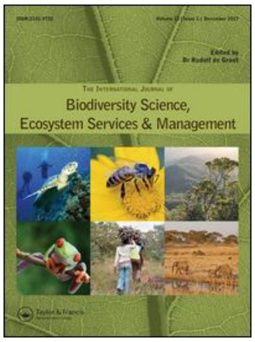

International Journal of Biodiversity Science, Ecosystem Services & Management

ISSN: 2151-3732 (Print) 2151-3740 (Online) Journal homepage: http://www.tandfonline.com/loi/tbsm21

State and transition model approach in native forests of Southern Patagonia (Argentina): linking ecosystem services, thresholds and resilience

Pablo Luis Peri, Dardo Rubén López, Verónica Rusch, Graciela Rusch, Yamina Micaela Rosas & Guillermo Martínez Pastur

To cite this article: Pablo Luis Peri, Dardo Rubén López, Verónica Rusch, Graciela Rusch, Yamina Micaela Rosas & Guillermo Martínez Pastur (2017) State and transition model approach in native forests of Southern Patagonia (Argentina): linking ecosystem services, thresholds and resilience, International Journal of Biodiversity Science, Ecosystem Services & Management, 13:2, 105-118, DOI: 10.1080/21513732.2017.1304995

To link to this article: http://dx.doi.org/10.1080/21513732.2017.1304995

Published online: 11 Apr 2017.

INTERNATIONAL JOURNAL OF BIODIVERSITY SCIENCE, ECOSYSTEM SERVICES & MANAGEMENT, 2017
VOL. 13, NO. 2, 105–118
http://dx.doi.org/10.1080/21513732.2017.1304995

Taylor & Francis
Taylor & Francis Group

Special Issue: Ecosystem Services Nexus Thinking

OPEN ACCESS Check for updates

State and transition model approach in native forests of Southern Patagonia (Argentina): linking ecosystem services, thresholds and resilience

Pablo Luis Peri[a], Dardo Rubén López [b], Verónica Rusch[c], Graciela Rusch[d], Yamina Micaela Rosas[e] and Guillermo Martínez Pastur [e]

[a]Department of Forestry, Agriculture and Water Management, Instituto Nacional de Tecnología Agropecuaria (INTA) EEA Santa Cruz - Universidad Nacional de la Patagonia Austral (UNPA) - Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Río Gallegos, Argentina; [b]Native Forest Research Department, INTA-Estación Forestal Villa Dolores (EEA Manfredi), Córdoba, Argentina; [c]Forestry Research Department, INTA EEA Bariloche, Bariloche, Argentina; [d]Department of Terrestrial Ecology, Norwegian Institute for Nature Research (NINA), Trondheim, Norway; [e]Agroforestry Resources Department, Centro Austral de Investigaciones Científicas (CADIC)- CONICET, Argentina

ABSTRACT
The sustainable use of ñire forests requires knowledge of its dynamics and management to maintain long-term main forest ecosystem services. The aim of this work was to develop a structural–functional state and transition model for ñire forests in southern Patagonia. For this, provincial inventory information was analyzed together with information from permanent PEBANPA plots (plots of Ecology and Biodiversity, natural environments in Southern Patagonia) and studies of ecology and eco-physiology in ñire forests. This allowed the description of plant communities on these ecological sites and the history of natural disturbances. Seven states and 10 negative transitions were described, as well the factors that trigger transitions (levels of grazing, fire and intense logging). Mature forests with low grazing, no extractive activity and complete canopy cover (>70%) correspond to the reference state or condition of greater integrity, and grassland or murtillar (dominance of *Empetrum rubrum*) with forest loss is considered the most degraded state. Negative transitions determine the threshold crossings associated with the reduction or loss of resilience to the previous or original state. The development of state and transition models allows for early warnings of deterioration and is a tool to achieve more productive and environmental value.

ARTICLE HISTORY
Received 21 October 2016
Accepted 2 March 2017

EDITED BY
Christine Fürst

KEYWORDS
Sustainability; resilience approach; degradation; disturbance; native forest

Introduction

Livestock grazing is one of the most widespread land uses in Latin America and is arguably the land use that has had the greatest impact on regional biodiversity (Peri et al. 2016a). In this region, more than 90 million ha of land is under pasture, in many cases as a result of forest conversion to cattle ranching, where meat and milk consumption probably assume greater political and economic importance than in any other region of the world. Forest degradation is a global environmental issue, resulting in biodiversity loss, increase in greenhouse gas emissions and a decrease in the generation of a number of ecosystem goods and services (Steege et al. 2015; Corlett 2016). However, choosing appropriate levels of use based on reference states, ecological thresholds and forest values still remains difficult. Advances in describing and quantifying ecosystem functioning have been fundamental in understanding forest dynamics and provide a promising framework by which degradation might be better understood (Ghazoul et al. 2015).

The southern beech, ñire (*Nothofagus antarctica* [G. Forster] Oerst.), one of the main deciduous native species in the Patagonian Andes, covers 342,094 ha in southern Patagonia (Santa Cruz and Tierra del Fuego Provinces) (Collado 2009; Peri & Ormaechea 2013a). Silvopastoral systems that combine trees and grasslands under grazing in the same unit of land have become a productive alternative in the region with the potential to generate various ecological and societal benefits. They enable the diversification of farm products by sustaining sheep and cattle production, which provides income from meat, wool and a range of wood products including poles, firewood and timber for rural construction purposes (Peri et al. 2016b). In addition to livestock and timber production, the silvopastoral system in the region provides other ecosystem services such as water regulation, biodiversity conservation, soil and water quality, carbon sequestration, recreation and cultural identity. Currently, ñire forests under silvopastoral use present a mosaic spatial distribution pattern with varying ecological condition, structure and floristic composition as a result of livestock grazing and silvicultural management in interaction with natural (e.g. drought) and anthropogenic (fires, introduction of species) factors (Peri & Ormaechea 2013a).

CONTACT Pablo Luis Peri peri.pablo@inta.gob.ar

In this context, one of the main goals of sustainable management in these ecosystems is the preservation of the ecological integrity and ecosystem functioning to maintain the provision of goods and services over time. A key property related to that objective is ecosystem resilience (Convention on Biological Diversity 2008). In this management context, tools that enable to identify thresholds associated with the loss of resilience and to determine the degree of vulnerability of an ecosystem to be degraded are needed (Briske et al. 2006, 2008; López et al. 2013).

Based on the framework of state and transition models (STM, Westoby et al. 1989), López et al. (2011) proposed the structural–functional state and transition model (SFSTM) as a conceptual framework to evaluate attributes of an ecosystem related to the resilience, such as elasticity, amplitude and resistance to disturbances factor (Box 1). The SFSTM approach, combined with conceptual advances of STM (e.g. Bestelmeyer et al. 2009; see Box 1), provides a tool that describes the dynamics of the vegetation and which supports decision-making that aims at preventing unwanted changes triggered by management and also provides a guide for management and restoration practices in degraded states. The SFSTM reinforces the STM by providing a methodological framework for assessing the resilience of an ecosystem based on two axes: ecosystem structure and ecosystem functions and/or processes. The SFSTM identifies critical structural and functional thresholds associated with the loss or decrease of resilience.

