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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

extraction (information provided by the National Park Administration of Argentina), and thus we sampled the communities least disturbed by other factors rather than fire that were available. In order to control the east-west rainfall gradient, we selected 25 sites whose mean annual rainfall only varies between 800 and 1600 mm/year, while communities located in the western edge of the rainfall gradient (i.e. 1600–3000 mm/year) were excluded. Besides, recently burned and old post-fire (i.e. >100 years) communities were selected at both east and west portions of the sampled rainfall gradient so that mean annual rainfall was not confused with time since last fire (Appendix C).

2.2. Sampling procedure

We used a chronosequence to reconstruct the recovery process of burned forests. Chronosequences are useful tools to study temporal dynamics in plant communities, especially when the temporal lengths of successional trajectories exceed the possibilities of continuous observational studies over time (Walker et al., 2010; Gosper et al., 2013). In general, chronosequences are more appropriate to measure plant community attributes that change predictably in time (e.g. vegetation cover and species richness) and identification of disturbance dates improves its application (Walker et al., 2010).

At each site, we delimited a 9 ha plot (300 m × 300 m) representative of each community. Within each plot, we laid two perpendicular transects of 300 m length (one in east-west direction and the other in north-south direction) crossed at their mid-point. In each transect, we recorded: (a) woody species cover and height at 1-m intervals, and (b) solar radiation, air temperature, relative humidity, and density of seedlings of woody species at 5-m intervals. Transects were located in flat areas or places with very gentle slopes (<3°), and at least 100 m away from the nearest unburned area to limit the influence of edge effects (Kitzberger and Veblen, 1999; Kitzberger et al., 2005).

We estimated woody species cover by the point-intercept method (Mueller-Dombois and Ellenberg, 1974), dividing the vertical space into three layers: low (<2 m height), medium (2–10 m) and high (>10 m) (Raunkiaer, 1934). Specifically, woody species cover was estimated by the number of times a woody species in the low, medium or high layer was intercepted by a pole positioned perpendicular to the transect (or its vertical projection in the case of medium and high layers). Thus, a given layer recorded 100% cover when woody species intercepted all 301 sampling points. Woody species cover was determined at 1-m intervals because the point-intercept method requires at least 200 points to generate reliable estimates (Mueller-Dombois and Ellenberg, 1974). In the first 50 m of each transect, woody species cover was recorded at intervals of 0.5 m in order to obtain accurate estimates, especially in communities with low vegetation cover (<4 years since last fire). Finally, in the first 100 points of each transect, when we found more than one individual per stratum, we recorded the height of the highest individual.

To estimate solar radiation in the understory we took hemispherical photographs (Nicotra et al., 1999; Gómez et al., 2004) at a height of 0.3 m by using a horizontally leveled digital camera (Coolpix 990™, Nikon Corporation, Tokyo, Japan) aimed at the zenith with a fisheye lens of 180° field of view (FC-E8™, Nikon Corporation, Tokyo, Japan). Temperature and relative humidity were recorded at 0.2 m from the floor surface, with a pocket weather station that provides instantaneous measurements (Kestrel 3000). The value considered for each point was the average of instantaneous measurements over a 10 min period. Temperature and relative humidity records were performed during sunny days. Environmental variables were recorded at 5-m intervals to reduce autocorrelation of consecutive records over space. Seedlings (i.e., individuals recruiting from seed <10 cm with cotyledons or cotyledon scars) of each woody species were sampled using 1 m^2 plots (Nicotra et al., 1999) centered on the same points where environmental variables were recorded (61 m^2 per transect).

2.3. Data analysis

2.3.1. Structural attributes

To interpret recovery dynamics we evaluated structural attributes based on the following variables: solar radiation and its standard deviation, standard deviation of temperature and relative humidity, and vertical and horizontal vegetation heterogeneity. Hemispherical photographs were analyzed with WinSCANOPY™ (Software for Hemispherical Image Analysis, Regent Instruments Inc., Quebec, Canada) to estimate total site factor (TSF). TSF is defined as the proportion of direct and diffuse radiation received under the canopy, expressed as a fraction of the radiation received above the canopy (Gómez et al., 2004).

Temperature and relative humidity were detrended in order to avoid the temporal autocorrelation produced by its sequential recording along the transects. We modeled the daily behavior of each variable in each transect from each community by using quadratic or higher polynomic regressions. Predicted values (obtained from the best model) were subtracted to raw data to obtain their residuals (R Development Core Team, 2006). We calculated standard deviation from temperature and relative humidity residuals as a measure of environmental heterogeneity. Total radiation was not detrended because, from each photograph, Winscanopy provides an expected daily mean for the entire growing season (November–April).

We used different variables to characterize vegetation structure. Based on vegetation samplings, we estimated the following dependent variables: total cover (summing cover per layer at each point, overlapping layers were considered as a single point for the calculation), cover per layer (low, medium and high), average patch size, average inter-patch size, patch and inter-patch number, coefficients of variation of patch and inter-patch size, and mean maximum height of each layer. A "patch" was considered as any group of woody individuals (shrubs and/or trees) whose continuous cover was interrupted by >1 m of bare soil or herbaceous species cover (hereafter "inter-patch") (Aguiar and Sala, 1999).

