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PLANT RICHNESS AND LIFE FORM DIVERSITY ALONG VEGETATION AND FOREST USE GRADIENTS IN NORTHWESTERN PATAGONIA OF ARGENTINA

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HIGHLIGHTS

Dense stands exhibited reduced solar radiation and plant diversity in the understory, and water content in the topsoil.

Rocky outcrops showed a restricted size but a high diversity of native plants.

Fenced vegetation units have a higher plant cover and diversity than their unfenced counterparts.

Compatibility between plant diversity and timber production requires fencing and an ample tree spacing.

Keywords:
Natural forest
Pinus ponderosa
Planted forest
Rocky outcrop
Wetland

ABSTRACT

The imbalace between the increase in the demand and the decrease in the supply of products from natural forests, partly explains the on-going development of exotic tree plantations. In northwestern Patagonia of Argentina, *Pinus ponderosa* (Pinaceae) afforestation plays a key role in ameliorate degraded soils, but may also reduce biodiversity. The ecological sustainability of this activity was assessed in Aguas Frías (38°46´ W, 70°54´ S) and Litrán (38°54´ W, 71°01´ S) forest stations, where species richness and life form diversity of plants were compared in vegetation units, fenced and unfenced against livestock. Eleven vegetation units were identified, including natural herbaceous-shrubby steppes, xerophilous and hygrophilous meadows, pure and mixed forests of *Nothofagus pumilio* (Nothofagaceae) and *Araucaria araucana* (Araucariaceae), and *P. ponderosa* planted forests of dissimilar canopy cover. Xerophilous meadows on rocky outcrops held 1/3 of total richness in an extremely restricted area. Hygrophilous meadows exhibited the largest number of families and native and exotic species, and lower diversity of life forms. Dense pine stands exhibited low values of light in the undergrowth, water in the topsoil, cover of undergrowth plants, frequency of hemicriptophytes and richness and diversity of life forms. As canopy cover decreased, values for these indicators resembled those of the steppe of reference. Within a plantation, greater compatibility between conservation of diversity and wood production requires maintenance of fencing, reduced tree spacing over long rotations and the development of buffer zones and biological corridors. Although such a project may represent a decline in productivity, it will promote enhanced ecosystem and aesthetic values, increasing the likelihood of further economic support from society.

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INTRODUCTION

Over the last 50 years natural forests of native species have been severely transformed by anthropogenic activities (Lindquist et al., 2013). At the same time, the need for goods and services from these ecosystems continues to increase (FAO, 2018). The current imbalance between the supply and demand of forest resources partly explains the growing establishment of tree plantations through afforestation and reforestation programmes (Overbeek et al., 2012). The environmental sustainability of these plantations generates conflicting views, considering them everything from valuable habitats for indigenous biota (Carnus et al., 2006), to "green deserts" (Overbeek et al., 2012). Biological diversity constitutes an indicator of ecosystem functioning and resilience, and therefore makes it possible to measure the relationship between environment and human activity (Haines-Young, 2009).

The interacting factors that control the species diversity of plants operate along gradients, and are linked to the local and regional gene pool and performance of populations, environmental conditions, spatial heterogeneity, and stress and disturbance (Drakare et al., 2006). In particular, the effect of plantations on diversity depends on the previous land use, the structure and conservation of original vegetation, the origin, composition, canopy cover and physiognomy of the trees, and the silvicultural prescriptions. Intensive silviculture tends to be detrimental to diversity, since it reduces the availability of essential aerial and subterranean resources, and also precludes the existence of stands in advanced stages of development, reducing the abundance of snags and large trees and encouraging the dominance of one or few species (Bremer and Farley, 2010).

Functional diversity is the constituent of plant diversity that measures the value of physical, biochemical, phenological or behavioural traits, observably or operationally defined, which potentially affect organism performance and ecosystem processes (Devictor et al., 2010). Weiher (2011) proposed that species coexistence depends on high degrees of trait dispersion, implying that community is structured by competition, and low levels of stress. In contrast, Kleidon et al. (2009) claimed that coexisting species tend to be phenotypically similar because habitat filters certain traits. Although functional diversity can predict productivity, stability and resource dynamics more accurately than taxonomic diversity, its measurement is complex due to the incomplete knowledge of exactly which species characteristics affect community functioning (Tilman, 2001). Therefore, patterns might be more easily interpreted when considering both taxonomic and functional diversity (Cadotte et al., 2011).

The life form of a plant represents plant morphology as an adjustment to ecological conditions. Individuals with a particular life form are expected to exhibit similar responses to environmental variation and to exert analogous effects on ecosystem processes (Tilman, 2001). Life form classification is based on the position and protection of renewal buds (Raunkiær, 1934). The life form structure of a community can be represented by both floristic and vegetational biological spectra. The floristic spectrum represents the relative number of species with each life form, and therefore every species makes the same contribution to the community. The vegetational spectrum considers species abundance, and consequently each class is weighted by frequency; it takes into account the occurrence of vegetation rather than flora and is more readily comparable to spectra from other sites (Batalha and Martins, 2004).

In northwestern Patagonia of Argentina, afforestation was initiated in the 1970s in non-irrigated areas within the forest - steppe transition of the Andes foothills, and comprises around 100000 ha. *Pinus ponderosa* ((Dougl.) Laws, Pinaceae) occupies 95% of this area due to its satisfactory growth under the prevailing dry, windy summer conditions and cold winters (MAGyP, 2014). Pines were mostly planted in natural pastures that were severely degraded, due mainly to overgrazing (MAGyP, 2014). These plantations contribute to reducing soil erosion, conserving fragile ecosystems and capturing CO_2 (Frugoni et al., 2016; Laclau et al., 2017). However, they can invade surrounding communities (Simberloff et al., 2010) and increase the fire hazard (Loguercio et al., 2011). The effect of these plantations on species richness has been evaluated in insects (Corley et al., 2006), birds (Lantschner et al., 2008) and mammals (Lantschner et al., 2011, 2012). Plants, with their enormous potential for regulation of ecosystem structure and function, have received little attention.

The overall aim of our study was to assess the ecological sustainability of afforestation with *P. ponderosa* at management unit level, within a single geomorphological zone and under different silvicultural regimes. In particular, we investigated the baseline of species richness and life form diversity for vascular plants in contrasting vegetation units. We described how diversity diverged from open units, dominated by herbs and shrubs in steppes and meadows, to closed units occupied by trees in natural and planted forests. We analysed the relationship between life form assemblage and the structural heterogeneity of pine stands, particularly in relation to the steppe as the ecosystem of reference. The effect of fencing was also evaluated, in terms of protection against consumption and trampling of livestock, both of which affect plant diversity. A species - assemblage study across a range of managed and unmanaged vegetation units, provides a means of exploring the value of plantations for harbouring wild plants, as a long term diversity conservation strategy complementary to that of the natural areas afforded by set-asides alone (Chown and McGeoch, 2011).