In this study, we build a SFSTM of ñire forests under silvopastoral use in southern Patagonia and evaluate the relationship between structural and functional variables to define and quantify the different states and transitions. Considering this approach, we include critical thresholds and an assessment of ecosystem resilience and stability to disturbance factors.

Material and method

Study area and measurements

The study was carried out in the main ecological site type of ñire forests in Santa Cruz province (southern Patagonia, Argentina) distributed in a narrow (100 km wide) and long (1000 km) strip of land from 46°00′ to 52°00′S. These forests reach in average <8 m height (Ivancich et al. 2011) and represent 80% of its total area (159,720 ha). Mean annual temperatures in the region range between 5.0 and 6.2°C, annual precipitation between 280 and 600 mm and mean annual potential evapotranspiration between 950 and 1650 mm. The ñire ecological site in the region occurs in slopes of 0–5° and an altitude below 450 m a.s.l. The soil effective depth is of 0.4–0.6 m, with a soil water retention capacity (field capacity at 0.3 m depth) of 50–60%.

The states (or phases within states) and transitions were defined based on the information gathered from the ñire provincial inventory (355 plots) established to provide information for a program aiming on sustainable forest management in Santa Cruz Province (Peri & Ormaechea 2013a). The inventory includes measurements of forest structure (development phases, canopy cover, height of dominant trees, site class, basal area, crown vigor, spatial distribution, state of regeneration, total volume, biomass), understory variables (species composition, above-ground net primary productivity, presence of woody debris and invasive alien species) and the presence of anthropogenic disturbances (livestock, browsed plants, forestry, fire and soil erosion) (Peri & Ormaechea 2013a, 2013b; Peri et al. 2013). Information from 145 permanent monitoring plots of PEBANPA Network (plots of Ecology and Biodiversity of natural environments in Southern Patagonia) that include diversity of vascular plants, structure and regeneration of tree species, physico-chemical characteristics of soils, degree of erosion, and climatic parameters has been used (Peri et al. 2016c). Also, information obtained in different studies addressing functional properties such as carbon sequestration capacity, nutrient and litterfall dynamics and decomposition rates have been included to define levels of the main functional variables (Peri et al. 2010; Bahamonde et al. 2013, 2015; Gargaglione et al. 2013, 2014). The structural variables of soil, vegetation and functional variables (n = 3) associated with the provision of ecosystem services and their ranges are summarized in Table 1.

The analyses that were conducted included (1) the definition of states based on the matrix of structural variables (Table 1), (2) identifying resilience levels, using the critical processes and (3) the relationship between states and the generation of ecosystem services (Table 2).

We first prepared a draft model of states and transitions that was discussed at a workshop with experts from the region where states, processes and variables that define negative transitions where discussed. To differentiate between ecosystems to absorb and/or reorganize after a disturbance phases and states, we evaluated the possibility of a natural reversal of the degradation condition. At a second stage, the definition of states was further refined by calculating the Structural Degradation Index (SDI) and regressions were adjusted to determine critical thresholds (see below). Finally, several forest stands were visited to verify and complete the description of the states.

Table 1. Variables used for the structural–functional state and transition model (SFSTM) in *N. antarctica* forests in southern Patagonia.

Structural variables	Range/units
Forest overstorey cover	0–90%
Understorey cover	5–92%
Invasive species cover	0–60%
Basal area	0–74 m^2/ha
Seedlings density (<1.3 m height, >2 years old)	0–90,000 ind/ha
Saplings density (>1.3 m height, <5 cm DBH)	0–62,000 ind/ha
Total stand volume	0–195 m^3/ha
Soil erosion	0–35%
Soil carbon (C) concentration	2.9–5.8%
Soil nitrogen (N) concentration	0.28–0.87%
Total C stock (aerial, roots and soil 0.6 m depth)	98–152 t C/ha
Understorey richness	4–21 Species/ha
Richness of introduced forage species (clover, grasses)	0–4 Species/ha
Understorey above-ground net primary productivity	90–420 kg DM/ha
Animal stocking rate	0–1.05 Ewes/ha
Functional variables as indicators of ecosystem services	**Range/units**
Stand forest growth	0–0.95 m^3/ha/year
Seedlings (>2 years old) establishment rate	0–37,300 Seedlings/ha/year
Understorey growth	1.2–9.3 kg DM/ha/day
Litter productivity	0–1,610 kg DM/ha/year
N return from litter	0–9.7 kg N/ha/year
Potassium (K) return from litter	0–3.5 kg K/ha/year
Phosphorus (P) return from litter	0–2.4 kg P/ha/year
Tree biomass growth rate	0–0.31 t DM/ha/year
Soil loss rate from erosion	0–98.9 t/ha/year
Mature tree (>200 years old) density and snags as an indicator of biodiversity habitat	0–100 ind/ha
Logs cover (coarse woody debris) as provision for biodiversity habitat	0–45%
Net N mineralization measured in soil (0–0.2 m)	10.8–67.8 kg N/ha/year
Decomposition constant (k) for *N. antarctica* tree leaves	0–0.37 (dimensionless)
Decomposition constant (k) for grass leaves	0.20–0.41 (dimensionless)

Table 2. List of indicators used as variables for the relationship between states and the generation of ecosystem goods and services in *N. antarctica* forests in southern Patagonia.

Ecosystem goods and services	Ecosystem functions	Indicators
Disturbance regulation	Capacitance, damping, resilience and integrity of the ecosystem	Forest Resilience Index
Erosion control and sediment retention	Retention of soil within the ecosystem	Annual soil loss rate
Nutrient cycling regulation	Storage, internal cycling, processing and acquisition of nutrients	Litter production, soil mineralization, nitrogen return, phosphorus return, potassium return, decomposition coefficient of ñire-leaves, decomposition coefficient of grass leaves
Biodiversity refugia	Habitat for resident and transient populations	Habitat for native biodiversity (mature trees and snags), coarse woody debris
Raw materials	That portion of gross primary production extractable as raw materials	Tree biomass productivity (growth rate), understorey net primary productivity

Classification adaptation of Costanza et al. (1997) adapted of de Groot et al. (2002) and Haines-Young and Potschin (2013).

Structural Degradation Index (SDI)

A SDI was generated to establish the degree of structural forest degradation (López et al. 2011, 2013). We used a matrix containing all the structural vegetation and soil variables (López et al. 2011; Briske et al. 2006) and calculated the Mahalanobis distance (MD) between plant community assessed (state and/or phase) (Legendre & Legendre 1998). Thus, the index was conformed as: $SDI_i = [(MD_i \times 100)/(MD_{max})]$, where MD_i is the MD between the i-th community and a reference ñire forest community (reference system of the ecological site type *sensu* Bestelmeyer et al. 2009, Box 1). The DM_{max} corresponds to a maximum MD value (thus, the community more distant related to the reference ecosystem according to structural and functional variables). Based on MD_{max}, all the MD values were standardized, determining that SDI varied between 0% and 100%.