We calculated two spatial vegetation heterogeneity indices: Horizontal (adapted from López et al., 2013) and Vertical (proposed in this study) since ecosystem structure can be characterized by three dimensional spatial distribution of biomass (Walker, 1995; Müller, 2005; Kandziora et al., 2013). According to Li and Reynolds (1995), spatial heterogeneity can be assessed based on the patch size of a variable and its variability (standard deviation = σ). Thus, we estimated Horizontal Vegetation Heterogeneity (HVH) as:

$$\begin{aligned} \text{HVH} = {} & (\sigma \text{ patch size/average patch size}) \times \text{patch number} \\ & + (\sigma \text{ inter-patch size/average inter-patch size}) \\ & \times \text{inter-patch number.} \end{aligned}$$

The first term in the formula indicates whether there is variability in patch size, while the second term in the formula indicates if patches are heterogeneously distributed in space (inter-patch size variability) (see more in López et al., 2013). HVH ranges from 0 to +∞, and is zero when no patches are found (average size patch = 0), when all patches are of equal size (patch size standard deviation = 0), or when patches are equally distributed over space (inter-patch size standard deviation = 0), independently of patch number. Patch number increases heterogeneity when there are

numerous differently sized patches unevenly distributed in space (different inter-patch size). The lower the HVH, the more homogeneous the horizontal spatial configuration of vegetation cover will be, whereas the higher HVH, the more heterogeneous vegetation cover configuration will be.

Vertical vegetation heterogeneity (VVH) was estimated as:

$$\mathrm{VVH} = (\bar{h}\mathrm{LL} \times \sigma \times \mathrm{PropLL}) + (\bar{h}ML \times \sigma \times \mathrm{PropML}) + (\bar{h}\mathrm{HL} \times \sigma \times \mathrm{PropHL}).$$

VVH is based on the average height ($\bar{h}$), standard deviation and cover (as a proportion of the total) of each layer. The cover per layer expressed as a proportion (Prop = cover/100) weighs the contribution of each layer to the VVH. If the high layer has a 50% cover (Prop = 0.5), then the high layer will contribute a 50% to VVH value. The contribution made by each layer is summed across layers because we assume that each layer adds vertical complexity to the community. Height is multiplied by its standard deviation because we assume that if two communities have the same average height for a given layer, the community that records greater height variability will have greater vertical heterogeneity. Finally, to assess whether there is a change in the dominant growth forms (i.e. shrubs vs. trees) in communities of different post-fire age we calculated the proportion of trees species as: tree species cover/(tree species cover + shrub species cover) (see the growth form of each species in Appendix B).

2.3.2. Functional attributes and post-fire recolonization strategies

To assess functional attributes, we analyzed variables associated with the regenerative capacity of the plant community (Briske et al., 2005; López et al., 2011), by considering: (a) different regeneration strategies: resprouting (i.e. species that survive fire and regenerate its biomass from dormant vegetative buds located on rhizomes or stumps, among others) vs. non-resprouting (i.e. species that usually do not survive fire and depend on seed dispersal from unburned sites to recolonize burned sites); and (b) the recruitment of new individuals (i.e. seedlings) from woody and tree species. To assess changes in regeneration strategies dominance in communities of different post-fire age we calculated the proportion of non-resprouting species as: non-resprouting species cover/(non-resprouting species cover + resprouting species cover). Regeneration strategy of each woody species was determined following Veblen et al. (2003) and Donoso (2006) (Appendix B).

To determine which variables exhibited a non-linear response we performed simple and piecewise regressions. Piecewise regressions are effective tools to model abrupt changes in a dependent variable as a consequence of continuous changes in an explanatory variable (Toms and Lesperance, 2003; Ficetola and Denoël, 2009) and are composed of two or more lines joined at unknown points (i.e. breakpoints: γ). We used straight lines to model each segment. Piecewise regressions were judged to better fit the data when significant differences were detected between models or when the Akaike Information Criterion (AIC) was at least 2 units lower than the AIC of simple regressions (Crawley, 2007) (Appendix D). Simple and piecewise regressions were performed with R software (lm package; R Development Core Team, 2006). Response variables were transformed with natural logarithm or $\ln(y+1)$ when did not met normality, heterocedasticity, and residuals independence assumptions.

2.3.3. Structure–function interrelation

In order to synthesize the structural attributes from each community, we calculated a Structural Recovery Index (SRI) (adapted from structural degradation index of López et al., 2011) considering the structural variables used to calculate vegetation heterogeneity indices (HVH and VVH). Mahalanobis distance (MD) between communities of different post-fire age was calculated based on these structural attributes. MD determines the similarity between units characterized by multidimensional data (Legendre and Legendre, 1998). MD considers correlation between variables, thus weighting each variable by its variance. So this distance measure is invariant to scale changes and is independent of measurement units (Legendre and Legendre, 1998). SRI was calculated as $\mathrm{SRI} = [(\mathrm{MD}_i \times 100)/\mathrm{MD}_{\max}]$, where MD_i is the MD between the ith community and the community that had the highest structural attribute values (i.e. $\mathrm{MD}_{\max}$). Finally, we performed a regression between SRI (explanatory variable) and tree species seedling density per hectare per year (dependent variable) to detect the recovery of structural and functional integrity (i.e. recovery of forest physiognomy and its functionality, estimated by the ability of the community to replace senescent adult trees).

3. Results

Communities varying in the time-since-last-fire were structurally and functionally different (Figs. 1–3). Furthermore, structural and functional attributes showed non-linear changes along the chronosequence studied. Although the communities we sampled differed in the degree of tree species dominance (i.e., mixed forests of *A. chilensis* and *N. antarctica* or *N. dombeyi* and pure forests of *Nothofagus* spp.), the structural and functional attributes recorded in this chronosequence were similar among them, mainly in communities younger than 36 years (Figs. 1–3).

