Environment and anthropogenic impacts as main drivers of plant assemblages in forest mountain landscapes of Southern Patagonia

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ABSTRACT

Management of natural areas generated multiple trade-offs, and changes in the plant assemblages was identified as one of the most critical ones. In this context, understanding the drivers of change of exotic plant diversity is critically important for biodiversity conservation and land planning. The aim of this work was to evaluate the relationships between environmental gradients in mountain landscapes and anthropogenic impacts related to human uses as drivers for plant assemblages (native and exotic species) in Southern Patagonian forests. The study was located in the Andorra Valley basin (12,934 ha) in the southern Tierra del Fuego Island (Argentina), where mountain landscape units (land-cover and land-use) were identified according to their vegetation types (forests and open-lands), elevational effects (< 400 and > 400 m.a.s.l.) and anthropogenic impacts derived from economic activities (harvesting and cattle grazing). Classification was based on Landsat 8 OLI images with fieldwork samplings, relevating a total of 101 landscape units. In each unit, forest structure and floristic surveys (dicots, monocots, pteridophytas and bryophytes) were conducted. Data were evaluated using ANOVAs and multivariate analyses (cluster, detrended and canonical correspondence analysis). A total of 104 plant species were surveyed (88% natives and 12% exotics), where managed deciduous forests (*Nothofagus pumilio*) had the highest values of exotic species occurrence frequency (20%). Multivariate analyses showed that environmental gradients and anthropogenic impacts highly affected the distribution of exotic species. Native species had higher cover values at upper elevations, while exotic plants had a higher cover at lower elevations, where the N-S aspects were strongly correlated with plant preferences for shaded/lighted aspects. The occurrence of exotic species can be specifically related to human activities (e.g., *Agrostis stolonifera* and *Rumex acetosella* with cattle grazing; and *Poa nemoralis*, *Ranunculus repens* and *Stellaria media* with harvesting), however one of them (*P. trivialis*) was related with unharvested forests. We conclude that environmental gradients and anthropogenic impacts define the plant assemblages at landscape level, and they also influence the occurrence of the exotic species, where the main driver was the harvesting. We propose that land-sharing conservation strategy in these mountain landscapes could be the better approach towards sustainability ensuring the preservation of the land-cover and the land-use at the low and upper elevations.

1. Introduction

Impacts on ecosystems by natural and anthropogenic-induced alterations span very different spatial levels, from the management of local ecosystems to understanding globally interconnected processes, and addressing them through international policies (Kueffer et al., 2014). An important example is a framework that distinguishes between the integration (land-sharing) and the separation (land-sparing) of conservation with production systems (Phalan et al., 2011). In a land-sparing scenario, the available land in a landscape is partitioned into some areas focused on producing mainly agricultural products, while others are devoted mainly to maintaining biodiversity and ecosystem services (e.g. maintaining and protecting areas of special interest); while in the land-sharing scenario, the available land is under lower-intensity management (e.g. harvesting or cattle grazing). The increased area of land in production compensates for its lower yield, and the decrease in intensity allows biodiversity to be conserved across the whole landscape (Phalan et al., 2011; Gabriel et al., 2013). However, trade-offs were produced among the different management objectives (e.g. harvesting vs. conservation) and the different ecosystem
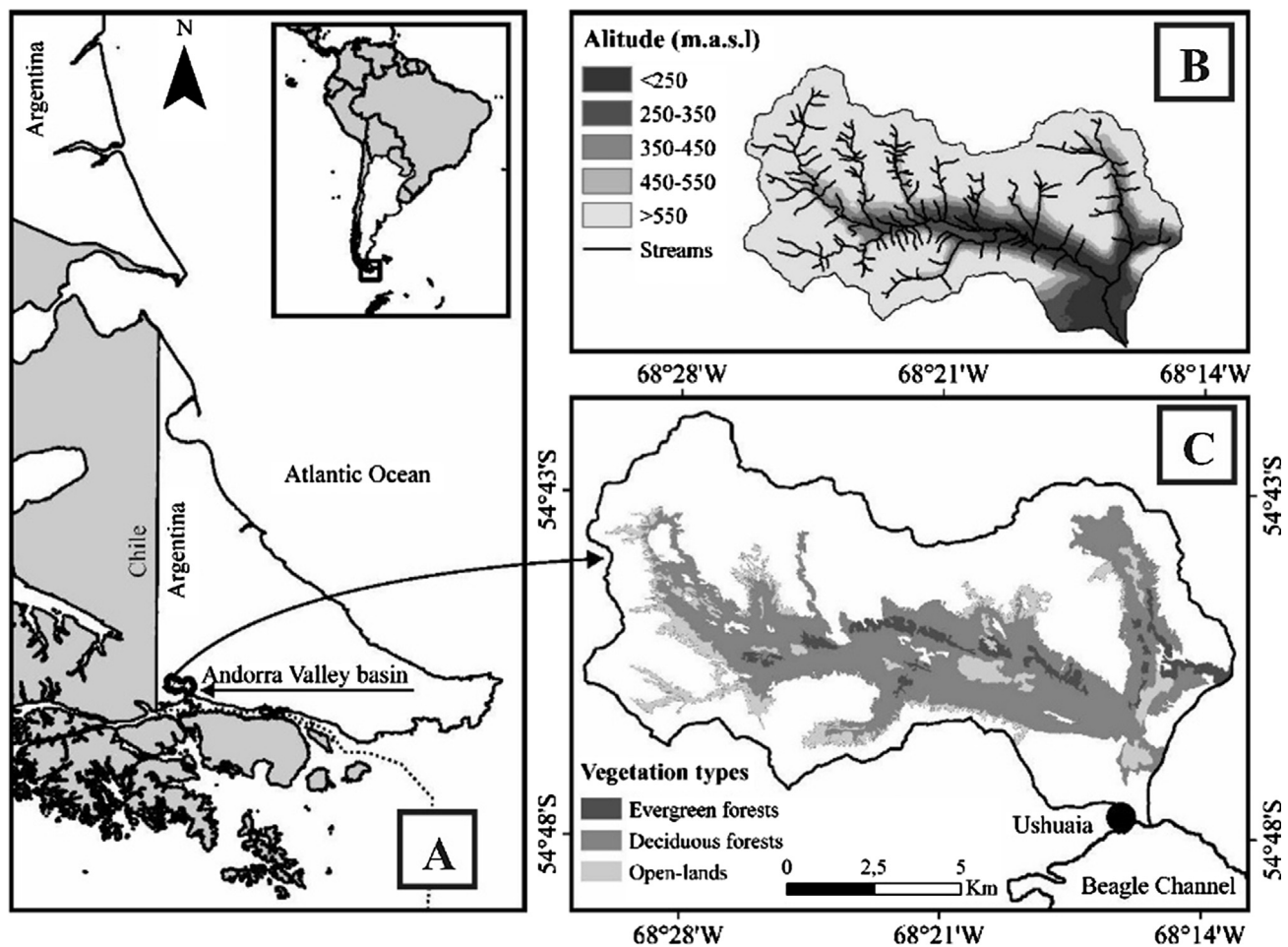

Fig. 1. Study area: (A) location of Andorra Valley, (B) river networking and elevation (m.a.s.l.), and (C) main vegetation types.

services that the landscape offers to the society (Martínez Pastur et al., 2017).

The occurrence of exotic species in the natural landscapes is one of the main proxies of anthropogenic impact of practical interest to ecosystems management (Butchart et al., 2010). In the case of plants, the occurrence of exotic species is widely recognized to alter ecosystem structure and function, community assemblage, and native species interactions (Sax, 2001; Lencinas et al., 2011), and could endanger the productive systems (e.g. trophic links) (Belnap et al., 2012; Peri et al., 2016). In mountain landscapes, the interest on species diversity has greatly increased during the last years, due to gaining further insight into patterns of invasion and mechanisms driving them along the environments (Alexander et al., 2011; Kueffer et al., 2014). Mountains provide several ecosystem services (Rodríguez-Rodríguez et al., 2011) and usually natural reserves were created in these landscapes (Arpin and Cosson, 2015). However, mountain regions are particularly vulnerable to socioeconomic pressures, where optimal land management to ensure the availability of the natural resources is needed (Grêt-Regamey et al., 2012).

In Southern Patagonia, remaining well-conserved wilderness areas are mainly located across the Andean Mountains, where *Nothofagus* represent the southernmost forested ecosystem on Earth (Peri et al., 2016) and the understory plants typically represented one of the most important components of biodiversity (Lencinas et al., 2011; Mestre et al., 2017). Land-cover includes forests dominated by deciduous (*Nothofagus pumilio* and *N. antarctica*) and evergreen trees (*N. betuloides*). These forests rarely constitute large continuous masses; rather the landscape is usually formed by a mosaic of several forest types and open-lands, where timber and unproductive forests are mixed (Lencinas

et al., 2008a). The deciduous forests (henceforth referred only to *N. pumilio*) grow in cool sites with well-drained soils (Frangi and Richter, 1994), while evergreen forests develop in softer environmental conditions at middle elevation on mountain valleys (Allué et al., 2010). The associated environments, such as open-lands, include unique species (Lencinas et al., 2008a, 2008b). The diversity of understory species is particularly associated with the ecology of each site, such as incident light and soil moisture at understory level (Mestre et al., 2017). These forests have very valuable timber species and valleys offered some grassland patches, for this, historical impacts occurred due to anthropogenic-influences such as harvesting and cattle grazing (Martínez Pastur et al., 2017), generating changes in the biodiversity, e.g. both activities reduce understory and insect richness, and significantly changes its original community's assemblage (Lencinas et al., 2011, 2017). Beside this, these mountain environments were also threat due to establishment of many new exotic plant species that established after the interventions (Lencinas et al., 2008a). The relationship between exotic plants, and environment and anthropogenic drivers, is still poorly understood at southernmost mountain landscapes, although they are strongly increasing in remote areas (Seebens et al., 2017, 2018), and was considered as an important pressure over biodiversity (Tittensor et al., 2014).