Functionality indices

The resilience of forest ecosystem to return to the initial vegetation community or condition previous to a disturbance once it is suppressed is associated with the recruitment process of key species and to its growth rate (López et al. 2011; Ghazoul et al. 2015). For this, a Forest Resilience Index (FRI) was generated to assess the resilience of the ñire forest ecosystem, based on seedling recruitment under 2 years old, and the trees growth, as follows:

$$FRI_i = \left[\left(\frac{x_i}{x_{max}}\right) \times 0.5\right] + \left[\left(\frac{y_i}{y_{max}}\right) \times 0.5\right]$$

Box 1. A brief definition of the key concepts of ecological sites and the state and transition model (STM) used in this article. The approach and definitions were adapted from Briske et al. (2008), Bestelmeyer et al. (2009) and López et al. (2011).

Ecological sites

Landscape units or elements with similar characteristics of soil, topography, geological formations and climatic regime that differs from other classes in:

(1) the production and plant species composition under the disturbance regime of reference conditions associated with soil properties, the natural dynamics of vegetation and the ecosystem services provided

(2) The responses to management, processes of degradation and restoration.

The Ecological Site classes are repeated in similar soil components, within either the same eco-region or other. Each ecological site has one states and transitions models with one or more alternative states

Concepts of STM

Ecological resilience: Capacity of an ecosystem to absorb and/or reorganize after a disturbance, maintaining structural-funtional integrity. This resilience approach assumes that ecosystems can be expressed as two or more alternative stable states and emphasizes the potential occurrence of state transitions based upon shifts between unique sets of organizing structures and processes. Each state has a specific resilience to different disturbance factors. Then, the original resilience of the ecosystem is associated to the ability of maintain and/or recover the ecosystem identity (i.e. reference state). The resilience can be evaluated by the properties: (1) elasticity or engineering resilience (rate at which an ecosystem can return to reference phase of reference state) following a perturbation, (2) amplitude (defined by a threshold beyond which the ecosystem diminishes or loses its resilience to the previous or original state) and (3) resistance (the sensitivity of system to undergo changes or degradation processes in response to a disturbance factor, thus, if the speed and magnitude of a particular change or degradation process is low, this means high resistance). Thresholds represent conditions that modify ecosystem structure and function beyond the limits of ecological resilience resulting in the transition to alternative states (see the other concepts of Box)

State: A set of plant communities temporary associated under dynamic soil properties (e.g. seasonal fluctuation of water table) that produce persistent attributes over time with particular structural and functional ecosystem characteristics

Reference state: The state that provides the great range of potential environmental services. All other states and phases of the same ecological site can be identified from this. A historical or natural range of variability represents the reference state, or it is represented for the set of conditions most preferred by society based on current scientific knowledge

Phases or communities of a state: Distinctive plant communities associated with the dynamics of varying soil levels and climate that fluctuate naturally over time within a single state. The phases change does not represent the crossing of a threshold and may be due to rotations with low or moderate anthropic use and/or climatic fluctuations (e.g. interannual climate fluctuations). Each state is characterized by a specific ecological resilience to different disturbance factors, and the dynamics between phases of the same state is associated to engineering resilience

Reference phase of an ecosystem: This is the plant community of the reference state with greater original resilience due to structural and functional properties key (i.e. the system tends to return to the reference phase in the absence of disturbance factors). Each alternative state can have a *potential phase*, which is the community plant toward the estate–ecosystem in the absence of disturbance factors

Risk phase: Within each state, it is the most vulnerable plant community to move through a negative transition to an alternative state more degraded (i.e. state with less structural–functional integrity respect to a reference forest-state). Represent the less resilient community within a state and the community more susceptible to degrade

Negative (or degradation) transitions: The mechanisms by which a state becomes another state more degraded (with lower levels of structural–functional integrity in relation to reference forest-state). It is defined based on *triggering factors* (natural and/or anthropic disturbance factor/s) that produce a process of change in a specific time and the *threshold*

Triggers: Events, factors, processes and/or drivers that start a transition to an alternative state. Triggers represent one (or more) factor(s) of disturbance (e.g. overgrazing, extreme droughts) that generate significant structural–functional changes in the ecosystem (e.g. disturbances in the system). If the change is to a degraded state, the trigger activates a negative transition (e.g. change determined by interaction between extreme drought and grazing). But if a transition toward a state with better structural–functional integrity of forest is triggered, it represents a positive or restoration transition (e.g. change triggered in a humid year under closure and/or reforestation practice)

Threshold: Key biotic and abiotic factors and processes modified during a negative transition that limit (or decreases significantly) the intrinsic recovery (without intervention or large external input) of the previous or original state. This is identified by threshold values of key indicators. Thresholds represent the structural–functional limits beyond which the ecosystem's resilience to the previous or original state has been significantly diminished or lost. If the thresholds are associated with the occurrence of more severe biotic and/or abiotic limitations (e.g. local species extinction, soil erosion), the likelihood of a transition to the original or previous state is very low (or the restoration will take more external input and time). In general, states with intermediate degradation (i.e. forest with intermediate levels of structural–functional integrity) significantly reduced their resilience to reference state (e.g. the ecosystem needs very long recovery periods with intermediate levels of inputs), while highly degraded states have lost their original resilience (e.g. the recovery is unlikely and/or needs very higher external inputs to recover or rehabilitate better levels of structural–functional integrity)

Restoration (or positive) transitions: Management practices or interventions (and time required) performed in a particular state, necessary to recover the structural–functional conditions of a previous state

where FRI_i is the index value for a particular site in the sample; x_i is the seedlings (≤2 years old) establishment rate (seedlings/ha/year) for the site; $x_{\max}$ is the maximum seedling establishment rate in all sampled sites; y_i is the tree biomass growth rate (t DM/ha/year) for each site; $y_{\max}$ is the maximum tree biomass growth rate in all sampled sites. Each variable was multiplied by a relative importance coefficient, which in our case, was equal for recruitment and growth, since some forest formations may have resilience associated with a medium or high level of seedling density, whereas others may be associated with a medium to high biomass growth rate at intermediate or advanced age.

An Ecosystem Services Provision Index (ESPI) was generated taking into account all functional variables. Then, to estimate the level of provision level of ecosystemic Goods and Services, we calculated:

$$\mathrm{ESPI}_i = \sum \left(\frac{x_i}{x_{\max}} \right)$$

where ESPI_i is the index value for a particular sampled site; x_i is a value from a ecosystem $function_i$ for a particular community (using each as functional variables of Table1); $x_{\max}$ is the maximum value for this ecosystem $function_i$ in all sampled sites.

Inferential statistical analysis

Segmented regression represents an efficient tool to model threshold responses, i.e. an abrupt change in the response variable (Clements et al. 2010), and to establish critical thresholds (*sensu* López et al. 2013). Segmented regressions were fitted between SDI, as an explanatory variable, and FRI, and its component processes (tree regeneration and tree growth rate) as the response variables to determine critical thresholds. The identification of ecological thresholds represents a key issue to differentiate between the multiple states of an ecosystem or between phases within a particular state. This analysis also helps identify which processes are the most affected in each state. The SFSTM allows to differentiate quantitatively between states by a threshold response (between structure–function). Each state would be defined between one or more critical thresholds, and therefore, the communities within each state would be phases with reversible transitions. It also enables to identify pre-threshold communities within each state that are more susceptible to a transition to another state (thus, communities or risk phases) providing useful information for making decisions (e.g. preventing crossing critical thresholds) (see more in Bestelmeyer et al. 2009; López et al. 2011) (Box 1). This quantification of the states (and phases) was used to validate and/or improve the conceptual model reported by Peri et al. (2015) which was generated based on empirical data, knowledge of local experts and the literature.