We hypothesized that although richness and life form diversity vary greatly between units, plantations show lower values than natural forests, regardless of their composition and structure. Within *P. ponderosa* stands, variability among structural types is mostly related to population pattern and competition. However, open *P. ponderosa* stand diversity approaches that of the steppe, due not only to greater heterogeneity, related to plant size, life form and habitat, but also a larger quantity of resources for understory plants, related to light and water. The silvicultural practice of fencing improves the conservation status of communities, which is evidenced in higher diversity values. Afforestation can be compatible with both timber production and provision of food, habitat and connectivity for wild flora and fauna. Such a strategy involves trade-offs that are plausible if plantation ecology is taken into account on temporal and spatial scales (CBD, 2019).

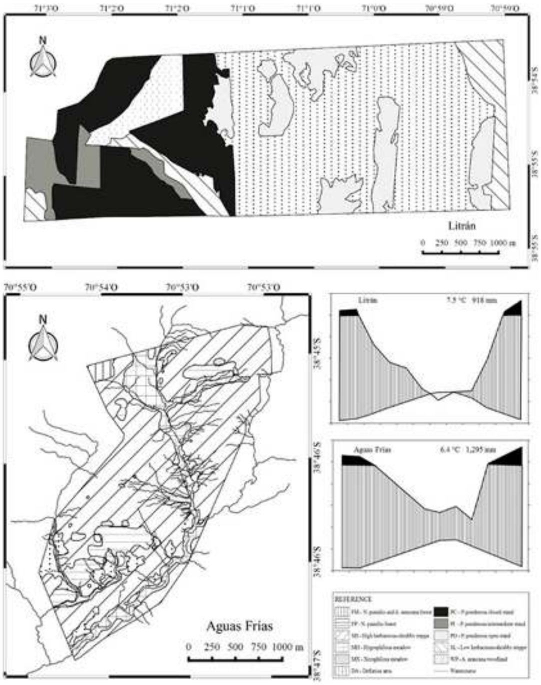

FIGURE 1 Vegetation units and climatic diagrams of Aguas Frías and Litrán..

MATERIALS AND METHODS

Study area

The study area comprised the forest stations Aguas Frías (38°46´ W, 70°54´ S, 1590 m a.s.l., 456 ha) and Litrán (38°54´ W, 71°01´ S, 1400 m a.s.l., 1310 ha). Climate is warm-summer Mediterranean (Csb) (Peel et al., 2007; AIC, 2015) (Figure 1). Geomorphology burden of Holocene tephra from the active volcanoes of the Andes. These rocks constitute the parent material of the well-developed and dominant allophanic Udivitrand and Endoaquand Andisols (Frugoni et al., 2016). The vegetation represents a transition between the semiarid Patagonian and the humid Subantarctic ecoregions, and steppe plants predominate in the bottomlands on zonal soils (Oyarzábal et al., 2018). *Nothofagus* (Nothofagaceae) forests grow at mid elevation on slopes of different exposures in the western part of the study area, and open woodlands of varying composition lie to the east, surrounded by the steppe (Frugoni et al., 2016). This area has traditionally been used as a migration route for the nomadic ranching of goats and sheep, as they went from bottom valleys in winter to higher elevations in summer. Here, higher pastures are located from 1,400 to 1,700 m a.s.l., approximately. Plants are intensely overgrazed and burnt as a consequence of this practice (Frugoni et al., 2016). Pines were planted in the deep, well-drained soils of the steppe between 1991 and 1995 in Litrán, and in 2010 in Aguas Frías. A fence against livestock circumscribed the forest stations, and a fire control system was implemented.

Vegetation units, soil features and solar radiation

Vegetation units were identified on an Aster satellite image (resolution 15 m, Gauss Krüger coordinates band 1, ellipsoid WGS 1984), using vegetation composition and structure as guiding criteria; the resulting cartography was verified in the field. In each unit, 10 sampling sites were equidistantly located within the boundaries of forest stations (fenced condition). In addition, 10 sampling sites were selected near Aguas Frías, in units covered by natural forest and steppe (unfenced condition). In each sampling site, geographical position (GPS), altitude (altimeter), slope (clinometer, metric tape) and exposure (compass) was recorded. Soil bulk density (*SBD*) was estimated during the dry season through the cylinder method, by randomly removing three samples of the soil A-horizon, which was then weighed in the laboratory (metal cylinder with three mobile rings, scale precision 0.001 g, n = 3) (SAMLA, 2004). During the dry season, soil moisture (*SM*) was estimated through the gravimetric method, by collecting soil samples of the A-horizon from each unit, which were hermetically stored and weighed in the laboratory, then dried for 24 h at 90 °C and weighed again (oven, scale precision 0.001 g, n = 3) (SAMLA, 2004). Photosynthetically active radiation (*PAR*) was measured at 0.2 m aboveground, as relative intensity in comparison with an adjacent fully open area, using a light receiver LI-250 and a quantum sensor LI-190SA (LI COR, Inc., n = 10) (Mottus et al., 2011).

Vegetation structure and diversity

In each unit covered by pure and mixed natural forests, a 1000 m^2- permanent sampling plot was chosen at random, and all living trees, including adults (diameter at base height $d_b \geq 0.1$ m) and saplings ($d_b < 0.1$ m, height $h > 0.1$ m), were measured for d_b (diameter tape, calliper) and *h* (hypsometer, metric tape). Seedlings ($d_b < 0.1$ m, $h \leq 0.1$ m) were counted in 20 0.5 m^2- square plots systematically located within the main plot. *Pinus ponderosa* stands were categorized as open (< 15 m^2/ha basal area, *BA*), intermediate (15 - 30 m^2/ha), and closed (> 30 m^2/ha) using a forest inventory classification (CFI, 2009). In each structural category, a 400 m^2- plot was randomly installed and trees were measured for d_b. Mean distance between pines (*d*, m) was estimated using tree density (*D*, ind/ha), according to $d = (10000 □ D)^{0.5}$. Four trees with the thickest and one with the thinnest trunk were measured for length of the five internodes above $h = 1.3$ m (l_5, m, metric tape). In each stand, site index for a reference age of 20 years (SI_{20}, m) was calculated as $SI_{20} = 4.37 + 14.86\, l_5 / 5$ (Andenmatten and Letorneau, 2003).

From the centre of each sampling site, four 10 m- transects were installed following the N, S, E and W directions. On each transect 10 sampling points were located 1 m apart to determine the frequency of bare soil (*BS*), crown cover of adult trees (*CC*), total (S_t) and mean (□) species richness, life form richness (*LFR*) and diversity (*LFD*), and floristic (*FBS*) and vegetational (*VBS*) spectra of vascular plants, based on frequency data and the point-intercept method (Kent, 2011). Plants were classified according to species, origin (native, exotic), life cycle (perennial, biannual, annual) (IBD, 2019) and life form (Raunkiær, 1934; Bertolami et al., 2008). All variables expressed as percentages were normalized through transformation into angular values prior to determining the effects of ANOVA. A *Chi-square* test was applied to verify whether spectra were significantly different from those expected under a random distribution of life forms. *LFR* and *LFD* were calculated through the FD package (Villéger et al., 2008; Laliberté et al., 2019). Comparisons of S_t, $\hat{S}$, *LFR* and *LFD* between units and fencing condition were performed with univariate and bivariate statistical methods.