Many countries of South America base their conservation strategy in natural parks located in remote areas (e.g. Argentina and Chile) (Martínez-Harms and Gajardo, 2008), however, land-use changes increased every year due to worldwide demand for more natural resources (e.g. food, wood, fiber) (FAO, 2014). In this context, land-sharing becomes the most realistic option in Andean mountain landscapes (Martínez Pastur et al., 2013), and the understanding of the

drivers related with exotic plant occurrence is critically important for biodiversity conservation and land planning. The aim of this study was to evaluate the relationships between environmental gradients (e.g. elevation, aspect, slope) and anthropogenic impacts (cattle grazing and harvesting) as drivers for plant assemblages in forested mountain landscapes at Southern Patagonia. Specifically, we want to answer the following questions: (i) how do plant assemblages change within the main vegetation types (forests and open-lands)?; (ii) how environmental gradients can explain these plant assemblages?; (iii) how anthropogenic impacts, in addition to environmental forces, can modify this plant assemblage?; and (iv) based on the previous answers, are these anthropogenic impacts a driver for the occurrence of exotic plant species?

2. Methods

2.1. Study area

The study was conducted in the Andorra Valley basin (54°41′ to 54°47′ S, 68°13′ to 68°30′ W) located in the Andean mountains of southern Tierra del Fuego Island (Fig. 1). It covers an area of 12,934 ha with elevation ranges from 0 to 1400 m.a.s.l. The dominant vegetation types consist in a mixed landscape of open-lands (grasslands and peatlands), and forests (evergreen and deciduous). The vegetation at low and middle elevation lands (< 400 m.a.s.l.) are predominantly conformed by Magellanic moorland formations (grasslands and peatlands), as well as evergreen (*N. betuloides*) and deciduous (*N. pumilio*) forests, while in the upper lands (> 400 m.a.s.l.) the area was dominated by deciduous forests (including krummholz formations) and alpine grasslands (Moore, 1983). The continuous range of highlands runs from west to east, and defines the relief and the main climate pattern of the basin, which is under the strong influence of Antarctica (Frederiksen, 1988; Martínez Pastur et al., 2016a), characterized by short-cool summers and long-snowy winters with frequent occurrence of frosts (Brancaleoni et al., 2003). Only three months per year are free of mean daily air temperatures below 0 °C, and the plant growing season extends approximately from November to March (Martínez Pastur et al., 2016a). Annual precipitations, including snowfall, ranging from 550 mm yr^{-1} at low elevation lands to 1190 mm yr^{-1} in the upper lands (Barrera et al., 2000). Annual average wind speed outside forests is 8 km h^{-1}, with strong winds reaching up 100 km h^{-1} during storms (Massaccesi et al., 2008). Soils are mainly Inceptisols (Cruzate and Panigatti, 2007), and highlands consist almost entirely of rocky promontories and mineral soil (Barrera et al., 2000; Brancaleoni et al.,

2003). Furthermore, glaciers and peatlands play an important role in the hydrology regulation, where small streams between peatlands carry groundwater and surface water into the main river, which drains the basin from west to east into the Beagle Channel (Grootjans et al., 2010). In the study area, harvesting occurred in deciduous forests within the past 50 years, mainly over primary forests (e.g. selective cuts), leaving the forest regeneration under a natural dynamic. However, the socio-economic development in the 1990s generate the suburban expansion of Ushuaia city, and some of their open-lands and forests were used for firewood extraction and cattle grazing (mainly Hereford breed). These land-use practices do not imply any technical management, but rather they responded to an extensive exploitation of the natural ecosystems (Peri et al., 2016). This mountain basin was selected because contains a set of land-cover and land-use units with a known history of changes in public and private lands and offers a wide variety of environmental gradients that comprise typical plant assemblages of Southern Patagonia.

2.2. Landscape characterization

Landscape units corresponded to vegetated surfaces, occupied 36% of the total study area. The remaining area (64%) corresponded to rocks (53%), glaciers (9%), lakes (1%) and urban settlements (1%). The landscape units were classified in land-cover units according to the main vegetation types (forests and open-lands) and elevation (< 400 and > 400 m.a.s.l.). Then, land-cover units with anthropogenic impact were classified in land-use units, according to the past or present uses (harvesting or cattle grazing). These classifications were made by analysis of medium spatial resolution imagery (year 2015) of sensor Landsat 8 OLI (30 m resolution) and fieldwork measurements (Appendix A). We used these images because it is readily and freely available, and often used for vegetation assessment (Jia et al., 2017), and is appropriate for this landscape-scale analysis (Chen et al., 2015). To undertake the spatial data analysis, we select images of summer (December to March) and winter (June to August) with clear sky conditions for adequate landscape cover assessments (e.g. land-cover discrimination between deciduous and evergreen forests). The images were processed by standard methods to reduce errors in the classification process (Hernández et al., 2015). Elevation was defined using the shuttle radar topography mission data (DEM) (Farr et al., 2007) allowed to calculate topography variables: elevation above sea level (ALT), slope (SLOPE), and aspect grids, which were calculated as sine and cosine functions of north magnetic direction (E-W and N-S) (Jenness, 2004). These data were analyzed with QGIS software version 2.14.
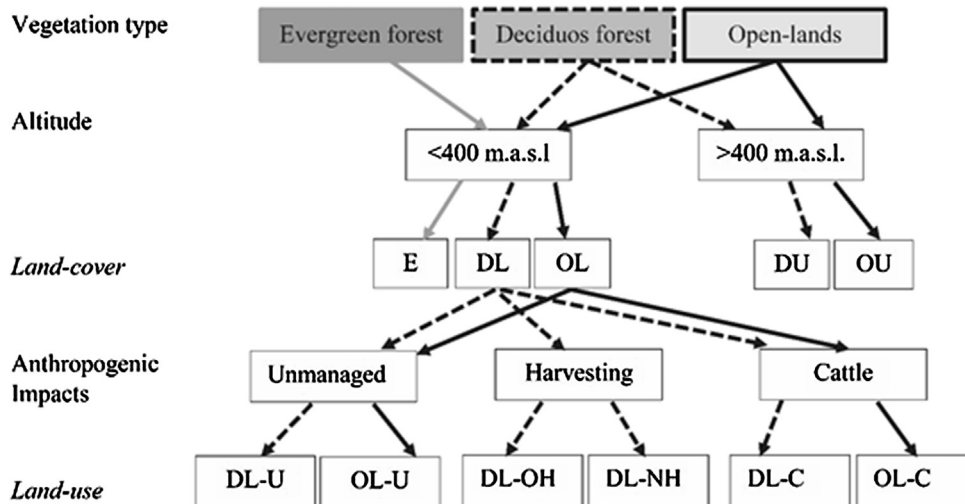

Fig. 2. Organizing framework for landscape unit treatments. Diagram showed how landscape units were categorized into land-cover units according to vegetations types and elevations, and into land-use subcategories according to the anthropogenic impacts (harvesting and cattle). E = evergreen forest at lower elevation, DL = deciduous forest at lower elevation, DU = deciduous forest at upper elevation, OL = open-land at lower elevation, OU = open-land at upper elevation, DL-U = deciduous unharvested forests at lower elevation, DL-OH = deciduous forests with old harvesting at lower elevation, DL-NH = deciduous forests with new harvesting at lower elevation, DL-C = deciduous forests with cattle grazing at lower elevation, OL-I = intact open-lands at lower elevation, and OL-C = open-lands with cattle grazing at lower elevation.

Ground-truth was conducted with field visits to each vegetation unit, allowed us to define five distinct land-cover units (Fig. 2): (1) E = evergreen forests at lower elevation, (2) DL = deciduous forests at lower elevation, (3) DU = deciduous forests at upper elevation, (4) OL = open-lands at lower elevation, and (5) OU = open-lands at upper elevation. In areas where anthropogenic impacts were detected, we defined the following categories: (1) DL-U = deciduous unharvested forests at lower elevation, (2) DL-OH = deciduous forests with old harvesting (> 50 years after harvesting-YAH) at lower elevation, (3) DL-NH = deciduous forests with recent harvesting (20–30 YAH) at lower elevation, (4) DL-C = deciduous forests with cattle grazing at lower elevation, (5) OL-I = intact open-lands at lower elevation, and (6) OL-C = open-lands with cattle grazing at lower elevation. The intact (I) or unharvested (U) conception, understanding as a natural ecosystem showing no signs of significant anthropogenic activity, and was defined based on the Intact Landscape concept (Potapov et al., 2008). In our study area, evergreen forests occurred only at lower elevations (< 400 m.a.s.l.) and no had significant anthropogenic impacts to be categorized, as well as none of the upper elevations land-cover units had significant anthropogenic impacts. Ground truth visits were the robust way to determine the present and historical pressures on the land-use units (e.g., cattle grazing within forests), being corroborated with local inhabitants and ranchers through informal interviews. Beaver impacts were considered in this study.

2.3. Sampling design and data taking

Along the landscape units (henceforth referred to both land-cover and land-use), data collection was conducted in summer during the growing season when plant structures can be better recognized (Lencinas et al., 2011). In each landscape unit, sampling areas (one per unit) were selected according to their homogeneity, accessibility and size (patches up to 5 ha). In the center of each unit, one plot was established measuring understory vegetation and/or forest structure. Understory vegetation census considering vascular plants (dicots, monocots and ferns) in 1.0 ha, where species cover was estimated using a modified Braun-Blanquet scale (Brancaleoni et al., 2003; Lencinas et al., 2011). Cover was also estimated for other ground variables including bryophytes (mosses and liverworts), bare soil without vegetation (including litter), rocky outcrop and woody debris (> 3 cm diameter). Plants were classified in taxonomic groups and its origin (native dicots, native monocots, exotic dicots, exotic monocots, and native pteridophyta) (Appendix B). We followed the taxonomy proposed by Correa (1969-1998) and Moore (1983). We could not differentiate species of mosses and liverworts, and they were considered together in the same group. Herbarium specimens were deposited in the Agroforestry Resources Lab (CADIC-CONICET) at Ushuaia city (Argentina).