To assess the relationship of the states with the level of ecosystem services provision, linear and segmented regressions were adjusted between SDI (as an explanatory variable) and ESPI (as the response variable). We first fitted single-linear regressions. When the relationship was not significant (p value > 0.05, and R^2 adj. <0.5), we fitted segmented regressions. For this, piecewise regressions were adjusted with two segments, and when this relationship was not significant, a segmented regression with three segments was fitted. For the analysis, we took into account the degradation pathways known as states and transitions defined a priori in the conceptual model developed by Peri et al. (2015). In this work, possible alternative states according to their vegetation structure and physiognomy had been differentiated. Thus, in the same regression, we took into account the sampled communities included a priori within two states defined by Peri et al. (2015) and that these are linked by a negative transition (degradation pathway). When more than one state (linked by a transition) was included in the same regression analysis, it had to have at least 15 points to fit a regression. This is because very degraded states had less number of sampled communities (states IV–VII) than less degraded states (states I–III). We considered adjusting regressions with few points reduces predictive power of adjustments.

Finally, for all functional variables associated with the provision of ecosystem services, an analysis of variance (ANOVA) among states defined according to the above-segmented regressions was performed (program-R).

Results

Conceptual model of states and transitions

From the analysis of the present work, the model of states and transitions developed by Peri et al. (2015) for ñire forests in Southern Patagonia had been modified (Figure 1). The description of seven states and its main phases are presented in Table 3. While the *S-I* state corresponds to the reference state or condition of greater integrity, the grassland or murtillar (dominance of *Empetrum rubrum*) with loss of forest (*S-VII*) is considered the state of major degradation. Also, the presence of *Hieracium praealtum* (an exotic invasive species) was important for the definition of states. The state *S-I* introduces the two phases as a result of its natural evolution where the very low intervention intensities allow recovering following disturbance. There are 10 negative transitions (T, Figure 1) where the main factors that trigger these transitions were related to the levels of grazing, fire and logging.

SFSTM

The regression of the FRI, seedling recruitment process for tree species and trees growth rate in relation to the SDI were adjusted to segmented and linear regressions (p values ≤ 0.05) [Figure 2 (a–c)]. These regressions were adjusted for plant communities included among: (1) State (S) S-I and S-II; (2) S-I, S-III and S-IV; (3) S-I, S-VI and S-VII; (4) S-I, S-IV and S-VI. This allowed quantitatively to differentiate the states (and phases within a particular state) and risk phases (pre-threshold communities), as well as the processes. Between the S-I and the rest of the states, there was a threshold response both between SDI and FRI, as well as between SDI and recruitment of new saplings (Figure 2(a,b)). All states showed lower values of seedlings recruitment than S-I, where S-III had intermediate values and other states had very low or zero values (Figure 2(a,b)). Regarding to the tree growth, except S-II, all states had lower growth than S-I showing a linear decrease from moderate-to-severe degradation status.

Regressions for each pathway of degradation were adjusted from S-I to other states. The structural threshold (considering the results of Figure 2(a)), in the transition T1 (Figure 1), the ecosystem supports 20.2% change in the structural level before crossing a critical threshold to S-II. In the transition T2, the ecosystem supports 42.5% change in the structural level before crossing the threshold into S-III. Finally, the ecosystem supports between 45.8% and 45.9%

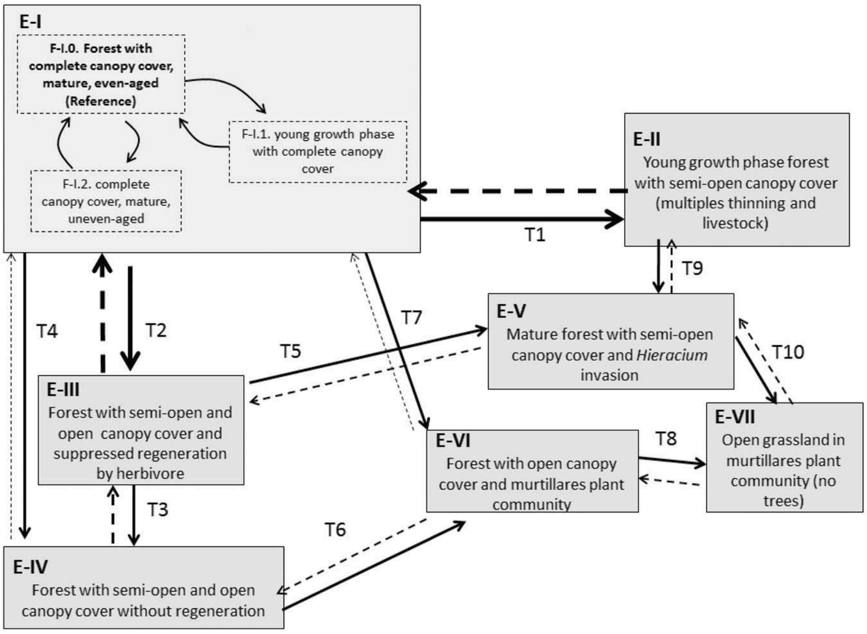

Figure 1. Conceptual Model of states and transitions for ñire forests in Southern Patagonia based on field data and empirical knowledge of experts (modified from Peri et al. 2015). The gray boxes represent states (Roman numerals), the dotted line boxes phases or plant communities within the same state (Arabic numerals) and whole curved arrows represent reversible pathways between phases. The straight arrows represent the negative transitions between states (degradation) and the straight dashed arrows represent the positive transitions (restoration) (labeled with letter T with Arabic numerals). A greater thickness of arrows represents a greater probability that negative or positive transitions may occur (thus, a lower external input from the ecosystem is needed to cross from one state to another). The definitions of states and transitions are described in Table 1. T1 = medium grazing pressure (continuous or seasonal) for at least 10 years (stabilization of grassland to disturbance) with successive thinning; T2 = high continuous grazing pressure, low fire severity events and low timber extraction with forest management; T3 = high grazing pressure, low timber extraction without fire events; T4 = High continuous grazing pressure, medium-to-high fire events and high wood extraction; T5 = high grazing pressure, high fire severity events, without silviculture practices, remove of deadwood post-fire and high availability of *Hieracium* (invasive exotic species) propagules; T6 = high grazing pressure, low or medium severity fire events, dead wood extraction post-fire and high availability of murtilla propagules; T7 = High grazing pressure for more than 20 years, high fire severity events, without silviculture practice, remove of deadwood post-fire and high availability of murtilla propagules; T8 = high grazing pressure, high fire severity events and high timber extraction; T9 = Medium continuous grazing pressure over 20 years and medium or high fire severity events; T10 = High grazing pressure, fire severity events and timber extraction with high availability of *Hieracium* propagules.

changes in the structural level before crossing thresholds from the state S-V to S-VI. Regarding the functional threshold, the values of RFI were above 0.6, and for seedling recruitment process for tree species, the values were higher than 20,000 individuals (less than 2 years) per hectare (Figure 2(a,b)).

