



Disturbance induced changes in species and functional diversity in southern Patagonian forest-steppe ecotone



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ABSTRACT

Ecotone areas are the most dynamic areas of the world where small changes in some condition produce rapid and abrupt responses such as shifts in the distribution of dominant species and associated community's patches. Studying southwestern Santa Cruz forest-steppe ecotone is an ideal landscape to explore potential feedbacks of grazing and fire on vegetation diversity because of the juxtaposition of fire-resistant forests dominated by obligate seeders with fire-sprouting shrublands and the prevalence of wild cattle since the early XX century. In this study, we analyzed how climate (precipitation, temperature and water balance), stand characteristics (basal area, quantity of cohorts and exotic species cover) and disturbances (fire and grazing) affect native species diversity, Plant Functional Types (PFTs) diversity and PFTs response in the forest-steppe ecotone of southern Patagonia. The study was conducted on 124 plots located on the eastern slope of the Andes (between 48°50' and 50°50'S) including forest-steppe ecotone sites between 1000 and 400 mm of annual precipitation. Native species and PFTs diversity indices modeling were carried out by generalized least squares and generalized lineal models. Stand characteristics, disturbance type and climate variables were used as factors over native species and PFTs diversity variables. An ordination and a Spearman rank correlation analysis were achieved between scores of the two first axes with total basal area, exotic species cover, mean annual temperature, annual precipitation, and water balance in order to explore PFTs responses to biotic or abiotic ecological conditions. The relationship between native species and PFTs richness (number of PFTs per plot) was modeled in order to evaluate the redundancy degree of PFTs under different disturbance types by fitting nonlinear power models to both richness measurements for each disturbance type. Fire impact over forest-steppe ecotone communities is one of the most important top down factor driving major increases on PFTs redundancy and heliophilous plants species abundance. At stand level, multicohort fire-disturbed stands support the highest native species diversity. Thus, mimicking this natural pattern on silvicultural practices could safeguard higher understory native species diversity than managing policies creating homogeneous conditions. Even if closed forest communities present lower native species diversity values than open canopy communities, they sustain different PFTs that present high conservation values for forest fauna. Grazing pressure represents a threatening agent diminishing native forest-steppe biodiversity. The coexistence of different stands at different development stages in the same landscape ensures the seed bank pools of shade tolerant and heliophilous species.

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1. Introduction

Ecotone areas are the most dynamic areas of the world where small changes in some condition, bottom up resource or top down

process will, when approaching some threshold, produce rapid and abrupt responses such as shifts in the distribution of dominant species and associated communities patches (Kitzberger, 2012). The forest-steppe ecotone of Patagonia is one of the areas with higher biodiversity values in southern South America (Brown et al., 2006). Tertiary connection between Brazilian and Bolivian rainforests has left interesting taxonomic endemism and relictual species patterns. These paleo-connections have defined modern

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regional diversity patterns (e.g. Ponce et al., 2002; Villagrán and Hinojosa, 1997). After the last glacial maximum, Southern Hemisphere atmospheric circulation patterns have driven major forest-steppe ecotone dynamics. However modern and Holocene disturbance regimes (e.g. fire, grazing) have been important forcings on determining vegetation shifts from local to regional scales in the forest-steppe ecotone (e.g. Fontana and Bennett, 2012; Kitzberger et al., 2012). Since late XIX century, anthropogenic introduction of species, logging and fire forest clearance became major driving factors on vegetation patterns (Huber et al., 2004; Martínez Pastur et al., 2002; Raffaele et al., 2011; Speziale and Ezcurra, 2011). A better understanding of the nature of ecotone and the complexity of interrelated natural and anthropogenic controls that regulate their internal dynamic is necessary before adequate assessments of their usefulness as early warning indicators of global changes can be made (Kitzberger, 2012). Studying south-western Santa Cruz forest-steppe ecotone is an ideal landscape to explore potential feedbacks of grazing and fire on vegetation diversity because of the juxtaposition of fire-resistant forests dominated by obligate seeders with fire-sprouting shrublands and the prevalence of wild cattle since the early XX century.

Understanding the processes shaping biological communities under disturbances is a core challenge in ecology and conservation science. Studying local and landscape forcings on understory species diversity and plant functional types composition is essential to understand ecosystems processes and services from the forest-steppe ecotone. In this study, we consider the term disturbance in its widest sense as any event, natural or human-driven, that causes temporary and localized shifts in species demographic rates (Mouillot et al., 2012). Understory vegetation in forest and tall shrublands of steppe communities is the baseline of trophic webs, offers refuge to most micro and mesofauna and protects soils from erosion especially on steep slopes (Whelan, 1995). Traditionally, ecologists have explored linkages between grade of severity, disturbance-types and taxonomic structure in Patagonian communities (e.g. Faggi and Cagnoni, 1996; Lencinas et al., 2008; Pisano and Dimitri, 1973; Quinteros et al., 2010; Vidal and Reif, 2011). However, few studies have focused on understory and plant functional diversity patterns of Patagonian forest-steppe ecotone (Damascos and Rapoport, 2002; Lencinas et al., 2008; Speziale et al., 2010).

The analysis of species traits dominance on different communities to assess functional structure of ecosystems, throughout the classification of species on Plant Functional Types (PFTs), have provided an alternative approach to disentangle how multiple disturbances affect ecosystems attributes (Díaz and Cabido, 2001; Mouillot et al., 2012). Much attention has been focused on PFTs diversity and PFTs richness patterns. For example how the species number within a given PFT varies in response to disturbances defining its degree of redundancy. It has been highlighted that the increase in PFTs redundancy improves reliability and resilience of ecosystem functioning, while its decrease may be a sign of a higher ecosystem vulnerability to disturbance agents (Lloret and Vilà, 2003). The influence of biotic and abiotic factors on community composition and species abundance is expected to affect the relationship between species and PFTs diversity (Cadotte et al., 2011; Naeem and Wright, 2003). Many authors showed that species diversity increased related to different sites characteristics such as multiple tree-layer structure, time since the last disturbance, but decrease related to even-age stands, abundant exotic species or grazing (Gallo et al., 2013; Lencinas et al., 2008; Ohlson et al., 1997; Veblen, 1979). Most of these studies have been carried out in forested areas under high precipitation values or in different harvesting scenarios.