RESULTS

Vegetation units, soil features and solar radiation

In the study area, 11 vegetation units were identified, covered by steppes, meadows, and natural and planted pure and mixed forests and woodlands. In Aguas Frías, units were categorized as "natural" because of the evolutive origin of the dominant plants. These were the high herbaceous-shrubby steppe (SH, 69.4% of the station area), the hygrophilous (MH, 15.1%) and xerophilous meadows (MX, 1.1%), the deflation area of pyroclastic material (DA, 5.8%), the pure forest of deciduous broadleaved *Nothofagus pumilio* ((Poepp. & Endl.) Krasser, Nothofagaceae) (FP, 7.6%) and mixed forest of *N. pumilio* and the evergreen conifer *Araucaria araucana* ((Molina) K. Koch, Araucariaceae) (FM, 1.0%). In Litrán, the natural units were DA (45.1%), the low herbaceous-shrubby steppe (SL, 8.8%) and the *A. araucana* woodland with dispersed *Nothofagus antarctica* ((G. Forst.) Oerst.) deciduous trees (WP, 4.8%). The "artificial" units with planted dominant species were the *P. ponderosa* open (PO, 12.8%), intermediate (PI, 5.1%) and closed forest (PC, 23.5%) (Figure 1).

Mean *SBD* was 0.66 g/cm^3 (SE = 0.05); means did not significantly differ between units (Table 1, Figure 2). Mean *SM* was 24.7% (SE = 5.8), with a minimum value in PC (9.6%, SE = 0.9) and a maximum in unfenced high steppe SH_u (78.8%, SE = 2.1); means significantly differed between units: PC (9.6%, SE =

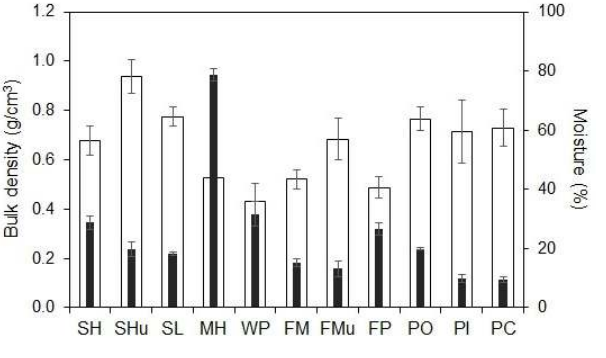

FIGURE 2 Bulk density (empty bar) and moisture (filled bar) of soil A-horizon in Aguas Frías and Litrán. Vertical bars indicate the standard error of the mean. Mean soil moisture differs among units (LSD test, $p < 0.05$, n = 3). SH: high herbaceous-shrubby steppe, fenced and (u) unfenced, SL: low herbaceous-shrubby steppe, MH: hygrophilous meadow, WP: *A. araucana* woodland, FM: *N. pumilio* and *A. araucana* forest fenced and (u) unfenced, FP: *N. pumilio* forest, PO: *P. ponderosa* open forest, PI: P. ponderosa intermediate forest, and PC: *P. ponderosa* closed forest..

0.9) and PI (9.9%, SE = 1.4) showed a lower value than PO (19.9%, SE = 0.4). Mean *SM* did not differ between FM (13.2%, SE = 2.6) and FM_u (15.2%, SE = 1.2), whereas it did vary between SH (28.7%, SE = 2.2) and SH_u (19.8%, SE = 2.5) (Table 1, Figure 2). In forest units, *SM* decreased as *CC* increased (ANOVA, F = 5.72, p = 0.042, n = 7) (Figure 3). Mean *BS* was 44.0% (SE = 2.6); means significantly differed between units (Table 1): PC (89.3%), PI (85.4%), and DA (83.6%) showed the greatest values, whereas MH (5.9%) and MX (17.5%) showed the lowest values. Mean *BS* was statistically lower in fenced than in unfenced condition (SH, 27.1%, SE = 4.4; SH_u, 40.2%, SE = 5.7; FM, 34.1%, SE = 9.2; FM_u, 51.4%, SE = 3.5) (*t* test, $p < 0.05$). *BS* in PI (83.6%, SE = 3.8) and PC (89.3%, SE = 3.6) was significantly lower than in PO (28.2%, SE = 3.7). *BS* showed a direct relationship with *CC* in pine stands (ANOVA, F = 93.01, $p < 0.001$, n = 30), and an inverse relationship with *SM* in all forest units (ANOVA, F = 157.46, $p < 0.001$, n = 11) (Figure 4). Mean *PAR* was 2.0% in PC (SE = 0.5), 13.0% in FM (SE = 9.7), 13.9% in FM_u (SE = 9.4), 16.3% in PI (SE = 7.3), 24.5% in WP (SE = 8.3), 31.9% in FP (SE = 7.9) and 42.0% in PO (SE = 3.9). These values were significantly different from each other, but FM and FM_u showed the same statistical mean (*t* test, F = 0.00, p = 0.946) (Table 1). In forest units, *PAR* decreased as *CC* increased (ANOVA, F = 44.49, $p < 0.001$, n = 7) (Figure 3).

TABLE 1 Analysis of variance for physical and biological variables of the vegetation units of Aguas Frías and Litrán. The degrees of freedom (df), F-quotient and sample size (n) are shown, (*) denotes significant differences of means between units, based on LSD test ($p < 0.05$), ns: non-significant. (1) Based on hemicryptophytes..

Variable	df	F	p	n
Soil bulk density (g/cm3)	44	2.0	0.063ns	3
Soil moisture (%)	41	47.4	< 0.001*	3
Bare soil (%)	129	38.2	< 0.001*	10
Light intensity bellow canopy (%)	69	2.7	0.019*	10
Species richness	129	17.8	< 0.001*	10
Plant families (number)	129	9.8	< 0.001*	10
Native species (%)	129	59.4	< 0.001*	10
Perennial species (%)	129	9.7	< 0.001*	10
Annual species (%)	129	5.7	< 0.001*	10
Tree species (%)	129	6.9	< 0.001*	10
Shrub species (%)	129	41.3	< 0.001*	10
Herb species (%)	129	62.5	< 0.001*	10
Floristic spectrum(1)	129	13.6	< 0.001*	10
Vegetational spectrum(1)	129	38.0	< 0.001*	10
Life form richness	129	3.4	< 0.001*	10
Life form diversity	129	12.1	< 0.001*	10

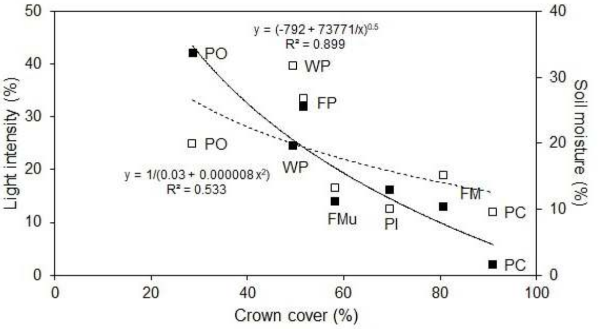

FIGURE 3 Light intensity (black square, continuous line) and soil moisture (white square, dashed line) related to crown cover in Aguas Frías and Litrán. The parameters of the regression function and the coefficient of determination (R2) are indicated (ANOVA, $p < 0.05$, n = 7). WP: A. araucana woodland, FM: N. pumilio and A. araucana forest fenced and (u) unfenced, FP: N. pumilio forest, PO: P. ponderosa open forest, PI: P. ponderosa intermediate forest and PC: P. ponderosa closed forest.