3.1. Structural attributes

Communities below 30 years had markedly higher environmental heterogeneity than communities over 30 years, where the standard deviation of temperature and relative humidity decreased considerably (Fig. 1c and d). Also, total radiation near ground was higher in communities younger than 35 years, while the highest values of standard deviation in total radiation were found in communities approx. 26 years old (Fig. 1a and b). Total cover increased sharply reaching its maximum values in communities > 10 years old (Fig. 2a). The average patch size increased steeply to its maximum in communities older than 28 years (Fig. 2c). In contrast, the response of patch number was more delayed reaching a minimum in communities over 40 years old (Fig. 2e).

Post-fire communities <5 years recorded low Horizontal Vegetation Heterogeneity (Fig. 2f). In these communities, low ground cover was distributed in a few small patches inmersed in a bare soil matrix (i.e. large inter-patches) (Fig. 2c, e, and f). The HVH reached its maximum values in communities around 9 years (Fig. 2f), characterized by numerous patches and inter-patches of varying sizes (Fig. 2c and e). On the other hand, minimum HVH values were recorded in communities >40 years old (Fig. 2f), characterized by high vegetation cover distributed in a few large patches and small inter-patches, both with low size variation (Figure 2c and e). In contrast, both Vertical Vegetation Heterogeneity and mean maximum height (Fig. 2b and d) reached their maximum values in communities older than 40 years. Finally, shrubs dominated in communities <36 years, whereas trees dominated in communities >36 years old (Fig. 3a).

3.2. Functional attributes and post-fire recolonization strategies

In communities <36 years old, resprouting species cover was higher than non-resprouting species cover (Fig. 3b). Whereas resprouting and non-resprouting species co-dominated in communities over 36 years old (Fig. 3b). The highest seedling density from

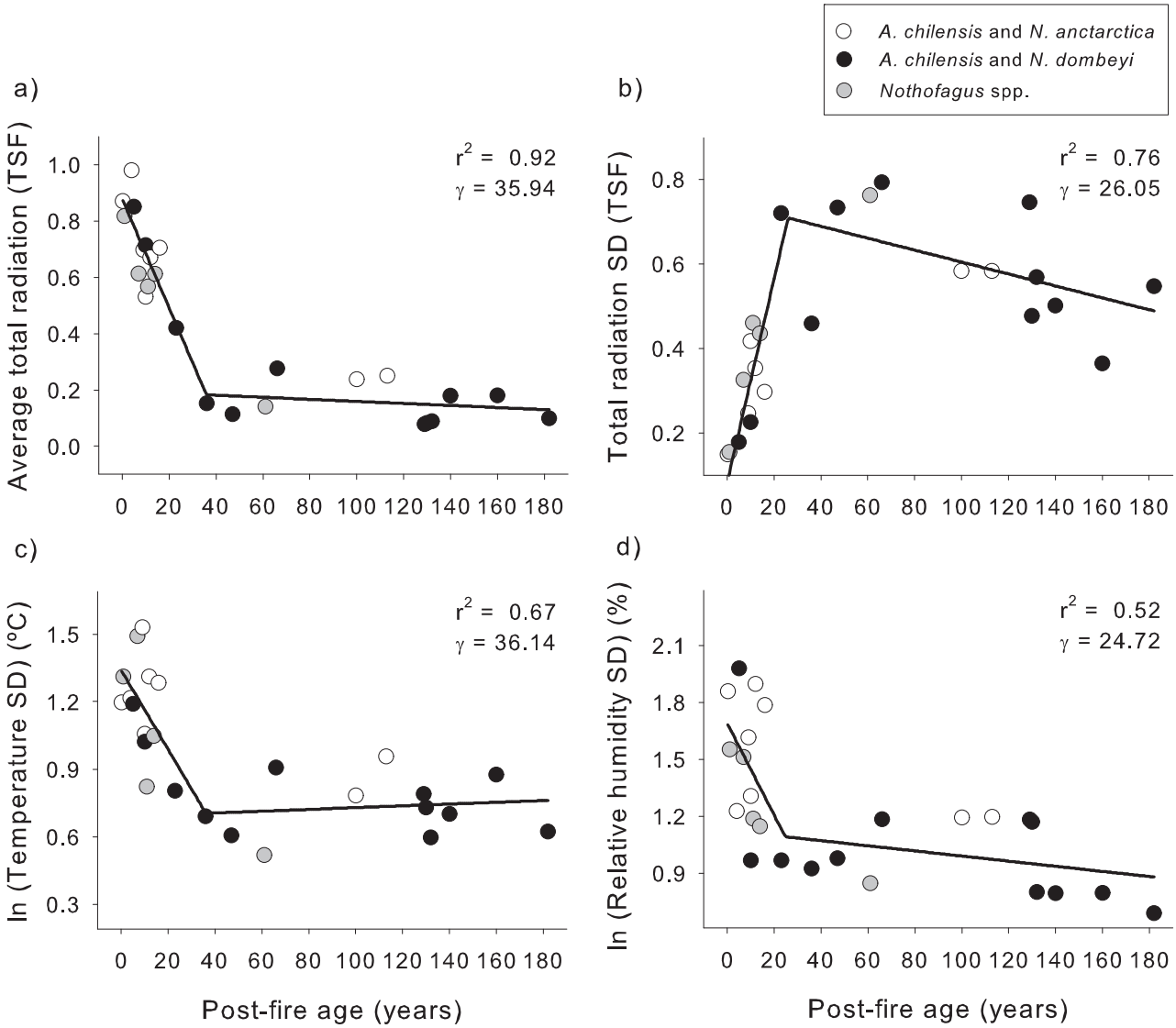

Fig. 1. Piecewise regressions of average total radiation (a), standard deviation of total radiation (b), standard deviation of temperature (c), and standard deviation of relative humidity (d) in function of post-fire age. The circles represent the average value for two transects on each community ($n = 25$). Each graph shows the adjusted coefficient of determination (r^2) and the estimated breakpoint (γ).

woody species was recorded in communities older than 28 years (Fig. 3c, Table 1). Whereas communities over 36 years recorded higher tree species seedling density than communities below 36 years (Fig. 3d).