In Patagonia, climate is the main factor that influence on vegetation distribution at regional scale. In the extra-Andean region, annual precipitation controls vegetation distribution and functional characteristics of the ecosystems (Paruelo et al., 2004), whereas mean annual temperature in conjunction with strong winds produces high evaporation rates having a strong effect on plant growth in southern Patagonia (Paruelo et al., 2001). Studies on ecotone dynamics in northern Patagonia have proposed direct or indirect effects of climate at different scales (Kitzberger, 2012). It is evident that ecotones respond to a complexity of inter-related factors, and other factors besides climate could drive vegetation dynamics at different scale of analysis. Nonetheless understandings how different biotic and abiotic factors (climate, disturbance and/or stand characteristics) affect species and PFTs diversity have not been achieved for Subantarctic forest-steppe ecotone communities of southern Patagonia. In this study, we present the first approach to understand how climate (precipitation, temperature and water balance), stand characteristics (basal area, quantity of cohorts and exotic species cover) and disturbances (fire and grazing) could affect native species diversity, functional diversity and plant functional types response in a selected ecotonal area.

2. Materials and methods

2.1. Study area

At the southern latitudes of Patagonia, the strong meridional pressure gradient and the presence of semi-permanent high pressure cells over south Pacific and south Atlantic oceans result in a dominant westerly circulation regime. The Andes produces a strong precipitation gradient from west to east (Paruelo et al., 1998). As moist Pacific air is forced up the western side of the Andes, copious precipitation falls on the windward slopes. In marked contrast, the leeward side of the Andes receives much less precipitation decreasing from ca. 1400 mm in mountainous areas to 300 mm at the eastern borderline of Argentino, Viedma and San Martín lakes. The study was conducted on eastern slope of the Andes (between 48°50' and 50°50'S, Fig. 1) including forest-steppe ecotone sites between 1000 and 400 mm annual precipitation, that is evenly distributed throughout the year, and mean annual temperature between 4 and 8 °C. A forest-steppe mosaic of trees dominated patches with low understory cover, and shrub-grass dominated patches with higher vegetation cover of woody and herb species, composes the forest-steppe ecotone. *Nothofagus pumilio* dominate forest patches. Sometime *N. pumilio* is usually accompanied by some evergreen *N. betuloides* trees in lowlands up to 1000 mm annual precipitation and deciduous *N. antarctica* small trees on eastward areas lower than 500 mm (Pisano and Dimitri, 1973). Forest communities present great heterogeneity in term of tree vertical and horizontal structure and floristic composition (Pisano and Dimitri, 1973). After autogenic or allogenic disturbances, shrublands of *Mulinum*, *Senecio*, *Gaultheria* and grass steppe communities dominated by *Festuca* and *Stipa* species replace forest patches. This study was carried out in Los Glaciares National Park (LGNP) and other minor protected areas surrounding LGNP. These protected areas have as main aim to conserve biodiversity of the forest and steppe communities in southwestern Santa Cruz, Argentina. Indeed, several taxonomic endemism develop in these areas such as *Drimys winteri*, *Embothrium coccineum*, carnivorous plants as *Pinguicula Antarctica* and saprophytic plants as *Arachnites uniflora*. Large native herbivores, such as huemul deer (*Hippocamelus bisulcus*) and guanaco (*Lama guanicoe*) were deeply hunted until the middle XX century and have been replaced by introduced herbivores specially