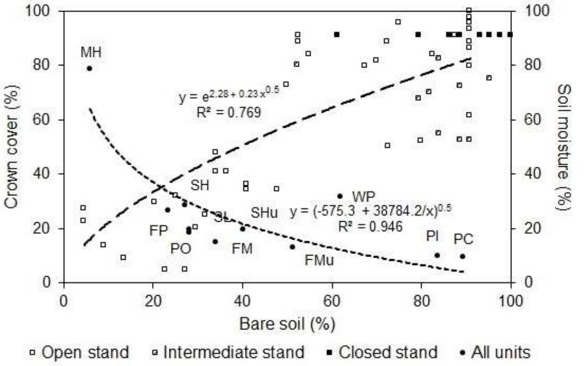

FIGURE 4 Crown cover (continuous line, primary y-axis) and soil moisture (dashed line, secondary y-axis) related to bare soil in the P. ponderosa stands (ANOVA, F = 93.01, $p < 0.000$, n = 30) and in all vegetation units (ANOVA, F = 157.46, $p < 0.000$, n = 11) of Aguas Frías and Litrán. The parameters of the regression function and the coefficient of determination (R2) are indicated. SH: high herbaceous-shrubby steppe, fenced and (u) unfenced, SL: low herbaceous-shrubby steppe, MH: hygrophilous meadow, WP: A. araucana woodland, FM: N. pumilio and A. araucana forest fenced and (u) unfenced, FP: N. pumilio forest, PO: P. ponderosa open forest, PI: P. ponderosa intermediate forest and PC: P. ponderosa closed forest.

Forest structure and plant richness

In woodland and forests, *D* varied from 95 ind/ha (WP) to 775 ind/ha (PC), and *BA* from 11.1 m²/ha (PO) to 97.7 m²/ha (FM). *Pinus ponderosa* stands differed in mean d_b, *D*, *BA* and *CC*; PO presented the lowest and PC the largest values. The potential for growth of the pine trees was equivalent, as stands belonged to the same site index class (Table 2). The diameter-class frequency distribution of natural forests differed between species. *Araucaria araucana* approached an irregular, multi-modal size distribution in which for mixed forest, small individuals (d_b = 10 -

TABLE 2 Structure of forests and woodlands in Aguas Frías and Litrán. nd: no data.

Variable		*N. pumilio* and *A. araucana* forest		*A. araucana*	*P. ponderosa* plantation		
		Mixed	Pure	woodland	Open	Intermediate	Closed
Density (ind/ha)	Adult	235	128	95	350	400	775
	Sapling	275	2105	10	-	-	-
	Seedling	1000	148000	-	-	-	-
Distance (m)		nd	nd	nd	5.3	5.0	3.6
Diameter (cm)		55.6	59.3	59.5	19.7	27.9	27.0
Height (m)		13.1	13.0	11.1	6.9	12.1	12.3
Site index (m)		nd	nd	nd	12.6	13.2	14.6
Basal area (m2/ha)		97.7	27.2	35.1	11.1	24.6	45.3
Crown cover (%)		80.7	51.6	47.1	28.6	69.5	90.9

39.9 cm) formed the largest category with 69.2% of total trees, and for the woodland, small (d_b = 10 - 19.9 cm) and intermediate (d_b = 60 - 69.9 cm) specimens formed the largest category, accounting for 68.4% of total trees. In contrast, *N. pumilio* approached a regular, normal distribution in which medium-sized trees comprised the most abundant class (Figure 5).

In the study area 154 species of plants were identified, *Carex* (Cyperaceae, 9 species), *Senecio* (Asteraceae, 8) and *Festuca* (Poaceae, 5) being the most diverse genera. S_t ranged from 16 (PC and PI) to 68 (MH). S_t was similar in FM (24) and FM$_u$ (23), whereas it differed in SH (47) and SH$_u$ (24) (Table 3). $\hat{S}$ statistically differed between units; the smallest value was found in PC (3.6) and the largest in MH (17.1). $\hat{S}$ was low and statistically similar in PC (3.6) and PI (4.9), but differed from PO (13.6). $\hat{S}$ did not differ between fenced and unfenced conditions; SH, $\hat{S}$ = 10.7 and SH$_u$, $\hat{S}$ = 8.5; FM, $\hat{S}$ = 7.5 and FM$_u$, $\hat{S}$ = 8.6 (*t* test, $p \geq 0.05$) (Tables 1 and 3). Plants belonged to 49 families, Asteraceae (27 species) and Poaceae (24) being the most diverse. Number of families statistically differed between units (Table 1); the lowest value was in PI (total 9, mean 3.2, SE = 0.5) and the largest in MH (23, 8.9, SE = 0.7). PI and PC (3.4, SE = 2.5) showed very low mean values, differing statistically from PO (8.4, SE = 0.3) (LSD test, $p < 0.05$). Although mean number of families tended to be higher in fenced than in unfenced condition, the differences were not significant (*t* test, $p \geq 0.05$). As a rule, *BS* and S_t showed an inverse relationship. In pine stands, there was a strong linear relation between these variables (ANOVA, $p < 0.001$, n = 30), whereas in natural units the function was polynomic, with lower goodness of fit (ANOVA, $p < 0.001$, n = 100); in both data sets, S_t variability was much higher below 60% of *BS* (Figure 6).