3.3. Structure–function interrelation

When analyzing a functional attribute (annual recruitment of tree species) in relation to structural attributes (Structural Recovery Index), communities of different post-fire ages separated in two clearly defined groups characterized by distinct structure–function feedbacks. Communities <36 years had the highest horizontal vegetation heterogeneity and scarce tree seedling density (<7000 seedlings ha^{-1} $year^{-1}$; Fig. 4), while exhibiting the highest incidence of shrub and resprouting species (74% and 90%, respectively). In contrast, communities >36 years had the highest vertical vegetation heterogeneity and tree species seedling density (>10,000 seedlings ha^{-1} $year^{-1}$) (Fig. 4).

4. Discussion

Post-fire logging and livestock grazing are common management practices in many forests worldwide (Belsky and Blumenthal, 1997; Beschta et al., 2004; Lindenmayer and Noss, 2006). However, these practices can hinder natural recovery of forest ecosystems (Beschta et al., 2004; Donato et al., 2006; Lindenmayer and Noss, 2006; Castro et al., 2010; Raffaele et al., 2011) and even drive transitions to alternative degraded states. Therefore, the detection of recovery indicators is critical because it allows to estimate the minimum structural and functional levels that a post-disturbance ecosystem should recover to maintain its resilience to anthropic pressure. Piecewise regressions of structural and functional variables in function of post-fire age helped us to select recovery indicators of burned forest communities (Figs. 1–3). The structural–functional approach (i.e. the assessment of annual tree species recruitment in function of a Structural Recovery Index) allowed us to differentiate successional phases with high- and low-risk of degradation (Fig. 4).

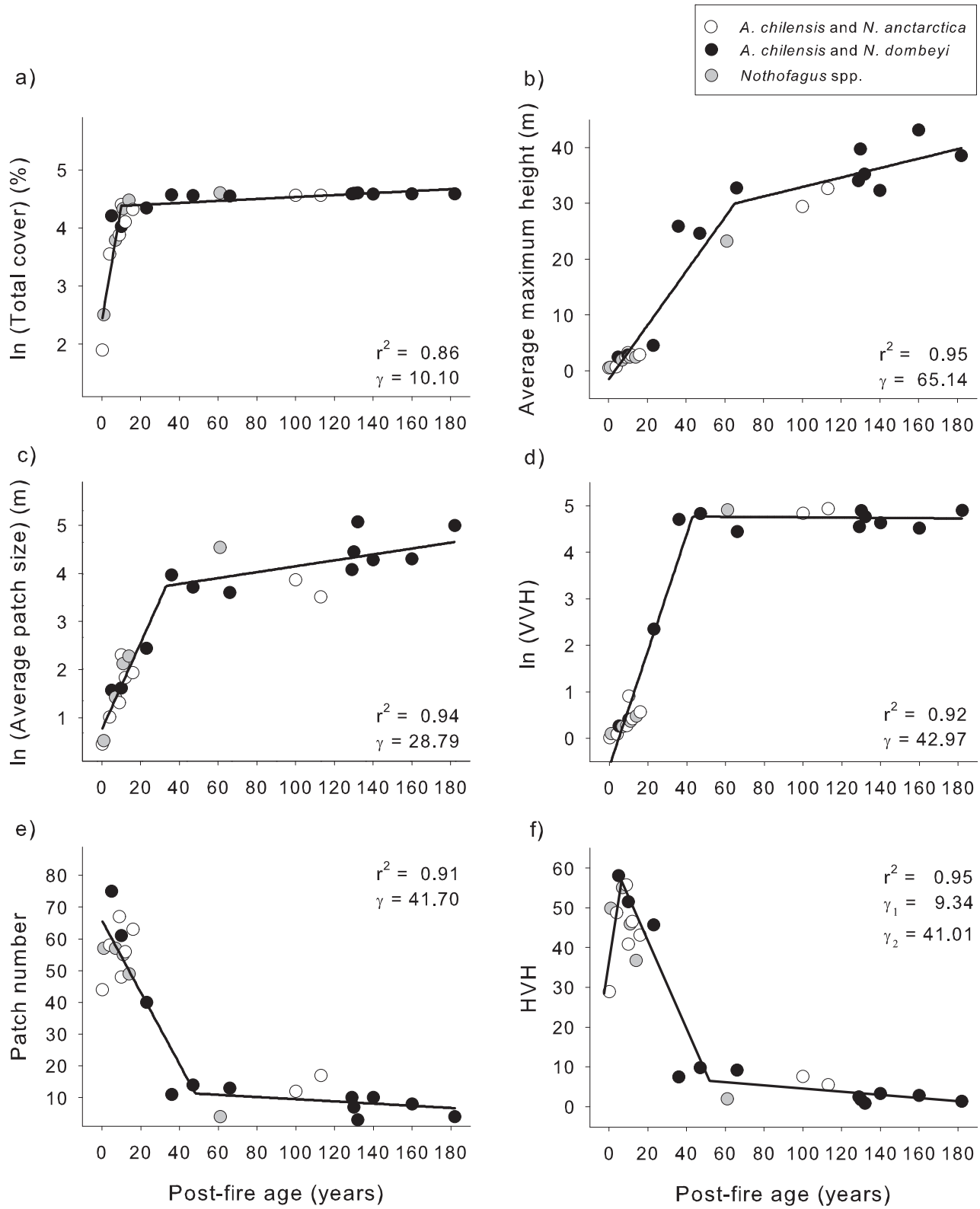

Fig. 2. Piecewise regressions of total cover (a), average maximum height (b), average patch size (c), vertical vegetation heterogeneity (VVH) (d), patch number (e), and horizontal vegetation heterogeneity (HVH) (f) in function of post-fire age. The circles represent the average value for two transects on each community ($n = 25$). Each graph shows the adjusted coefficient of determination (r^2) and the estimated breakpoint (γ).