Segmented regressions were also adjusted between SDI explaining the x axis and the response variable ESPI (y-axis) for ñire forests in Southern Patagonia (Figure 3). For each degradation pathway from S-I to other states, the thresholds responses between SDI and ESPI (Figure 3) had similar values to those recorded between SDI and RFI (Figure 2(a)). From this analysis, the threshold responses were 17.1% of SDI between S-I and S-II, 43.0% of SDI between S-I and S-III (and S-IV), 45.9% of SDI between S-I and S-VI, and 41.3% of SDI between S-I and S-IV (i.e. threshold structural values). Also, the values of functional thresholds in ESPI were above 9, after which a significant decrease in the provision level of ecosystem goods and services occurs (i.e. increases the loss rate of functions) (Figure 3).

Specifically, for ecosystem goods and services provision, the main variables with higher values explaining the difference between S-I and all the other states were understorey growth, habitat for biodiversity and coarse woody debris (Figure 4(a,k,l)).

Except for decomposition (coefficient K) of grasses leaves and ñire leaves, and annual soil loss rate, state S-I showed the highest values of all other variables and S-VII the lowest (Figure 4(a–g,k,l)). In contrast, site S-VII had the highest values of annual soil loss rate followed by S-VI (Figure 4(j)). For decomposition of ñire-leaves, only state S-VII had the lowest values (Figure 4(h)).

Discussion

In Patagonia, ecosystem sustainable management should preserve its capacity to adapt to actual anthropic disturbances or future climate changes, and maintain the main provision of goods and services from the native forest. There are several definitions of forest degradation because of different perceptions

Table 3. Description of states from the conceptual states and transitions model for ñire forests in Southern Patagonia.

State	Description	Threshold
E I Forest with complete canopy cover, mature, even-aged (Reference)	These mature forests (>120 years old) are the least anthropic, with low grazing use, no extractive logging activity or land use conversion, and with complete canopy cover (>70%). This state contains two reversible stages: F-1.1 complete canopy cover, mature and uneven-aged stand with good regeneration and F-1.2 young growth phase stand with complete canopy cover	
E II Thickets of Ñire (matorrales): Young growth forest with semi-open canopy cover (multiples thinning and livestock)	In this young development growth stage (advanced regeneration 20–40 years old), intense thinning or successive thinning is performed that determines low canopy cover (<40%) with a stand density of <1000 trees/ha, and it is characterized by a linear growth phase in biomass, DBH and volume. For this, the presence of tree-seedlings is low for regeneration but this state represents an unstable system with high grass understorey biomass for grazing. In this state, the resilience to S-I has decreased significantly (natural recovery >50 years), and from a management perspective, rotations with long rest times (unused >40–50 years) are difficult to implement. The silvicultural practices are necessary to accelerate the forest recovery to S-I	Biotic limitations associated with high competition among the many young tree individuals, determining a stage of competitive exclusion, which significantly slows forest recovery
E III Forest with semi-open and open canopy cover and suppressed regeneration by herbivore	Anthropized forests with intermediate upper canopy cover (10–20%, or basal area, BA, 8–15 m^2/ha) and regeneration (>5 years old) cover less than 5% (or density <300 plants/ha) mostly browsed (rabbit or sheep) which determines a height <20 cm. These forests need protection of individual trees to ensure their continuity over time	Biotic limitations associated with low-density tree regeneration (and low growth) due to competition with grasses
E IV Forest with semi-open and open canopy cover without regeneration	Sites with intense grazing and logging use together with the occurrence of fire events. The forest structure had been strongly modified and herbaceous understorey stratum dominates the site	This state is characterized by the lack of regeneration that limits the forest continuity due to competitive grasses (biotic limiting) and soil erosion (abiotic limiting: least amount and/or quality of micro-sites for recruitment seedlings)
E V Mature forest with semi-open canopy cover and *Hieracium* invasion	Anthropized forests with a canopy cover between 20% and 50% (or BA 15–35 m^2/ha) with regeneration (>5 years old) cover >5% (or density >200 plants/ha) not browsed, but with a cover of *Hieracium praealtum* (exotic invasive species) >20%	The exotic understory specie limits the development of ñire regeneration by physically occupying the forest floor (biotic limitations)
E VI Forest with open canopy cover and murtillares plant community	Mature (>120 years old) ñire forests of very low (<10%, or BA <8 m^2/ha) or medium (20–50%, or BA 15–35 m^2/ha) with low or without regeneration due to soil loss by wind erosion, and occupation (cover >30–40%) of murtilla (*Empetrum rubrum*). Generally, these are shrubby forests (<5 m height of dominant trees), exposed to strong winds, growing in sandy or sandy loam soil and in sites with evidence of intense fires that determined the loss of the thin organic soil layer and facilitate the occupation of murtilla	The lack or absence of ñire regeneration due to soil loss by wind erosion and occupation of murtilla that limits forest continuity
E VII Open grassland or murtillares plant community with forest loss	The arboreal layer disappears and replaced by a murtillar or grassland due to long-term severe uses of timber and grazing and/or occurrences of fire	Lack of ñire seed bank (biotic limiting) and microsites to emergency for tree seedlings establishment (abiotic limiting)

and values that scientists, government and stakeholders give to a loss of attributes, functions or services in response to disturbances. In this context, the proposed SFSTM developed for ñire forests in Southern Patagonia has large implications for forestry research and management, facilitating the understanding and integration of key concepts to enhance the STM. Our results provide concrete evidence of a relationship between the decrease (or loss) of forest resilience (i.e. reference state) (Figure 2) and the decrease in the provision level of ecosystem goods and services (Figure 3). Thus, the reference state is the state that provides a wider range of environmental goods and services (Bestelmeyer et al. 2010). The number of states (and its phases) and transitions found in the present work were less than those established for ñire forests in Northern Patagonia (Rusch et al. 2015). This would indicate a difference in the intensity and type of historical use interacting with climatic and soil conditions.

In the present work, it was possible to differentiate between states and phases within states. A critical threshold was integrated by the relationship between a structural threshold and a functional threshold (Briske et al. 2005). Thus, the regression of FRI, seedling recruitment process and tree growth