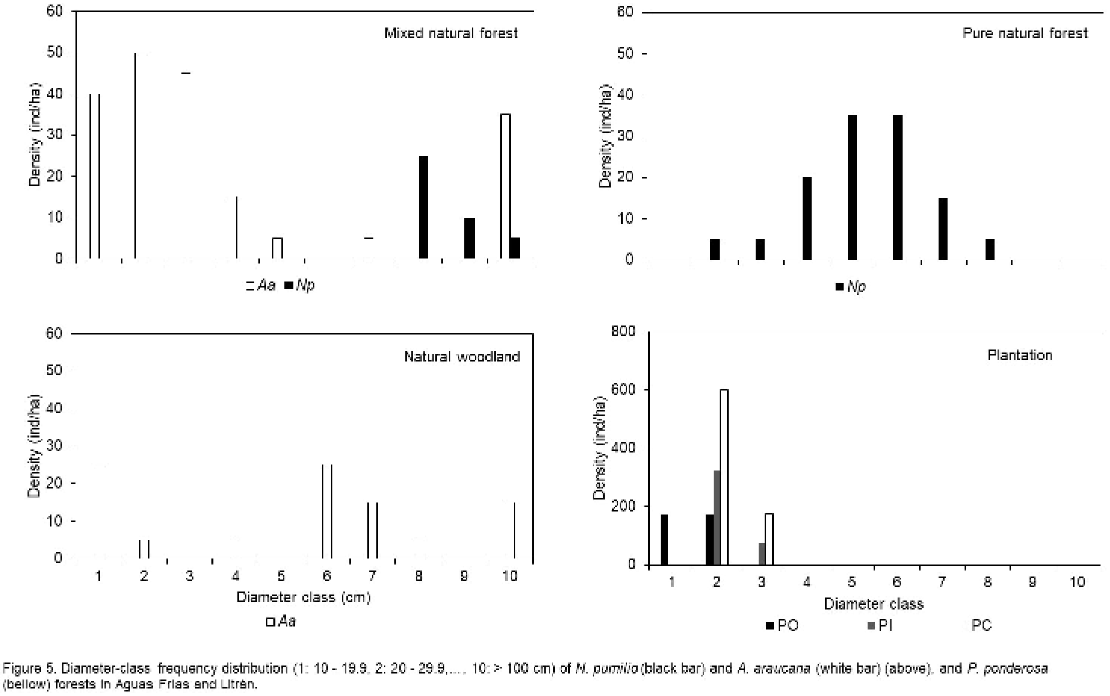

FIGURE 5 Diameter-class frequency distribution (1: 10 - 19.9, 2: 20 - 29.9,…, 10: > 100 cm) of N. pumilio (black bar) and A. araucana (white bar) (above), and P. ponderosa (bellow) forests in Aguas Frías and Litrán.

TABLE 3 Species richness and frequency (%) of native, perennial, annual, tree, shrub and herb species, difference (as the module) between the floristic (FBS) and vegetational (VBS) spectra and life form richness (LFR) and diversity (LFD) in the vegetation units of Aguas Frías and Litrán. Mean ($\bar{x}$) and standard error (SE) are shown. SH: high herbaceous-shrubby steppe, fenced and (u) unfenced, SL: low herbaceous-shrubby steppe, MH: hygrophilous meadow, MX: xerophilous meadow, DA: deflation area, WP: A. araucana woodland, FM: N. pumilio and A. araucana forest fenced and (u) unfenced, FP: N. pumilio forest, PO: P. ponderosa open forest, PI: P. ponderosa intermediate forest and PC: P. ponderosa closed forest.

Unit	Richness			Native		Perennial		Annual		Tree		Shrub		Herb		FBS-VBS		LFR		LFD	
	Total	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
SH	47	10.7	1.4	90.6	5.1	98.4	0.8	1.6	0.8	1.4	1.0	1.4	1.0	77.6	4.8	4.9	1.2	3.7	0.3	0.23	0.03
SHu	24	8.5	0.7	97.2	1.0	99.3	0.8	0.8	0.8	0.7	0.3	0.7	0.3	81.4	1.0	2.5	1.5	2.8	0.3	0.21	0.01
SL	38	14.8	1.0	82.2	0.9	99.2	0.5	0.7	0.5	1.3	0.7	1.3	0.7	94.2	1.5	3.5	2.0	2.6	0.3	0.08	0.02
MH	68	17.1	1.2	82.0	5.4	92.9	1.6	1.9	1.5	0.5	0.2	0.5	0.2	89.2	1.8	1.2	0.6	3.3	0.3	0.15	0.02
MX	50	12.1	0.9	98.5	0.8	100	0.0	0.0	0.0	10.5	3.2	10.5	3.2	55.7	4.5	1.7	0.8	3.0	0.2	0.29	0.01
DA	23	4.6	1.0	90.4	4.8	99.6	0.4	0.4	0.4	1.3	0.9	1.3	0.9	69.1	6.1	2.0	0.7	2.6	0.3	0.24	0.03
WP	28	9.1	1.1	78.7	4.3	99.0	0.5	1.0	0.5	44.9	6.0	1.7	0.9	52.9	5.8	9.5	5.6	2.9	0.4	0.26	0.02
FM	24	7.5	1.0	94.5	2.2	99.4	0.3	0.3	0.2	44.4	7.3	0.2	0.2	37.4	4.8	11.5	6.4	3.1	0.2	0.28	0.03
FMu	23	8.6	0.6	80.5	7.0	97.6	0.7	1.8	0.7	38.0	6.3	0.0	0.0	50.7	6.2	8.3	4.6	3.4	0.2	0.27	0.02
FP	42	11.9	1.1	83.1	3.7	97.8	0.9	1.9	0.9	28.5	3.8	0.9	0.5	54.0	2.7	10.5	3.8	4.2	0.2	0.31	0.01
PO	30	13.6	0.8	65.3	3.4	100	0.0	0.0	0.0	22.1	4.8	2.3	0.3	72.6	4.8	4.7	2.5	3.5	0.2	0.20	0.03
PI	16	4.9	1.0	9.7	2.9	99.6	0.2	0.4	0.2	90.6	2.9	3.3	0.9	6.0	2.2	17.1	8.3	2.9	0.4	0.09	0.02
PC	16	3.6	0.8	12.6	2.1	93.0	1.4	6.8	1.3	83.7	3.6	0.0	0.0	16.1	3.5	15.9	8.9	2.6	0.2	0.14	0.02
$\bar{x}$	33.0	9.8		74.1		98.1		1.3		28.5		1.9		58.1		7.2		3.1		0.21	
SE	4.2	1.1		2.7		0.3		0.3		2.8		0.4		2.5		1.5		0.13		0.02	

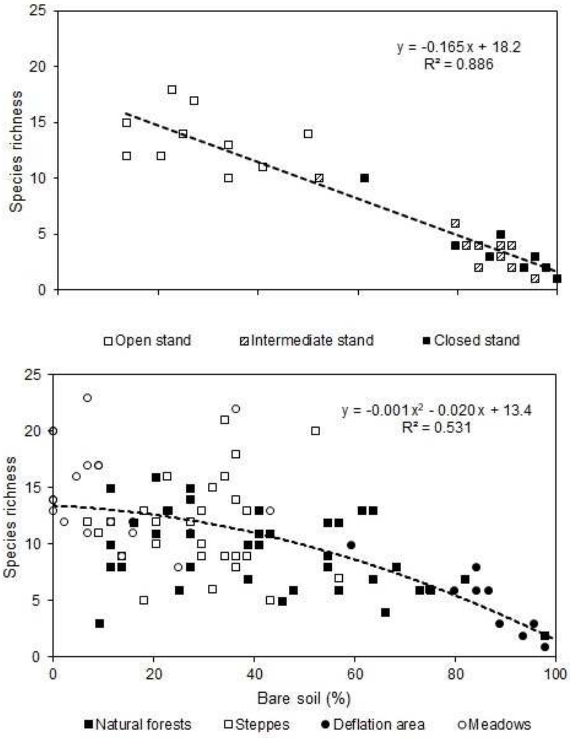

FIGURE 6 Bare soil and plant richness in the *P. ponderosa* stands (left) and natural vegetation units (right) of Aguas Frías and Litrán. The parameters of the regression function and the coefficient of determination (R^2) are indicated (ANOVA, $p < 0.05$).