4.1. Structural indicators

We evaluated environmental and vegetation attributes to select indicators of structural recovery after fire. We found that both environmental and vegetation variables were sensible indicators of the post-fire recovery process. Specifically communities <24–36 years old were more heterogeneous (i.e. temperature and humidity were more variable and recorded more extreme values Fig. 1c

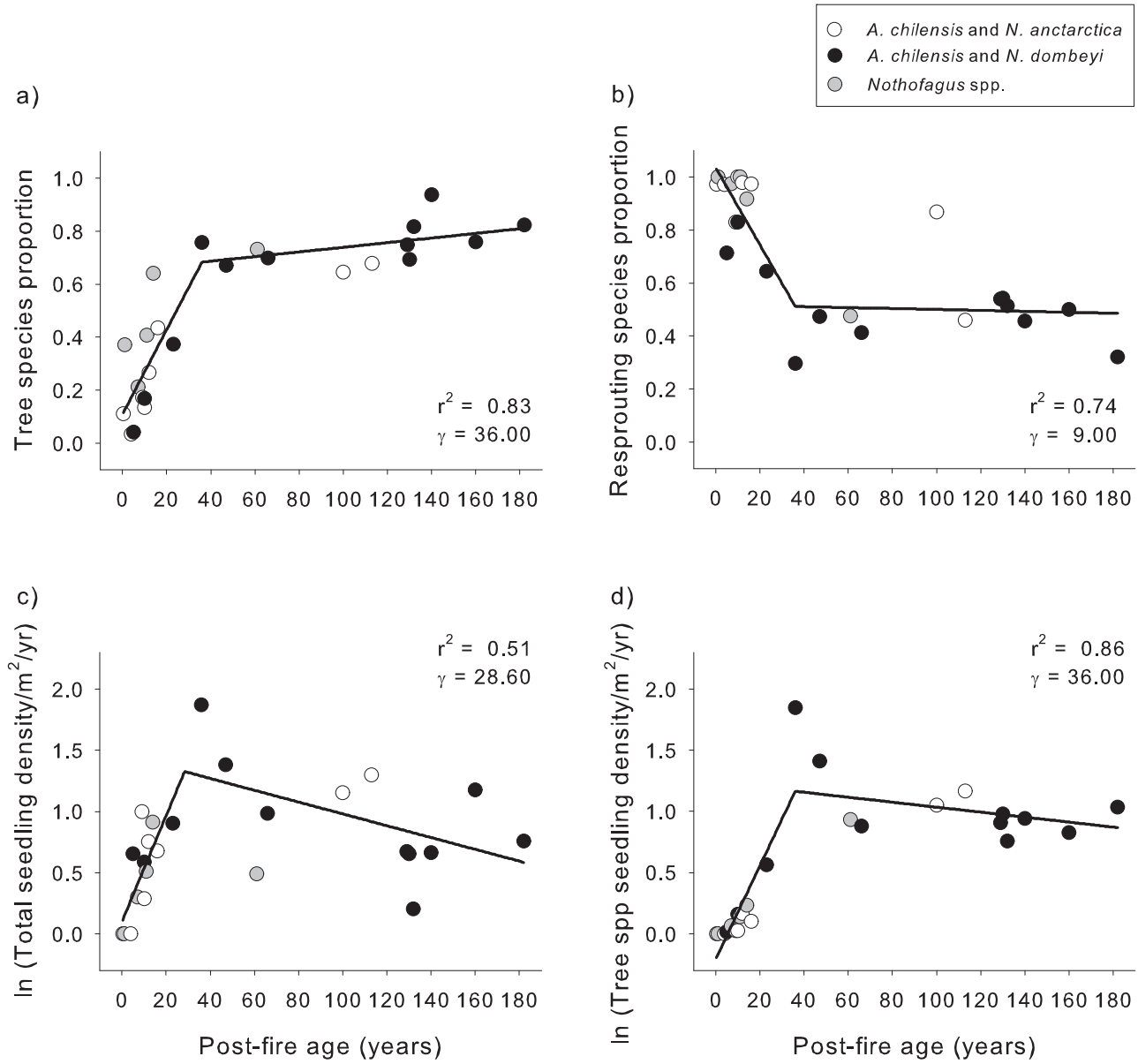

Fig. 3. Piecewise regressions of tree species proportion (a), resprouting species proportion (b), total seedling density (c) and tree species seedling density (d) in function of post-fire age. The circles represent the average value for two transects on each community ($n = 25$). Each graph shows the adjusted coefficient of determination (r^2) and the estimated breakpoint (γ).

and d), received higher radiation at ground level (Fig. 1a), and had a higher number of small plant patches (Fig. 2c and e) than communities >24–36 years old. This could be due to the biotic ecosystem components affect the spatial and temporal patterns of the abiotic habitat ecosystem features (Müller, 2005), since vegetation removal increases radiation, temperature, and evaporation levels, and also thermal amplitude (Knapp, 1984; Hulbert, 1988; Paritsis et al., 2006; Cavallero and Raffaele, 2010). We suggest to use vegetation variables as indicators of structural recovery of post-disturbed plant communities, considering that (1) indicators should be easy to measure and monitor under field conditions, (2) have low cost from both economic and sampling effort perspectives, and (3) show differences between unrecovered and reference communities (Kandziora et al., 2013). This is justified because (1) environmental variables recorded similar breakpoints to vegetation variables (Figs. 1 and 2), and (2) the measurement of environmental variables is more costly in time (e.g. hemispherical photographs processing is a time consuming task) and money (e.g. expensive equipment, such as data loggers, is needed) than measuring vegetation attributes.

