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Conservation values of understory vascular plants in even- and uneven-aged *Nothofagus antarctica* forests

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Abstract

Usually, stands with aging trees are considered forests with higher conservation values, regardless their structural diversity and other functional attributes. Natural stands present a wide range of age structures, from even-aged stands growing at different development growth phases (e.g. CO = stands at initial or final optimum development growth phase, MD = stands at mature or decaying development growth phases) to uneven-aged stands with mixed development growth phases (e.g. UOG = stands combining mature or decaying development growth phases with initial or final optimum development growth phases, UMD = stands combining only mature and decaying development growth phases). The aim of this work was to compare richness and cover of understory vascular plants of even- and uneven-aged stands of *Nothofagus antarctica* (ñire) forests in Tierra del Fuego (Argentina), and relate these characteristics with abiotic, soil and forest structure variables. A total of 75 stands were sampled across the natural range distribution of the forests, where understory (point intercept method), forest structure (angle count sampling and eye-fish photos) and environmental (soil) variables were measured. 17 one-way ANOVAs were conducted using Tukey test at $p < 0.05$ to compare the means. Among forest structure and environmental variables, cover ($F = 4.3$, $p = 0.007$), radiation ($F = 4.4$, $p = 0.006$), phosphorous ($F = 3.9$, $p = 0.012$), tree density ($F = 10.3$, $p < 0.001$), tree diameter ($F = 10.3$, $p < 0.001$) and stand growth ($F = 4.9$, $p = 0.004$) showed significant differences, and in general with a positive or negative trend across the MD—UMD—UOG—CO gradient. Total ($F = 6.5$, $p < 0.001$) and native species richness of the understory ($F = 7.2$, $p < 0.001$) were significantly different among forest types, where UMD > UOG > MD > CO (17–28 total, and 13–24 native species, respectively). Neither exotic species richness (4–5 species) nor understory cover significantly changed among treatments (total, dicots, ferns and bryophytes). However, monocots cover significantly differed among treatments ($F = 3.9$, $p = 0.012$), where UMD > MD > UOG > CO. Finally, indicator species cover for environmental degradation did not present significant differences ($F = 2.1$, $p = 0.106$), but they were positive related to forests growing in mature stages. We concluded that uneven-aged stands presented significantly higher conservation values compared to even-aged stands, where mature/decay stands have better conservation values

than optimum growth development phases. These findings can be used for better silviculture practices that combine silvopastoral use and conservation strategies.

Introduction

Natural forests present dissimilar forest structure derived from tree species ecology, regional climate, topography, and natural disturbances (e.g. wind, landslides, etc.) that modify their forest dynamics (Duncanson et al. 2015; Hakkenberg et al. 2016). At higher latitudes, natural forests show simple structures dynamic paths, usually with one or two species and few overstory strata, such as *Nothofagus antarctica* (Forst. f.) Øerst. (commonly named ñire) forests in Tierra del Fuego. These forests grow in pure stands and regenerate by seeds or root sprouts under simple and predictable gap dynamic (Peri et al. 2016a). The natural forests can present even- or uneven-aged structures depending on the stand dynamic history, e.g. massive wind-blown leads to even-aged structures (Ivancich 2013; Peri et al. 2017).

An important goal in forest management is to preserve biodiversity and the multiple ecosystem services that they provide to society (Perera et al. 2018). Usually, forest conservation strategies prioritize areas with stands under a natural dynamics with the lowest human impact, leading many times to select isolated and remote forests despite other specific ecosystem functions and biodiversity values (Sandifer et al. 2015; Oliver et al. 2015). However, there are natural forests with different conservation values (Ishii et al. 2004; Hilmers et al. 2018), being necessary to determine which characteristics are specifically related to these high biodiversity values. In example, the concept of old-growth forests is strongly related to high biodiversity values, and many times this concept was simplified and just considered stand age (e.g. higher tree age in the stand, higher old-growthness). The concept of old-growth must consider other characteristics and attributes in addition to the stand age, e.g. (i) towering trees, multiple canopy layers, large snags, and coarse woody debris (Beese et al. 2003; Fahey 2018); (ii) number and quality of tree cavities (Boyle et al. 2008); (iii) structural and functional complexity of the stands (Bauhus et al. 2009); (iv) site quality of the stands (Bahamonde et al. 2018); or (v) position of the stands in the landscape (Martínez Pastur et al. 2016; Ratcliffe et al. 2017; Rosas et al. 2019). In fact, the concept of old-growth was actually expanded to other ecosystems (e.g. grasslands, savannas, and woodlands) (Veldman et al. 2015), mainly related to the capacity of biodiversity maintenance as well as other ecological attributes.

In order to define better conservation and silviculture management strategies is necessary to determine the stand characteristics that support higher biodiversity values. In this sense, it is more effective to implement conservation strategies based on land-sharing than in land-sparing. The creation of natural reserves was proposed as one alternative to protect biodiversity using a land-sparing strategy, but fails in protect many species at landscape level (Lindenmayer et al. 2006; Phalan et al. 2011). For example, managed stands have lower richness and abundance than the original species assemblage of the primary unmanaged forests (Deferrari et al. 2001; Spagarino et al. 2001; Martínez Pastur et al. 2002; Lencinas et al. 2017). The silviculture in ñire forests (e.g. silvopastoral systems) (Peri et al. 2016a) proposes to simplify the natural structures at the stand level, by opening the canopy and maintaining homogeneous tree age distributions for livestock shelter and

wood production. This management increases the provision of some ecosystem services (e.g. animal and timber production) and decreases other services (e.g. supporting or regulating) (Martínez Pastur et al. 2017), and significantly modified the biodiversity conservation values. This proposal also increases the grass production of understory, affecting the original species assemblage including birds and insects, as well as several ecosystem functioning (e.g. decomposition and nutrient cycling) (Bahamonde et al. 2013, 2015; Peri et al. 2016b; Soler et al. 2017).

Ecologically sustainable forest management was proposed as a solution for many ecological and socio-economic problems associated with forest uses (Perera et al. 2018). The aims were designed to preserve ecosystem integrity while providing wood and non-wood values by maintaining forest structural complexity, species diversity and composition, and the ecological processes and functions within the bounds of normal disturbance regimes (Lindenmayer et al. 2012). To achieve both conservation and production in future silviculture proposals, we need to determine the natural forest structures that conserve more biodiversity values and other desirable ecosystem functions. The most employed proxy for biodiversity conservation includes the understory vascular plant species (e.g. richness and cover) (Martínez Pastur et al. 2016; Rosas et al. 2019), acting as good bio-indicators in the *Nothofagus* forests of Southern Patagonia (Soler et al. 2016, 2017; Lencinas et al. 2017). Therefore, the aim of the present work was to compare richness and cover of vascular plants in the understory of even and uneven-aged stands of ñire forests in Tierra del Fuego (Argentina), and relate these characteristics with abiotic and forest structure variables. We tried to answer the following questions: (i) do the stand characteristics (abiotic, soil and forest structure variables) change according to the age structure?; (ii) is there any age structure that favor the understory richness and cover?; and (iii) do species assemblage of the understory change with the age structure of the stands?