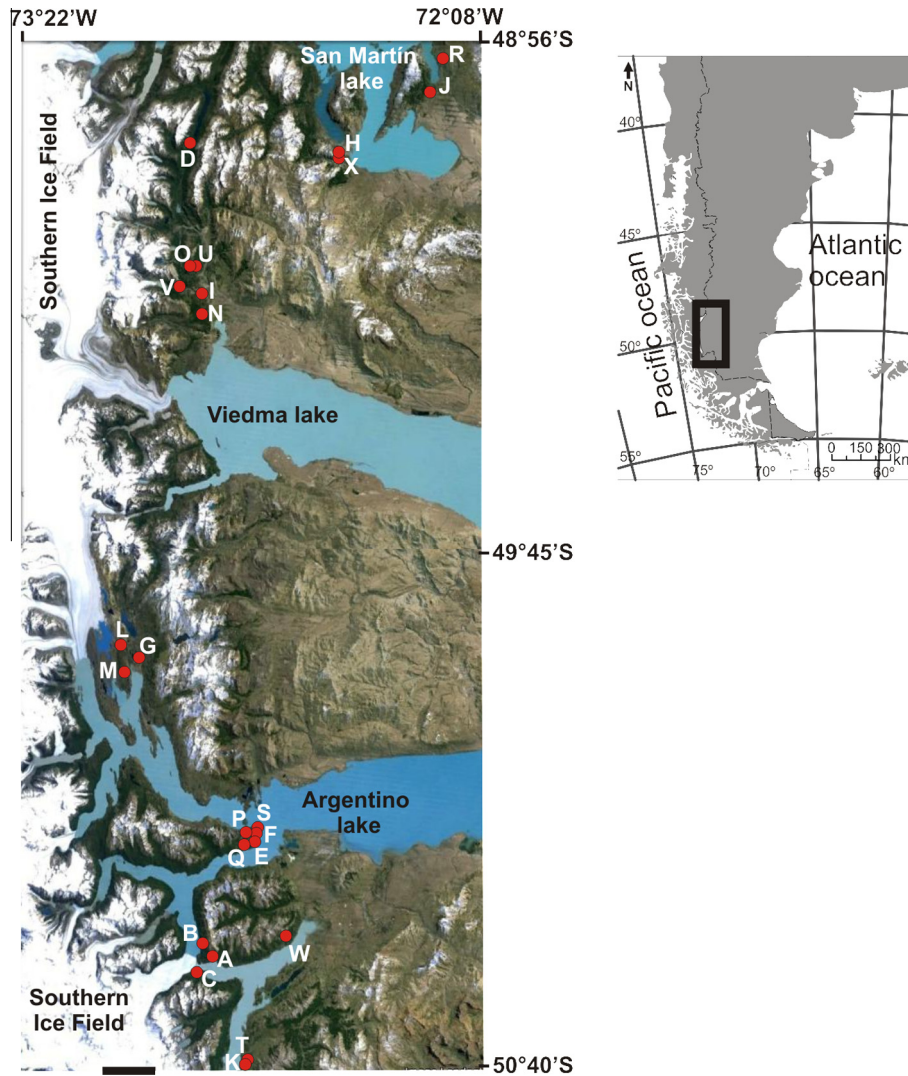


Fig. 1. Study area. Sampling sites are pointed with letters. See Appendix A1 for detailed information.

livestock and the European hare (*Lepus europaeus*) (Merino et al., 2009).

2.2. Vegetation sampling, stand characteristics and disturbance types

During January 2008 and February 2010, understory and tree vegetation was sampled on 120 plots distributed on 24 different sites (5 plots by site) under different disturbance types in the forest-steppe ecotone, between 48° and 50.5°S. The five plots within each site were distributed randomly within a 100 m radius area. Understory species censuses were performed in 25 m² plots. Ocular estimates of every understory species cover (%) was registered on each plot. Each understory native species cover (%) was related to total understory native species cover. Exotic understory species cover (%) was calculated separately and related to the total understory species cover. Species nomenclature follows Correa (1969–1984) and synonymies follow Missouri Botanical Garden (<http://www.tropicos.org>).

Every plot was described by stand characteristics and disturbance type (Appendix A1). Stand characteristics involves total basal area (m² ha⁻¹, BA), quantity of cohorts, and exotic species cover. Quantity of cohorts was obtained from the analysis of tree diameter at the breast height (dbh) distribution. The quantity of

cohorts coincides between tree species in those sites composed by two or more tree species. Tree stand size was adjusted to include a minimum of thirty trees in each stand to allow a reliable interpretation of the tree population structure.

Disturbance types were classified as non-disturbed stand (ND), grazing (G) and recent (f) or historical (F) fire, and thereof combination. Fire disturbance were differentiated in two categories according to the time since the last fire event: recent fire (f) when fire events occurred during the last 30 years and historical fire (F) when fire events occurred during the early–middle XX century. All sites affected by grazing pressure (G) supported small population of cattle because most of them are included in protected areas. The presence/absence of feces was used as sign of grazing disturbance. Fire history and cattle presence were assessed from Los Glaciares National Park authorities, farm owners and were verified by our own field observations.

2.3. Climate data

Annual precipitation (Pann), temperature (T°) and water balance (WB) were selected as environmental independent variables for modeling species and functional diversity. Since that the instrumental meteorological record in Patagonia is fragmentary and only

two meteorological stations are active on the east side of the Andes between 48 and 50°S, climate data were extracted from WorldClim database (<http://www.worldclim.org/current.htm>; Hijmans et al., 2005). Data were imported into GIS software (ArcGis 9.3), interpolated by krigging method and then monthly values were extracted and the mean values were calculated for each sampled site. The WB index was calculated for each site as the ratio between annual precipitation and potential evapotranspiration. Potential evapotranspiration values were estimated according to Thornthwaite (1948).

2.4. Species and functional diversity estimation

Native species and PFTs diversity were calculated by the Shannon-Wiener index; $H' = -\sum p_i \log p_i$; at each sampling plot, where p_i represents each understory native species cover in native species diversity index, and each PFT cover in PFTs diversity index. Classification of native species in Plant Functional Types (PFTs) was based at first on growth form (Hobbs, 1997). Then different growth forms were classified following the former functional traits: morpho-ecological leaf characteristics (presence of hairy or sclerophilous leaves), plant response to environment (e.g. mesophytes, higrphytes), and light/water gradient–architecture relation (plano-philous versus erectophilous architecture). Species functional traits follow species descriptions by Boelcke et al. (1985), Correa (1969–1984), Damascos (1997), and Damascos and Rapoport (2002) (Appendix A2).

2.5. Diversity patterns modeling

Native species and PFTs diversity values (dependent variables) were modeled as function of stand characteristics (quantity of cohorts, total basal area, exotic species cover) and disturbance type (ND, G, F, f or combination of disturbances) as independent variables. At first, a Spearman rank correlation and variance inflation factors were achieved between explanatory variables in order to detect collinearity. No collinearity was found between the stand characteristics and disturbance variables. Then, modeling of native species and PFTs diversity indices was carried out by Generalized Least Squares models (GLS). Since diversity data presented different variance spread patterns (see Fig. 2), the homogeneity assumption may be violated. In order to deal with this violation, a variance structure (VarIdent Variance Structure) was included into GLS analyses. This variance structure considers that the spread differs per stand characteristics or disturbance type factor (Zuur et al., 2009).

In GLS analyses, a model without any independent variable (i.e. null model), a global model, and models with different number and combinations of explanatory variables were constructed during the comparison procedure. Models were fitted by maximum likelihood and Information-Theoretic (IT) procedures and were performed to get the best model, computing AICc (akaike information criterion), Δi (AICc differences) and w_i (normalized weights of AIC) of all possible models (Jonhson and Omland, 2004; Symonds and Moussalli, 2011). We also calculated 95% confidence intervals for parameters estimated in the best model. Spearman rank correlation and GLS models fitting were performed by Open Access Software R (R Development Core Team, 2011), with the “nlme” package (Pinheiro et al., 2013). Model selection was performed with the “MuMIn” package (Barton, 2009) which has a range of functions to automate an IT-AIC approach.