Vegetation heterogeneity indices proved to be good indicators of structural recovery because they reflected spatial vegetation reorganization after fire. In our study, fire produced spatial homogenization in the short term (i.e., during the first 5 years after fire) (Turner et al., 1994; Pérez and Moreno, 1998), due to total vegetation removal (Figs. 1a, b and 2a). The first breakpoint of HVH (9 years) was similar to the breakpoint of total cover (Fig. 2a and f), suggesting that ground cover would have been rapidly recovered by resprouting species (Fig. 3b). The maximum values of HVH indicate that plant cover was spatially distributed in numerous patches, formed by the individuals who survived and resprouted after fire (Fig. 3b). This could be because, as vegetation recovers, the spatial aggregation of vegetation increases (Pausas and Lloret, 2007), and positive interactions between individuals prevail (e.g. seed capture by shrubs and facilitation between sprouted shrubs to emerging seedlings) (Bertness and Callaway, 1994; Gómez-Aparicio et al.,

Table 1
Estimated breakpoint (γ), slope of the first (β_1) and second (β_2) segment ± standard error of the estimate (SE), p-value (p) and adjusted coefficient of determination (r^2 Adj.) of the piecewise regression for each response variable in function of post-fire age. The transformation of the variables that did not met normality and heteroscedasticity assumptions is indicated. SD = standard deviation; CV = coefficient of variation; Ln = natural logarithm.

Response variables	Transf.	Adjust. r^2	γ (breakpoint)			β_1 ($y<\alpha$)			β_2 ($y>\alpha$)		
			Coef.	SE	p	Coef.	SE	p	Coef.	SE	p
Average total radiation		**0.9161**	35.9390	6.2708	**<0.0001**	0.1825	0.0487	**0.0012**	0.1293	0.0487	**0.0148**
Average total radiation SD		**0.7238**	26.0559	4.4740	**<0.0001**	0.7092	0.0645	**<0.0001**	0.4888	0.0630	**<0.0001**
Temperature SD	Ln	**0.6276**	36.1362	10.1053	**0.0018**	0.7038	0.1140	**<0.0001**	0.7616	0.1039	**<0.0001**
Relative humidity SD	Ln	0.4576	24.7196	11.8183	**0.0488**	1.0915	0.1796	**<0.0001**	0.8790	0.1547	**<0.0001**
Total cover	Ln	**0.8416**	10.1014	0.9234	**<0.0001**	4.3806	0.1044	**<0.0001**	4.6707	0.1327	**<0.0001**
Average patch size	Ln	**0.9343**	28.7909	4.8735	**<0.0001**	3.6878	0.2095	**<0.0001**	4.9587	0.2674	**<0.0001**
Average patch size CV	Ln	0.3056	14.000	3.7493	**0.0012**	4.7648	0.0962	**<0.0001**	4.3830	0.1071	**<0.0001**
Total patch number		**0.8996**	41.7008	6.2009	**<0.0001**	12.3779	5.3373	**0.0306**	4.1875	6.3356	0.5158
Average inter-patch size		**0.9290**	1.8039	0.2539	**<0.0001**	2.9398	0.2314	**<0.0001**	0.3912	0.3701	0.3024
Average intepatch size CV		**0.8381**				−0.5923	0.0529	**<0.0001**			
Total inter-patch size	Ln	**0.8556**	47.8636	11.7919	**0.0006**	1.7395	0.4204	**0.0005**	0.8391	0.3123	**0.0138**
Average maximum height		**0.9486**	65.1381	9.7276	**<0.0001**	29.9756	3.3247	**<0.0001**	39.8670	2.4010	**<0.0001**
Vertical vegetation heterogeneity	Ln	**0.9663**	42.9726	3.7377	**<0.0001**	4.7664	0.2478	**<0.0001**	4.7297	0.2376	**<0.0001**
Horizontal vegetation heterogeneity		**0.9441**	9.3383	0.2770	**0.0001**	59.9848	2.5260	**<0.0001**			
			41.0148	4.9573	**<0.0001**	8.1226	3.4530	**0.0296**	0.6633	3.0988	**0.0016**
Tree species proportion		**0.8346**	36.0000	11.273	**0.0044**	0.1140	0.0623	0.0814	0.6829	0.0724	**<0.0001**
Resprouting species proportion		**0.7417**	36.0000	11.213	**0.0042**	0.5116	0.0898	**<0.0001**	0.4856	0.0792	**<0.0001**
Total seedling density	Ln	0.4430	28.5892	8.0383	**0.0019**	1.3351	0.1893	**<0.0001**	0.5785	0.1970	**0.0079**
Tree species seedling density	Ln	0.8603	36.0000	6.2397	**<0.0001**	1.1649	0.1322	**<0.0001**	0.8679	0.1251	**<0.0001**

Bold fonts denote significant results considering an $\alpha = 0.05$.