Methods

Study area

The study area covers most of the natural distribution of ñire forests in the Argentinean sector of Tierra del Fuego (53° 38′ to 54° 37′ S, 66° 28′ to 68° 36′ W), including 181,500 ha of pure forests (Collado 2001). These forests present different forest structures (even-aged or uneven-aged), depending on natural (e.g. windstorms) and human-derived impacts during the last century (e.g. fires, harvesting, implantation of pastures, cattle grazing) (Peri et al. 2016a, b). We sampled 75 stands (Fig. 1) with the following characteristics: (i) at least 2 ha with a homogeneous forest structure; (ii) a complete crown cover (up to 50%) without harvesting or fire events during the last 50 years; and (iii) an acceptable conservation condition, without large degradation impacts due to over-uses (e.g. heavy soil erosion, livestock over-grazing).

Sampling of the stands

In each stand, we placed at random a 50 m transect to characterize each plot. Canopy structure and solar radiation transmittance were measured using hemispherical photographs taken in the center of each transect at ground level with an 8-mm fish eye lens (Sigma, Japan) mounted on a 35 mm digital camera (Nikon, Japan) with a tripod leveling head to ensure horizontal lens position. Each photograph was orientated with the upper edge
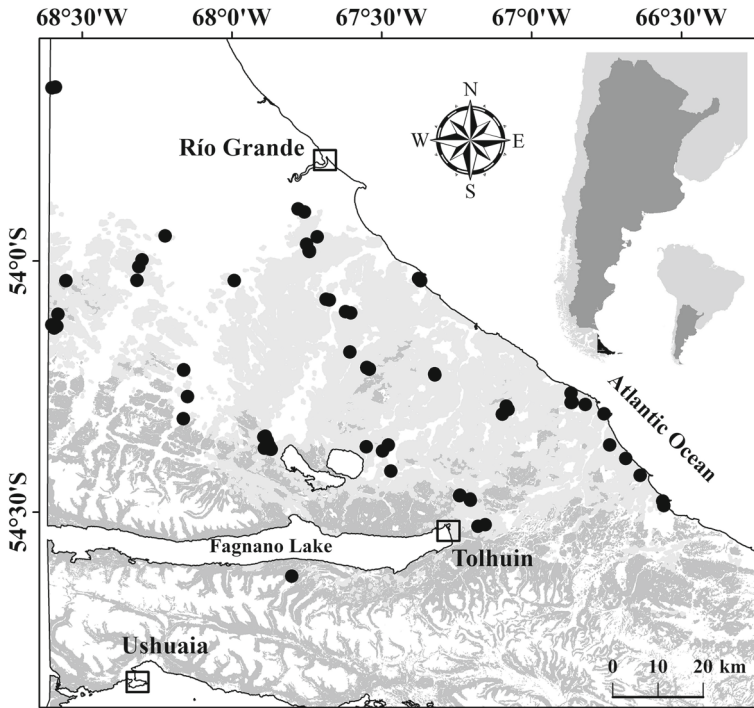
Fig. 1 Location of the sampled stands (black dots). Pale grey shadow shows *Nothofagus antarctica* forests and dark grey shadow shows *N. pumilio* and *N. betuloides* forests, while squares show the cities

towards the magnetic north, avoiding direct sunlight. Gap Light Analyzer software v.2.0 (Frazer et al. 2001) was used to define cover (overstory crown and debris up to 1.3 m height) (CC), as a percentage of open sky relative to the cover, and total radiation at ground level (TR), as the amount of direct and diffuse radiation transmitted through canopy and debris. Modeling of solar radiation and the user-supplied input variables and radiation details were presented in Martínez Pastur et al. (2011a).

Four soil samples (0–10 cm depth) were collected along each transect using a field borer (after removing the litter layer) during middle summer. Samples were weighted and then air-dried in laboratory conditions (24 °C) until constant weight. Soil bulk density and soil water content (SWC) for each stand were obtained from the four samples. After that, coarse root debris > 2 mm had been removed by sieving. For chemical analyses, we pooled individual soil samples into one combined sample per stand. Each sample was finely ground to below 2 mm using a tungsten-carbide mill, and then it was determined: (i) total organic carbon (C) from soil samples washed with HCl (50%) with an automatic analyzer (LECO CR12, USA); (ii) total nitrogen (N) by a semi-micro Kjeldahl method; and (iii) extractable phosphorous (P) according to the method of Bray and Kurtz (1945). Data for nutrient contents were presented as kg m^2 30 cm depth, using the average soil bulk density data of each stand.

Forest structure was characterized by two plots located at the beginning and the end of each transect, using the point sampling method (BAF = 4) (Bitterlich 1984) with a Criterion RD-1000 (Laser Technology, USA). In each sampling-point we measured: (i) diameter at breast height (DBH) with a forest caliper; (ii) development stage of each tree

(IGP = initial growth phase 0–30 years-old, FGP = final growth phase 30–60 years-old, M = mature phase 60–120 years-old, D = decaying phase > 120 years-old) (based on Ivancich 2013); (iii) vigor (VIG) of each tree (one to three, where higher values indicated more crown vitality); (iv) dominant height (DH) of the stand using a TruPulse 200 laser clinometer and distance rangefinder (Laser Technology, USA) by averaging the height of the two tallest trees per transect. These data allowed us to determine tree density (DEN), basal area (BA), total over bark volume (TOBV), and annual growth (GRO) of each stand. For further details on the applied models see Peri et al. (2010) and Ivancich et al. (2011, 2014). Finally, a homogeneity index (HI) was determined based on the deviation of the percentage of basal area occupancy of trees with different development stage (IGP, FGP, M or D). The values of the index were standardized for further analyses, where zero indicates uneven-aged stand, where all the development stages are equally represented, and one indicates even-aged stands, where only one development stage is present in all the trees of the stand.

For further analyses, the stands were classified according to the different age structures of sampled trees (proxy: development stage of each tree). For this, we considered the basal area for the different development stage trees, and classified the stands as: even-aged stands as those forests that concentrate > 70% of the basal area in one development stage (IGF, FGP, M, or D even-aged stands), and uneven-aged stands when more than one development stage is needed to concentrate > 70% of the basal area (UOG = stands combining trees of mature or decaying phases and initial or optimum growth phases, or UMD = stands combining mostly mature and decaying phases). For some analyses, we simplified the even-aged stands in just two categories: CO = stands with trees growing at initial or optimum growth phase, and MD = stands with trees growing at mature or decaying phases.

