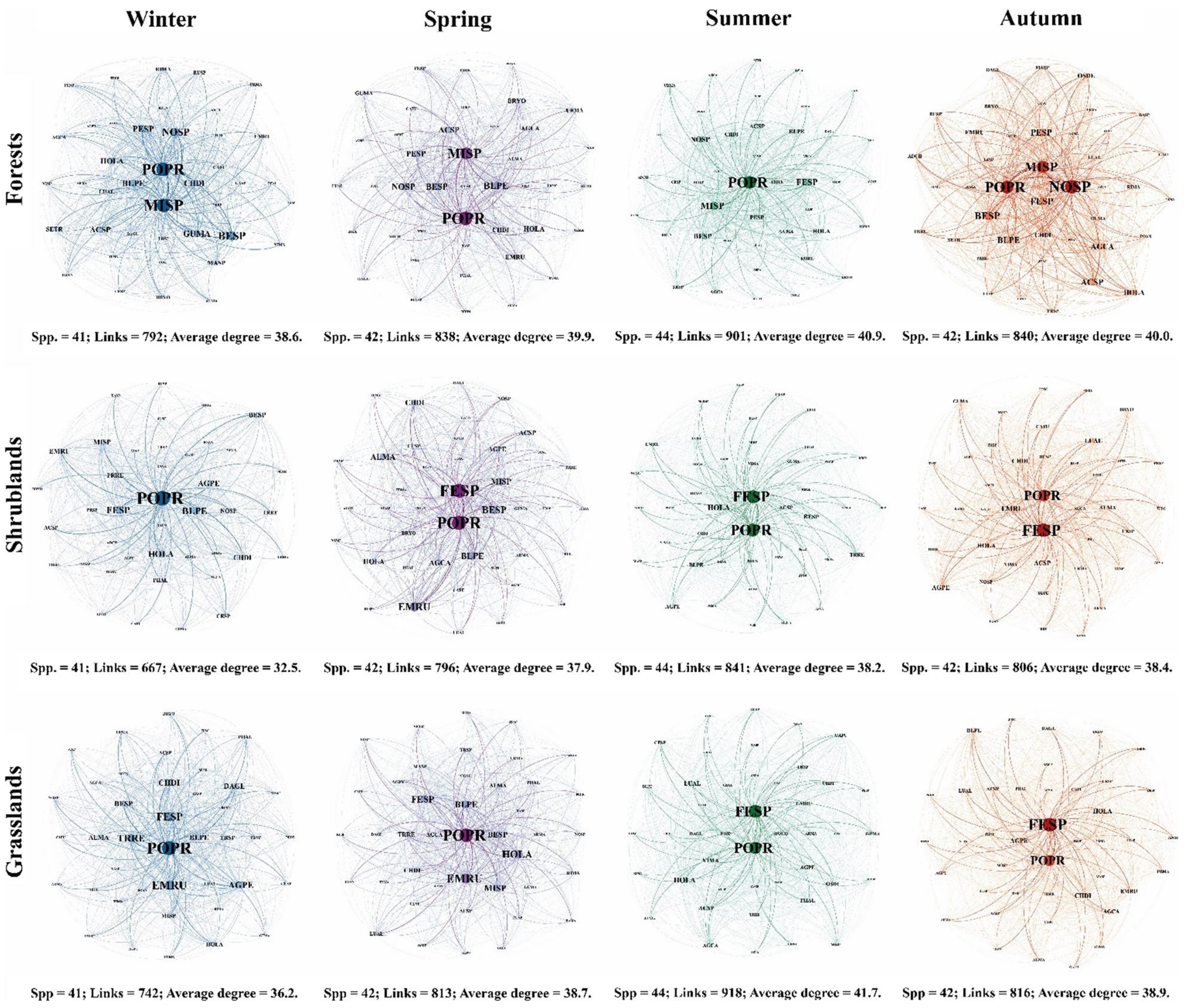

Fig. 4 Rabbit's forage intake networks in the studied vegetation types for each season. The circles indicate the species (sp.) observed in the pellets, and the lines indicate the intake links between the species. The average degree indicates networks connected to a species with many or few links. The larger the letters of the name of each circle and the lines of the links, the more important the species are in the network