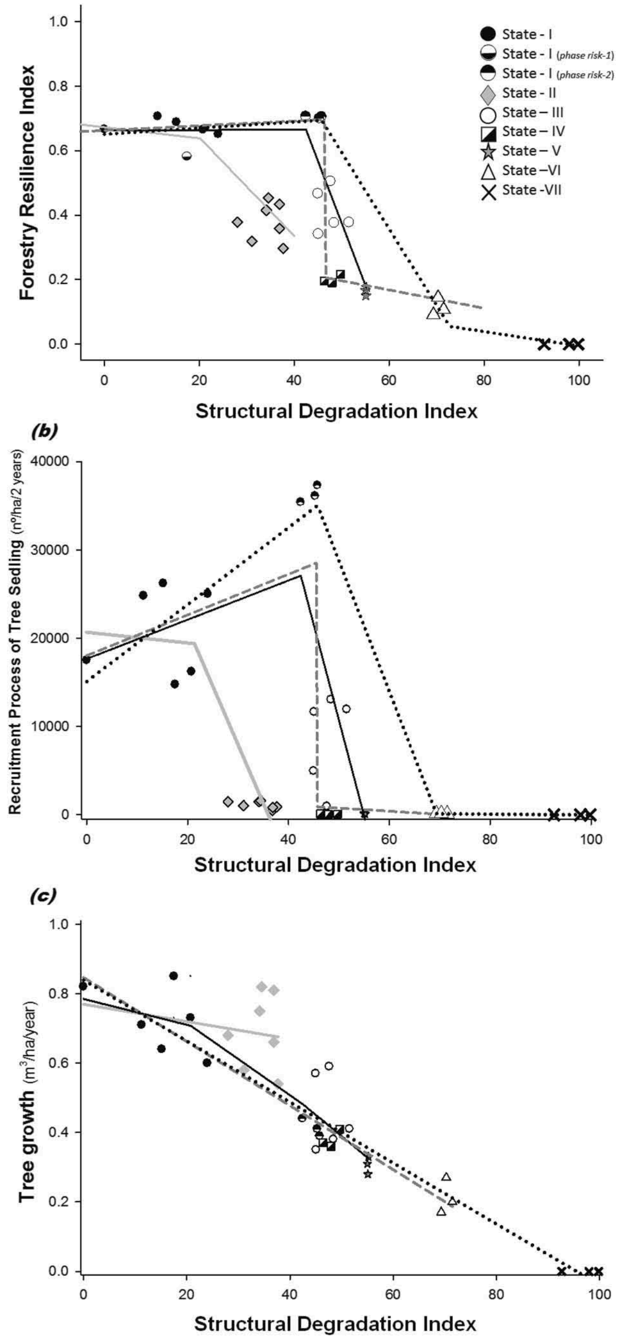

Figure 2. Structural–functional state and transition model (SFSTM) approach (López et al. 2011) for ñire forests in Southern Patagonia. Segmented and linear regressions were adjusted between Structural Degradation Index (SDI explaining the *x* axis) (*sensu* López et al. 2013) and the following variable responses (*y* axis): (a) Forest Resilience Index (FRI); (b) seedling recruitment process for tree species and (c) trees growth rate. Adjusted regressions for: State (S) S-I and S-II (gray solid line); S-I, S-III and S-IV (black solid line); S-I, S-VI and S-VII (black dotted line); S-I, S-IV and S-VI (dashed gray line). Adjusted R^2 and *x* axis (SDI) values are indicated when the inflection point T (response threshold) occurs (T_1 represents the first inflection point and T_2 represents second inflection point when segmented regressions with three segments were adjusted). (a) Gray solid line: segmented regression, $R^2_{adj} = 0.51$,$T_1 = 42.5$, $p < 0.05$; black solid line: segmented regression, $R^2_{adj} = 0.81$, $T_1 = 45.5$, $p < 0.05$; dashed gray line: segmented regression, $R^2_{adj} = 0.98$, $T_1 = 45.3$, $T_2 = 45.9$, $p < 0.05$; black dotted line: segmented regression, $R^2_{adj} = 0.99$, $T_1 = 45.8$, $T_2 = 72.7$, $p < 0.05$. (b) Gray solid line: segmented regression, $R^2_{adj} = 0.70$, $T_1 = 21.4$, $p < 0.05$; black solid line: segmented regression, $R^2_{adj} = 0.51$, $T_1 = 42.5$, $p < 0.05$; black dotted line: segmented regression, $R^2_{adj} = 0.90$, $T_1 = 45.8$, $T_2 = 69.4$, $p < 0.05$; dashed gray line: segmented regression, $R^2_{adj} = 0.82$, $T_1 = 45.7$, $T_2 = 44.8$, $p < 0.05$. (c) Gray solid line: linear regression, $R^2_{adj} = 0.0007$, $p > 0.05$; black solid line: segmented regression, $R^2_{adj} = 0.77$, $T_1 = 27.9$, $p < 0.05$; black dotted line: linear regression, $R^2_{adj} = 0.95$, $p < 0.05$; dashed gray line: linear regression, $R^2_{adj} = 0.90$, $p < 0.05$.

rate in relation to SDI using 15 variables (biotic and abiotic) allowed quantitatively to differentiate the states (and phases within a particular state) and risk phases (pre-threshold communities). This type of response between functional indexes in relation to SDI was used for grasslands steppe in North Patagonia indicating that the overgrazing decreased the recruitment process of foundational or key

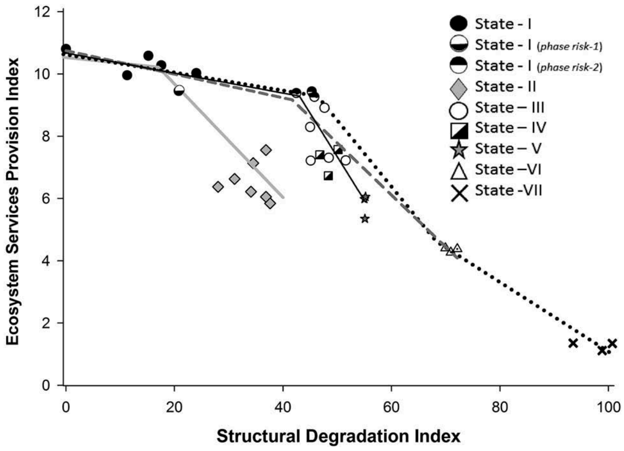

Figure 3. SFSTM approach (López et al. 2011) for ñire forests in Southern Patagonia. Segmented regressions were adjusted between Structural Degradation Index (SDI explaining the *x* axis) (*sensu* López et al. 2013) and the response variable Ecosystem Services Provision Index (ESPI) (*y* axis). Black solid line: segmented regression between state (S)-I and S-II (R^2_{adj} = 0.79, T_1 = 17.1). Grey solid line: segmented regression between S-I, S-III and S-IV (R^2_{adj} = 0.85, T_1 = 43.0). Black dotted line: segmented regression between S-I, S-VI and S-VII (R^2_{adj} = 0.99, T_1 = 45.9, T_2 = 67.7). Dashed gray line: segmented regression between S-I, S-IV and S-VI (R^2_{adj} = 0.91, T_1 = 41.3).

species, and it could be associated with a loss of the ecosystem functional integrity (López et al. 2013). Similarly, this approach allowed differentiation in the successional phases with high- and low-risk of degradation in recovery postfire of North Patagonia forests (Cavallero et al. 2015).