To evaluate the understory, we used the point-intercept method (Levy and Madden 1993) with 50 intercept points (e.g. every 1 m) along each transect in the sampled stands. In each point, we recorded all vascular plants (dicots, monocots, and ferns) including tree regeneration less than 1.30 m height (e.g. *Nothofagus antarctica* and *N. pumilio*), identifying dominant and suppressed layers. We also recorded the presence data of the species occurring on transects but that were not intercepted by the points. These data was used to determine richness and plant species cover, bare soil or litter (BS) and woody debris (DEB) (> 2.5 cm diameter). Vascular plants were identified and classified according to their life-form (prostrate herb, erect herb, shrub, dwarf-shrub, tree, caespitose grass, and rhizomatous grass) following Moore (1983) and Correa (1969–1998). With these measurements, we determined: (i) total species richness (TR), classified in native (NR) or exotic (ER) according to the origin of the species; and (ii) understory cover calculated as total cover (TC), which included all the layers (dominant and suppressed layers), tree regeneration (RC), dicots (DC), monocots (MC), ferns (FC), bryophytes including mosses and liverworts (BC). This cover was also discriminated as native (NC) or exotic (EC) plants. Finally, we determined the cover of key species as indicator for environment (PD) or economic (ED) degradation. The first ones included early seral species that settled after major disturbances, generating mounds (e.g. *Azorella caespitosa*, *A. trifurcata* and *Bolax gummifera*) and significant changes in the natural conditions of the stands. The second ones are species that reduce the quality of the understory for grazing purposes (e.g. *Achillea millefolium*, *Hieracium pilosella* and *Rumex acetosella*). The vascular plant species list is presented in Table 5, including the species code, type (dicot, monocot or fern), origin (native or exotic), life-form, and the mean cover measured in each forest type according to their age structure.

Statistical analyses

One-way ANOVAs were conducted using Fisher test, and Tukey test at p < 0.05 was used to separate means, comparing stands with different age structures (CO, UOG, UMD, MD) and analyzing: (i) abiotic and soil variables (CC, TR, SWC, C, N, P); (ii) forest variables (DH, DEN, DBH, BA, TOBV, GRO, VIG, HI); (iii) richness and forest floor cover (BS, DEB, TR, NR, ER, PD, ED); and (iv) the different plant type cover in the understory (TC, RC, DC, MC, FC, BC, NC, EC). Multivariate analyses were conducted with plant species cover to analyze similarities among the different even- and uneven-aged stands: (i) cluster analysis was performed using complete linkage method with Euclidean distance to link the different stand types (IGP, FGP, UOG, UMD, M, D); and (ii) detrended correspondence analyses (DCA) were performed to relate the understory species for each age structure, comparing CO, MD and UOG, and CO, MD and UMD. We used a matrix of average species cover, and classified them according to type and origin (Table 5). Analyses were based on species relative cover matrix without down-weighting for rare species and with axis rescaling (Hill 1979), and were performed using PC-Ord software (McCune and Mefford 1999).

Results

Even- and uneven-aged stands presented differences in the studied abiotic and soil variables (Table 1), where crown cover and total radiation at understory level followed inverse patterns. Crown cover was higher and total radiation was lower in young even-aged stands (CO) in comparison with even-aged old stands (MD), and where uneven-aged stands (UOG and UMD) presented intermediate values. Soil moisture, carbon and nitrogen content did not present significant differences, while phosphorous did not present a clear variation pattern (UMD < CO < MD < UOG). While some forest structure variables did not show significant differences among the studied stands (Table 2, e.g. dominant height, basal area, and total over bark volume), other variables presented changes as was expected, e.g. tree density, stand volume growth and vigor of the trees decreased and diameter of the trees

Table 1 Analyses of variance to characterize abiotic and soil variables in *Nothofagus antarctica* stands with different age structures (CO = even-aged stands at initial or final optimum development growth phase, UOG = uneven-aged stands combining mature or decaying development growth phases and initial or final optimum development growth phases, UMD = uneven-aged stands combining mature and decaying development growth phases, MD = even-aged stands at mature or decaying development growth phases)

Treatment	CC	TR	SWC	C	N	P
CO	81.3b	25.7a	44.9	17.2	1.05	0.39ab
UOG	77.6b	29.6a	32.6	15.6	0.95	0.54b
UMD	70.8ab	37.7ab	37.2	16.7	0.96	0.29[a]
MD	65.5a	43.3b	54.6	17.1	1.08	0.47b
F (p)	4.34 (0.007)	4.46 (0.006)	0.77 (0.517)	0.93 (0.429)	1.44 (0.239)	3.89 (0.012)

Analyzed variables were overstory crown cover (CC, %), percentage of total radiation at the understory level (TR, W.m^2), soil water content (SWC, m^3.m^{-3}), soil carbon content (C, kg m^2 30 cm), soil nitrogen content (N, kg.m^2.30 cm), and soil phosphorous content (P, kg m^2 30 cm)

F = Fisher test, (p) probability. Different letters showed differences with Tukey test at p < 0.05

Table 2 Analyses of variance to characterize forest variables in *Nothofagus antarctica* stands with different age structures (CO = even-aged stands at initial or final optimum development growth phase, UOG = uneven-aged stands combining mature or decaying development growth phases and initial or final optimum development growth phases, UMD = uneven-aged stands combining mature and decaying development growth phases, MD = even-aged stands at mature or decaying development growth phases)

Treatment	DH	DEN	DBH	BA	TOBV	GRO	VIG	HI
CO	10.3	3928c	18.1a	36.0	173.4	3.9b	2.5b	0.82c
UOG	9.2	2439b	25.5a	35.6	167.3	2.9a	2.0a	0.46a
UMD	9.1	1054a	33.9b	35.3	184.0	2.4a	2.0a	0.57b
MD	9.8	900a	35.9b	30.9	171.8	2.2a	1.9a	0.78c
F (p)	0.65 (0.585)	10.25 (< 0.001)	10.34 (< 0.001)	0.87 (0.459)	0.14 (0.933)	4.86 (0.004)	9.82 (< 0.001)	33.98 (< 0.001)

F = Fisher test, (p) probability. Different letters showed differences with Tukey test at $p < 0.05$

(DBH) increased from stands with more young trees to stands with older trees (CO > UOG > UMD > MD).

As it was expected, the homogeneity index was lower at uneven-aged (0.46–0.57) compared to even-aged stands (0.78–0.82), but distant of the theoretical fully uneven- or even-aged values (zero or one). This was due to mixed tree development stages were present in all the forest types (Fig. 2) derived from gap dynamics or due to some trees survive for longer periods after massive death of the trees in the stands.

Forest floor cover significantly changed according to the structure age of stands. Bare soil was exposed more in young stands (CO) compared to other treatments, while woody debris did not show significant changes (Table 3). Cover of total understory, regeneration, dicots, ferns, bryophytes, as well as native or exotic plants, did not significantly change according to the age structure of the stands (Table 4). However, monocot cover was significantly higher in mature stands (even-aged MD > uneven-aged UMD) than in stands with young trees (uneven-aged UOG > even-aged CO). Total species richness and native species richness (Table 3) significantly varied with treatments, following UMD > UOG > MD > CO (17–28 total and 13–24 native species, respectively). However, exotic species richness did not present significant differences among treatments (4–5 species). Finally, the cover of key plant species for environmental and productive degradation did not show significant differences among the studied treatments, but the trend showed an increase from young to older stands (0.21 to 1.23 and 0.03 to 0.81, respectively).