for each vegetation type. Besides, many plant species (e.g., *Acaena magellanica* and *Cotula scariosa*) were not detected in the pellets analyses, which means that rabbits avoided that species. Although we expected an explicit spatial correspondence between the vegetation type and the rabbit's intakes, the evidence showed that rabbits move freely across the landscape, foraging at different vegetation types during the day. For example, the offer of hemiparasites (e.g., *Misodendrum* sp.) only occurred in forests, but it was found in pellets in all the studied vegetation types. According to Marín-García et al. (2021) and Marín-García and Llobat (2021), rabbits explore different vegetation strata and adapt their feeding strategies to the quantity and quality of available plant resources. This ability confirms the generalist nature of rabbits and corresponded to our results.

On the other hand, in some cases, rabbits preferred specific vegetation types according to seasonally available forage. Then, the rabbits showed a slightly lower forage activity in forests, but there was no difference between seasons for the consumption of tree regeneration (only the consumption of hemiparasites was higher in spring). Another example is what happened with shrubs and ferns, where consumption does depend on the season, probably due to the decrease in the grass and forb availability (e.g., snow accumulation). Rabbits generally prefer grasses over other plant groups (Chapman and Flux 2008), so they take in less grass in the winter and spring

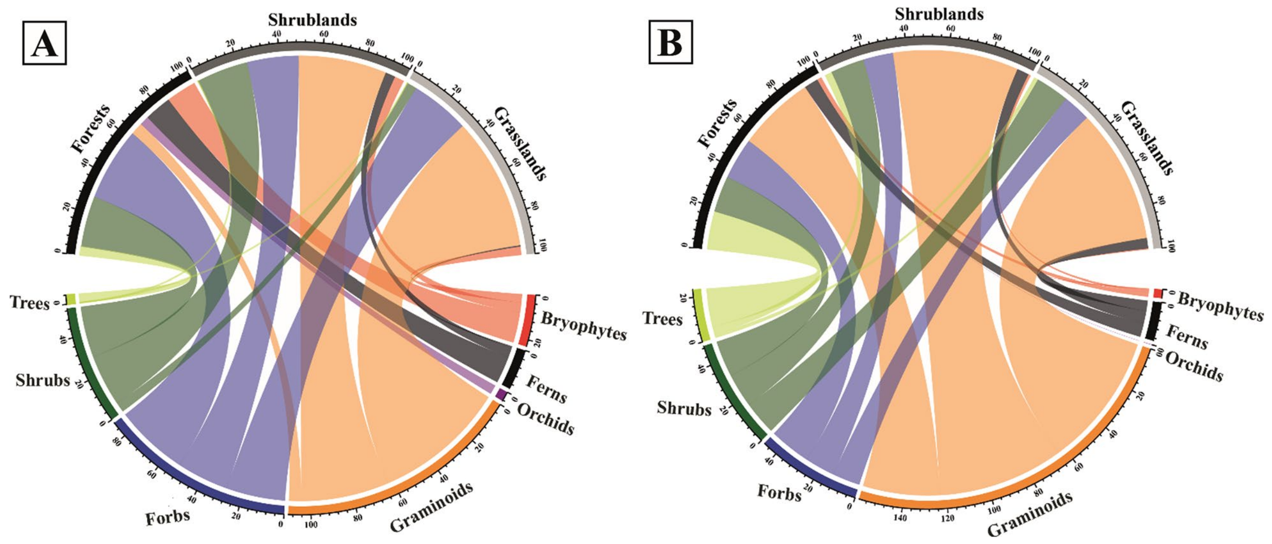

Fig. 5 Relationship between vegetation types and life forms for: **A** forage offer (based on ground cover, %) and **B** rabbit forage intakes (based on occurrence frequency in microhistological analyses, %). The coloured ribbons represent the links of each life form within the vegetation types

