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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 seedlers 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 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 seedlers 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 interrelated 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 leeside 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

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