Multivariate analyses allowed us to link the different treatments according to their similarities in the understory species assemblage. Cluster analyses showed that mature stands were most similar to even-aged mature (M) and uneven-aged stands that combined mature and young trees (UOG) (Euclidean distance of 7.5) (Fig. 3), while these stands were closely linked to other uneven-aged stands that combined older structures (UMD) (Euclidean distance of 11), and far-away these were linked with even-aged older stands
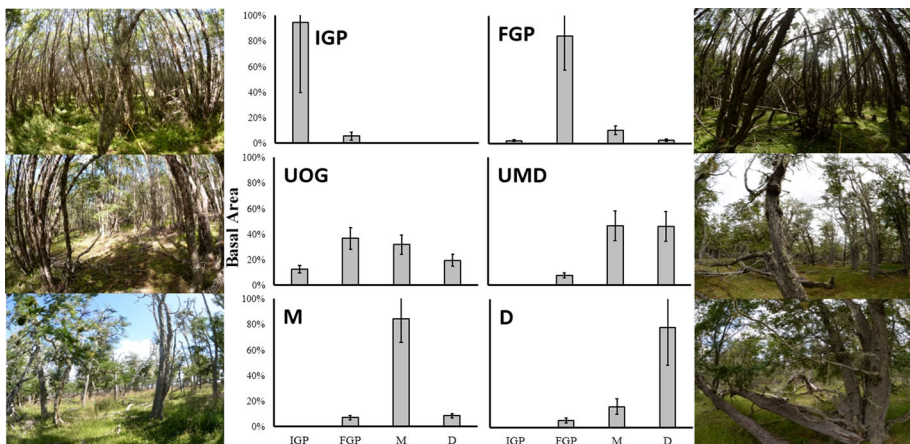
Fig. 2 Proportion of the basal area (%) classified according to development growth stage of the trees (IGP = even–aged stands at initial optimum development growth phase, FGP = even–aged stands at final optimum development growth phase, UOG = uneven–aged stands combining mature or decaying development growth phases and initial or final optimum development growth phases, UMD = uneven–aged stands combining mature and decaying development growth phases, M = even–aged stands at mature development growth phase, D = even–aged stands at decaying development growth phase) of the different even–and uneven–aged *Nothofagus antarctica* stands

Table 3 Analyses of variance to characterize forest floor cover, understory richness and indicator vascular plants in *Nothofagus antarctica* stands with different age structures (CO = even-aged stands at initial or optimum development growth phase, UOG = uneven-aged stands combining mature or decaying development growth phases and initial or optimum development growth phases, UMD = uneven-aged stands combining mature and decaying development growth phases, MD = even-aged stands at mature or decaying development growth phases)

Treatment	BS	DEB	TR	NR	ER	PD	ED
CO	11.4b	15.0	17.0a	13.0a	4.0	0.03	0.21
UOG	4.8a	11.6	24.4bc	19.8bc	4.6	0.96	0.97
UMD	3.1a	12.7	28.0c	23.5c	4.5	0.57	1.49
MD	5.1a	13.4	23.3b	19.0b	4.3	0.81	1.23
F (p)	3.49 (0.021)	0.64 (0.592)	6.49 (0.001)	7.16 (< 0.001)	0.29 (0.832)	0.76 (0.519)	2.11 (0.106)

Analyzed variables were bare soil or litter without vegetation (BS, %), woody debris (DEB, %), total species richness (TR, n species), native species richness (NR, n species), exotic species richness (ER, n species), cover of indicator species of productive degradation (PD, %), and cover of indicator species of environmental degradation (ED, %)

F = Fisher test, (p) probability. Different letters showed differences with Tukey test at p < 0.05

Table 4 Analyses of variance to characterize understory cover of vascular plants in *Nothofagus antarctica* stands with different age structures (CO = even-aged stands at initial or optimum development growth phase, UOG = uneven-aged stands combining mature or decaying development growth phases and initial or optimum development growth phases, UMD = uneven-aged stands combining mature and decaying development growth phases, MD = even-aged stands at mature or decaying development growth phases)

Treatment	TC	RC	DC	MC	FC	BC	NC	EC
CO	148.9	4.8	80.8	49.3a	6.9	11.9	109.7	39.2
UOG	172.5	2.8	91.5	56.4ab	10.2	14.4	116.1	56.4
UMD	177.3	4.2	90.3	73.0bc	5.9	8.1	136.5	40.8
MD	176.9	3.6	71.8	85.9c	10.1	9.1	113.9	63.0
F (p)	1.15 (0.334)	0.31 (0.818)	1.03 (0.384)	3.86 (0.012)	0.28 (0.840)	0.77 (0.516)	0.73 (0.537)	0.43 (0.712)

Analyzed variables were total cover (TC, %), tree regeneration cover (RC, %), dicots cover (DC, %), monocots cover (MC, %), ferns cover (FC, %), bryophytes cover (BC, %), native species cover (NC, %), and exotic species cover (EC, %)

F = Fisher test, (p) probability. Different letters showed differences with Tukey test at $p < 0.05$
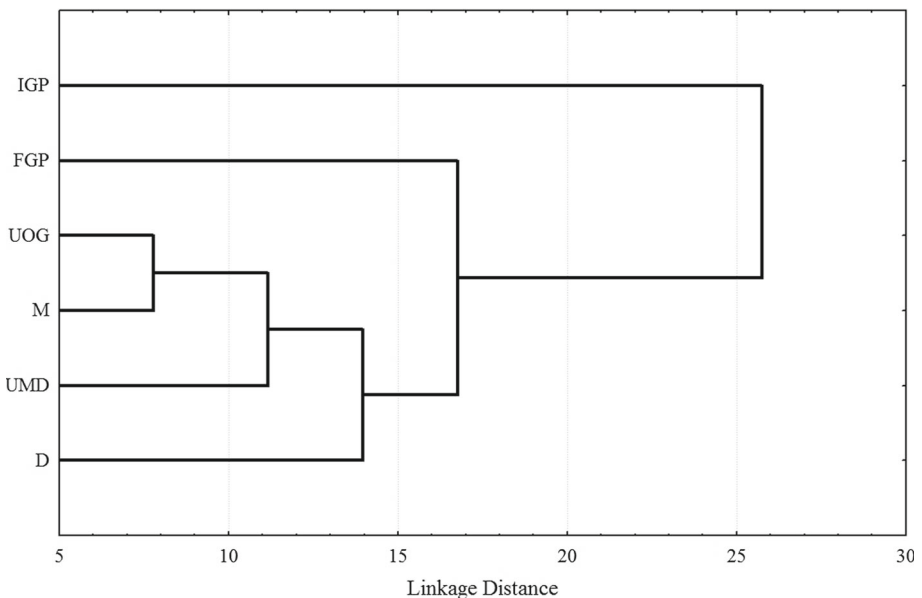

Fig. 3 Cluster analysis of *Nothofagus antarctica* forests with different age structures analyzing the cover of the understory vascular species (IGP = even–aged stands at initial optimum development growth phase, FGP = even–aged stands at final optimum development growth phase, M = even–aged stands at mature development growth phase, D = even–aged stands at decaying development growth phase, UOG = uneven–aged stands combining mature or decaying development growth phases and initial or final optimum growth development growth phases, UMD = uneven–aged stands combining mature and decaying development growth phases)