PLANT FEATURES

The vast majority of plants in all units were native (94.2% of total species), whereas MH had the largest number of exotic species (7). Mean frequency of native species varied from 9.7% (PC) to 98.5% (MX), values which differed statistically between units (Tables 1 and 3). In pine stands the frequency of native plants was significantly higher in PO (65.3%) than in PI (12.6%) and PC (9.7%) (LSD test, F = 119.6, $p < 0.001$) (Tables 1 and 3). Mean frequency of native species did not differ between fenced and unfenced conditions; FM = 94.5% and FM_u = 80.5%, whereas SH = 90.6% and SH_u = 97.2% (*t* test, $p \geq 0.05$) (Table 3). Mean frequency of perennial species varied from 92.9% (SE = 1.6) in MH to 100% in PO and MX; these values differed statistically between units (Tables 1 and 3). Mean frequency of perennial species within the mixed forest and high steppe did not differ between fenced and unfenced conditions (*t* test, $p \geq 0.05$). Mean frequency of herbaceous species ranged from 6.0% in PO to 94.2% in SL; these values differed statistically between units (Tables 1 and 3). Within pine stands, herbs were less frequent in PC (6.0%) and PI (16.1%) than PO (72.6%) (LSD test, F = 96.9, $p < 0.001$). Herb frequency did not differ between fenced and unfenced conditions within the mixed forest or high steppe; for example, FM = 37.4%, and FM_u = 50.7% (ANOVA, F = 2.86, p = 0.108) (Table 3).

Life forms and biological spectra

Plants were classified as hemicryptophytes (63.1% of total species), chamaephytes (14.9%), geophytes (7.1%), nanophanerophytes (6.5%), therophytes (5.8%) and mesophanerophytes (2.6%). *FBS* differed statistically between units from that expected under a random distribution of frequencies (X^2 test, $p < 0.05$, n = 6). Although hemicryptophytes tended to dominate overall (62.1%, SE = 1.9), *FBS* differed significantly between

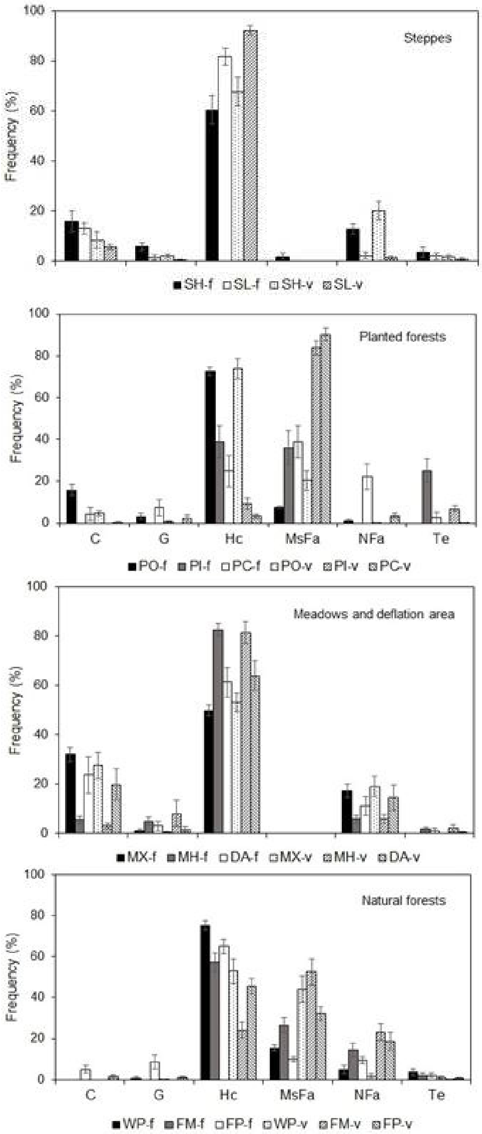

FIGURE 7 Floristic (f) and vegetational spectrum (v) of the vegetation units of Aguas Frías and Litrán. Vertical bars indicate the standard error of the mean (n = 10). C: chamaephytes, G: geophytes, Hc: hemicryptophytes, MsFa: mesophanerophytes, NFa: nanophanerophytes, and Te: therophytes. SH: high herbaceous-shrubby steppe, SL: low herbaceous-shrubby steppe, MH: hygrophilous meadow, MX: xerophilous meadow, DA: deflation area, WP: *A. araucana* woodland, FM: *N. pumilio* and *A. araucana* forest, FP: *N. pumilio* forest, PO: *P. ponderosa* open forest, PI: *P. ponderosa* intermediate forest and PC: *P. ponderosa* closed forest.

units, judging from differences in the frequency of this life form (Table 1, Figure 7). Hemicryptophyte frequency ranged from 24.8% in PC (SE = 7.6) to 82.6% in MH (SE = 2.7), whereas mesophanerophytes formed the largest class in PC (38.8%, SE = 7.8). Hemicryptophyte frequency did not differ between FM (57.1%, SE = 4.4) and $\mathrm{FM_u}$ (60.9%, SE = 3.4) (*t* test, p = 0.499), whereas frequency in SH (60.5%, SE = 5.8) was lower than in $\mathrm{SH_u}$ (77.3%, SE = 2.8) (*t* test, p = 0.017) (n = 10). In pine stands, hemicryptophytes increased significantly as *CC* decreased (ANOVA, F = 16.40, p < 0.001, n = 10); in PC, PI and PO frequency was 24.8% (SE = 7.6), 38.8% (SE = 7.9) and 72.6% (SE = 2.1), respectively (LSD test, p < 0.05, n = 10). Hemicryptophyte frequency was similar in PO and steppe units (SH, 60.5%, SE = 5.8; SL, 81.7%, SE = 3.5). Geophytes constituted the least frequent life form, ranging from 0% (PI and FM) to 8.6% (FP) (Figure 7).

VBS differed statistically from that expected under a random distribution of life forms (X^2 test, p < 0.05, n = 6). It was dominated by hemicryptophytes (52.7%, SE = 2.6), with therophytes (1.2%, SE = 0.2) and geophytes (1.3%, SE = 0.2) constituting the least frequent life forms. This spectrum differed between units, judging from differences in hemicryptophyte frequency; maximum frequencies were recorded in SL (92.2%, SE = 1.9), SH (81.4%, SE = 4.5) and MH (81.3%, SE = 4.5), while the minimum value was found in PC (3.3%, SE = 1.1) (Table 1, Figure 7). Hemicryptophyte frequency differed between FM (24.1%, SE = 3.9) and $\mathrm{FM_u}$ (42.0%, SE = 7.2) (*t* test, p = 0.042), but not between SH (67.7 is = 5.7) and $\mathrm{SH_u}$ (76.2%, SE = 1.7) (*t* test, p = 0.169) (n = 10). In pine stands, hemicryptophyte frequency increased significantly as *CC* decreased: PC, 3.3% (SE = 1.1); PI, 9.3% (SE = 2.7); PO, 74.0% (SE = 4.9) (LSD test, F = 141.40, p < 0.001, n = 10). Frequency in PO resembled that in SH (67.7%, SE = 5.7). In tree-dominated units, mean mesophanerophyte frequency ranged from 20.4% (BA, SE = 4.8) to 90.2% (PC, SE = 3.0) (Figure 7). Hemicryptophyte frequency was very low in PC (3.3%), and increased in PO (74.0%) to resemble values from the steppe (SH, 67.7%; SL, 92.3%). The difference between *FBS* and *VBS* ranged from 1.2% in MH to 17.1% in PC; differences larger than 5% were found only in FM, FP, PI and PC (Table 3). Hemicryptophyte frequency differed significantly between the spectra only in forest units (Kolmogórov-Smirnov test, p < 0.05).