A transition from one state to another implies that threshold values in the state variables have been reached, resulting in a shift in vegetation structure and composition (Bestelmeyer et al. 2009). Usually, there are overlaps in the attributes of states where not all variables (structural and functional) equally contribute to a transition from one state to another (Rumpff et al. 2011). In our work as an example, a transition away from the reference state (T1) implies that most of the defined state variables decline in value where the ecosystem supports 20.2% change in the structural level before crossing a critical threshold to S-II. However, it is the degree of seedlings (≤2 years old) establishment rate and stand tree growth (as driven by land-use history) that determines the site-negative transitions. The importance of seedlings establishment rate has been reported previously as a key functional variable since there are positive and negative interactions among trees, pasture and livestock, proper forest management aim to encourage the positive interactions in order to ensure tree regeneration for long-term viability (Peri et al. 2016b). Thus, one of the main ecological indicators that define the success of forestry proposal is the effective establishment of natural regeneration to ensure the continuity of the tree layer defining the capacity of forest ecosystems to sustain itself in time and space (Martínez Pastur et al. 2009). It is also important to highlight that survival of seedlings and saplings depends on the species' ecophysiological traits. *Notofagus antarctica* is considered less 'shade tolerant' from a physiological perspective compared to other closely related species such as *N. pumilio* (Peri et al. 2009b). It provides competitive advantages for this tree species to grow in open areas. Another less known regeneration strategies of ñire is the great ability of agamic regeneration (e.g. stump regrowth and suckers from roots) under natural conditions (Steinke et al. 2008), which represents a reproductive advantage over the other *Nothofagus* species. Vegetative reproduction is a key mechanism of persistence for those species facing natural anthropic disturbances that cause partial loss of above-ground biomass (e.g. thinning, browsing damage). This vegetative reproduction provides higher resilience and it has been identified in Santa Cruz and it is particularly evident after disturbances like fire and tree logging. In Santa Cruz, 25% of ñire forest with high regeneration cover (>25%) originated from root suckers and it was referred to fire disturbance (Peri & Ormaechea 2013a). Stand tree growth (both, saplings from seed or sprouts) is a functional variable that determines the state resilience and states transitions (Figure 2(a, c)), and that also is associated with other processes (carbon accumulation) and is very sensitive to forest management. For example, in Santa Cruz, the total over bark volume growth rate at stand level was 4.3 ± 0.65 and 3.7 ± 0.43 m^3/ha/year for the thinned stand and primary forest, respectively (Peri et al. 2016d). In this context, we recognize that the models (the METs in general and SFSTM in particular) represent a simplification of complex reality. Therefore, our approach aims to differentiate states of the forest with different resilience determined by their structure–functional integrity that needs different management practices (Briske et al. 2005, 2006, 2008; López et al. 2011, 2013) (Box 1). While plant communities of states II and III (with intermediate values of FRI; Figure 2) would significantly diminished their resilience to state I, other states would have lost their original resilience (e.g. by the extinction of key species, invasions and/or soil erosion). This influences resilience management at the landscape level. Thus, different management practices are needed (at each state level and at a

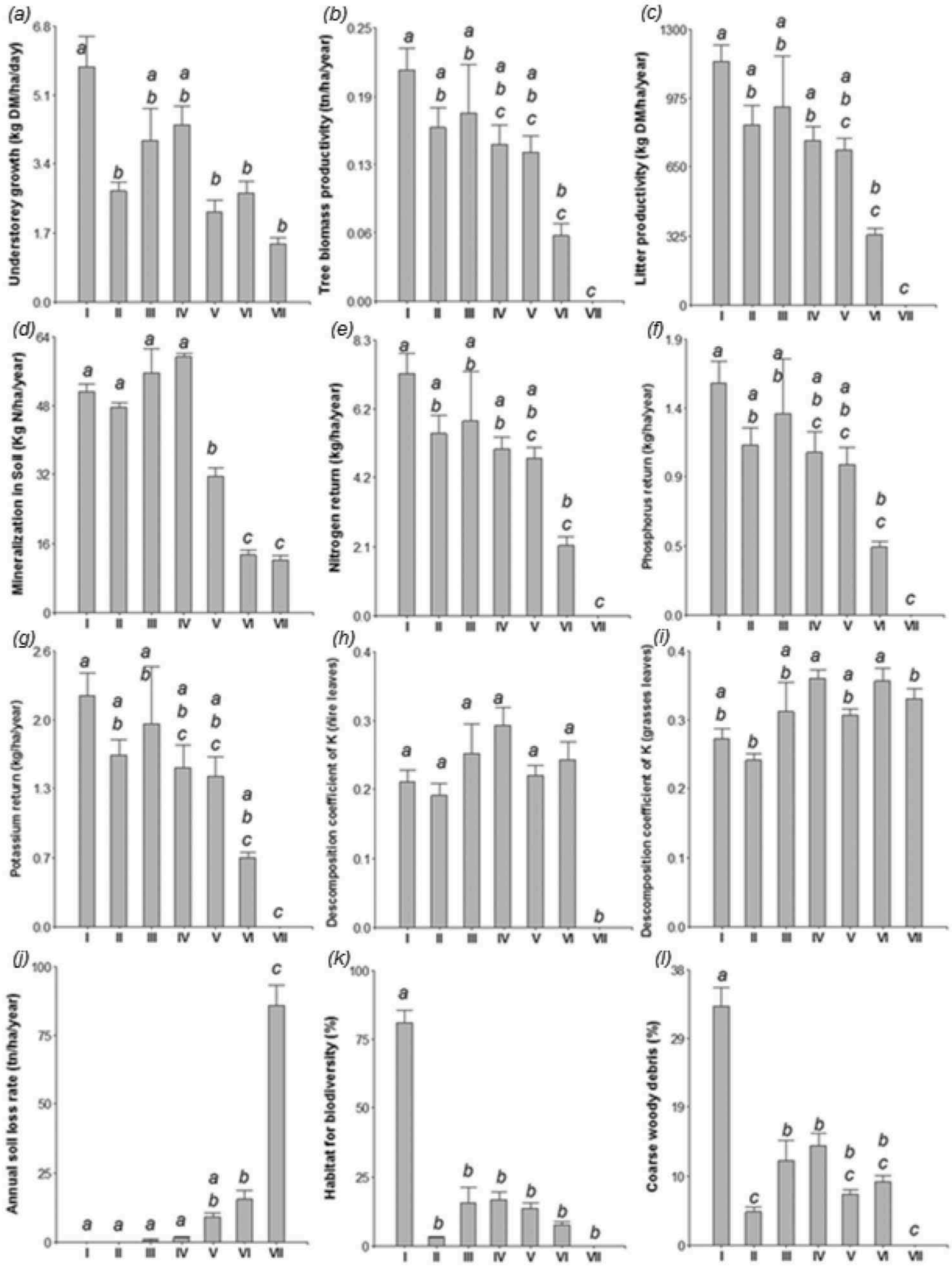

Figure 4. Ecosystem goods and services provision in alternative state of ñire-forests. (a) Understorey growth (dry material – DM – in kg/ha/year); (b) tree biomass productivity (tn/ha/year); (c) litter productivity (kg DM/ha/year); (d) mineralization in soil (kg N/ha/year); (e) nitrogen return (kg/ha/year); (f) phosphorus return (kg/ha/year); (g) potassium return (kg/ha/year); (h) decomposition coefficient of K for ñire leaves; (i) decomposition coefficient of K of grasses leaves; (j) annual soil loss rate (tn/ha/year); (k) habitat for biodiversity (%); (l) coarse woody debris (%). Significant differences within each site are indicated by p^*. Significant differences between the state (I, II, III, IV, V, VI and VII) are indicated with different lowercase letters (α = 0.05). The table (top right corner) indicated the relationship between each response variable and ecosystem goods/services provided ((a–l)). According to De Groot et al. (2002), the response variables are associated to production function (a,b); regulation function (a, b, c, d, e, f, g, h, j, l); habitat function (k, l).

landscape level) if forests are dominated by highly (e.g. S-IV to S-VII) or less (e.g. S-I to S-III) degraded states.