Forest structure in the forest land-use units was characterized using two different methods: in forests at a lower elevation (< 400 m.a.s.l.) the point sampling method (Bitterlich, 1984) was performed using a Criterion RD-1000 (Laser Technology, USA) with a variable BAF (basal area factor between 6 and 9); while in forests at upper elevation (> 400 m.a.s.l.) fixed plots of 200 m^2 (transects of 50 × 4 m) were used, due to the presence of krummholz. Each tree species was identified, and diameter at breast height (DBH) was measured with a forest caliper. Also, the dominant height (DH) was measured in each plot using a Trupulse 360 (Laser Technology, USA). With these data, we calculated basal area (BA), total over-bark volume (TOBV) and tree density (DEN) (Martínez Pastur et al., 2002). Additionally, overstory crown cover (OCOV) was estimated using a spherical densiometer (Lemmon, 1956), and expressed as a percentage. We also considered the structure of different forests with respect to the distinct development stages: optimal initial growth and final growth, maturing and crumbling following. The development phases were estimated through the observation of external morphological characteristics (e.g., bark and crown development).

2.4. Data analyses

Occurrence frequency, defined as the proportion of plots in which each species occurred, was estimated to define the importance and variation of each species across landscape units. One-way ANOVAs for forest structure variables (dominant height, basal area, tree density, total over-bark volume, overstory crown cover) were carried out using forest land-cover (E, DL, DU) and forest land-use (DL-U, DL-OH, DL-NH, DL-C) units as main factors. Understory cover classified by its taxonomic group (dicots, monocots, pteridophytas, bryophytes) and origin (native, exotic), as well as the other ground cover variables (bare soil, woody debris) were compared by one-way ANOVAs considering land-cover and land-use units as main factors. Species richness for taxonomic groups and origin was analyzed by one-way ANOVAs comparing landscape units. In all cases, Shapiro-Wilk and Levene methods were used to test normality and homogeneity. When the assumptions were not achieved, variables were log-transformed to normalize its distribution, but non-transformed data are shown in the tables. Finally, we used post-hoc Tukey test (p < 0.05) to separate mean significant values. Statistical analyses were conducted using Statgraphics software (Statistical Graphics Corp., USA). Multivariate statistical methods of classification (clusters) and ordination (constrained and unconstrained) were used to analyse the data of richness and understory vegetation cover (Dray et al., 2012; ter Braak and Šmilauer, 2015). Cluster analyses were performed using Ward's linkage method with Euclidean distance to evaluate the relation among the plant assemblages of the different land-cover and land-use units, and aspects. Detrended correspondence analyses (DCA) using understory species relative cover, without down weight for rare species and with axis rescaling, were performed to compare the plant assemblages among land-cover and land-use units, as well as among anthropogenic impacts discriminating the species by its taxonomic groups and origins. We selected DCA due to provides simultaneously analyses of species and samples units (Hill and Gauch, 1980), allowing the examination of ecological interrelationships between them in a single-step analysis (Ludwig and Reynolds, 1988). Canonical correspondence analyses (CCA) based on plants species cover data were used to analyze the relationships between plant assemblages and environmental variables, discriminating the species by its taxonomic group and origin, plus the presence of exotic species. Moreover, sampling units were analyzed according to land-cover, land-use (excluding E and OU sampling units), and richness of exotic species. Species covers were used as response variables, and 14 environmental site characteristics were tested as explicatory variables (Appendix C). Likewise, Monte-Carlo method with 499 permutations was employed to test the significance of each axis in CCA. Selected explicatory variables (p-values < 0.05) were: dominant height (DH), total over-bark volume (TOBV), overstory crown cover (OCOV), woody debris (DEB), elevation above sea level (ALT), slope (SLOPE), east-west aspect (E-W), and north-south aspect (N-S). All multivariate analyses were performed using PC-ORD (McCune and Mefford, 1999).

3. Results

A total of 101 landscape units were identified among the vegetated surfaces (Appendix A(A)). Land-cover units reach to 4602 ha of the study area, where land-use units occupied near 50% (2469 ha) (Table 1). A total of 104 plant species were surveyed: 88% natives (92 species, where 61 dicots, 28 monocots and 3 ferns) and 12% exotic (12 species, where 8 dicots and 4 monocots) (Appendix B). The most common plants were native dicots, including *N. pumilio, Senecio acanthifolius, Gunnera magellanica, Osmorhiza chilensis* and *Rubus geoides* (40–64% occurrence frequency). Among exotic species, the most abundant were two dicots (*Taraxacum officinale* and *Cerastium fontanum*) (29% and 21% occurrence frequency, respectively) and two monocots (*Poa pratensis* and *P. nemoralis*) (22% occurrence frequency each). In land-cover units, the exotic species were more frequent in

Table 1

Landscape units of the studied area (mean ± standard error) (ha and %). Land-cover units (E = evergreen forest at lower elevation, DL = deciduous forest at lower elevation, DU = deciduous forest at upper elevation, OL = open-land at lower elevation, OU = open-land at upper elevation); and (B) land-use units (DL-U = deciduous unharvested forests at lower elevation, DL-OH = deciduous forests with old harvesting (> 50 years after harvesting) at lower elevation, DL-NH = deciduous forests with new harvesting (20–30 years after harvesting) at lower elevation, DL-C = deciduous forests with cattle grazing at lower elevation, OL-I = intact open-lands at lower elevation, OL-C = open-lands with cattle grazing at lower elevation).

Landscape units		*n*	Area (ha)	%
Land-cover	E	16	24.0 ± 4.6	8
	DL	45	45.8 ± 5.2	45
	DU	21	61.1 ± 8.9	28
	OL	10	41.0 ± 12.2	9
	OU	9	61.8 ± 20.6	10
Land-use	DL-U	12	46.4 ± 11.1	23
	DL-OH	19	45.8 ± 7.2	35
	DL-NH	6	55.9 ± 15.2	14
	DL-C	8	37.1 ± 13.6	12
	OL-I	5	40.2 ± 16.8	8
	OL-C	5	41.9 ± 19.7	8

deciduous forests (20% occurrence frequency) than evergreen forests (< 5% occurrence frequency), and at lower than higher elevations. In land-use units, the old harvested forests comprised the greater occurrence of exotic species (22%), followed by recent harvested forests (9%). Finally, the lowest occurrence frequency of exotic species was found across deciduous forests and open-lands with cattle grazing (< 5%).

Understory cover among land-cover units presented significant differences for all taxonomic groups, except dicots (p = 0.139) (Table 2). Monocots were dominant in open-lands, both at lower and upper elevations, pteridophyta presented more cover at lower elevations and bryophyte at deciduous at upper elevations, evergreen forests and lower open-lands. Also, native species had higher covers at upper elevations, whereas exotic plants had greater covers at lower elevations. Total vegetation cover ranged from 51% to 63% in forests, and from 84% to 96% in open-lands. As was expected, woody debris had higher covers in forested lands (> 15%), which significantly decreased with elevation.

Table 2

One-way ANOVA results for cover and richness of understory plants at different land-cover units. E = evergreen forest at lower elevation, DL = deciduous forest at lower elevation, DU = deciduous forest at upper elevation, OL = open-land at lower elevation, and OU = open-land at upper elevation. *F* (*p*) = Fisher test and significance between brackets. Different letters for each row show differences by Tukey test at *p* < 0.05.

Variables	E	DL	DU	OL	OU	*F* (*p*)
Cover (%)						
Dicots	28.8	40.2	31.8	44.0	47.4	1.78 (0.139)
Monocots	0.7a	8.7ab	3.2a	21.6bc	35.5c	13.58 (< 0.001)
Ferns	0.2a	0.8b	0.0a	0.4ab	0.0a	3.94 (0.005)
Bryophytes	21.2bc	9.6ab	27.8c	30.2c	1.4a	8.62 (< 0.001)
Natives	50.7a	51.0a	62.7ab	85.1b	83.0b	6.16 (< 0.001)
Exotics	0.1a	8.3bc	0.2a	11.2c	1.3ab	2.87 (0.027)
Total	50.8a	59.3a	62.9ab	96.3c	84.4bc	6.91 (< 0.001)
Bare soil	37.8b	25.2ab	26.5ab	2.8a	14.4ab	3.57 (0.009)
Woody debris	11.4b	15.6b	10.6b	1.0a	1.1a	13.10 (< 0.001)
Richness (species per plot)						
Dicots	10.3	8.8	9.5	8.9	7.6	0.83 (0.508)
Monocots	2.3	2.6	2.0	2.3	2.3	0.30 (0.879)
Ferns	0.6	0.4	0.3	0.8	0.1	1.71 (0.153)
Natives	11.8	9.6	11.5	11.1	8.8	1.26 (0.292)
Exotics	1.3ab	2.2b	0.5a	0.9ab	1.2ab	2.95 (0.024)
Total	13.1	11.8	11.9	12.0	10.0	0.45 (0.769)

Also, bare soil cover was significantly higher in forests than open-lands. Richness of native species did not differ among forest and open-land units. However, significant differences were found for exotic species richness, where deciduous forests in lower lands presented the highest values (2.2 species per plot), and deciduous forests in upper lands presented the lowest values (0.9 species per plot).

