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Structural–functional approach to identify post-disturbance recovery indicators in forests from northwestern Patagonia: A tool to prevent state transitions

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ABSTRACT

The disruption of the natural post-disturbance recovery process, either by changes in disturbance regime or by another disturbance, can trigger transitions to alternative degraded states. In a scenario of high disturbance pressure on ecological systems, it is essential to detect recovery indicators to define the period when the system needs more protection as well as the period when the system supports certain use pressure without affecting its resilience. Recovery indicators can be identified by non-linear changes in structural and functional variables. Fire largely modulates the dynamic and stability of plant communities worldwide, and is this the case in northwestern (NW) Patagonia. The ultimate goal of this study is to propose a structural–functional approach based on a reference system (i.e. chronosequence) as a tool to detect post-disturbance recovery indicators in forests from NW Patagonia. In NW Patagonia (40–42°S), we sampled 25 *Austrocedrus chilensis* and *Nothofagus* spp. communities differing in post-fire age (0.3–180 years). In each community we recorded structural (woody species cover and height, solar radiation, air temperature, relative humidity) and functional (annual recruitment of woody and tree species) attributes. We modeled these attributes in function of post-fire age and analized the relationship between a functional attribute and a Structural Recovery Index (SRI). Communities varying in time-since-last-fire were structurally and functionally different. Moreover, response variables showed non-linear changes along the chronosequence, allowing the selection of recovery indicators. We suggest to use vegetation variables instead of environmental variables as structural recovery indicators. Horizontal and Vertical Vegetation Heterogeneity indices provided the information necessary to describe vegetation spatial reorganization after fire. Tree species annual recruitment was a good indicator of the functional recovery of forest communities. The relationship between a functional attribute and SRI allowed us to detect phases with high- and low-risk of degradation during post-fire succession. High-risk phases (<36 years old) had the highest horizontal vegetation heterogeneity and scarce tree seedling density (<7000 seedlings ha^{-1} $year^{-1}$). Whereas, low-risk phases (>36 years old) had the highest vertical vegetation heterogeneity and tree species seedling density (>10,000 seedlings ha^{-1} $year^{-1}$). Due to the low structural–functional levels, communities at high-risk phases would be more vulnerable to antropic pressure (e.g. livestock raising, logging) than communities at low-risk phases. The proposed approach contributes to the sustainable management of forest communities because it allows to estimate the minimum structural–functional levels from which forest communities could be harvested.

1. Introduction

Ecosystems can be resilient to particular disturbance regimes, however the disruption of the natural post-disturbance recovery process, either by an increase in disturbance frequency/intensity or by another disturbance, can significantly decrease or even cause the loss of its resilience. In ecosystems dominated by slow growing, long-lived plants, changes in vegetation structure, composition and functionallity after stand-replacing disturbances may occur

Abbreviations: NW, northwestern; HVH, horizontal vegetation heterogeneity; VVH, vertical vegetation heterogeneity; TSF, total site factor; LL, low layer; ML, medium layer; HL, high layer; SRI, Structural Recovery Index; MD, Mahalanobis distance.

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over decadal time-scales (Haslem et al., 2011; Gosper et al., 2013). In these slow recovery ecosystems, an increase in disturbance frequency/intensity (e.g. climatic cycles, fires) or the interaction between natural disturbance events (e.g. fire, droughts) and subsequent anthropic use (e.g. cattle raising, logging) can interrupt the natural recovery process, triggering transitions to alternative degraded states (Westoby et al., 1989). These triggers can produce soil erosion and compaction (Beschta et al., 2004; Lindenmayer and Noss, 2006; Marañón-Jimenez et al., 2011) and reduce the effect of physical and biological legacies (Foster et al., 1998; Turner, 2010; Peters et al., 2011), affecting the ecological integrity of the ecosystem and reducing its ability to provide goods and services over time. In a scenario of high disturbance pressure on ecological systems by anthropogenic and/or natural factors, there is a growing need to detect recovery indicators to define the period when the system needs more protection as well as the period when the system supports certain use pressure without affecting its resilience (Müller et al., 2000; Briske et al., 2005, 2006).

Even though ecosystem recovery after disturbances is a complex process, it can be characterized by changes in structural and functional variables. As in degradation processes (Briske et al., 2005; López et al., 2011), recovery dynamics can be analized by plotting the values of these variables as a function of time since last disturbance. Specifically, structural and functional attributes used to estimate recovery dynamics can show non-linear changes in response to time since last disturbance. Therefore, recovery indicators can be detected based on the point where the slope of this function shows an abrupt change in value and/or sign (Clements et al., 2010). In terrestrial ecosystems, structural variables used to characterize degradation/recovery responses are based on environmental and vegetation traits. This attribute category includes solar radiation incidence, plant community diversity and composition, vertical and horizontal biomass distribution, relative abundance of different growth forms and incidence of invasive species, among others (Briske et al., 2005). Functional variables that can be used to characterize ecosystem responses can be also based on vegetation, including community-level processes such as pollination, seed dispersal, and plant recruitment as well as ecosystem-level parameters such as nutrient cycling and primary productivity (Briske et al., 2005; López et al., 2011). Here we tested for the existence of recovery indicators based on environmental and vegetation structural and functional variables in post-fire forested communities from northwestern (NW) Patagonia. Analyzing post-disturbance recovery dynamics and establishing when an ecosystem recovers certain structural and functional levels associated with the maintainace of its resilience is essential for its sustainable management.