(D) (Euclidean distance of 14). At a higher distance, these groups were linked to young stands at final (FGP) and initial (IGP) growth development phases (Euclidean distances of 17 and 26, respectively). Detrended correspondence analyses showed a differential species relationship with tree age structure of the stands (Fig. 4). Most of the species were generalists (center of the triangle graphs) or shared between two different forest types (both native and exotic species). However, some species mostly occurred in particular forest types. For example, (i) some monocots (*Agrostis inconspicua*, *Phaiophleps biflora* and *Uncinia lechleriana*), dicots (*Chilliotrichum diffusum*, *Gamochaeta spiciformis*, *Ranunculus peduncularis* and *Viola magellanica*) and one exotic species (*Hieracium pillosella*) were related to uneven-aged stands that combined mature or decaying phases and initial or final optimum growth development phases (UOG). (ii) Some monocots (*Luzula alopecurus*
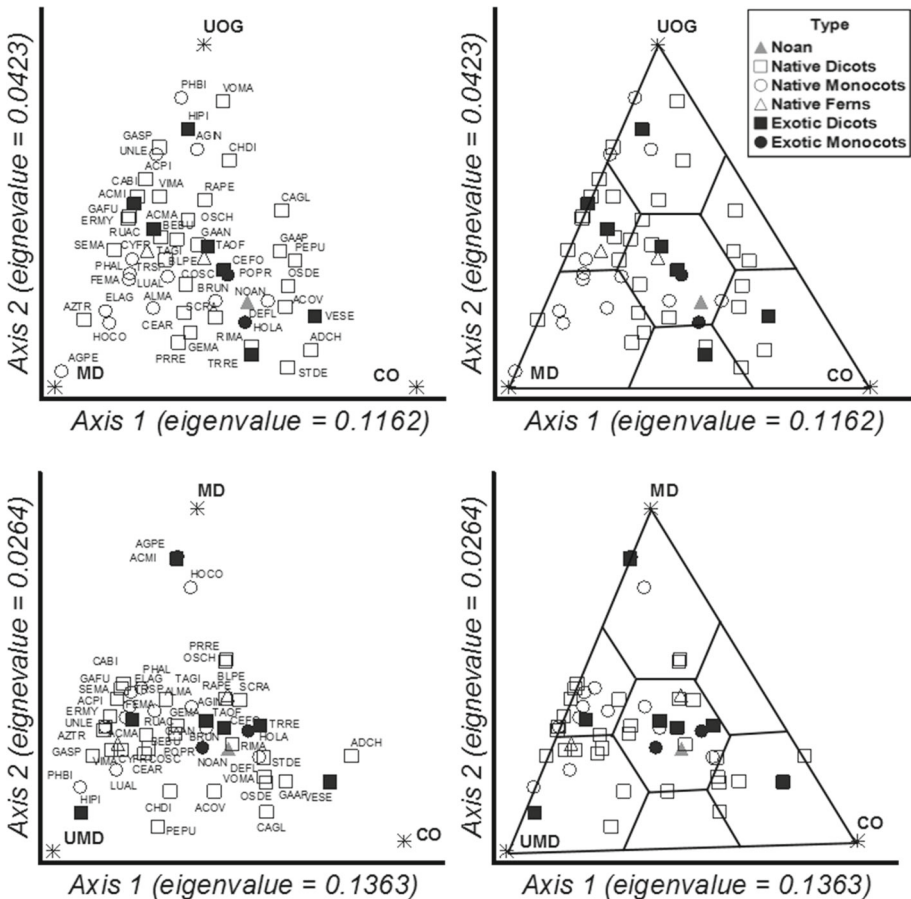
Fig. 4 Detrended correspondence analyses relating the understory vascular plant species in *Nothofagus antarctica* stands with different age structures (CO = even–aged stands at initial or final optimum development growth phase, UOG = uneven–aged stands combining mature or decaying development growth phases and initial or final optimum development growth phases, UMD = uneven–aged stands combining mature and decaying development growth phases, MD = even–aged stands at mature or decaying development growth phases). Symbols and color differentiate tree regeneration (Noan), native ferns, and native and exotic dicots and monocots. See species codes in the Table 5

and *P. biflora*), dicots (*Berberis buxifolia*, *Cerastium arvense*, *Ch. diffusum*, *Cotula scariosa*, *G. spiciformis*, *Pernettya pumila* and *Viola magellanica*), one fern (*Cystopteris fragilis*) and one exotic species (*H. pillosella*) were related to uneven-aged stands combining mature and decaying phases (UMD). (iii) Young even-aged stands (CO) were related to several dicots (*Acaena ovalifolia*, *Adenocaulon chilensis*, *Cardamine glacialis*, *Galium aparine*, *Osmorhiza depauperata* and *V. magellanica*) and one exotic species (*Veronica serpyllifolia*). Finally, (iv) the older even-aged stands (MD) were related to several monocots (*Agrostis perennans*, *Alopecurus magellanicus*, *Elymus agropyroides*, *Festuca magellanica* and *Hordeum comosum*), dicots (*Azorella trifurcata*, *Cerastium arvense*, *Geum magellanicum*, *Osmorhiza chilensis* and *Pratia repens*), and one exotic species (*Achillea millefolium*).

Discussion

Structural diversity of even- and uneven-aged stands influences over forest variable attributes

Forest characteristics (abiotic, soil and forest structure variables) varied according to the age structure of the stands. Some forest structure attributes were directly related to the stand age (e.g. decrease tree density, increase DBH, decrease stand growth or tree vigor), which is consistent with the literature (Martínez Pastur et al. 2002; Peri et al. 2010, 2017; Duncanson et al. 2015). Our sampled plots were distributed across the species occurrence in the landscape and across the site quality gradient (proxy: dominant height), without significant differences in basal area and total volume (Fig. 1 and Table 2). We did not find both fully even- or uneven-aged stands, but some forest types were more related to one of the age structure classes defined for this study (Table 2). The homogeneity index showed, that some mix of age classes in natural stands (e.g. in young stands some old trees also survive) influenced over the total volume of the stands. This is because in natural ñire forests, some legacies of primary forests survived in the secondary even-aged forests (Keeton and Franklin 2005).

The differences in the forest structure were associated to changes in the crown cover, e.g. young vigorous trees had the highest canopy cover and lowest total radiation at the understory level, as it was described for other *Nothofagus* forests (Promis et al. 2009; Martínez Pastur et al. 2011a; Penone et al. 2019). It was expected that these differences caused by fluctuations in soil moisture (higher values in open canopies), nutrient contents (e.g. C and N), natural cycles (e.g. decomposition rates) or micro-climate conditions (e.g. temperature and soil moisture). However, these changes were not detected across the studied age structures, as it was described in other studies (Martínez Pastur et al. 2011a, b; Lozano-García et al. 2016). The variations in soil P content did not clearly change with the stand characteristics, and maybe are related to soil variations at landscape level (Diehl et al. 2003; Romanyà et al. 2005; Toro Manríquez et al. 2019). Beside this, there were changes in the understory cover and bare soil, in concordance with previous studies (Martínez Pastur et al. 2002; Lencinas et al. 2017). Finally, woody debris accumulation did not change across the stands, maybe due to the low decomposition rates or other natural processes that usually occurs in temperate forests at higher latitudes (Frangi et al. 1997; Wesely et al. 2018).