Dicot cover were not significantly different (p = 0.446) across land-use units (Table 3), while monocot cover differed between unharvested forests and open-lands and all anthropogenic-altered units (henceforth referred to both harvesting and cattle grazing), while pteridophyta cover was significantly lower at forests and open-lands with cattle grazing. Likewise, bryophyte cover showed significantly lower values in old than recent harvested forests (4% and 7%, respectively). Bare soil and woody debris covers also significantly changed among anthropogenic-altered units. Bare soil was greater in unharvested and old harvested units (39% and 23%, respectively), and considerably lower in open-lands. As was expected, woody debris was higher inside forests than open-lands. In harvested forests, woody debris was significantly greater at DL-NH than DL-OH, and it was inversely proportional to bare soil cover. Considering species richness, dicots, monocots and ferns showed significant differences among anthropogenic-altered units. However, significant differences were not found for native species richness between any pair of landscape units. In contrast, exotic species richness showed significant differences among these units, varying from 3.8 species per plot in harvested forests to 0.4 in DL-U. The forests with cattle grazing have lower values of exotic richness (1.8 species per plot) than harvested forests (both DL-NH and DL-OH, with 3.8 species per plot), similar than open-lands with or without cattle grazing (1.6 and 1.0 species per plot, respectively).

Multivariate analyses showed that plant composition were not driven by a single factor and they are better explained by a combination of natural gradients and anthropogenic impacts. Cluster analyses highlighted the differences between open-lands and forests, and the differences between elevations for each land-cover unit (Fig. 3A), with minor variations between low and high elevation deciduous forests, followed by evergreen forests and open-lands which joint themselves at higher distances. Regarding to the aspect, E and W (more lighted aspects) were more similar than N and S (more shaded aspects) (Fig. 3B), which were also similar at shorter distances. Land-use units also remarked the differences between forests and open-lands, and land units with or without impacts (Fig. 3C). Old harvested forests were more similar to unharvested forests, followed by the recent harvested forests. The most dissimilar forests were those impacted by cattle grazing.

Canonical correspondence analysis (CCA) showed similar trends than those described before (Fig. 4). The analysis presented a total inertia of 9.6 and Eigenvalues of 0.651 in Axis 1 and 0.425 in Axis 2, with a cumulative percentage variance of species-environment correlation of 55%. Axis 1 was influenced by the forest structure (OCOV, DH, TOBV, DEB), and Axis 2 was more related to environmental variables (ALT, SLOPE, N-S and E-W aspects). When taxonomic group and origin of the species were analyzed (Fig. 4A), the Axis 1 showed differences between native species more related to open-lands on the right (e.g. *Deschampsia kingii*, *Carex magellanica*, *Azorella fuegiana*), and the more typical forest species on the left (e.g. *Dysopsis glechomoides*, *O. chilensis*, *Ranunculus fuegianus*). Exotic species were more related to Axis 2, located at lower elevations and north aspects (e.g. *Cerastium fontanum*, *Stellaria media*, *Poa pratensis*, *Taraxacum officinale*, or *Ranunculus repens*). Considering the taxonomic groups, native dicots and monocots species were homogeneously distributed along forests and open-lands, and across slope and elevation gradients. When land-cover units were analyzed (Fig. 4B), differences can be showed between forests and open-lands, and between lower and upper elevations. Evergreen forests conformed a conspicuous group with characteristics shared by lower and upper elevation deciduous forests. When land-use units were represented (Fig. 4C), recent harvested and unharvested forests, as well as intact open-lands conformed the less dispersed groups, with DL-NH

Table 3
One-way ANOVA results for cover and richness of understory plants at different land-use units. DL-U = deciduous unharvested forests at lower elevation, DL-OH = deciduous forests with old harvesting (> 50 years after harvesting) at lower elevation, DL-NH = deciduous forests with new harvesting (20–30 years after harvesting) at lower elevation, DL-C = deciduous forests with cattle grazing at lower elevation, OL-I = intact open-lands at lower elevation, and OL-C = open-lands with cattle grazing at lower elevation. $F(p)$ = Fisher test and significance between brackets. Different letters for each row show differences by Tukey test at $p < 0.05$.

Variables	DL-U	DL-OH	DL-NH	DL-C	OL-I	OL-C	$F(p)$
Cover (%)							
Dicots	28.2	45.2	37.4	41.5	45.3	48.8	0.97 (0.446)
Monocots	1.2a	9.0ab	14.9ab	11.8ab	25.5b	22.5ab	3.06 (0.018)
Ferns	0.2a	1.3b	1.0ab	0.1a	0.7ab	0.0a	2.83 (0.025)
Bryophytes	20.7b	3.5a	6.7ab	19.4b	22.6b	25.7b	3.24 (0.013)
Natives	50.2a	50.1a	44.8a	61.6ab	90.6b	82.5ab	3.52 (0.009)
Exotics[a]	0.1a	8.9ab	15.2b	11.3ab	3.4ab	14.5ab	3.47 (0.009)
Total	50.3a	59.0a	60.0ab	72.7ab	94.0b	97.0b	4.94 (< 0.001)
Bare soil	38.9b	23.2ab	17.5ab	17.1ab	4.4a	3.0a	3.28 (0.012)
Woody debris	10.8ab	17.8bc	22.5c	10.1ab	1.6a	0.0a	10.12 (< 0.001)
Richness (species per plot)							
Dicots	8.8a	12.7b	12.0ab	8.5a	8.8a	8.0a	3.79 (0.006)
Monocots	1.5a	3.4b	4.7b	2.5ab	3.4ab	4.4b	3.88 (0.005)
Ferns	0.6ab	0.9b	1.2b	0.3ab	0.4ab	0.0a	3.97 (0.004)
Natives	10.4	13.3	14.0	10.8	11.6	9.4	2.06 (0.086)
Exotics	0.4a	3.8b	3.8b	1.8ab	1.0ab	1.6ab	5.37 (< 0.001)
Total	10.8a	17.1b	17.8b	11.3a	12.6ab	12.4ab	4.36 (< 0.001)

[a] Exotics was $\ln(Y + 1)$ transformed prior to the analysis, but non-transformed data are shown.

concentrated at lower elevations and slope in N aspects, while DL-U and OL-I intermingled with the different impacted land-use units. Beside this, cattle-grazed units were distributed along Axis 2, both in forests and open-lands. Finally, when analysis were classified by richness of exotics species per plot (Fig. 4D), the units with > 3 exotics were grouped at lower elevations and S aspects, corresponding with DL-NH and DL-OH (only 2 plots with > 3 exotics were OL, and only one was cattle-grazed). Meanwhile, 1–2 exotic group included plots from all land-cover and land-use categories, as well as for plots without exotic species, which were concentrated at upper elevations and higher slopes. Finally, this analysis not included effects for the different forest development stages (Appendix C).

The first DCA (Eigenvalues of 0.39 for Axis 1 and 0.11 for Axis 2) defined the relationships among vegetation types: forests (E, DL) and open-lands (Fig. 5A). This graph markedly split forest and open-land plant species, with more exotic species related to OL than DL than E. Likewise, few species were sharing among the vegetation types (23%), highlighting that few generalist species exists in the study area (e.g., *Pernettya mucronata*). The second DCA analyzed harvested and unharvested forest units (Fig. 5B). The ordination with Axes 1 (Eigenvalue

of 0.38) and 2 (Eigenvalue of 0.03) showed higher quantity of shared species among the three forest types (35%), with greater quantity of exclusive species in U than in OH than in NH. Likewise, there were very few species shared only between NH and U (*Caltha sagittata* and *Trisetum spicatum*), while the species shared only between NH and OH were mainly exotics, and the species shared only between OH and U were mainly native, despite some exotic species such as *P. trivialis* and *Rumex acetosella* presented greater covers in U compared with OH. The third DCA (Eigenvalues of 0.2885 for Axis 1 and 0.0894 for Axis 2), comparing anthropogenic impact types (Fig. 5C), showed much more equitable plant species ordination (e.g., 44% of the species were observed in the center of the graph). However, there were too many plants exclusively found in the unharvested forests, being all of these natives. Beside this, several species presented greater covers in harvested and cattle grazed areas, e.g., exotic species such as *Agrostis stolonifera* and *R. acetosella* were more represented in cattle grazing, while *P. nemoralis*, *Ranunculus repens* and *S. media* were more related with harvested forests, whereas only one exotic species (*P. trivialis*) presented greater cover in the unharvested forests compared with H and C.
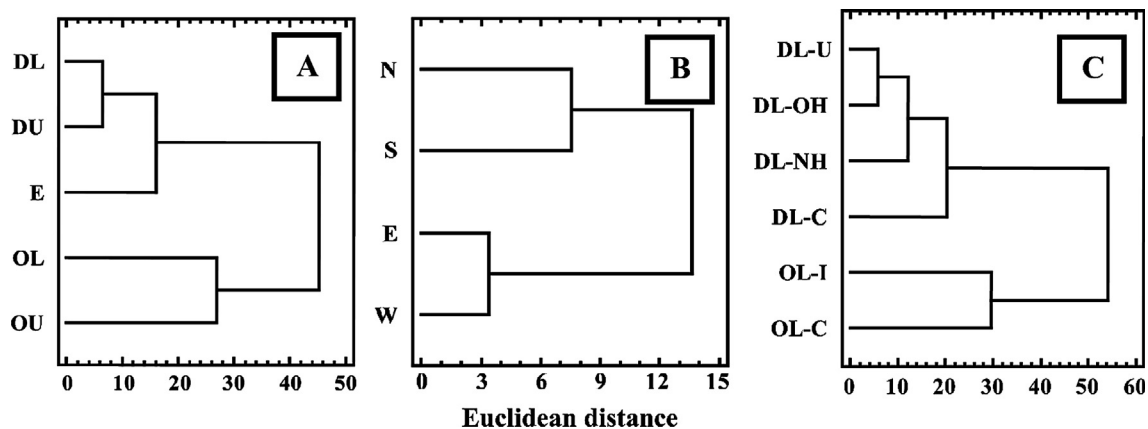