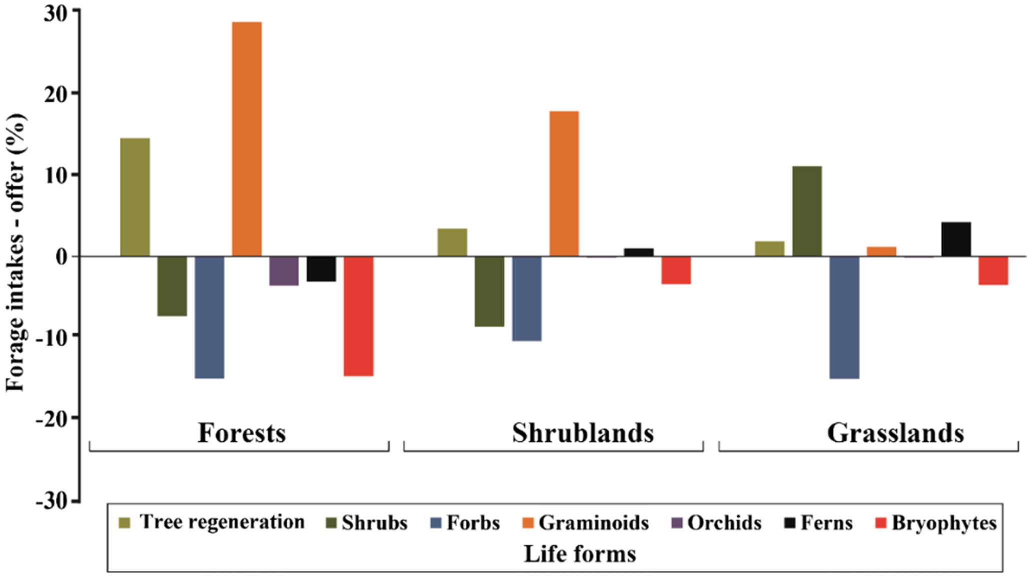

Fig. 6 Difference between forage rabbit intakes and offer, by life forms at the studied vegetation types (forest, shrublands, and grasslands). Negative responses indicated that rabbits avoid it (e.g., less intakes than offer), while a positive response indicated that rabbits prefer it (e.g., more intakes than offer)

because the offer is lower. Besides, rabbits consume most plants from the Poaceae, Fabaceae, and Asteraceae families in their natural habitat (Delibes-Mateos et al. 2008) and insular ecosystems where rabbits have been introduced (Cubas et al. 2019). Many Asteraceae ($n = 11$ species) and Poaceae ($n = 15$ species) were consumed by rabbits in our study area, much similar to that in their natural habitat. However, there were only two species of Fabaceae (*Trifolium repens* and *Vicia magellanica*) in the vegetation types (Appendix 1). The other plant families in which rabbits consumed more species were Rosaceae (*Acaena magellanica*, *Acaena ovalifolia*, and *Acaena pinnatifida*) and Caryophyllaceae (*Arenaria serpens*, *Cerastium arvense*, *Cerastium fontanum*, and *Stellaria media*).