Native species and PFTs diversity values (dependent variables) were also modeled as function of climate variables (T° , Pann and WB) as independent variables using Generalized Linear Model analyses to rule out any climate effects on diversity patterns in

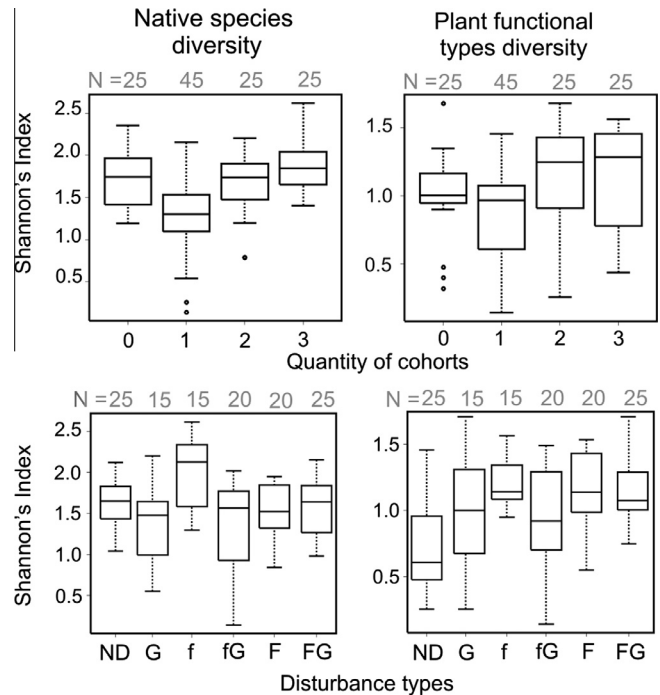


Fig. 2. Native species and plant functional types diversity related to stand characteristics (quantity of cohorts), disturbance types (ND – Non-disturbed, G – Grazing, f – Fire events occurred during the last 30 years, F – Fire events occurred during early–middle 20th century). Number of plot sampled per stand characteristic or disturbance type is pointed above each boxplot (N).

our study sampling design. Models have a Gaussian distribution and its canonical link was specified (Crawley, 2005).

2.6. PFTs responses

An ordination was carried out to explore PFTs cover patterns and to evaluate the correlation between the two first axes of variation with total basal area (BA) and exotic species cover (Ex). Climate variables (T° , Pann, and WB) were also correlated to the two first axis of variation to evaluate if any PFT group could be limited to some climatic conditions. First, a DCA (detrended by segments and untransformed data) was applied to PFTs data in order to estimate compositional gradient length. Linear ordination methods perform better for short gradients (<1.5 SD units) and unimodal methods are more suitable for long gradients (>3 SD units), whereas both methods may be appropriate for intermediate gradient lengths (Legendre and Birks, 2012). The PFTs data presented a gradient length of 3.20 standard deviation units indicating that numerical methods based on a unimodal response as Correspondence Analysis (CA) is the most appropriate. Multivariate analysis was performed by PAST 2.16 software (Hammer et al., 2001). Then, a Spearman rank correlation analysis was achieved between scores of the two first axes with BA, Ex, T° , Pann, and WB.

Differences between PFTs cover values under different disturbance types were tested by a Games-Howell Post Hoc multiple comparison test not assuming equal variance. Correlation and multiple comparison analysis were performed by SPSS 13.0 software.

2.7. PFTs redundancy degree analysis

The relationship between native species and PFTs richness (number of PFTs per plot) was modeled in order to evaluate the redundancy degree of PFTs under different disturbance types. A

simple nonlinear model explaining this proportionality is the power function: $F = aD^b$; where D is species richness, F is PFTs richness, “ a ” is intercept and “ b ” is shape parameter (Cadotte et al., 2011). Due to our interest in species and PFTs richness relationship, parameter “ b ” is the only relevant. Thus, a nonlinear power model was fitted to both richness measurements for each disturbance type (Fire-including F or f, Grazing, Fire-Grazing and Non-disturbed stands). Parameters estimations for four power curves were performed using maximum likelihood and 95% confidence intervals (Table 4). Then, in order to evaluate differences in the relationship between species and PFTs richness under different disturbance types, the shape parameters (b) of each power function model were compared using confidence intervals (Zuur et al., 2009). Analyses were performed by Open Access Software R (R Development Core Team, 2011) with the “bbmle” package (Bolker and R Development Core Team 2013).

3. Results

3.1. Diversity patterns modeling

The best model explaining native species diversity included disturbance type, quantity of cohorts and total basal area (AICc = 74.5, Table 1) whereas the best model to explain PFTs diversity included disturbance type and quantity of cohorts (AICc = 19, Table 1). In all GLS models, residual deviance was less than residual degrees of freedom, indicating that models fitted data well (Zuur et al., 2009).

Factors for disturbance type were relative to non-disturbed stands (ND). The significant factors of disturbance type for the native species diversity best model are: fG, F and G. Stands with these disturbance types present low native species diversity (Table 2, Fig. 2). In PFTs diversity best model, all disturbance type factors were significant except G (Table 2, Fig. 2). Stands with f, F and FG disturbance types present higher values of diversity than fG stands (Fig. 2).

Factors for quantity of cohorts were relative to zero (absence of trees), where high diversity values were found (Fig. 2). The significant factors of quantity of cohorts for the native species diversity best model were one and three cohorts. Notice that these parameters matched the lowest and the highest values of species diversity respectively (Fig. 2). The quantity of cohorts significant factors (2 and 3 cohorts) for PFTs diversity best model agreed with the highest PFTs diversity values (Table 2, Fig. 2).

Basal area (BA) improved significantly species diversity model (Table 1; $w_i = 0.005$ to $w_i = 0.714$). This factor describes high (low) diversity values under low (high) BA values. Exotic species (Ex) was not a significant parameter neither to species nor to PFTs diversity models.