Fig. 3. Cluster analysis for cover of understory plant. (A) Land-cover units (E = evergreen forest at lower elevation, DL = deciduous forest at lower elevation, DU = deciduous forest at upper elevation, OL = open-land at lower elevation, OU = open-land at upper elevation); (B) aspects (N = north, S = south, E = east, W = west); (C) land-use units (DL-U = deciduous unharvested forests at lower elevation, DL-OH = deciduous forests with old harvesting (> 50 years after harvesting) at lower elevation, DL-NH = deciduous forests with new harvesting (20–30 years after harvesting) at lower elevation, DL-C = deciduous forests with cattle grazing at lower elevation, OL-I = intact open-lands at lower elevation, OL-C = open-lands with cattle grazing at lower elevation).
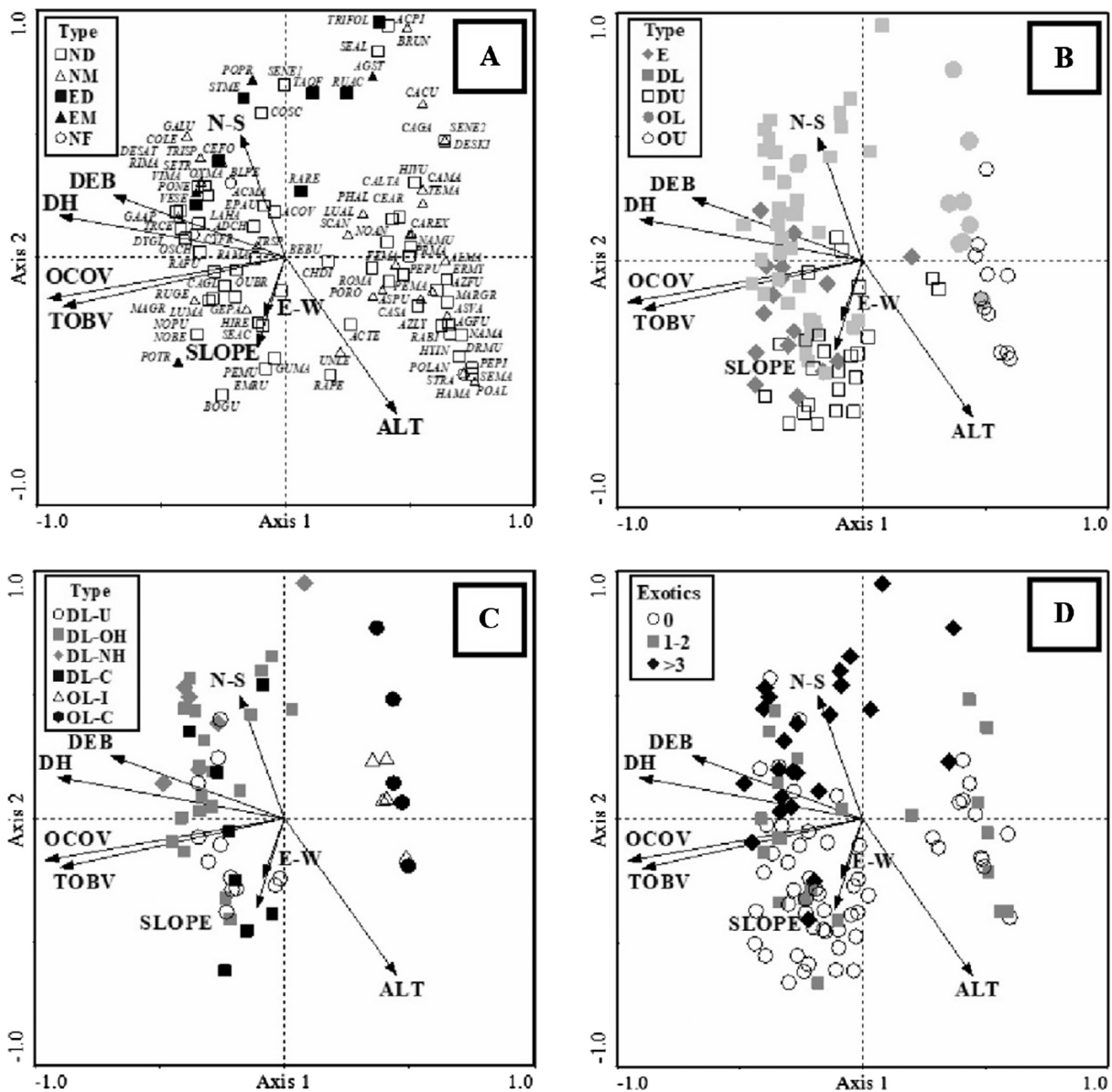
Fig. 4. Canonical correspondence analysis (CCA) based on plant species cover. (A) Plants classified by taxonomic group and origin (ND = native dicots, NM = native monocots, ED = exotic dicots, EM = exotic monocots, NF = native ferns); (B) sampling units classified by land-cover units (E = evergreen forest at lower elevation, DL = deciduous forest at lower elevation, DU = deciduous forest at upper elevation, OL = open-land at lower elevation, OU = open-land at upper elevation); (C) sampling units classified by land-use units (DL-U = deciduous unharvested forests at lower elevation, DL-OH = deciduous forests with old harvesting (> 50 years after harvesting) at lower elevation, DL-NH = deciduous forests with new harvesting (20–30 years after harvesting) at lower elevation, DL-C = deciduous forests with cattle grazing at lower elevation, OL-I = intact open-lands at lower elevation, OL-C = open-lands with cattle grazing at lower elevation); and (D) sampling units classified by the quantity of exotic plant species per plot (0 species, 1–2 species, > 3 species). Explicatory variables were dominant height (DH) (m), total over bark volume (TOBV) ($m^3 ha^{-1}$), overstory crown cover (OCOV) (%), woody debris (DEB) (%), elevation (ALT) (m.a.s.l.), slope (SLOPE) (%), east-west aspect (E-W), and north-south aspect (N-S). Species codes are presented in Appendix B.

4. Discussion

4.1. Plant assemblages at different vegetation types

Andorra Valley basin is dominated by forests (evergreen and deciduous) intermingled with open-lands (grasslands, peat-lands and alpine vegetation), where forests mainly corresponded to unmanaged stands. Harvesting changed the forest structure from primary to secondary forests, mainly in the *Nothofagus pumilio* stands closest to Ushuaia city (Gutiérrez, 1994). Forest structure affects to the dynamic of regeneration, composition of different organism communities, and biodiversity conservation (e.g. Tilman, 1994; Frangi et al., 2005; Martínez Pastur et al., 2013). In our study, forest land-cover units

varied its forest structure with elevation, as was previously cited, influencing over: (i) tree and regeneration growth patterns (Massaccesi et al., 2008); (ii) natural biogeochemical cycles (Barrera et al., 2000); and (iii) the associated biodiversity (e.g., understory plants) (Frangi et al., 2005). Plant assemblages strongly depend with the different vegetation types and the studied environmental gradients. Richness and cover varied among forest types and open-lands across elevation gradients, and the different human uses, which was identified as drivers of change for richness and cover (e.g. exotic plant occurrence). Some authors suggest that differences in plant assemblages are associated with topography or the location into the landscape (Mestre et al., 2017), which can also be related to regional climate (Frangi et al., 2005). Land-cover units showed differences in their species
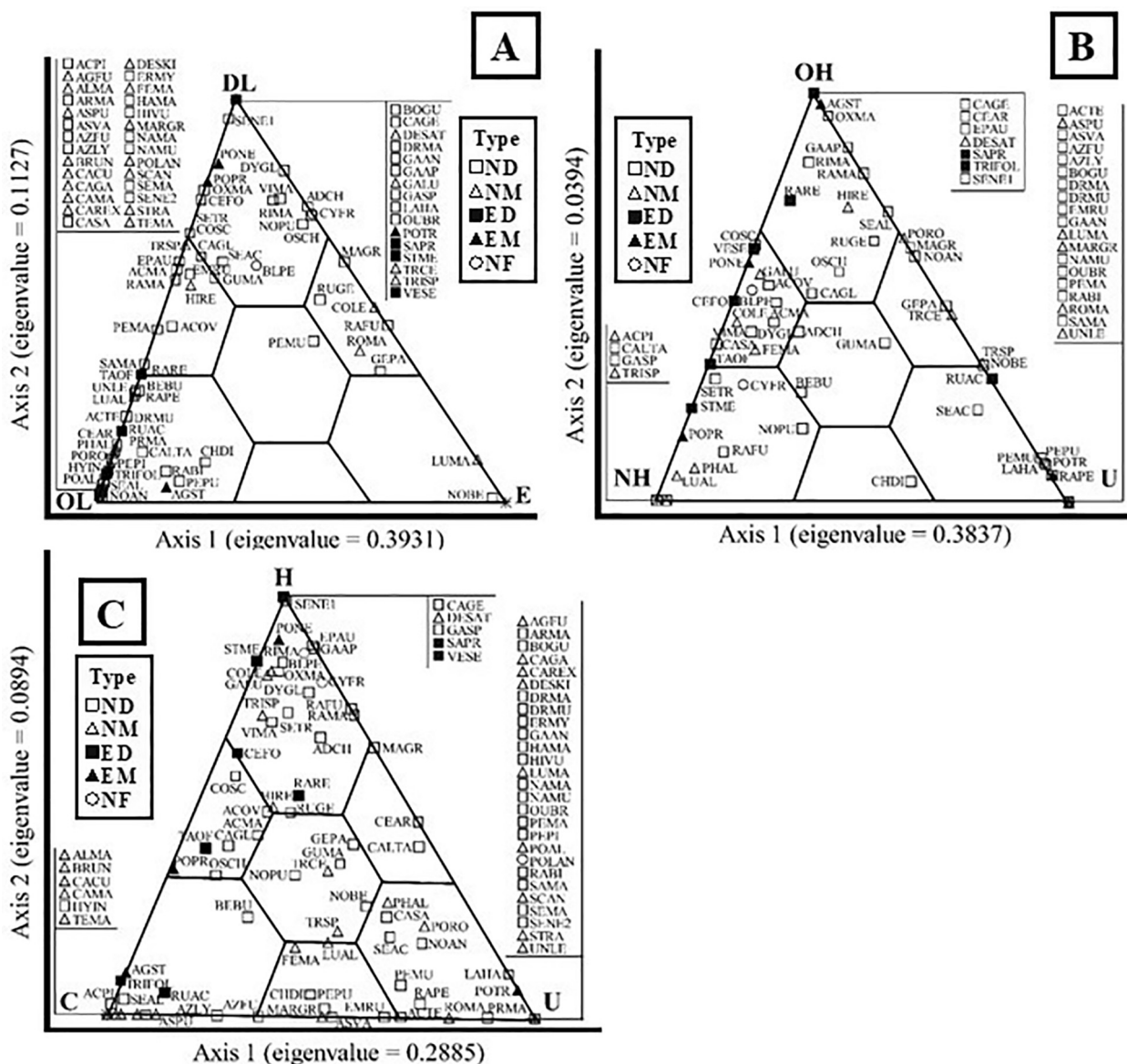
Fig. 5. Detrended correspondence analysis (DCA) based on cover of understory plant scores by taxonomic group and origin (ND = native dicots, ND = native monocots, ED = exotic dicots, EM = exotic monocots, NF = native ferns). (A) Land-cover units (E = evergreen forest at lower elevation, DL = deciduous forest at lower elevation, OL = open-land at lower elevation); (B) forest land-use units (U = unharvested, OH = old harvesting, NH = recent harvesting); and (C) anthropogenic impact types (U = unharvested, H = harvesting, C = cattle grazing).