The structural characteristics detected across the different even- and uneven-aged stands offer great variety of microenvironmental conditions that may influence over the habitat of

different species (e.g. birds, mammals), the natural regeneration dynamics, and also over other natural cycles (Martínez Pastur et al. 2012; Nolet et al. 2018; Penone et al. 2019; Lelli et al. 2019). The specific niche requirements can change according to the species and its life span, e.g. requirements for nesting, breeding, foraging (Boyle et al. 2008; Lencinas et al. 2017; Lelli et al. 2019; Rosas et al. 2019). For this, it is necessary to determine if one specific forest type can be indispensable for some particular species, despite it presents higher or lower species diversity (Martínez Pastur et al. 2015).

Structural diversity of even- and uneven-aged stands influences over understory diversity

The studied gradient of age structure influenced the understory richness, cover and species assemblage. There was a direct relationship between structural diversity of the stands (uneven-aged > even-aged) and the understory plant richness (total and native species) than just the age of the trees in the stand (e.g. even-aged stands with oldest trees did not support the greatest diversity of the landscape). Thus, the forest structure that sustains more plant richness was the uneven-aged stands that combined mature and decaying growth development phases, which was significantly greater than in even-aged stands with only mature or decaying growth development phases. Tree age was identified as the main proxy for biodiversity (e.g. Pinto Correia et al. 2017); however, in the present study structural diversity was more important for ñire forests. The best forest structure that sustained greater biodiversity (UMD) had middle values of canopy cover, with gaps that favored incoming radiation and rainfall, and therefore increasing decomposition rates and decreasing immobilization of nutrients (e.g. N and P was lower than in other treatments). These environmental characteristics increased the stand heterogeneity and consequently the biodiversity that sustain these forests (McIntosh et al. 2016; Bohn and Huth 2017; Penone et al. 2019). The stands structural diversity only influenced on monocots cover, which was directly related to the overstory cover of the stands (MD > UMD). Beside this, neither the structural diversity nor the tree age influenced over exotic species (richness or cover) or indicator species for productive or environmental degradation of the stands.

The conservation values of the different forests mostly reside in the species assemblage that different structural diversity can sustain, and the increase of the monocot cover in open stands. Total richness included 78 dicot species (80.6% of the total richness, 13 exotics), 37 monocot species (16.9% of the total richness, seven exotics) and three native ferns (2.5%). The greatest dicots richness developed better under middle covers, while monocots increased its biomass and cover in open canopies, as it also was observed by Peri et al. (2016a). Thus, dicots compete with monocots, and usually grasses displace the herbs when light availability increases (Henn et al. 2014). For this, the environmental conditions and the heterogeneity of the uneven-aged stands generated more diverse micro-habitats that enhance the niche requirements for more understory plant species.

Despite the understory diversity that can supported for each forest type, they presented unique conservation values that should be considered in an integrative conservation strategy at landscape level. The most valuable stands (UMD) presented special niche conditions mainly for dicot species (two shrubs, one dwarf-shrub, three prostrate herbs, and one erect herb) than other taxa (one caespitose grass, one monocot erect herb, and one fern). Some of these species also grow in dense *Nothofagus pumilio* forests (e.g. *Viola magellanica* or *Cystopteris fragilis*) (Martínez Pastur et al. 2002; Lencinas et al. 2017). Other uneven-aged stands with more young trees and closed canopies (UOG) had similar

special niche conditions for four of these species (one shrub, one prostrate herb, one dicot, and one monocot), but presented special features for other three species (one erect herb, one caespitose, and one rhizomatous grass).

The young even-aged stands (CO) with closed canopies also offered special niche conditions for several species that were not listed before for UMD or UOG, including five dicots (two prostrate, and three erect herbs) that also usually occurred in dense *N. pumilio* forests (Martínez Pastur et al. 2002; Lencinas et al. 2017). Finally, the even-aged mature (MD) stands with more open canopies, offered special niche conditions for several monocots (four caespitose and one rhizomatous grasses) and some dicots (one prostrate and two erect herbs). Beside this, all the forest types were vulnerable to exotic species invasion (e.g. *Hieracium pillosella* or *Achillea millefolium*) or to species from the open-environments due to some processes of degradation (e.g. *Azorella trifurcata*), mainly associated to over-grazing, clear-cuttings or intense human-related fires (Peri et al. 2017; Huertas Herrera et al. 2018).

Recommendations for the landscape planning

Management and conservation planning in ñire forests in southern Patagonia were conducted through the implementation of compulsory plans that ranch owners must present to the Regional Forest Office according to provincial forest regulations (law 145/94) and according to three conservation categories (national law 26,331/07). The planning considers: (i) the regulation of livestock stocking rate in paddocks, (ii) the implementation of thinning to promote silvopastoral uses, and (iii) conservation of intact areas with special features. Animal stocking rate is defined according to the pasture biomass availability (quantity and quality) in different seasons. The thinning practices homogenize the forest structure by selecting the middle age trees (60–100 years-old with good crown development), and promoting the understory grass growth (Peri et al. 2016a; Martínez Pastur et al. 2017). The last point is implemented without clear criteria about conservation values (Martínez Pastur et al. 2016), where protected forests had been selected according to past uses (e.g. without previous harvesting), continuous close canopy cover (e.g. homogeneous stands with mature trees), soil protection in high slopes, and riverbank buffers.

The findings of this work provide information to improve the management and conservation planning under land-sharing strategies in ñire forests. Thus, the conservation of intact forest patches provides a degree of structural diversity that enhances species habitats. We suggest the conservation of uneven-aged stands with major presence of mature trees (mature and decay stages) (see UMD in Fig. 2). However, in the conservation matrix at landscape level, open forests with large old trees and closed young stands must also be protected to conserve the full species assemblage. On the other hand, management must include some strategies to maintain the natural heterogeneity of uneven-aged stands at a ranch level by: (i) maintaining some retention patches in the managed stands; (ii) maintaining some regeneration patches with close canopy (e.g. old gaps that are naturally regenerated); (iii) promoting the conservation of trees with different age, leading to some heterogeneity inside the managed stands; and (iv) conserving some legacies associated to biodiversity (e.g. large woody debris, snags).

Conclusions

We can conclude that uneven-aged forests showed high conservation values compared to even-aged stands, and where mature trees have better values than young growth stages. These results provide novel insights into the important ecological associations between understory plant communities and structural diversity of the ñire forests. It was widely recognized that the maintenance of biodiversity associated with structural and functional complexity could not rely solely on large old trees in the stands or left-aside reserves. It is necessary to consider the attributes at stand level to improve sustainable management planning. Therefore, in managed forests, silvicultural systems must be able to develop or maintain forest attributes related to the biodiversity. Further research and monitoring are still required to optimize silvopastoral proposals for a wide variety of management and conservation objectives.