The climate variables Pann and WB presented high collinearity as their variance inflation factor (VIF) values were >1 (3.59 and 3.78 respectively) and were highly correlated ($r^2 = 0.84$, $p < 0.01$). Therefore Pann and WB were used separately as independent variables for modeling diversity patterns (Table 3). No competent model was found to explain the relationship between native species or PFTs diversity values with climate variables (Table 3). Therefore, in the ecotone communities included in this research, we assume that climate variables have minor effects driving diversity patterns at landscape scale.

3.2. PFTs responses

The first two CA axes explained 52.3% of variance (see biplot figure in Appendix A3). Variation related to the first CA axis is positively correlated to total basal area ($r^2 = 0.68$) and negatively correlated to exotic species ($r^2 = -0.58$) (Table 4). Thus,

Mesophytic shrubs, Hicrophytic herbs and Mesophytic rosette herbs high cover is associated to high BA values and low values of exotic species cover. Meanwhile Helio-sclerophilous shrubs, Heliophilous hairy herbs and Helio-erectophilous herbs dominate under low BA values and high values of exotic species cover.

The second CA axis present a negative significantly correlation to annual temperature (T°) ($r^2 = -0.4$, Table 4). Thus, Mesophytic shrubs and Hicrophytic herbs high cover is associated to high T° values. Meanwhile Mesophytic rosette herbs and Dwarf shrubs dominates under low T° values. Pann and WB present no significant correlation to either axis 1 or axis 2.

PFTs cover varies significantly between disturbed and non-disturbed stands (except for Mesophytic shrubs) (Fig. 3). Mesophytic rosette herbs present the highest values on non-disturbed stands meanwhile other PFTs present high cover values on grazed, fire or grazed-fire stands. The highest values of Helio-sclerophilous shrubs, Heliophilous hairy herbs, Dwarf shrubs and Helio-erectophilous herbs are related to fire affected stands. Grazing disturbance is related to high values of Hicrophytic herbs. Helio-erectophilous herbs cover is associated to grazing and fire disturbance. Those stands affected both by grazing and fire disturbances are associated with high values of Helio-sclerophilous shrubs and Heliophilous hairy herbs cover (Fig. 3).

3.3. PFTs redundancy degree analysis

Shape parameters (b) show differences between models. It means that different relationships exist between native species and PFTs richness under different types of disturbance. Non-disturbed stands shape parameter (0.971, Table 5) differs from stands affected by fire (0.426, Table 5) while those stands affected by Grazing and Grazing-Fire present intermediate shape parameters values (Table 5). Values of b close to 1 show a linear relationship between native species and PFTs richness, indicating low PFTs redundancy (Cadotte et al., 2011). Therefore, non-disturbed stands show low PFTs redundancy. On the contrary, Fire shape parameter and scatterplot graphics show a nonlinear relationship between native species and PFTs richness, suggesting the highest degree of redundancy (Table 5, Fig. 4).

4. Discussion

4.1. Diversity patterns modeling and PFTs responses

The high native species and PFTs diversity values on multi-cohort stands detected on this study has been highlighted in other template forests, related specially to silvicultural practices (Cellini et al., 2013; Kern et al., 2014; Lencinas et al., 2011). Modern silvicultural management policies tend to emulate natural disturbance regimes to restore or maintain biodiversity in managed forests (Seymour et al., 2002). This approach assumes that the patterns and processes characteristic of unmanaged forests support native flora and fauna; therefore, when management practices mimic patterns of natural disturbances, native biodiversity is more likely to persist (Kern et al., 2014; Mitchell et al., 2002). Our results suggest that the likely uneven canopy-structure of multi-cohort stands present heterogeneous light conditions that may create a wider range of niches and support a greater number of species than those of single cohort stands. Thus, mimicking this natural pattern on silvicultural practices could safeguard higher understory native species diversity than managing policies creating homogeneous conditions (Kern et al., 2014; Seymour and Hunter, 1999).

Disturbance events (as fire) modifying stand characteristics (e.g. basal area and tree cohort establishment) indirectly affect water-energy conditions through light availability. Air

Table 1
Least squares set of best-ranked models ($w_i > 0.005$) examining effect of disturbance and stand characteristics variables on species and functional type diversity. AICc, akaike information criterion for small samples; Δ_i , AICc differences; w_i , normalized weights of AIC; acc w_i , cumulative Akaike weight. DT, disturbance types; QC, quantity of cohorts, Ex, Exotic species cover, BA, total basal area.

Species diversity				Plant functional types diversity			
Candidate models	AIC	Δ_i	w_i	Candidate models	AIC	Δ_i	w_i
DT + QC + BA	74.5	0.00	0.714	DT + QC	19	0.00	0.553
DT + QC + BA + Ex	77.0	2.50	0.204	DT + QC + BA	20.7	1.70	0.236
QC + BA	79.8	5.30	0.050	DT + QC + Ex	21.7	2.70	0.143
QC + Ex + BA	81.1	6.60	0.026	DT + QC + BA + Ex	23.4	4.40	0.061
DT + QC	84.3	9.80	0.005	QC + BA	27.9	8.90	0.006
Null	136.1	56.30	0.000	Null	85.1	63.40	0.000

Table 2

Parameter estimate (SE) from least squares models describing the effect of disturbance and stand characteristics on native species and plant functional type diversity. Significant statistical differences were considered when "0" is not included into confidence interval (CI). Asterisks mark statistical factors with significant SE. The models are the best model selected from all models that can be built for each dependent variable. DT, disturbance types (G, Grazing, f, Fire events occurred during the last 30 years, F, Fire events occurred during early–middle 20th century); QC, quantity of cohorts; BA, total basal area.