assemblages even within the same vegetation type, topography, climate, soil properties and water regime. Beside this, the occurrence of exotic species was higher in forests than open-lands, including those belonging at lower and upper elevations. It was interesting that land-cover units with the same forest type presented different assemblage of species, which contradicted the idea that *Nothofagus* forests configured continuous ecological elements from sea level to the tree-line. Other studied also found that these forests greatly varied across the landscape within the same vegetation type (Martínez Pastur et al., 2016a, 2017; Lencinas et al., 2017).

4.2. Environmental variables explain variations in plant assemblages

Mountain ecosystems are characterized by environmental gradients that greatly varied in short distances, where higher elevations present low temperatures and severe conditions for plant growth (Bacaro et al., 2015), e.g. in Tierra del Fuego deciduous forests changes across the elevation gradient with a decrease in temperature and increase in

rainfall (also ratio between water and snow) (Barrera et al., 2000). Low temperatures can affect water availability along the year, decreasing the amplitude of the growing season, increasing frost or mechanical damages due to snow impacts, and influencing over biological functions such as foliar phenology, growth and decomposition rates (Barrera et al., 2000; Massaccesi et al., 2008). Also, this rainfall pattern, together with edaphic and topographic variations, influenced over the vegetation distribution (Peri et al., 2017). Temperate forests of Northern hemisphere showed that forest structure and natural gradients are more related to understory composition than to tree specific forest types (Bonari et al., 2017), where the assemblages of the understory plants could be related both to environmental gradients and particular tree species functional traits (Terwei et al., 2016). In our study, aspect and elevation were the most important natural drivers on richness and cover of understory species among the landscape units. Forest types partially explained the understory diversity, considering that deciduous tree species grow in well-drained soils (Frangi and Richter, 1994) and evergreen required less extreme environmental conditions (e.g. middle

elevation or closeness to water bodies) (Gutiérrez, 1994; Allué et al., 2010).

4.3. Anthropogenic impacts modifies the original plant assemblage

In Southern Patagonia, plants have been used as useful indicators of biodiversity modifications under different scenarios of impacts generated by anthropogenic activities such as forestry (Lencinas et al., 2011, 2017) or cattle grazing (Peri et al., 2013). We have shown here that native and exotic plant assemblages were related to environmental gradients, but also they were related to the anthropogenic economic activities. We found several exclusive species in the different land-covers, and also found exclusive species in harvested and cattle grazed units. In harvested forests, the recorded species can be inhabitants of these areas previously to the disturbances and survive to the impacts or arrive after found appropriate conditions to growth (e.g. light, moisture, nutrient availability, competition with other species). This could be the case for two exotic species exclusively found in harvested stands: one of them that appeared only in unharvested forests (*Sagina procumbens*), and other that colonize harvested forests during the first years after harvesting (*Veronica serpyllifolia*). On the other hand, the exclusive species found in cattle grazed units were natives, and the exotic species presented here were also occurred in harvested and unharvested forests, denoting the generalist role and their naturalization capability. Beside this, exotic plants were absent in most of the cattle grazed units, and only one presented more than 3 exotic species, therefore the cattle grazing impact in this study could not be the main driver for exotic species occurrence in these ecosystems.

Some studies showed the plasticity of some plant species to occupy different habitats, as timber forests and associated non-productive environments (Lencinas et al., 2008a, 2008b), where some species can quickly reacted after the impacts when conditions changed favorably. Other studies also suggest that greater specific diversity is associated with forest quality site of the stands (e.g. Gallo et al., 2013), which should be probably first affected by harvesting operations. Beside this, harvesting modifies forest structure variables and directly affect the autecology of tree species, the canopy structure and their composition, and indirectly, the environmental associated variables (e.g. light and soil moisture), and can generate trade-offs with regeneration (Martínez Pastur et al., 2013). These, direct and indirect effects, affects the ecosystem organisms (vascular plants, insects, birds and other biotic components) (Lencinas et al., 2011, 2017), allowing to incorporate exotic species from associate environments (Lencinas et al., 2011, 2017). We observed that some exotics species, such as *Poa trivialis* and *Rumex acetosella*, colonized unharvested forests, probably through streams or winds, or through cattle or wildlife (e.g. *Lama guanicoe*); or were seeded at lower elevations to improve grass for cattle (e.g. *Trifolium repens*). These exotic species could be dispersed by cattle or wildlife (e.g. *P. pratensis* was preferred in the diet and quickly dispersed through dungs). Moreover, the selective foraging during grazing favored selection of some species adapted to periodic and recurring cuts, which trend to homogenize the area (e.g. *T. repens* in OL-C). Also, cattle generate trade-offs with other native herbivores (e.g. *L. guanicoe*) (Martínez Pastur et al., 2016b), which in turn might impact other environments due to their displacement by cattle. Our analyses remark that cattle grazing was an important driver of change, generating greater differences among the landscape units with or without cattle uses (Fig. 3C). However, although cattle generated important changes in the plant assemblage, it did not present a greater impact of exotic species compared to forest harvesting, as was previously discussed.

Several primary forests were transformed into secondary forests with a more regular structure, which allowed to the exotic species to settle in these stands and changed the plant species assemblage after harvesting (Lencinas et al., 2011, 2017). However, these stands recovered the forest structure and become similar to primary forests (e.g. closeness of overstory canopy), e.g. understory assemblage in old

harvesting forests recovered the original values, both in richness and cover (e.g. sharing more native species with unharvested than with recent harvested forests). However, once the exotic species settled the harvested forests, their maintained its presence on time (e.g. *C. fontanum*, *P. nemoralis*), or even could not arrive initially but colonize later (e.g. *S. procumbens* and *T. repens*).

4.4. Anthropogenic impacts as a driver of exotic plant species occurrence

Previous research showed that anthropogenic impacts, elevation and land-use influenced over the occurrence of exotic plant species in Northern Patagonia (Pauchard and Alaback, 2004). This might imply that at higher elevations native communities were better preserved in their composition because most of the exotic species find greater difficulty to establish (Pauchard et al., 2009). Besides this, some exotic plant species have been reported as invasive in South Patagonia (e.g. *T. officinale*, *Agrostis stolonifera*, *P. pratensis*) (Peri et al., 2016), and some of them are capable of transforming the potential uses of the forests, e.g. *Hieracium pilosella* (Díaz-Barradas et al., 2015). Many authors highlight the risk of increasing the direct introduction of exotic species with specialized ecophysiological adaptations to mountain environments that in the future could increase the risk of occurrence (e.g. McDougall et al., 2005; Alexander et al., 2011). Many of the detected exotic plant species are not yet considered as invasive by ecologist and managers, but other anthropogenic impacts could modify the current conditions and favor their invasive capability. The study of occurrence mechanisms could provide some tools to prevent or develop strategies to control or minimize this threat over the ecosystem integrity (Kueffer et al., 2014).

Future improvements in our understanding of forest management and conservation can be based on the knowledge derived from the opportunities offered on the examination of landscape-scale patterns in managed and unmanaged forests (Binkley et al., 2018). In our study area, a recent history of impacts (less than 100 years including harvesting and cattle grazing), including areas with great impacts and others without evident impact, give us a unique opportunity to understand the occurrence process in the short-term. In relation to this, land-sharing instead of land-sparing appear as the most useful management tool to moderate the availability of areas that could be invaded, by the generation of more spatial heterogeneity at farm and basin landscape level. Likewise, the conservation of some structural legacies and microenvironments in forests (e.g. different retention types), could provide habitats for native plant species in the managed stands, and improve their survival in front to occurrence of exotic plants (Peri et al., 2016). Since land-sharing becomes the most realistic option of southern mountain landscapes, anthropogenic practices can be developed to preserve the balance between management and conservation in the framework of the exotic species occurrence, because it may define most fundamentally their habitability across the land-cover and land-use units.

5. Conclusions

Environmental gradients and anthropogenic impacts defined the plant assemblages at the landscape level, and they also influenced over distribution of exotic species, where the main driver was the forest harvesting. Across the landscape units, understory plants were mainly related with forest type and topographic variables (elevation and aspect). Native species represented the largest component of plant assemblages, which maintained their intactness at higher elevations, while exotic plants significantly changed the assemblages at lower elevations and in anthropogenic impacted land-use units. Both land-cover and land-use showed differences in their plant species assemblage even within the same vegetation type, both in forests and open-lands. Harvesting changed the forest structure, allowing to a rapid development of the understory including the exotic species occurrence. The

recovering of the forest structure in time allowed to the re-establishment of the original understory assemblage, however, the exotic species remained in the ecosystem after the impacts.