Marín-García and Llobat (2021) suggested that rabbits have requirements that apparently cannot be covered for one specific vegetation type. Fuentes et al. (1983) also showed that rabbits browse and consume shrub seedlings when another forage offer is scarce. It has been observed that nutrition can limit the abundance and density of this herbivorous species, where plants with a higher amount of crude protein are more consumed (Llobat and Marín-García 2022). In fact, effective vegetation management, including the use of native plants and the use of protein as a limiting factor, can also help increase rabbit density, according to Llobat and Marn-Garca (2022). Thus, rabbits prefer an equilibrium between food and shelter and look for the best choice across the season in the landscape. Certain plant species help the rabbit to survive, finding plant food destinations at a landscape level. Previous studies indicate that rabbit alterations seriously affect plant communities' function in the invaded vegetation types (Delibes-Mateos et al. 2008). These impacts cause disturbances in the ecosystem function (e.g., natural seed banks and regeneration plants of shrub and tree species) in the areas where they have been introduced (Courchamp et al. 2003; Cuevas et al. 2016). For example, they markedly alter the assemblage of plant species and vegetation structure through browsing and seed dispersal (e.g., Bobadilla et al. 2020). Rabbits develop new interactions with exotic plants, which may aid their spread (e.g., accelerating the increase in the number of introduced species and their impact on the native community) (Bobadilla et al. 2020). In many ecosystems, their activities produce novel structures that modify resource availability and/or alter environmental circumstances for other taxa (Gálvez Bravo et al. 2009). This study did not provide enough evidence to conclude tree regeneration limitations in the affected stands. Other studies are needed to evaluate their influence, as for other similar herbivores in other *Nothofagus* forests of the region (e.g., *Lepus europaeus* foraging in *Nothofagus pumilio* forests, as was studied by Huertas Herrera et al. 2022). However, rabbit forage can affect iconic or emblematic native species (e.g., the Orchids *Codonorchis lessonii* and *Gavilea lutea*). In this context, it may be essential to know the use that rabbits make of the different plant resources as an approach to the knowledge or evaluation of the possible impact over native vegetation and its potential dispersion (e.g., exotic species such as *Poa pratensis*, which was preferred over other natural grams). For instance, if rabbits take in a plant species in short supply (e.g., orchids), they could threaten the survival of those plants.

Conclusions

The present work indicates that rabbits have a generalist ingestion capacity of the different plant life forms available in forests, shrublands, and grasslands. The forage offered at each vegetation type consisted of graminoids, shrubs, and forbs life forms from the Asteraceae, Poaceae, Rosaceae, and Caryophyllaceae families and was comparable to that consumed in its natural habitat. The rabbit's dietary intakes occur in all vegetation types, covering all the landscape, where the forage supply was available seasonally. The strongest links between rabbit intake and vegetation types were found in graminoids like *Poa pratensis* (all four seasons) and *Festuca* sp. (mainly in spring, summer, and autumn), hemiparasites like *Misodendrum* sp. (mainly in winter, spring, and autumn), shrubs like *Empetrum rubrum* (mainly in spring, summer, and autumn), and trees like *Nothofagus* sp. (mainly in autumn). As hypothesized, rabbits' food intake varies depending on the seasonal availability of forage, e.g., some life forms, such as shrubs, were higher consumed during winter and spring, while others, such as ferns were avoided. In other words, rabbits differently use the available forage according to the seasons. As a result, seasonality, rather than vegetation types, is a key indicator for rabbit management. To conclude, the fact that there is a different diet intake between the life forms beyond the understory (e.g., *Misodendrum* sp.) indicates that rabbits have another forage use according to the vegetation types across the seasons (balance between food offer and shelter).

Appendix 1. Forage offer (cover, %) by plant species in the studied vegetation types (forests, shrublands, and grasslands)