Response variable	Explanatory variable	Parameter estimate (SE)	CI	
			Lower	Upper
Native species diversity	Intercept	1.79 (0.08)	1.64	1.95
	DT – f	0.09 (0.12)	–0.15	0.34
	DT – fG*	–0.24 (0.10)	–0.44	–0.05
	DT – F*	–0.21 (0.11)	–0.42	–0.01
	DT – FG	–0.13 (0.10)	–0.32	0.06
	DT – G*	–0.30 (0.14)	–0.57	–0.03
	QC – 1*	–0.19 (0.09)	–0.36	–0.02
	QC – 2	0.15 (0.11)	–0.04	0.34
	QC – 3*	0.58 (0.12)	0.34	0.82
	BA*	–0.006 (0.001)	–0.009	–0.003
Plant functional types diversity	Intercept	0.58 (0.08)	0.42	0.73
	DT – f*	0.54 (0.08)	0.40	0.69
	DT – fG*	0.22 (0.10)	0.03	0.42
	DT – F*	0.53 (0.08)	0.37	0.69
	DT – FG*	0.54 (0.08)	0.38	0.70
	DT – G	0.23 (0.12)	–0.01	0.46
	QC – 1	–0.07 (0.05)	–0.16	0.02
	QC – 2*	0.30 (0.08)	0.15	0.46
	QC – 3*	0.31 (0.05)	0.21	0.42

temperature and humidity are dependent on canopy structure and their variations are correlated with light regimes. Thus, light can be used as a single synthetic factor grouping these microclimatic variations (Barbier et al., 2008). Light is an important limiting factor on forest diversity through canopy structure (Barbier et al., 2008; Damascos and Rapoport, 2002; Lencinas et al., 2008; Martínez Pastur et al., 2002; Quinteros et al., 2010). The negative relationship between BA and native species diversity is consistent with a

classic competitive exclusion explanation, because increasing abundance of the dominant overstorey trees is associated with greater light pre-emption, resulting in lower understory plot-scale native diversity (Kern et al., 2014). In addition, the higher understory native diversity values related to high irradiance (low BA values) indirectly suggest heliophilous PFTs species redundancy. On the contrary, lower understory native species diversity under high BA values (closed forest) highlight the importance of each understory species occupying different shade niches. These results may suggest that closed forest understory communities and related ecosystem functions present high degree of vulnerability against overstorey disturbances.

Crown and moderate fire disturbances increase post-fire species diversity by realizing growing space in terms of light at floor level, as well as, increasing soil nutrient abundance (Oliver and Larson, 1996; Whelan, 1995). This assumption is coincident with the positive shape parameter of recent fires ($f = 0.09$, Table 2) over native species diversity even though it was not statistically significant. Stands with recurrent disturbance events of moderate or low severity (e.g. gaps dynamics, fire) characterized by a canopy structure composed by uneven cohorts sustain higher species diversity values than even-aged stands. The Intermediate Disturbance Hypothesis (Wittaker et al., 2001) predicts maximal diversity whereby repeated local disturbances occur frequently enough to prevent competitive exclusion over an area, but not so frequent as to eliminate most species. Species coexistence may be favored by resource partitioning related to the heterogeneous canopy structure composed by old large tree survivors to fire, or sparse tree recruitments cohorts under other disturbances. PFTs diversity might be interpreted as an ecological niche availability indicator (Gillison et al., 2013). Thus, the high values of PFTs diversity on fire affected communities recorded in this study, support resource partitioning after disturbance.

Otherwise, high selective pressure by livestock favors reduced Mesophytic rosette herbs (Fig. 3). The communities under grazing are mainly dominated by Helio-erectophilous herbs (mostly grasses) (Fig. 3) which present intercalary meristems that allow

Table 3

Generalized linear set of best-ranked models examining effect of climatic variables on native species and plant functional types diversity. AICc, akaike information criterion for small samples; Δ_i , AICc differences; w_i , normalized weights of AIC; acc w_i , cumulative Akaike weight. T° , mean annual temperature; Pann, annual precipitation; WB, water balance. Notice that null models present the lowest AICc.

Native species diversity					Functional type diversity				
Candidate model	AICc	Δ_i AICc	w_i	acc w_i	Candidate model	AICc	Δ_i AICc	w_i	acc w_i
1. Null	147.1	0	0.455	0.455	1. Null	93.2	0	0.314	0.314
2. T°	148.2	1.1	0.263	0.718	2. Pann	93.2	0.006	0.305	0.619
3. T° + Pann	148.8	1.76	0.189	0.907	3. Pann + T°	93.6	0.46	0.25	0.869
4. Pann	150.2	3.17	0.093	1	4. T°	94.9	1.75	0.131	1
1. Null	147.1	0	0.424	0.424	1. Null	91.3	0	0.465	0.465
2. T°	148.2	1.1	0.245	0.669	2. WB + T°	92.1	0.79	0.313	0.778
3. T° + WB	148.9	1.81	0.172	0.841	3. T°	93.6	2.32	0.146	0.924
4. WB	149	1.96	0.159	1	4. WB	94.9	3.61	0.077	1

Table 4

Rho' Spearman correlation values between PFTs, stand characteristics, climatic variables (mean annual temperature – T° , annual precipitation – Pann, water balance – WB) with scores on the two first axis of the CA. Significant correlation values are marked by asterisks: ** $p < 0.05$ or * $p < 0.01$.

		Rho' Spearman correlation values	
		Axis 1	Axis 2
PFTs	Mesophytic shrubs	0.49*	-0.50*
	Higrophytic herbs	0.66*	-0.51*
	Mesophytic rosette herbs	0.71*	0.46*
	Helio-sclerophilous shrubs	-0.70*	-0.21**
	Heliophilous hairy herbs	-0.70*	-0.20**
	Helio-erectophilous herbs	-0.57*	0.07
	Dwarf shrubs	0.02	0.46*
Stand characteristics	Exotic species	-0.58*	-0.15
	Total basal area	0.68*	0.14
Climatic variables	T°	0.06	-0.40*
	Pann	0.11	0.05
	WB	-0.07	0.04

regrowing after damage by grazing herbivores. The synergic pressure of fire plus grazing affects native species diversity negatively (Fig. 2, Table 2). This pattern suggests grass species higher competitive aptitude than Heliophilous hairy herbs, Dwarf and Helio-sclerophilous shrubs species. Livestock or fire pressure on closed forests stands favors PFTs composition turnovers replacing Mesophytic rosette herbs by Helio-erectophilous herbs which are adapted to sprout after foddering/fire. This compositional shift may have major consequences over pollination services (Kremen et al., 2007) because most Mesophytic rosette herbs present zoophilous pollination whereas most Helio-erectophilous herbs are grasses with anemophilous pollination. The importance of animal-plant mutualistic interaction on *Nothofagus* forests have been extensively discussed (Aizen and Ezcurra, 1998; Aizen et al., 2002; Arroyo et al., 1983). Aizen and Ezcurra (1998) highlighted that deforestation, fragmentation and habitat degradation may be particularly threatening for mutualistic-dependent plants due to low redundancy in alternative animal partners.