Acknowledgements

The authors gratefully thank the Centro Austral de Investigaciones

Appendix A. . Analyzed landscape units of Andorra Valley basin: (A) land-cover units (E = evergreen forest at lower elevation, DL = deciduous forest at lower elevation, DU = deciduous forest at upper elevation, OL = open-land at lower elevation, OU = open-land at upper elevation); and (B) land-use units (DL-U = deciduous unharvested forests at lower elevation, DL-OH = deciduous forests with old harvesting (> 50 years after harvesting) at lower elevation, DL-NH = deciduous forests with new harvesting (20–30 years after harvesting) at lower elevation, DL-C = deciduous forests with cattle grazing at lower elevation, OL-I = intact open-lands at lower elevation, OL-C = open-lands with cattle grazing at lower elevation).
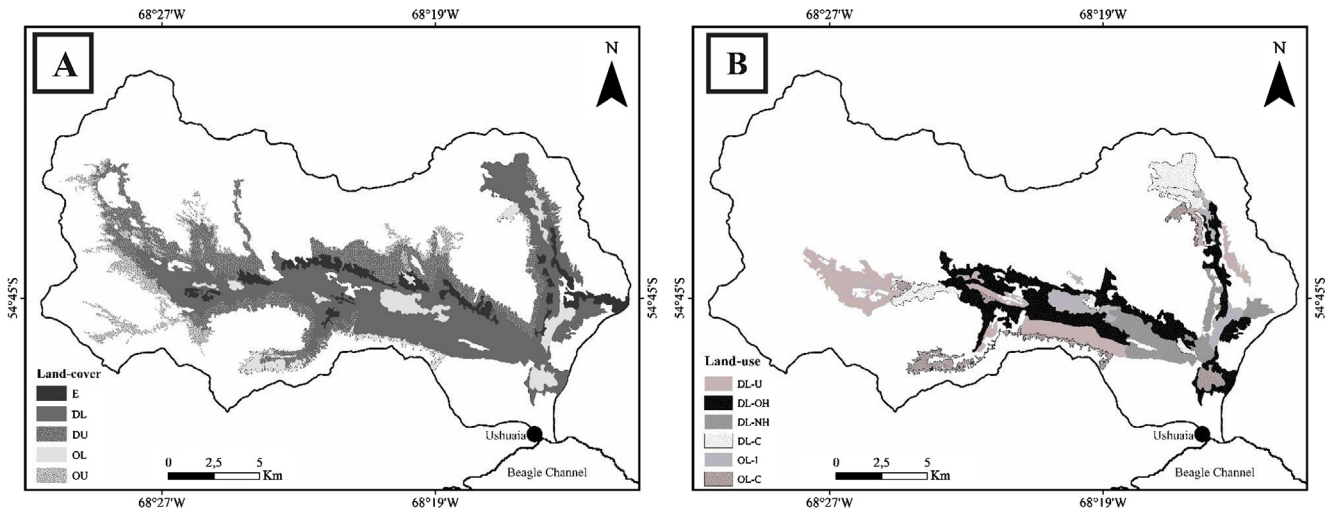
Appendix B. . Occurrence frequency (%), taxonomic group (D = dicots, M = monocots, F = ferns), origin (N = native, E = exotic) and codes for the sampled vascular plants in the analyzed at land-cover units (E = evergreen forest at lower elevation, DL = deciduous forest at lower elevation, DU = deciduous forest at upper elevation, OL = open-land at lower elevation, OU = open-land at upper elevation), and land-use units (DL-U = deciduous unmanaged forests at lower elevation, DL-OH = deciduous forests with old harvesting (> 50 years after harvesting) at lower elevation, DL-NH = deciduous forests with new harvesting (20–30 years after harvesting) at lower elevation, DL-C = deciduous forests with cattle grazing at lower elevation, OL-I = intact open-lands at lower elevation, OL-C = open-lands with cattle grazing at lower elevation).

Code	Species	Group	Origin	Land-cover						Land-use						
				E	DL	DU	OL	OU	Total	DL-U	DL-OH	DL-NH	DL-C	OL-I	OL-C	Total
NOPU	*Nothofagus pumilio* (Poeppig & Endl.) Krasser	D	N	9.9	33.7	18.8		2.0	64.4	20.0	25.5	7.3	14.5			67.3
SEAC	*Senecio acanthifolius* Hombron & Jacquinot	D	N	6.9	23.8	19.8		5.9	56.4	18.2	20.0	1.8	9.1		1.8	50.9
GUMA	*Gunnera magellanica* Lam.	D	N	3.0	19.8	17.8	4.0	8.9	53.5	7.3	20.0	7.3	7.3	5.5	5.5	52.7
OSCH	*Osmorhiza chilensis* Hooker & Arn.	D	N	5.9	29.7	5.0	1.0	1.0	42.6	9.1	29.1	9.1	10.9	1.8		60.0
RUGE	*Rubus geoide* Sm.	D	N	8.9	18.8	9.9	1.0	1.0	39.6	12.7	12.7	3.6	5.5	1.8		36.4
DYGL	*Dysopsis glechomoides* (A. Richard) Müller Arg.	D	N	3.0	24.8	6.9			34.7	10.9	25.5	5.5	5.5			47.3
CAGL	*Cardamine glacialis* (Forster F.) DC.	D	N	3.0	25.7	5.0		1.0	34.7	10.9	23.6	5.5	10.9		1.8	52.7
EMRU	*Empetrum rubrum* Vahl ex Willd.	D	N	5.0	4.0	15.8	5.0	4.0	33.7	7.3			5.5	5.5	5.5	23.6
VIMA	*Viola magellanica* Forster f.	D	N	3.0	22.8	3.0	1.0		29.7	7.3	23.6	7.3	3.6	1.8		43.6
ACOV	*Acaena ovalifolia* Ruiz & Pavón	D	N	1.0	23.8	1.0	2.0	2.0	29.7	9.1	20.0	9.1	5.5	1.8	1.8	47.3
FEMA	*Festuca magellanica* Lam.	M	N		11.9	6.9	2.0	7.9	28.7	3.6	9.1	7.3	5.5	3.6	3.6	32.7
TAOF	*Taraxacum officinale* Weber	D	E		21.8	1.0	2.0	4.0	28.7	7.3	16.4	10.9	5.5	1.8	1.8	43.6
RIMA	*Ribes magellanica* Poiret	D	N	2.0	22.8	1.0		2.0	27.7	7.3	25.5	7.3	1.8			41.8
BLPE	*Blechnum penna-marina* (Poiret) Kuhn	F	N	3.0	20.8	1.0	2.0		26.7	7.3	21.8	7.3	1.8	3.6		41.8
PEPU	*Pernettya pumila* (L. f.) Hooker	D	N	5.0	3.0	4.0	5.9	6.9	24.8	3.6			1.8	7.3	7.3	20.0