Life form	Family	Species	Code	Forests	Shrublands	Grasslands
Bryophytes	Liverworts and mosses	*Bryophytes*	BRYO	7.5	4.5	3.8
Graminoids	Poaceae	*Agropyron pubiflorum*	AGPU			0.1
	Poaceae	*Agrostis capillaris*	AGCA	0.1	1.2	5.6
	Poaceae	*Agrostis perennans*	AGPE		3.8	6.3
	Poaceae	*Alopecurus magellanicus*	ALMA	0.1	0.1	4.4
	Poaceae	*Bromus unioloides*	BRUN	0.1	0.1	0.1
	Poaceae	*Dactylis glomerata*	DAGL	0.1	0.1	16.2
	Poaceae	*Festuca magellanica*	FEMA	0.1	1.2	16.3
	Poaceae	*Festuca ovina*	FEOV	0.1		15.8
	Poaceae	*Festuca rubra*	FERU		22.3	11.2
	Poaceae	*Holcus lanatus*	HOLA	0.2	3.6	3.8
	Poaceae	*Hordeum comosum*	HOCO			8.0
	Poaceae	*Phleum alpinum*	PHAL		2.0	
	Poaceae	*Poa annua*	POAN	0.5		
	Poaceae	*Poa pratensis*	POPR	1.8	6.5	4.2
	Poaceae	*Trisetum spicatum*	TRSP	0.1	0.1	4.5
	Cyperaceae	*Carex fuscula*	CAFU	0.1	0.1	2.8
	Juncaceae	*Juncus scheuzerioides*	JUSC	0.1	0.1	0.3
	Juncaceae	*Luzula alopecurus*	LUAL	0.1	0.6	0.1
	Juncaginaceae	*Tetroncium magellanicum*	TEMA	0.1		1.0
Shrubs	Asteraceae	*Baccharis magellanica*	BAMA	0.1	12.0	0.1
	Berberidaceae	*Berberis buxifolia*	BEBU	0.4	4.3	0.6
	Berberidaceae	*Berberis ilicifolia*	BEIL	3.8		
	Asteraceae	*Chiliotrichum diffusum*	CHDI	1.8	12.8	3.3
	Empetraceae	*Empetrum rubrum*	EMRU	0.1	1.6	0.1
	Ericaceae	*Pernettya mucronata*	PEMU	1.5	1.4	0.3
	Ericaceae	*Pernettya pumila*	PEPU	3.0	2.6	0.1
	Celastraceae	*Maytenus disticha*	MADI	4.3	0.1	0.1
	Saxifragaceae	*Ribes magellanicum*	RIMA	1.8		0.1
Trees	Celastraceae	*Maytenus magellanica*	MAMA	1.5		
	Nothofagaceae	*Nothofagus pumilio*	NOPU	1.3	0.1	0.1
	Winteraceae	*Drymis winterii*	DRWI	1.0		
Forbs	Rosaceae	*Acaena magellanica*	ACMA	2.7	5.7	4.8
	Rosaceae	*Acaena ovalifolia*	ACOV	0.1	5.0	
	Rosaceae	*Acaena pinnatifida*	ACPI		3.0	2.5
	Asteraceae	*Adenocaulon chilense*	ADCH	3.3	0.1	0.1
	Plumbaginaceae	*Armeria maritima*	ARMA	0.1	0.1	0.7
	Caryophyllaceae	*Arenaria serpens*	ARSE		3.0	3.0
	Asteraceae	*Aster vahlii*	ASVA	0.1		3.0
	Asteraceae	*Bellis perennis*	BEPE			6.0
	Caryophyllaceae	*Cerastium arvense*	CEAR		1.0	
	Caryophyllaceae	*Cerastium fontanum*	CEFO	0.1	0.1	0.7
	Asteraceae	*Cotula scariosa*	COSC	0.1	0.1	0.2
	Euphorbiaceae	*Dysopsis glechomoides*	DYGL	5.1		
	Rubiaceae	*Galium aparine*	GAAP	1.5		0.1
	Rubiaceae	*Galium fuegianum*	GAFU	1.5		
	Asteraceae	*Gamochaeta spiciformis*	GAPI	0.1		
	Gentianaceae	*Gentianella magellanica*	GEMA			2.0
	Haloragaceae	*Gunnera magellanica*	GUMA	0.3	3.5	2.8
	Asteraceae	*Hypochoeris radicata*	HYRA			3.0