Life form diversity

LFR ranged from 2.6 (PC, DA, SL) to 4.2 (FP), values differing statistically between units. Although *LFR* was greater in PO (3.5) than in PC, these differences were not significant (ANOVA, p = 0.075, F = 2.86). *LFR* did not differ between FM (3.1) and $\mathrm{FM_u}$ (3.4) (*t* test, p = 0.232), but did vary between SH (3.7) and $\mathrm{SH_u}$ (2.8) (*t* test, p = 0.023) (n = 10) (Tables 1 and 3). *LFD* was lowest in SL (0.08) and PC (0.09) and highest in FP (0.31); these values differed statistically between units. In pine stands, *LFD* tended to increase significantly as cover decreased: PC, 0.09; PI, 0.14 and PO, 0.20 (LSD test, p

= 0.023). *LFD* in FM (0.28) and FM_u (0.27) were similar (ANOVA, $p = 0.828$, $F = 0.05$) and *LFD* in SH (0.23) and SH_u (0.21) were similar (ANOVA, $p = 0.399$, $F = 0.74$) (Tables 1 and 3). Within plantations, *LFD* was large in PI with 30 to 60% of *BS*, but decreased in PO and PC, which exhibited *BS* apart from this range (ANOVA, $p < 0.001$, $n = 30$) (Figure 8).

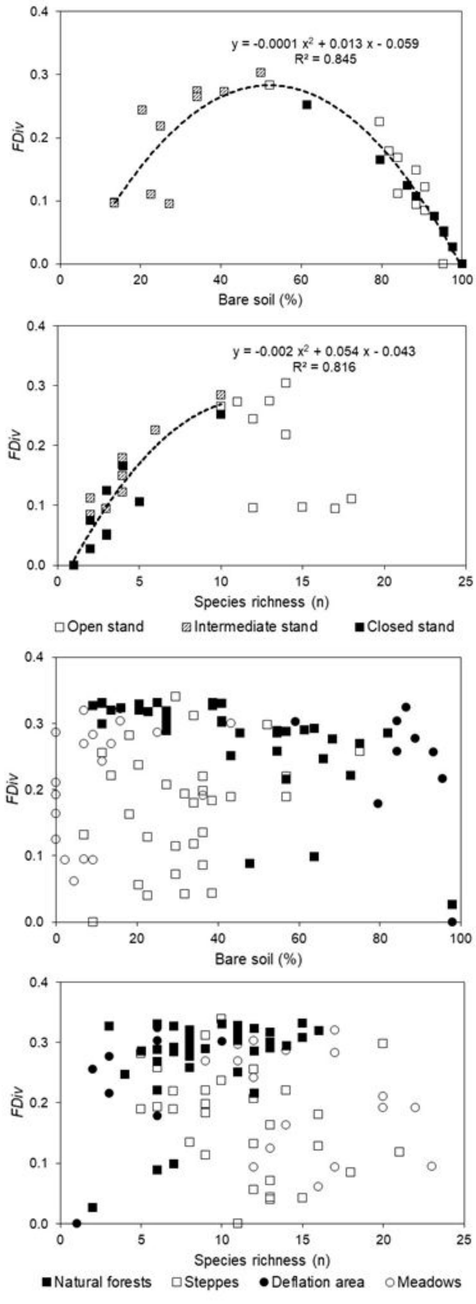

FIGURE 8 Bare soil, species richness and life form diversity (FDiv) in the *P. ponderosa* stands (left) and natural vegetation units (right) of Aguas Frías and Litrán. The parameters of the regression function and the coefficient of determination (R^2) are indicated when slope is statistically different from 0 (ANOVA, $p < 0.05$).

Units covered by natural *vegetation* showed no significant relationship between *BS* and *LFD*, either when the entire database was analysed together or when separated in units (ANOVA, $p \geq 0.05$, $n = 100$) (Figure 8). In PC and PI, *LFD* tended to increase asymptotically as S_t increased (ANOVA, $p < 0.001$, $n = 20$). In contrast, PO and units covered by natural vegetation showed no significant statistical relationship between these variables, either when the entire database was analysed together or when separated into different units (ANOVA, $p \geq 0.05$) (Figure 8). There was no bi-dimensional relationship between *LFR* and *LFD* (ANOVA, $F = 3.78$, $p = 0.078$, $n = 13$). Multiple regression (stepwise, forward selection method) among *LFD*, *BS* and S_t for PO, PI and PC produced the function $LFD = 0.00072\ BS + 0.0131\ S_t$ (MANOVA, $p < 0.001$, $R^2 = 0.803$, $n = 30$), whereas for the remaining units the function was $LFD = 0.00228\ BS + 0.0123\ S_t$ (MANOVA, $p < 0.001$, $R^2 = 0.793$, $n = 100$). Goodness of fit between observed and modelled values was very low for the entire data set (MANOVA, $p = 0.005$, $R^2 = 0.061$, $n = 130$).

DISCUSSION

The effect of *plantations* on species richness was evaluated in regional studies. Bremer and Farley (2010) found a decrease in the richness of native species in plantations compared to pastures, shrublands, and primary forests. However, richness increased when reference communities were secondary forests, degraded grasslands and deforested grazing areas. In the Argentinean Patagonia, dense plantations of *Pinus* exhibited lower diversity of plants (Paritsis and Aysen, 2008), insects (Corley et al., 2006), birds (Lantschner et al., 2008) and mammals (Lantschner et al., 2011, 2012), compared to the surrounding natural forest, grassland, and open plantations. Animal diversity tended to correlate positively with understory complexity and landscape heterogeneity, and negatively with stand cover (Paritsis and Aysen, 2008; Lantschner et al., 2011, 2012). In structurally simple *Pinus radiata* stands from Chile, depletion of diversity was documented in reptiles (Uribe and Estadés, 2014), birds (Tomasevic and Estadés, 2008; Vergara and Armesto, 2009; Najera and Simonetti, 2010), and terrestrial and flying mammals (Ramirez and Simonetti, 2011; Rodríguez-San Pedro and Simonetti, 2013; Meynard et al., 2014). Stratified undergrowth within *P. radiata* stands provided habitat for medium-sized mammals and natural regeneration of the original vegetation (Guerrero and Bustamante, 2007; Simonetti et al., 2013).