Shade tolerant PFTs such as Mesophytic rosette herbs and Hygrophytic herbs are negatively associated to exotic species cover (Table 3). This might suggest shade species competitive exclusion by exotic species. Some exotic species traits such as short life span and sprout strategies represent an ecological advantage against most native perennial herb species. On the other hand, Heliophilous herbs are positively related to exotic species. Speziale and Ezcurra (2011) suggested that dominant exotic herbaceous annual and biennial species might fill open niches accessing resources that are not exploited by native species in northern

Patagonia forest-steppe ecotone. This hypothesis could explain also southern Patagonia forest-steppe ecotone heliophilous and exotic species coexistence. Grazing pressure history on each site could be another important driving factor influencing native and functional diversity which should be explored on future studies.

Fire occurrence slightly increases dwarf shrubs cover. Some of these species like *Empetrum rubrum* have been reported as sprouting after fire in *Nothofagus* forests communities (Vidal and Reif, 2011). Indeed, first colonization of the substrate by this Dwarf shrub may facilitate trees and other shrubs seedling by decreasing temperature and humidity day/night variability (Henríquez and Lusk, 2005). Dwarf shrubs and Mesophytic rosette herbs cover in the forest-steppe ecotone are favored by low temperatures (Table 4) suggesting the presence of morphoecological attributes that allow them to survive under snow level during autumn-winter. The opposite trend is observed on Mesophytic shrubs and Higrophytic herbs, this pattern indicates a functional divergence between understory plants traits especially in plots with high BA values (Norman et al., 2005; Appendix A3). Thus, temperature may represent an important functional divergence driver between closed forest understory species communities. However, temperature, precipitation and water balance would have a minor effect on driving species and functional diversity patterns at our research area. Species or plant functional types turnover associated to climate variables may not necessarily result in changes on diversity patterns.

The high correlation between PFTs and BA, suggests differences microclimatic conditions in biological terms at the understory level. The same situation was recorded by Paritsis et al. (2014) between unburned closed forest patches and shrub-dominated sites in northern Patagonia. The authors showed that significantly lowest maximum temperatures and higher relative humidity characterized unburned *N. pumilio* forest for the 10% of the warmest and driest days, respectively. Comparing our results to those carried out by Paritsis et al. (2014), we conclude that understory species overcome high temperature and low relative humidity by presenting hairy/sclerophilous/erectophilous leaves. Meanwhile hygrophytic, mesophytic and rosette leaves domain under closed forest canopy communities. The use of these PFTs may be a useful tool to explore indirectly different microclimatic conditions characterizing different forest-steppe ecotone communities under other disturbances not included in our study such as blowdowns and snow avalanches.

4.2. Plant functional types redundancy

Non-linear models suggested that non-disturbed communities present low degree of PFTs redundancy (Table 4, Fig. 4). On the

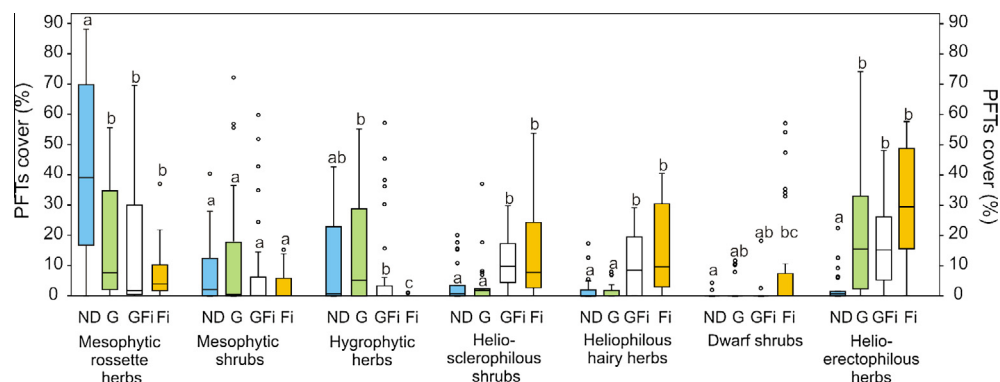


Fig. 3. Plant functional types cover under different disturbance types (ND – Non-disturbed, G – Grazing, Fi – Includes fire events occurred during the last 30 years and fire events occurred during early–middle 20th century). Different lowercase letters indicate significant differences after applying Games-Howell Post Hoc test ($p < 0.05$).

Table 5

Simple nonlinear model shape parameter “b” for each disturbance type. CI: confidence interval. Asterisks denote statistical differences between the shape parameter “b”.