Ethical statement The authors inform that there are no conflicts of interest in the content of this article, and does not contain any studies with human or animal subjects.

Appendix

See Table 5.

Table 5 Vascular plant species list indicating code, taxonomy type (D = dicots, M = monocots, F = ferns), origin (N = native, E = exotic), life-form (PH = prostrate herb, EH = erect herb, S = shrub, DS = dwarf-shrub, T = tree, CG = caespitose grass, RG = rhizomatous grass) and mean cover (%), classified according to the different age structures of *Nothofagus antarctica* stands (IGP = even-aged stands at initial optimum development growth phase, FGP = even-aged stands at final optimum development growth phase, M = even-aged stands at mature development growth phase, D = even-aged stands at decaying development growth phase, UOG = uneven-aged stands combining mature or decaying development growth phases and initial or final optimum development growth phases, UMD = uneven-aged stands combining mature and decaying development growth phases)

CODE	Species	Type	Origin	Life-form	IGP	FGP	M	D	UOG	UMD
ACMA	*Acaena magellanica*	D	N	PH	–	0.25	0.76	0.79	0.75	1.66
ACOV	*Acaena ovalifolia*	D	N	PH	0.67	1.80	0.45	1.21	0.67	1.75
ACPI	*Acaena pinnatifida*	D	N	EH	–	–	0.14	0.14	0.22	0.22
ADCH	*Adenocaulon chilensis*	D	N	EH	0.33	1.25	0.05	1.29	0.17	–
AGCO	*Agoseris coronopifolium*	D	N	EH	–	–	0.05	–	0.19	–
ARPA	*Arjona patagonica*	D	N	EH	–	–	–	–	0.33	–
ARMA	*Armeria maritima*	D	N	EH	–	–	–	–	0.03	0.06
ASVA	*Asther valhi*	D	N	EH	–	–	0.02	–	–	–
AZCE	*Azorella cespitosa*	D	N	DS	–	–	–	–	–	0.06
AZFU	*Azorella fuegiana*	D	N	DS	–	–	–	–	0.03	0.03
AZTR	*Azorella trifurcata*	D	N	DS	–	–	0.07	1.14	0.08	0.63
BAMA	*Baccharis magellanica*	D	N	S	–	–	–	–	–	0.03
BEBU	*Berberis buxifolia*	D	N	S	1.83	0.20	1.76	0.71	1.58	2.41
BOGU	*Bolax gummifera*	D	N	DS	–	–	0.02	–	–	–
CABI	*Calceolaria biflora*	D	N	EH	–	–	0.12	–	0.11	0.09
CAGL	*Cardamine glacialis*	D	N	EH	0.17	0.50	0.10	–	0.53	0.25
CASA	*Caltha sagittata*	D	N	PH	–	–	0.02	–	–	–
CEAR	*Cerastium arvense*	D	N	PH	–	0.40	0.67	0.36	0.25	1.22
CHDI	*Chilliotrichum diffusum*	D	N	S	1.83	0.15	0.29	0.50	1.72	1.16
COSC	*Cotula scariosa*	D	N	PH	3.50	1.70	5.31	0.50	2.67	7.72
DRMA	*Draba magellanica*	D	N	EH	–	0.05	0.07	–	0.08	–
DYGL	*Dysopsis glechomoides*	D	N	PH	–	0.15	–	0.14	0.14	0.06
EMRU	*Empetrum rubrum*	D	N	S	0.33	0.05	0.21	0.29	0.06	–
EPAU	*Epilobium australe*	D	N	EH	–	–	0.02	–	–	–
ERMY	*Erigeron myosotis*	D	N	EH	–	–	0.14	0.14	0.14	0.25
EUAN	*Euphrasia antarctica*	D	N	EH	–	–	0.02	–	–	0.09
GAAN	*Galium antarcticum*	D	N	PH	0.83	0.20	0.74	–	0.64	0.75
GAAP	*Galium aparine*	D	N	PH	3.33	5.60	1.88	0.79	4.39	1.97
GAFU	*Galium fuegianum*	D	N	PH	–	–	0.48	0.14	0.39	0.44
GASP	*Gamochaeta spiciformis*	D	N	EH	–	–	0.02	0.07	0.08	0.09
GEPO	*Gentiana postrata*	D	N	PH	–	–	0.05	–	–	–

Table 5 continued

CODE	Species	Type	Origin	Life-form	IGP	FGP	M	D	UOG	UMD
GNMA	*Gentianella magellanica*	D	N	EH	–	–	0.02	0.14	0.06	0.09
GEMA	*Geum magellanicum*	D	N	EH	0.17	0.30	0.48	0.43	0.14	0.56
GUMA	*Gunnera magellanica*	D	N	PH	–	–	0.12	0.14	0.06	–
HYAR	*Hypochaeris arenaria*	D	N	EH	–	–	0.07	0.07	0.06	–
CODE	Species	Type	Origin	Life–forms	IGP	FGP	M	D	UOG	UMD
LEVU	*Leucanthemum vulgare*	D	N	EH	–	–	–	–	0.03	–
LEHA	*Leucheria hahnii*	D	N	EH	–	–	–	–	0.03	0.03
LEPU	*Leucheria purpurea*	D	N	EH	–	–	–	–	0.03	–
NOAN	*Nothofagus antarctica*	D	N	T	16.00	1.50	3.64	3.64	2.78	4.22
NOPU	*Nothofagus pumilio*	D	N	T	–	–	0.05	–	–	0.03
OSDE	*Osmorhiza depauperata*	D	N	EH	15.00	13.30	4.14	6.50	7.69	7.38
OSCH	*Osmorhiza chilensis*	D	N	EH	2.00	1.40	3.40	2.50	4.50	1.03
OXEN	*Oxalis enneaphylla*	D	N	PH	–	–	–	0.07	0.06	0.13
OXMA	*Oxalis magellanica*	D	N	PH	–	0.05	0.02	–	–	0.03
PELA	*Perezia lactucoides*	D	N	EH	–	–	0.02	–	0.03	0.13
PEPU	*Pernettya pumila*	D	N	DS	0.17	0.05	0.02	–	0.06	0.19
PRRE	*Pratia repens*	D	N	PH	1.33	–	0.67	0.50	0.14	0.22
PRMA	*Primula magellanica*	D	N	EH	–	–	0.02	–	–	–
RABI	*Ranunculus biternatus*	D	N	PH	–	–	0.10	–	0.03	0.03
RAMA	*Ranunculus maclovianus*	D	N	EH	–	0.05	0.05	–	–	0.06
RAPE	*Ranunculus peduncularis*	D	N	EH	–	0.10	0.07	0.21	0.22	0.06
RARE	*Ranunculus repens*	D	N	EH	–	–	–	–	–	0.03
RASE	*Ranunculus sericocephalus*	D	N	EH	–	–	–	–	–	0.03
RIMA	*Ribes magellanicum*	D	N	S	0.17	0.10	0.10	0.07	0.03	0.09
RUGE	*Rubus geoides*	D	N	DS	–	–	0.07	–	–	0.06
SCRA	*Schizeilema ranunculus*	D	N	PH	2.00	0.55	1.26	0.50	0.50	0.53
SEAC	*Senecio acanthifolius*	D	N	EH	–	–	–	–	–	0.03
SEMA	*Senecio magellanicum*	D	N	EH	–	–	0.02	0.43	0.08	0.16
SEPA	*Senecio patagonicus*	D	N	EH	–	–	–	–	–	0.06
STDE	*Stellaria debilis*	D	N	PH	–	0.40	0.21	–	0.03	0.16
TAGI	*Taraxacum gilliesii*	D	N	EH	–	0.15	0.40	0.21	0.28	0.34