PAR on the floor of the closed stand (2%) was probably low because of high reflection and absorption of light caused by extensive canopy cover (91%) (Canham et al., 1990). A well-developed canopy would also imply higher rates of evapotranspiration, and interception and consumption of water (Weigandt et al., 2015), which would explain the reduced soil water content measured during the dry season (9.6%). However, a denser stand structure can also promote lower air temperatures, reducing evaporation and partly compensating for water losses through the canopy (Canham et al., 1990; Geiger et al., 2003). A decrease in canopy cover caused an increase in luminosity on the forest floor, and probably in soil water content, to attain levels similar to the steppe. The open stand showed 29% canopy cover, 42% light intensity, and 20% soil moisture, whereas in the high and low steppe soil moisture was 29% and 18%, respectively. In the closed stand, lower values of light intensity and soil moisture, given a large canopy cover, would have promoted large amounts of bare soil (89%); in the open stand, soil cover decreased to 28%, resembling the values found for the high (27%) and low steppe (28%). Low richness of understory plants in the closed stand (3.6) was probably related to the restricted possibility of establishment in an environment with a shortage of essential aerial and underground resources. However, species richness in the open stand (13.6) and in the low steppe (14.8) was similar.

Although the high frequency of exotic species in the closed stand (90%) was associated with the exotic *P. ponderosa*, the amount of this plant type was very low on the whole (2/16) and comparable with that of other units (e.g. high steppe, 4/47 and low steppe, 4/38). A pine stand would not provide a particularly advantageous habitat for exotic herbs and shrubs, reducing the possibility of biological invasion. The conversion of steppe to forest, and the resulting increase in tree canopy cover, was linked to the severe decline in hemicryptophytes and herbs. Hemicryptophytes were dominant within the floristic spectrum in all natural units, reflecting plant adaptation to cold winters and dry summers (Bertolami et al., 2008). Chamaephytes attained relevance in the xerophilous meadow, as in other southern rocky outcrops, a phenomenon also interpreted to be a consequence of the harsh climate (Speziale and Ezcurra, 2012). Evergreen and deciduous mesophanerophytes, namely tall perennials with buds emerging from aerial parts, were dominant at the mid elevation of south and east facing slopes, indicating a more humid environment.

Nanophanerophytes, which are low-height phanerophytes, increased their participation in the understory of pine stands as cover developed, reflecting the role of a closed canopy in microclimate amelioration. Within the closed stand, mesophanerophyte dominance, higher values for canopy cover and bare ground, and a small number of species in the understory led to low taxonomic and life form diversity, which increased significantly in the intermediate and open stands to resemble values of the high steppe. The attenuation of light and precipitation on the forest floor is likely to act as an environmental filter, restricting the pool of viable habits and reducing community diversity (Kleidon et al., 2009). The xerophilous meadow was one of the most diverse habitats in terms of life forms. It comprised around 1/3 of total plant species and a large number of families in an extremely restricted area, which barely exceeded 1% of Aguas Frías. The vast majority of plants were native species not found in the matrix, as only 42% were commonly found in the steppe, 30% in natural forest, and 18% in the closed stand. This unit also presented high life form diversity, equivalent to that of the natural forests and 3.2 times higher than the closed stand. These rocky outcrops have higher temperature, insolation and wind frequency and intensity, plus lower air humidity, water and nutrient content than the surrounding ecosystems (Szarzynski, 2000). This setting, together with a variety of microhabitats such as cracks and overhangs, and lower fire and grazing pressure, enhances "specialist" diversity (Milchunas and Noy-Meir, 2002; Galende and Raffaele, 2013). It probably also represents refuges of cold-adapted glacial relict paleofloras (Speziale and Ezcurra, 2012).

The hygrophilous meadow of Aguas Frias had a high number (10%) and frequency (18%), of exotic plant species, low life form diversity (0.15) and the largest number of plant families (23) and species (68). This richness was 4.3 and 1.6 times that of the closed stand and the pure forest, respectively. Wetlands in northwestern Patagonia are very productive and biodiverse ecosystems mainly threatened by overgrazing, which causes an increase in bare soil, gully formation and drainage, and the risk of plant invasion (Chimner et al., 2011). There is also concern about the potential effect replacing grassland with plantation may have on water recharge (Weigandt et al., 2015). The deflation area is an intense human-degraded unit, which shows a large proportion of unvegetated soil and reduced taxonomic and life form richness (Frugoni et al., 2016).

The fenced steppe of Aguas Frías showed a significantly lower amount of bare soil (27%) and higher taxonomic (47 species) and life form richness (3.7) than the unfenced steppe (40%, 24 species, 2.8, respectively). Grace and Jutila (1999) found that reduction in the species pool of grazed areas was predominantly caused by selective herbivory. Grime (2006) hypothesized that the decline in richness is because herbivory reduces competition, although herbivory can intensify the effects of competition. Besides, such generalization ignores the evolutionary relation between plants and grazers (Milchunas and Noy-Meir, 2002). In the mixed forest, the amount of bare soil was lower in the fenced than in the unfenced condition (34% and 51%, respectively). In Patagonia, the enclosing of forest stations protects young trees against the herbivory of livestock and native and introduced wildlife. However, this practice also confers significant ecological benefits on the surrounding natural and semi-natural environments, which usually exhibit substantial degradation due to fire and overgrazing (Frugoni et al., 2016).

CONCLUSIONS

In Aguas Frías, ecological indicators improved after seven years of project implementation. In Litrán, dense stands of *P. ponderosa* negatively affected soil cover, plant richness, and life form diversity. These variables came close to the values of the steppe of reference as canopy cover decreased. Projects for the production of goods and services crucial for the biota and people, demand functional ecosystems over time and space. Greater compatibility between harbouring a wide variety of wild species and timber production in this anthropogenic habitat requires, as a priority, the maintenance of fencing and reduced tree spacing. Although such a project may represent a decline in productivity, the resulting enhanced ecosystem and aesthetic value will increase opportunities for further economic support from society.

List of abbreviations used in the text.

Initial	Meaning
BA	Basal area
BS	Bare soil
CC	Crown cover
D	Tree density
d	Distance between trees
DA	Deflation area
db	Diameter at base height
FBS	Floristic biological spectrum
FM	*Nothofagus pumilio* and *Araucaria araucana* fenced forest
FMu	*Nothofagus pumilio* and *Araucaria araucana* unfenced forest
FP	*Nothofagus pumilio* forest
h	Tree height
I5	Length of the five internodes above 1.3 m
LFD	Life form diversity
LFR	Life form richness
MH	*Hygrophilous meadow*
MX	*Xerophilous meadow*
PAR	Photosynthetically active radiation
PC	*Pinus ponderosa* closed forest
PI	*Pinus ponderosa* intermediate forest
PO	*Pinus ponderosa* open forest
Ŝ	Mean species richness
SBD	Soil bulk density
SH	High herbaceous-shrubby fenced steppe
SHu	High herbaceous-shrubby unfenced steppe
SI20	Site index at 20 yr
SL	Low herbaceous-shrubby steppe
SM	Soil moisture
St	Total species richness
VBS	Vegetational biological spectrum
WP	Araucana araucana woodland

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