2004; Cavallero et al., 2012, 2013). The second breakpoint of HVH (41 years) was similar to the breakpoints recorded by patch size and number and by VVH (Fig. 2c–f), indicating a change in the spatial organization of post-fire plant communities. Thus, communities >40 years old, recorded the lowest values of HVH, which it was associated with the growth and coalescence of vegetation patches (Fig. 2c, e, and f), whereas the highest values of VVH, which it was mainly associated with the appearance of a high layer dominated by tree species (>20 m; Figs. 2b, d, and 3a). Thus, Horizontal and Vertical Vegetation Heterogeneity indices provide complementary information that enables to interpret the structural recovery process of post-disturbance forest communities. Consequently, heterogeneity indices would represent key indicators of ecosystem structure as they provide information on the capacity of an ecosystem to provide suitable habitats for different species, for functional groups of species and for processes (see also Kandziora et al., 2013).

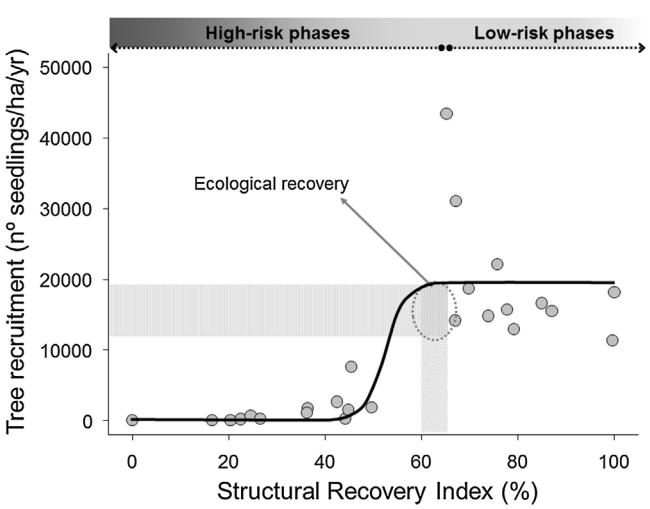

Fig. 4. Structural–functional characterization of post-fire recovery process. Number of seedlings of tree species per hectare and per year in function of Structural Recovery Index (SRI). The data adjusted to a sigmoid curve ($r^2 = 0.68$, $p < 0.0001$). Gray dots represent the sampled communities ($n = 25$). The recovery process scheme is proposed for the precipitation range considered in this study (800–1600 mm/year).

4.2. Functional indicators

We found a similar non-linear response in annual recruitment of woody and tree species. However, tree species annual recruitment would be a better indicator of the functional recovery of forest communities because it meets certain requirements. First, a noble indicator must have an integrating and synoptical value about certain phenomena (Wiggering and Müller, 2004). Seedling recruitment provides aggregated information from other factors and processes, including plant vigor and fertility, pollination, seed dispersal and germination, seedling emergence and survival, among others (Zeiter et al., 2006; López et al., 2011). Despite both functional attributes have an integrating and synoptical value, forest communities depend largely on seedling recruitment of tree species to maintain its composition and structure across time and to recover after disturbances (Leck et al., 2008). Second, a good indicator should show the difference between unrecovered and reference communities (Angeler and García, 2005; Kandziora et al., 2013). Woody and tree species seedling density were significantly higher in reference communities (i.e. >28 and 36 years old, respectively; Fig. 3d, Fig. 4). However, compared to woody species, the recruitment of tree species (i.e. foundational species *sensu* Ellison et al., 2005) provides a better assessment of the degree of recover of forest communities after fire, since a limited or null recruitment of foundational species can produce significant changes on the structure and composition of plant communities, driving negative transitions to alternative stable states (i.e. shrubland states) (Leck et al., 2008). Third, a noble indicator should be inexpensive and easy to measure in field conditions (Angeler and García, 2005; Kandziora et al., 2013). The economic cost and sampling effort required to record annual seedling recruitment are scarce compared to the cost of measuring other functional indicators such as nutrient cycling or hydrological processes. Finally, a good indicator must have high utility for early warning purposes (Kandziora et al., 2013). The assessment of tree species recruitment enables to anticipate drastic ecosystem changes that could occur in the long-term if there were no restocking of tree species. For

example, if a certain management practice (e.g. livestock grazing) causes a decrease in the recruitment of tree species (e.g. due to herbivory) in forest communities, its consequences will appear in the long-term when there will not be regeneration to replace senescent adult trees. Besides, a high seedling density of woody species in mature communities may not indicate functional recovery but can indicate a transition to a shrubland state, if a high proportion of these seedlings is from shrub species. In addition to the strengths listed above, seedling recruitment has already been used as functional indicator in dry grasslands (Zeiter et al., 2006) and in wetlands (Angeler et al., 2004). However, this indicator has the limitation that is sensitive to inter-annual climatic variability, and to mast-seeding events. An alternative to correct the association of seedling recruitment to inter-annual climatic variability is to perform samplings during years with average rainfall (Fig. 4) or to relativize annual recruitment by the rainfall amount fell during the growing season (Fig. E.II on Appendix E).