Life form	Family	Species	Code	Forests	Shrublands	Grasslands
	Apiaceae	*Osmorhiza depauperata*	OSDE	1.5	0.1	0.1
	Lobeliaceae	*Pratia repens*	PRRE	0.1	0.3	0.1
	Primulaceae	*Primula magellanica*	PRMA			5.0
	Ranunculaceae	*Ranunculus peduncularis*	RAPE	0.5	5.0	
	Polygonaceae	*Rumex acetosella*	RUAC	0.1		
	Polygonaceae	*Rumex crispus*	RUCR			2.0
	Apiaceae	*Schizeilema ranunculus*	SCRA		1.0	
	Asteraceae	*Senecio tricuspidatus*	SETR	2.4	0.1	
	Caryophyllaceae	*Stellaria media*	STME	0.8		
	Asteraceae	*Taraxacum gillesii*	TAGI		1.5	
	Asteraceae	*Taraxacum officinale*	TAOF	1.3	5.9	5.9
	Fabaceae	*Trifolium repens*	TRRE	0.1	1.3	2.5
	Urticaceae	*Urtica magellanica*	URMA	6.5	3.0	5.0
	Fabaceae	*Vicia magellanica*	VIMA	0.1		2.0
	Violaceae	*Viola magellanica*	VOMA	1.3		
	Violaceae	*Viola reicheii*	VIRE	1.0		
Orchids	Orchidaceae	*Codonorchis lessonii*	COLE	1.3		
	Orchidaceae	*Gavilea lutea*	GALU	2.0		
Ferns	Polypodiaceae	*Asplenium dareoides*	ASDA	1.0		0.1
	Blechnaceae	*Blechnum penna-marina*	BLPE	5.8	4.6	0.6
	Athyriaceae	*Cystopteris fragilis*	CYFR	0.9		

Appendix 2 Rabbit's forage intakes (cover, %) by plant species in three vegetation types (forest, shrublands, and grasslands) along the four seasons of the year

Life form	Species	Code	Autumn			Spring			Summer			Winter		
			Forests	Shrublands	Grasslands	Forests	Shrublands	Grasslands	Forests	Shrublands	Grasslands	Forests	Shrublands	Grasslands
Bryophytes	Bryophytes	BRYO	1.4	1.9	0.5	3.5	1.5	0.5	1.2	1.2	0.3	0.8	1.7	0.2
Graminoids	*Agropyron pubiflorum*	AGPU			1.5			0.4				0.1		
	Agrostis capillaris	AGCA	4.4	1.3	3.7	3.1	4.6	2.9	2.7	2.1	3.6	1.5	1.7	
	Agrostis perennans	AGPE		4.4	6.3		3.8	2.5		3.6	2.9	7.2		6.3
	Alopecurus magellanicus	ALMA	0.4	3.3	1.5	1.7	5.9	3.4	0.2	0.6	1.5	3.8	0.5	
	Bromus unioloides	BRUN				0.1			0.8	1.0	0.3		0.2	
	Dactylis glomerata	DAGL	1.3		2.8	0.8	0.6	1.6			2.1	5.4	0.9	
	Festuca sp.	FESP	6.1	19.8	23.2	1.9	14.8	8.1	9.3	23.0	18.4	9.6	0.9	9.7
	Holcus lanatus	HOLA	4.1	5.3	6.1	4.2	4.3	9.2	4.5	8.8	6.8	3.2	5.0	8.4
	Hordeum comosum	HOCO									1.9			
	Phleum alpinum	PHAL		0.5	1.2	0.4	1.2	2.5		1.6	3.1	2.5		3.3
	Poa annua	POAN	1.0						0.1				1.0	