Disturbance type	“b” Parameter estimate (SE)	CI	
		Lower	Upper
Non-disturbed	0.971 (0.154)*	0.644	1.344
Grazing	0.809 (0.108)	0.596	1.047
Grazing and fire	0.778 (0.097)	0.540	1.024
Fire	0.426 (0.083)*	0.244	0.597

other hand, fire occurrence favors PFTs redundancy (Table 4, Fig. 4). Even though resource distribution across niche space (in this case in terms of light/water availability conditions) on post-fire stands is even, high values of native species diversity suggest that heliophilous species may have higher niche complementarity than mesophytic species in the studied communities. Some native species adapted to similar light/water conditions present different traits in response to other filtering factors such as pollination mode e.g. unspecialized zoophilous – *Senecio filaginoides* (Aizen and Ezcurra, 1998) versus anemophilous – *Mulinum spinosum*; both Helio-sclerophilous shrubs (see Appendix A2), seed dispersal e.g. wind – *Symphotrichum vahlii* versus animals – *Acaena pinnatifida*; both Heliophilous hairy herbs (see Appendix A2), among others. The diversity of morphoecological traits shows the complexity of microenvironmental heterogeneity in spite of the apparent homogeneity of one niche space dimension (light/water availability intra-stands conditions). This more complete use of available resources within a community may allow a high invasion resistance and help to buffer ecosystem processes against climatic fluctuations (Mason et al., 2005). Our results suggest that fire-stand structure interactions drives PFTs redundancy mainly through heliophilous PFTs. However, the effect of disturbance over plants pollination syndrome and dispersal types should be analyzed empirically in future studies.

The high degree of PFTs redundancy after fire occurrence might be a result of long-millennial time scales evolutionary mechanisms acting over understory species. Paleoecological studies based on pollen and charcoal analysis from lakes and peat-bog sequences have shown fires occurrence in southern Patagonia since the late Glacial Maximum (ca. 20,000 years before present) (e.g. de Porras et al., 2012; Sottile et al., 2012; Whitlock et al., 2007). Changes on atmospheric circulation during the last 13,000 years favored forest-steppe west-east displacements. Those shifts showed to be synchronous to the increase in fire frequency along the ecotone (Sottile et al., 2012). Landscape heterogeneity composed by forest

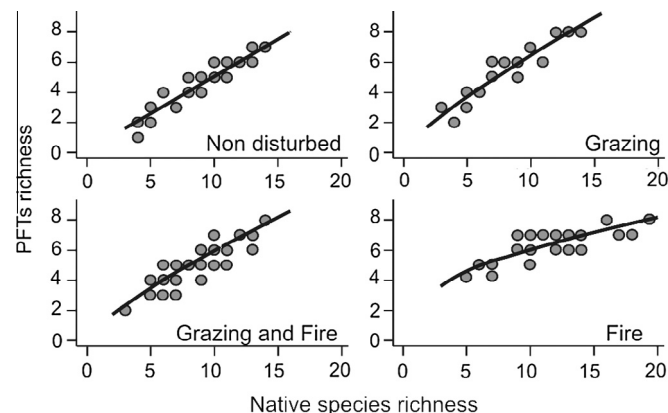


Fig. 4. Scatter plots and simple nonlinear models between native species and Plants Functional Types richness under different type of disturbance.

and steppe patches because of climate-fire dynamics, probably favored PFTs redundancy during this period. These features might have decreased the probability of species extinction during periods of major climatic changes.

4.3. Conservation and management implications

Multi-cohort forest stands support the highest levels of native species and PFTs diversity. The complex heterogeneity of these stands supports the coexistence of several species traits that probably sustain complex interactions between plants, insects and vertebrates. Historically, undisturbed forest areas have been the focus of conservation policies in Patagonia (Defossé and Urretavizcaya, 2003). Nonetheless, our results suggest that these policies should also include areas covered by multi-cohort and post-fire stands as well to protect highly native species diverse communities. On the other hand, our results highlight different PFTs under undisturbed and closed forest patches (high BA values) versus disturbed and open landscape communities (lower BA values). Even if closed forest communities present lower native species diversity values than open canopy communities, they probably sustain different biota than heliophilous communities. Therefore, closed undisturbed forest present high conservation values to southern Patagonia flora and fauna.

Kitzberger et al. (2012) and Paritsis et al. (2014) probed that post fire forest stands are highly flammable due to the coexistence of flammable resprouting shrubs and bamboo in the main canopy, the accumulation of dead stems from heliophilous shrubs and the self-thinning process. Despite the absence of bamboo in southern Patagonia forests, some helio-sclerophilous shrubs (e.g. *Gaultheria mucronata*; *Berberis microphylla*) together with small trees (*E. coccineum* and *Maytenus magellanica*) and some climbing stems herbs (*Vicia nigricans* and *Galium fuegianum*) would favor vertical fuel continuity increasing crown fire probabilities. Thus, landscapes dominated by post-fire stands (with intermediate values of BA) are more vulnerable to wildfires or accidental-tourist fires.

Several Los Glaciares National Park and other Chilean protected areas never recovered their tree communities after the anthropogenic crown fires occurred after mid-XX century. In these cases, both European settlement and modern livestock pressures over forest stands may have exceeded resilience thresholds of forest toward shrubland communities (Vidal and Reif, 2011). Paritsis et al. (2014) showed that there is a narrow strip bordering unburned forest patches with dense populations of *N. pumilio* seedlings and saplings. Given the slow dispersal of *N. pumilio* seed from unburned edges or scarce survivors of fire, succession from shrubland back to forest is a slow process requiring at least several to many decades (Paritsis et al., 2014; Veblen et al., 1996). However, the more flammable shrublands surrounding unburned forest could burn again, killing the *N. pumilio* juveniles during a lengthy window. Thus, management policies focusing on forest restoration should establish cattle exclusion areas bordering forest patches. This action would not only favors tree recruitment, but also shade tolerant understory species and PFTs recovery.

5. Conclusions

Our results allowed us to identify how stand characteristics factors, grazing and fire disturbance affect forest-steppe ecotone communities in terms of diversity patterns. At the forest-steppe ecotone, disturbance dynamics produce major changes over stand structure driving main species, PFTs diversity and PFTs dominance through changes in light/water gradients. Fire impact over forest-steppe ecotone communities is one of the most important top down factor driving major increases on PFTs redundancy and

heliophilous plants species abundance. On the contrary, grazing pressure represents threatening agents diminishing native forest-steppe biodiversity. The coexistence of different stands at different development stages in the same landscape ensures the seed bank pools of shade tolerant and heliophilous species. This fact probably favors hysteretic grade of major plant communities' distribution.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2015.05.025>.

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