Table 5 continued

CODE	Species	Type	Origin	Life-form	IGP	FGP	M	D	UOG	UMD
THMA	*Thlaspi magellanicum*	D	N	EH	–	–	–	–	–	0.06
VIMA	*Vicia magellanica*	D	N	PH	–	0.05	0.33	–	0.36	0.56
VOMA	*Viola magellanica*	D	N	PH	–	0.30	0.07	0.14	1.61	0.13
VORI	*Viola richei*	D	N	PH	0.17	–	0.19	0.07	0.22	0.06
ACMI	*Achillea millefolium*	D	E	EH	–	–	1.14	0.93	1.25	0.19
CABU	*Capsella bursa–pastoris*	D	E	EH	–	–	–	0.07	0.03	0.06
CEFO	*Cerastium fontanum*	D	E	PH	–	1.00	1.00	0.14	0.81	0.69
CRCA	*Crepis capillaris*	D	E	EH	–	0.05	–	–	–	–
HIPI	*Hieracium pillosella*	D	E	PH	–	0.05	0.10	0.21	0.50	0.97
RUAC	*Rumex acetosella*	D	E	EH	–	0.40	2.05	0.57	1.69	2.41
RUCR	*Rumex crispus*	D	E	EH	–	–	–	–	–	0.03
SAPR	*Sagina procumbens*	D	E	PH	–	0.05	–	–	–	–
STME	*Stellaria media*	D	E	PH	–	0.70	0.05	0.14	0.03	0.03
TAOF	*Taraxacum officinale*	D	E	EH	2.00	9.20	10.93	7.00	12.11	9.25
TRDU	*Trifolium dubium*	D	E	EH	–	0.20	–	–	–	–
TRRE	*Trifolium repens*	D	E	EH	–	2.30	1.60	0.86	0.33	0.81
VESE	*Veronica serpyllifolia*	D	E	PH	–	0.55	0.14	–	0.14	0.06
AGIN	*Agrostis inconspicua*	M	N	CG	0.17	–	0.07	0.07	0.25	0.06
AGLE	*Agrostis leptotricha*	M	N	RG	–	–	0.17	0.07	0.11	–
CODE	Species	Type	Origin	Life–forms	IGP	FGP	M	D	UOG	UMD
AGME	*Agrostis meyenii*	M	N	CG	–	–	–	–	–	0.03
AGPE	*Agrostis perennans*	M	N	CG	–	–	0.52	0.71	0.03	0.09
AGUL	*Agrostis uliginosa*	M	N	CG	–	–	0.05	–	–	–
AGFU	*Agropyron fuegianum*	M	N	CG	–	–	0.05	–	–	–
AGPU	*Agropyron pubiflorum*	M	N	RG	–	–	0.12	–	0.03	–
ALMA	*Alopecurus magellanicus*	M	N	CG	–	0.25	0.81	0.14	0.25	0.75
ARUN	*Arachnitis uniflora*	M	N	EH	–	–	–	0.07	–	–
BRUN	*Bromus unioloides*	M	N	CG	0.17	4.30	3.86	4.43	2.47	4.09
CACU	*Carex curta*	M	N	RG	–	–	0.52	–	–	–
CAFU	*Carex fuscula*	M	N	RG	–	–	0.05	–	–	–
CAMA	*Carex macloviana*	M	N	RG	–	–	0.29	–	0.03	0.06
COLE	*Codonorchis lesonii*	M	N	EH	–	–	–	0.07	–	0.03
DEAN	*Deschampsia antarctica*	M	N	CG	–	–	0.24	–	0.03	0.03
DEFL	*Deschampsia flexuosa*	M	N	RG	11.33	2.95	2.43	3.36	2.53	2.63

Table 5 continued

CODE	Species	Type	Origin	Life-form	IGP	FGP	M	D	UOG	UMD
ELAG	*Elymus agropyroides*	M	N	RG	–	0.20	2.14	2.71	0.69	2.50
FEGR	*Festuca gracillima*	M	N	CG	–	–	–	0.71	0.06	–
FEMA	*Festuca magellanica*	M	N	CG	0.50	0.70	4.21	8.29	2.69	7.59
FEPY	*Festuca pyrogea*	M	N	CG	–	0.05	0.02	–	–	0.03
HIRE	*Hierochloë redolens*	M	N	RG	–	–	0.02	–	–	–
HOCO	*Hordeum comosum*	M	N	CG	–	0.10	0.67	1.07	0.19	0.16
JUSC	*Juncus scheuzeroides*	M	N	RG	–	–	–	–	0.11	0.19
KOFU	*Koeleria fueguina*	M	N	RG	–	–	0.05	–	–	–
LUAL	*Luzula alopecurus*	M	N	CG	–	0.10	0.17	0.36	0.14	0.63
PHBI	*Phaiophleps biflora*	M	N	EH	–	–	0.05	–	0.19	0.16
PHAL	*Phleum alpinum*	M	N	CG	0.50	0.45	4.57	2.00	2.17	3.91
POAL	*Poa alopecurus*	M	N	CG	–	–	–	–	0.03	0.03
TRSP	*Trisetum spicatum*	M	N	CG	0.33	0.30	1.60	7.00	1.94	3.75
UNLE	*Uncinia lechleriana*	M	N	RG	–	–	0.10	0.50	0.42	0.34
AGCA	*Agrostis capillaris*	M	E	RG	–	0.10	0.02	–	0.86	0.16
DAGL	*Dactylis glomerata*	M	E	CG	–	0.05	0.02	–	1.28	0.06
FEOV	*Festuca ovina*	M	E	CG	–	–	2.38	0.71	0.83	0.03
HOLA	*Holcus lanatus*	M	E	CG	1.67	4.85	2.67	3.57	2.28	2.25
POAM	*Poa ampla*	M	E	CG	–	–	–	–	–	0.03
POPR	*Poa pratensis*	M	E	RG	0.67	14.35	11.86	7.50	10.69	14.75
POTR	*Poa trivialis*	M	E	CG	–	0.05	–	–	–	–
BLPE	*Blechnum penna–marina*	F	N	PH	1.00	4.20	3.36	9.57	5.06	2.66
CYFR	*Cystopteris fragilis*	F	N	EH	–	0.05	0.14	0.43	0.17	0.44
LYMA	*Lycopodium magellanicum*	F	N	PH	–	–	–	–	0.03	0.03

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