Life form	Species	Code	Autumn			Spring			Summer			Winter		
			Forests	**Shrublands**	**Grasslands**	**Forests**	**Shrublands**	**Grasslands**	**Forests**	**Shrublands**	**Grasslands**	**Forests**	**Shrublands**	**Grasslands**
	Poa pratensis	POPR	11.1	16.4	18.0	14.5	15.2	17.3	19.0	22.6	17.3	16.6	12.7	21.2
	Trisetum spicatum	TRSP	1.8	1.0	1.8	0.4	0.3	2.6	2.3	0.7	2.7	2.7	0.7	
	Carex fuscula	CAFU	0.2	2.8	1.7	0.4	0.4	0.4	0.3	1.0	2.6	0.3	1.4	0.1
	Juncus scheuzerioides	JUSC		0.8	0.4	0.0		0.3	0.3	1.0	0.2		0.7	0.2
	Luzula alopecurus	LUAL	1.5	4.4	2.4	0.6	0.9	2.7	0.6	1.9	4.8	0.8	2.6	0.4
	Tetroncium magellanicum	TEMA				0.1						1.0		
Shrubs	*Baccharis magellanica*	BAMA	0.0	0.0	0.2			0.2						
	Berberis sp.	BESP	7.0	2.8	0.6	6.5	7.3	6.8	7.0	5.5	1.3	5.2	7.8	5.2
	Chiliotrichum diffusum	CHDI	3.0	5.5	5.7	3.9	5.1	4.0	3.9	1.9	1.8	6.2	5.0	5.8
	Empetrum rubrum	EMRU	3.1	6.1	4.7	3.2	8.7	11.6	2.6	2.8	3.8	9.9	2.5	5.2
	Ribes magellanica	RIMA	1.2			0.7		0.1	0.7				2.2	
	Pernettya sp.	PESP	5.3	0.8	0.6	5.1	1.0	0.7	5.2	0.7	0.4	0.9	5.9	1.4
Trees	*Maytenus* sp.	MASP	1.3			1.6	0.3	0.1	0.9			0.5	3.4	
	Nothofagus sp.	NOSP	12.0	3.0	1.6	8.4	1.7	0.7	7.7	1.0	1.4	1.1	6.8	3.6
Forbs	*Acaena* sp.	ACSP	5.1	5.0	3.5	5.7	4.3	1.7	4.4	4.5	4.5	2.0	4.4	2.9
	Adenocaulum chilensis	ADCH	1.4	0.3	0.4	0.9	0.2		1.8		0.2		0.2	
	Armeria chilensis	ARMA		1.3	0.2	0.2	0.4	0.2	0.1	0.1	1.0	0.1		
	Aster vahlii	ASVA	0.2								0.3			
	Cerastium sp.	CESP	0.8	2.7	1.8	1.0	1.7	1.0	0.9	1.6	1.9	0.7	0.5	2.4
	Cotula scariosa	COSC	0.0	0.4	0.3	0.1		0.1	0.3	1.4	0.3	0.1		
	Galium sp.	GASP	0.7						0.1		0.0		0.5	
	Gunnera magellanica	GUMA	1.5	2.3	0.6	2.1	0.9	0.9	2.6	0.9	1.8		5.3	0.4
	Osmorhiza depauperata	OSDE	3.3		0.3		0.1				3.1			
	Pratia repens	PRRE	0.5	0.6	0.4		0.2			0.4	0.2			4.5
	Rumex sp.	RUSP	1.2			0.3			0.1				1.2	
	Senecio tricuspidatus	SETR	1.7			1.7			0.3				2.8	0.7

Life form	Species	Code	Autumn			Spring			Summer			Winter		
			Forests	Shrublands	Grasslands	Forests	Shrublands	Grasslands	Forests	Shrublands	Grasslands	Forests	Shrublands	Grasslands
	Taraxacum sp.	TASP	0.7	0.4		0.2	0.2				0.2	0.2		0.5
	Trifolium repens	TRRE	1.2	0.7	1.7	1.3	0.4	4.9	2.2	4.5	1.2	8.8	0.3	2.4
	Urtica magellanica	URMA		0.8	1.3	3.4			1.7	0.3			1.0	
	Vicia magellanica	VIMA		2.1									0.7	
	Viola sp.	VISP				0.3	0.8	0.5		1.1	4.7		1.1	
Orchids	*Codonorchis lessonii*	COLE							0.1					
	Gavilea lutea	GALU	0.4			0.0								
Ferns	*Asplenium daeroides*	ASDA									0.2			
	Blechnum pennamarina	BLPE	4.9	1.7	4.6	7.9	7.0	7.4	4.4	3.9	1.5	5.2	5.9	9.4
Hemiparasites	*Misodendrum* sp.	MISP	10.0	1.6	0.7	13.8	6.3	5.0	10.8	0.5	1.7	3.5	12.7	5.7

Abbreviations
ANOVA: Analysis of variance; DCA: Detrended correspondence analyses; SD: Standard deviation.

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