4.3. Ecological recovery: identification of phases with high- and low-risk of degradation

In the context of the State and Transitions Model, different phases connected by reversible transitions can be identified for a given state (see Bestelmeyer et al., 2009, 2010). Specifically, the 'reference phase' is defined by the community which exhibits the potential characteristics of the reference state, and is considered to be the most resilient within the state. In states featuring a natural or normal disturbance regime, this would be a phase that has not been disturbed recently, such as a late seral stage. On the contrary, the 'risk phase' is identified as the community most vulnerable to suffer a transition to an alternative state, and thus is considered to be the least resilient within the state (Bestelmeyer et al., 2010). Under this reasoning, transitions occur when a community in risk-phase is affected by a disturbance factor (e.g. extreme drought) or by a management decision (e.g. logging) (Bestelmeyer et al., 2009). In this context, our study provides a set of tools to identify phases having high- and low-risk of suffering a transition to an alternative state. The Structural Recovery Index (SRI) allows to estimate what percentage of the vegetation structure recovered after a disturbance compared to a fully recovered community (Fig. 4). In turn, vegetation heterogeneity indices provide complementary information to SRI as they serve to describe how vegetation reorganizes in space, considering horizontal and vertical dimensions. Although structural characterization has a great management value because it is most easily quantified, it does not provide dynamic information about the system. In other words, structural levels represent the information provided by a community snapshot (e.g. ground cover percentage), whereas functional levels can be linked to processes that occur over a specific period of time (e.g. net primary productivity by year) and can forecast future structural changes. These tools allowed us to identify phases with different risk to degradation during post-fire succession (Fig. 4). High-risk phases (SRI < 60%) would correspond structurally with shrublands (<10 m) dominated by resprouting shrub species, characterized by low VVH but high HVH that generated highly variable and extreme environmental conditions. From a functional perspective, tree seedling density was scarce (Fig. 4). In contrast, low-risk phases (SRI > 60%, within which the communities in reference phase are found) would correspond structurally with tall forested communities (>20 m) with a high layer dominated by tree species. These communities could be characterized by a continuous woody species cover, where HVH was the lowest whereas VVH the highest. From a functional perspective tree seedling density increased at least seven orders of magnitude, indicating full funtional integrity recovery (Fig. 4). These forest communities would have low-risk of degradation because they recorded the maximum structural–functional levels, suggesting the recovery of the biophysical legacy (e.g. seed and/or seedling banks). On the contrary, communities with low structural–functional levels would have a high-risk of degradation. In these less complex communities, any disturbance factor (e.g. overgrazing, extreme droughts) that maintains low ground cover and low vegetation heterogeneity for long periods will increase the likelihood of triggering hydric and/or eolic erosion. Also, anthropic use (e.g. livestock raising, logging) and/or increase in fire frequency (e.g. in a context of climate change) can favor the persistence of highly flammable sprouting species (Blackhall et al., 2014), stabilizing these communities in degraded states by enhancing vegetation-fire feedback processes (Raffaele et al., 2011; Paritsis et al., 2014; Pausas, 2014;).

The structural–functional approach allowed us to validate indicators of ecological recovery after fire. Although the post-fire age ranges can provide an indication of community recovery, it is more appropriate to use the values from structural and functional attributes to estimate ecological recovery. This is because the time that may take a specific community to reach certain structural–functional levels can vary depending on several factors (e.g. location along the rainfall gradient, fire intensity and extent, and the occurrence of wet and dry climatic cycles). In other words, if several wet years occur after a fire, vegetation recovery will be probably faster than if after the same fire several dry years occur. From a practical perspective, the structural and/or functional indicators we tested here should allow to assess the degree of ecological recovery (i.e. structural–functional levels) in a given site without knowing in detail its previous history (e.g. fire date, occurrence of climatic events during the recovery process), and thus we encourage their implementation in management programs. For our study system, a community that records a tree layer ≥20 m tall, >80% woody species cover, vegetation patches >35 m and more than 10,000 tree seedlings ha^{-1} $year^{-1}$ would have recovered its structural–functional integrity, regardless of how long it took to achieve those attribute levels.

While other approaches, such as remote sensing, have been used to study the post-fire recovery process (Goetz et al., 2006; White et al., 1996; Minchella et al., 2009), the structural–functional approach using a chronosequence allows a better understanding of such process. Although remote sensing techniques allow to study larger areas with low cost and sampling effort compared to community-level studies, they have certain limitations. First, investigations of post-fire recovery are restricted to a 30–35 years time frame as satellite images became available just after 1970s. Second, in forest ecosystems (with several vegetation layers) spectral indices used to estimate vegetation recovery (e.g. NDVI) record prompt saturation and despite they have been improved (e.g. EVI, Jiang et al., 2008), field controls are essential for their interpretation, losing the advantage of low sampling effort. Third, spectral indices do not allow to estimate spatial vegetation reorganization considering the vertical dimension. Related to this last point, our results suggest that it is very important to analyze the spatial reorganization of vegetation not only considering the horizontal dimension, which could be estimated by remote sensing techniques, but also the vertical dimension (a key issue in forest ecology studies). This is because ground cover, that recorded the breakpoint 10 years after fire (Fig. 2a), did not provide the information necessary to characterize the structural recovery of the vegetation but rather reflected the recovery of the released space by resprouting species, mainly shubs from low layer (Fig. 3a and b). Instead, the breakpoint recorded by VVH index reflected an increase in the vertical complexity of post-fire communities mainly given by the constitution of the high layer by tree species (Figs. 2b, d, and 3a). Therefore, the chronosequence approach and the proposed indices (HVH, VVH and SRI) allow a more detailed characterization and interpretation of the post-fire recovery process, as well as they will allow a more precise validation of spectral indices estimated by remote sensing techniques.

5. Conclusions

The detection of ecological recovery indicators and the differentiation of high- and low-risk phases are essential for the sustainable management of ecosystems, as its characterization can be used to prevent the occurrence of undesirable states (Briske et al., 2006; Bestelmeyer et al., 2010). The significantly lower structural and functional levels recorded in communities at high-risk phases suggest that during post-fire recovery, forest communities would be more vulnerable to anthropic pressure and/or natural disturbance events. Consequently, to maintain the ecosystem resilience and its ability to provide goods and services, harvesting practices should be conducted in communities at low-risk phases. Our study contributes to the sustainable management of forest communities because it allows to estimate the minimum structural–functional levels from which forest communities could be used.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolind.2014.11.019.

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