Code	Species															
ACMA	*Acaena magellanica* (Lam.) Vahl	D	N	1.0	16.8	4.0	2.0		23.8	3.6	18.2	3.6	5.5	3.6		34.5
ADCH	*Adenocaulon chilense* Less.	D	N	3.0	20.8				23.8	1.8	23.6	9.1	3.6			38.2
BEBU	*Berberis buxifolia* Lam.	D	N	2.0	9.9	5.0	3.0	4.0	23.8	9.1	3.6	3.6	1.8	3.6	3.6	25.5
PONE	*Poa nemoralis* L.	M	E	1.0	19.8		1.0		21.8		23.6	9.1	3.6	1.8		38.2
POPR	*Poa pratensis* L.	M	E		19.8		2.0		21.8	1.8	21.8	7.3	5.5	1.8	1.8	40.0
MAGR	*Macrachaenium gracile* Hooker f.	D	N	4.0	14.9	3.0			21.8	14.5	12.7					27.3
COLE	*Codonorchis lessonii* (D'Urv.) Lindley	M	N	5.0	15.8				20.8	7.3	12.7	7.3	1.8			29.1
PHAL	*Phleum alpinum* L.	M	N		12.9	3.0	2.0	3.0	20.8		10.9	9.1	3.6	1.8	1.8	27.3
NOBE	*Nothofagus betuloides* (Mirbel) Oersted	D	N	15.8	2.0		2.0	1.0	20.8		1.8			1.8	3.6	7.3
CEFO	*Cerastium fontanum* Baumg.	D	E		19.8		1.0		20.8		23.6	7.3	5.5	1.8		38.2
PEMU	*Pernettya mucronata* (L. f.) Gaudich	D	N	5.9	6.9	5.0	1.0	1.0	19.8	9.1	1.8		1.8	1.8		14.5
GEPA	*Geum parviflorum* Comm. ex Sm.	D	N	1.0	5.0	10.9		2.0	18.8	1.8	7.3			1.8	3.6	14.5
RARE	*Ranunculus repens* L.	D	E		9.9	1.0	2.0	4.0	16.8		14.5	1.8	1.8	1.8	3.6	23.6
CYFR	*Cystopteris fragilis* (L.) Bernh.	P	N	1.0	12.9				13.9	5.5	10.9	5.5	1.8			23.6
MARGR	*Marsippospermum* sp. Desv.	M	N			3.0	5.0	5.9	13.9					7.3	3.6	10.9
HIRE	*Hierochloë redolens* (Vahl) Roemer & Schultes	M	N	2.0	5.9	3.0	1.0	2.0	13.9	1.8	7.3	1.8	1.8	1.8	1.8	16.4
NOAN	*Nothofagus antarctica* (Forster f.) Oersted	D	N		1.0	5.0	5.9	1.0	12.9		1.8			7.3	3.6	12.7
SETR	*Senecio tricuspidatus* Hooker & Arn.	D	N		10.9	1.0	1.0		12.9	1.8	7.3	9.1	1.8	1.8		21.8
COSC	*Cotula scariosa* (Cass.) Franchet	D	N		11.9		1.0		12.9	0.0	12.7	5.5	3.6	1.8		23.6
GALU	*Gavilea lutea* (Pers.) Correa	M	N		11.9				11.9	3.6	10.9	5.5	1.8			21.8
CHDI	*Chiliotrichum diffusum* (Forester f.) O. Kuntze	D	N	1.0	5.9	1.0	3.0	1.0	11.9	5.5	1.8	1.8	1.8	5.5	1.8	18.2
ACTE	*Acaena tenera* Alboff	D	N			4.0		6.9	10.9					3.6		3.6
STME	*Stellaria media* (L.) Vill.	D	E		10.9				10.9		10.9	3.6	5.5			20.0
TRSP	*Trisetum spicatum* (L.) K. Richter	M	N		5.9	2.0	1.0	1.0	9.9	5.5	1.8		5.5	1.8		14.5
CALTA	*Caltha* sp. l.	D	N	1.0	1.0	2.0	3.0	3.0	9.9			1.8		5.5	1.8	9.1
ASPU	*Astelia pumila* (Forster f.) Gaudich.	M	N			4.0		5.0	8.9					3.6		3.6
LUAL	*Luzula alopecurus* Desv.	M	N		4.0	1.0	1.0	3.0	8.9	1.8	1.8	1.8	1.8	1.8	1.8	10.9
CASA	*Caltha sagittata* Cav.	D	N		3.0			5.9	8.9		3.6	1.8		1.8		7.3
AZFU	*Azorella fuegiana* Speg.	D	N				2.0	5.9	7.9					3.6		3.6
AZLY	*Azorella lycopodioides* Gaudich.	D	N				1.0	5.9	6.9					3.6		3.6
RAFU	*Ranunculus fuegianus* Speg.	D	N	2.0	2.0	3.0			6.9		1.8	1.8				3.6
RAPE	*Ranunculus peduncularis* Sm.	D	N		1.0	2.0		4.0	6.9		1.8			1.8		3.6
PRMA	*Primula magellanica* Lehm.	D	N		1.0		2.0	4.0	6.9					3.6	1.8	5.5
EPAU	*Epilobium australe* Poeppig & Hausskn.	D	N		5.0			2.0	6.9		9.1					9.1
AGST	*Agrostis stolonifera* L.	M	E	2.0	2.0		2.0		5.9		3.6				3.6	7.3
RAMA	*Ranunculus maclovianus* D'Urv.	D	N		4.0	1.0		1.0	5.9		7.3					7.3
SEAL	*Senecio alloeophyllus* O. Hoffm.	D	N		2.0	1.0	1.0	2.0	5.9	1.8	1.8				1.8	5.5
ASVA	*Aster vahlii* (Gaudich.) Hooker & Arn.	D	N	1.0			2.0	3.0	5.9					3.6	1.8	5.5
ALMA	*Alopecurus magellanicus* Lam.	M	N			1.0	1.0	3.0	5.0				1.8	3.6		5.5
TRCE	*Trisetum cernuum* Trin.	M	N		5.0				5.0	1.8	5.5		1.8			9.1
PORO	*Poa robusta* Steudel	M	N		1.0	1.0		3.0	5.0		1.8				1.8	3.6
OXMA	*Oxalis magellanica* Forster f.	D	N		2.0	1.0		2.0	5.0		3.6				1.8	5.5
ROMA	*Rostkovia magellanica* (Lam.) Hooker f.	M	N	1.0		2.0	1.0		4.0						1.8	1.8
DRMU	*Drapetes muscosus* Banks ex Lam.	D	N			1.0		3.0	4.0							0.0
VESE	*Veronica serpyllifolia* L.	D	E		4.0				4.0		5.5	1.8				7.3
NAMU	*Nanodea muscosa* Banks ex C. F. Gaertner	D	N			2.0	1.0	1.0	4.0					1.8		1.8
RABI	*Ranunculus biternatus* Sm.	D	N	1.0		1.0		2.0	4.0							0.0
RUAC	*Rumex acetosella* L.	D	E		2.0	1.0	1.0		4.0		3.6				1.8	5.5
PEMA	*Perezia magellanica* (L. f.) Lag.	D	N			2.0	1.0	1.0	4.0					1.8		1.8
LUMA	*Luzuriaga marginata* (Banks & Sol. ex Gaertner) Bentham & Hooker	M	N	1.0	2.0				3.0	3.6						3.6
TEMA	*Tetroncium magellanicum* Willd.	M	N				3.0		3.0					1.8	3.6	5.5
TRISP	*Trisetum* sp. Pers.	M	N		2.0	1.0			3.0				1.8	1.8		3.6
DESAT	*Deschampsia atropurpurea* (Wahlenb.) Scheele	M	N		3.0				3.0		5.5					5.5
AGFU	*Agropyron fuegianum* (Speg.) F. Kurtz	M	N					3.0	3.0							0.0
CAMA	*Carex magellanica* Lam.	M	N				3.0		3.0					1.8	3.6	5.5
SAMA	*Saxifraga magellanica* Poiret	D	N		2.0			1.0	3.0	3.6						3.6
TRIFOL	*Trifolium* sp.	D	E		2.0		1.0		3.0		3.6				1.8	5.5
NAMA	*Nassauvia magellanica* J. F. Gmelin	D	N					3.0	3.0							0.0
SENE1	*Senecio* sp. 1	D	N		2.0		1.0		3.0		3.6			1.8		5.5
BRUN	*Bromus unioloides* Humb. Bonpl. & Kunth	M	N				1.0	1.0	2.0						1.8	1.8
POTR	*Poa trivialis* L.	M	E		1.0	1.0			2.0		1.8					1.8
CAREX	*Carex* sp. l.	M	N				2.0		2.0					3.6		3.6

Code	Species												
UNLE	*Uncinia lechleriana* Steudel	M	N	1.0			1.0	2.0	1.8				1.8
GAAP	*Galium aparine* L.	D	N	2.0				2.0	1.8	1.8			3.6
ACPI	*Acaena pinnatifida* Ruiz y Pavón	D	N	1.0	1.0			2.0			1.8	1.8	3.6
HYIN	*Hypochoeris incana* (Hooker & Arn.) Macloskie	D	N				2.0	2.0				1.8	1.8
ERMY	*Erigeron myosotis* Pers.	D	N				2.0	2.0					0.0
LAHA	*Lagenifera hariotii* (Franchet) T. Dudley	D	N	2.0				2.0	1.8	1.8			3.6
PEPI	*Perezia pilifera* (D. Don) Hooker & Arn.	D	N				2.0	2.0					0.0
CEAR	*Cerastium arvense* L.	D	N	1.0			1.0	2.0		1.8			1.8
POLAN	*Polystichum andinum* Phil.	P	N				1.0	1.0					0.0
POAL	*Poa alopecurus* ssp. fuegiana (Hooker f.) D. M. Moore & Doggett	M	N				1.0	1.0					0.0
DESKI	*Deschampsia kingii* (Hooker f.) Desv.	M	N				1.0	1.0					0.0
STRA	*Stipa rariflora* (Hooker f.) Bentham	M	N				1.0	1.0					0.0
CAGA	*Carex gayana* Desv.	M	N				1.0	1.0					0.0
SCAN	*Schoenus antarctucus* (Hooker f.) Dusén	M	N		1.0			1.0			1.8		1.8
CACU	*Cartex curta* Gooden.	M	N		1.0			1.0				1.8	1.8
BOGU	*Bolax gummifera* (Lam.) Sprengel	D	N			1.0		1.0					0.0
OUBR	*Ourisia breviflora* Bentham	D	N			1.0		1.0					0.0
GAAN	*Galium antarcticum* Hooker f.	D	N	1.0				1.0	1.8				1.8
HAMA	*Hamadryas magellanica* Lam.	D	N				1.0	1.0					0.0
ARMA	*Armeria maritima* (Miller) Willd.	D	N				1.0	1.0					0.0
HIVU	*Hippuris vulgaris* L.	D	N		1.0			1.0				1.8	1.8
CAGE	*Cardamine geraniifolia* (Poiret) DC.	D	N	1.0				1.0		1.8			1.8
DRMA	*Draba magellanica* Lam.	D	N	1.0				1.0	1.8				1.8
SEMA	*Senecio magellanicus* Hooker & Arn.	D	N				1.0	1.0					0.0
SENE2	*Senecio* sp. 2	D	N				1.0	1.0					0.0
GASP	*Gamochaeta spiciformis* (Sch. Bip.) Cabrera	D	N	1.0				1.0			1.8		1.8
SAPR	*Sagina procumbens* L.	D	E	1.0				1.0		1.8			1.8

Appendix C. . Conditional effects obtained from the environmental explicatory variables tested (Monte Carlo test with 499 permutations) in canonical correspondence analysis (CCA). Abbreviations of environment explicatory variables: DBH = diameter at breast height, DH = dominant height, BA = calculated basal area, TOBV = total over-bark volume, DEN = tree density, OCOV = overstory crown cover, PHASE = distinct development stages (optimal initial growth and final growth, maturing and crumbling following), ALT = elevation above sea level, SLOPE = slope, E-W = east-west aspect, N-S = north-south aspect, IMACT = harvesting or cattle grazing, SOIL = percent cover of bare soil, DEB = percent cover of woody debris, REG = tree regeneration density.

Variable	LambdaA	*P*	*F*
OCOV	0.61	0.002	6.71
ALT	0.32	0.002	3.56
N-S	0.23	0.002	2.58
SLOPE	0.20	0.002	2.40
DEB	0.16	0.010	1.81
E-W	0.16	0.004	1.85
DH	0.15	0.008	1.82
IMPACT	0.14	0.028	1.71
TOBV	0.15	0.024	1.76
SOIL	0.13	0.028	1.58
REG	0.11	0.124	1.41
DEN	0.11	0.224	1.31
PHASE	0.10	0.208	1.18
BA	0.09	0.264	1.15

Appendix D. Supplementary material

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.foreco.2018.08.033.

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