Fire largely modulates vegetation distribution and composition worldwide, influencing the dynamic and stability of most plant communities (Bond and Van Wilgen, 1996). By removing vegetation biomass, fire increases radiation and temperature, and decreases soil and environment moisture (Guo et al., 2002, 2004). Also, by releasing space as well as nutrients (Guo et al., 2002, 2004), fire increases ecosystem susceptibility to degradation by soil erosion (Beschta et al., 2004; Lindenmayer and Noss, 2006) and/or biological invasions (Hughes and Vitousek, 1993; Didham et al., 2007), among other processes. Consequently, understanding plant community responses to fire is essential to predict vegetation recovery dynamics, guide management practices, and evaluate restoration strategies in fire-prone landscapes (Turner et al., 1998; Turner, 2010).

In NW Patagonia, fires, both natural and human-set, have largely modulated the structure and dynamics of forests and woody communities (Veblen and Lorenz, 1988; Kitzberger and Veblen, 1999; Veblen et al., 1999). In this study, we describe vegetation recovery after fire in *Austrocedrus chilensis* and *Nothofagus* spp. forests from NW Patagonia following a chronosequence approach (i.e. time by space replacement; Walker et al., 2010; Gosper et al., 2013). The existence of non-linear changes in structural and functional attributes during post-fire recolonization, would allow the identification of successional phases that could be more vulnerable to antropic pressure. The ultimate goal of this study is to propose a structural–functional approach based on a reference system (i.e. studied chronosequence) as a tool to detect recovery indicators.

2. Materials and methods

2.1. Study area

The study area is located in the northern Patagonian Andean region of Argentina. Soils are mostly derived from volcanic ash (andisols) and show a high capacity to stabilize soil organic matter, retain phosphorus and water and buffer pH (Colmet-Daage et al., 1993). Precipitation in this region is seasonally distributed; occurring mainly from April to September, as snow and rain, whereas the dry season extends from December to February. At this latitude, mean annual precipitation decreases abruptly from *c.* 4000 mm/year on the western side of the Andes to less than 500 mm/year, only 80 km to the east (Veblen et al., 2003). However, in the studied area mean annual precipitation ranges from 800 to 1600 mm/year. Along this precipitation gradient, two *Nothofagus* species (*Nothofagus dombeyi* and *Nothofagus antarctica*) form pure stands, or mixed with a native conifer *A. chilensis* in drier sites. A common feature of these forests is the presence of the same accompanying tree and shrub resprouting species (i.e. *Lomatia hirsuta*, *Maytenus boaria*, *Schinus patagonicus*, *Embothrium coccineum*, *Diostea juncea*, and *Berberis* spp.).

Fire represents the dominant stand-initiating disturbance in the Argentine forests of NW Patagonia (Veblen et al., 1992). The fire season in this region is coincident with the period with the strongest water deficit (i.e. from October to April) and the largest fires are concentrated in the summer months (i.e. January through March) (Kitzberger and Veblen, 1999). The minimum fire return interval occurring in the middle sectors of the rainfall gradient (about 700–1700 mm/year) is driven by a combination of moisture, which promotes a sustained accumulation of continuous fuel loads, and the occurrence of dry periods, which facilitates the drying of accumulated fuel material (Mermoz et al., 2005; Veblen et al., 1992).

The study area encompasses approximately 2,520,000 ha from Lanín and Nahuel Huapi National Parks and southward to Epuyén Lake in Chubut province (from 40° S to 42° S latitude, and the west-east belt of 71° W longitude, see Appendix A). During the summer seasons of 2007–2008, 2008–2009 and 2009–2010, we sampled a total of 25 plant communities belonging to potential vegetation states ('reference states' *sensu* Bestelmeyer et al., 2009) but that differred in time since last fire. Post-fire ages range from <1 to 180 years (Appendix A). All sampled sites were affected by stand-replacing fires. For the selection of communities whose fire date is prior to 1938 we used vegetation maps compiled in 1913 (Willis, 1914; Kitzberger and Veblen, 1999) and historical photographs taken between 1883 and 1948 (Veblen and Lorenz, 1988). For the selection of communities burned after 1938 we used the complete fire record of the Nahuel Huapi National Park and information extracted from published literature (Kitzberger and Veblen, 1999; Veblen et al., 1999; Mermoz et al., 2005). Besides being severe, all fires were extensive (i.e. burned area was >500 ha in all sites, except at three sites in which burned area was smaller) (Willis, 1914; Veblen and Lorenz, 1988; Kitzberger and Veblen, 1999; Veblen et al., 1999; Mermoz et al., 2005). When selecting each community, we prioritized the absence or scarcity of livestock and fuelwood