The ecosystem service concept (direct and indirect contributions of ecosystems to human well-being) is currently the focus of both scientific activities (Seppelt et al. 2011) and environmental policy actions. The relationship between SDI and the response variable ESPI for ñire forests in Southern Patagonia provided a quantitative approach for ecosystem goods and services provision. The main variables with higher values explaining the difference between the reference state and all the other states were understorey growth, habitat for biodiversity and coarse woody debris. The S-I was the state that provided the most range of environmental services (Figures 3 and 4). This is because S-I has a largest amplitude defined by the threshold value with a variety of phases (Figure 1, Box 1) from closed forests (reference phase) to open forests with grassland (risk phase).

Ñire forests are usually immersed in a landscape spatial matrix alternate with rangelands, peat-lands and other *Nothofagus* forests. The existence of species that only occurs in ñire forests denotes the importance of this unique environment, which is usually undervalued due to the lack of natural provincial and national reserves that preserve habitat wilderness (Rusch et al. 2004). In addition, variations in forest structure through modifications in overstorey canopies (more closed or open canopies) generate differences in richness and relative abundance of different organisms, which could be minima as for understory vascular plant, insect and bird richness and bird density, or very important as in vascular plant cover or insect abundance (Peri et al. 2016b). Livestock use (anthropic disturbance) in ñire forests usually diminishes the original biodiversity, both richness and relative abundance, mainly due to loss of sensitive species to animal pressure and selective grazing on more palatable species. But this effect could be masked by incoming species, which could generate similar values of richness. However, high livestock charge produced greater reduction in vascular plant richness. Coarse woody debris as a structural variable was important in the present work to maintain good ESPI values. In ñire forest, it is recommended to leave coarse woody debris because it plays a substantial role in several ecological processes in forest ecosystems and because a large number of organisms (fungi, insects) are dependent on decaying wood for nutrients or habitat (Franklin et al. 1987). Understory growth also was a relevant functional variable to keep desire ESPI values. Understory dry matter production in ñire forest largely depends on the interaction of soil water availability and light intensity reaching the sward, and it is sensitive to thinning, grazing management and weed invasion (Peri et al. 2016a).

The capacity of a particular ñire state to supply particular services that benefit people should be considered a service-providing unit, thus the ecosystem structures and processes that provide a specific ecosystem service at a particular spatial scale. If this capacity is changed by disturbances, the satisfaction of social demands for the ecosystem service might be affected (Burkhard et al. 2012). In this context, it is important to identify models that relate ecosystem state to ecosystem services. The range of tools available to unravel patterns and mechanisms of ecosystem change and incorporate this knowledge in models allowing the projection of the future state of biodiversity and ecosystem services in particular decision-making and management contexts is needed.

Practical implications

Ñire forests use should be designed to avoid crossing critical thresholds, beyond which, forest stand loses or significantly decreases its resilience to its previous or original state once the disturbance is suppressed, and therefore, the system needs external input (e.g. sulvicultural practices or reforestation) to be restored. In 2007, the Argentinean government enacted National Law 26.331 for the Environmental Protection of Native Forests and the objectives are to promote the conservation of native forests through land planning, sustainable management and tightening the regulations associated with land-use change. In the last few years, more than 50% of the budget has been destined to silvopastoral system plans in the Yellow category that includes forestry inventories, silvicultural practices, adjustment of stocking rate and fencing for strategic separation in homogenous areas (grass steppe, forest and riparian meadows) covering planning areas of ñire forest from 22 to 13,000 ha. However, most ranchers in Patagonia have been slow to adopt an integral silvopastoral system management plan, possibly because of lack of convincing evidence of positive economic returns or long-term benefits from ecosystem service values.

In this context, the resilience approach is the management best suited for coping with external shocks and surprises given the nonlinear complex dynamics arising from linked social–ecological systems (Allen et al. 2011; Bestelmeyer & Briske 2012). This is based on managing adaptively for resilience and consists of actively maintaining a structural–functional levels, associated with functional diversity and homeostatic feedbacks, trying to keep the ecosystem in a dynamic equilibrium away from a critical threshold (risk phases, *sensu* Bestelmeyer et al. 2010) (Allen et al. 2011; López et al. 2011; Cavallero et al. 2015).

The adaptive management of ecosystem resilience should be aimed to (1) reduce uncertainty and to avoid thresholds in situations where maintaining resilience is desired (e.g. forest or reference state); and/or (2) contemplate landscape scale in the range management, taking into account both the ‘spatial contagion’ of degradation, and the practices to reinforce the resilience at landscape level (Allen et al. 2011; Bestelmeyer et al. 2011). Thus, considering the resilience approach, silvopastoral systems in Southern Patagonia could be managed in states S-I, S-II and

S-III, accompanied with a suitable spatial design and clear management guidelines. Thus, for biodiversity maintenance and conservation at landscape or ranch level is advisable to create a complete array of forest successional stages and their structures (e.g. phases within the S-I, *see* Cavallero et al. 2015), including sectors with old-growth forest conditions and retaining standing dead trees and fallen logs. The ideal objective of sustainable management would be to maintain a landscape with different proportions of phases from S-I, which provides a high range of environmental services and goods, and where the original resilience is maintained (Figures 2–4). However, in Patagonia, nowadays, there are forests with different states of degradation (mainly S-II and S-III). Some state transitions (which their resilience to S-I decreased) are feasible to recover through management practices or restoration. Sapling protection from livestock herbivory could allow recovery from *S-III* to *S-I* (T2). For example, in Santa Cruz, sapling trees are protected as individual specimens or as small groups by using individual tree guard or small fences (Peri et al. 2009a). The authors suggest to protect a final number of 250 seedlings/ha for dry sites and 150 seedlings/ha for better site conditions until saplings reach >2 m height. The results indicated that tree guard can be effectively used to protect individual seedlings from cattle by enhancing height growth (10.0 cm/year for protected trees vs. 1.8 cm/year for unprotected). When there are no regeneration in the stand, as in the case of desire to move from S-IV to S-I (T4), it is necessary to conduct a plantation with ñire seedlings and then protect those from browsing by herbivores (such as rabbits, hare and livestock).

Furthermore, the proposed approach provides a tool for forest assessment regarding the identification of states that can be restored and those that might be more susceptible to degradation. In general using the results of the present work, we promote a strategy of adaptive management to improve management of ñire native forest in Patagonia that is widely advocated in scientific and management literature because it provides an explicit framework for motivating, designing and interpreting the results of monitoring. Then, for adaptive management can be used as reference points the thresholds (or risk phases) as key tool for monitoring of system response to the anthropic use (Briske et al. 2008; Bestelmeyer & Briske 2012). Adaptive Management is a 'learning by doing' approach that acknowledges management action must proceed in the face of uncertainty but facilitate iterative updating of knowledge and management strategies (Duncan & Wintle 2008). Rumpff et al. (2011) reported this approach on the use of a STM in the Adaptive Management of native woodland vegetation in south-eastern Australia.

A further step to assist forest managers is the premise of combining STMs and Bayesian belief networks (BBNs) (also known as belief networks, causal nets, causal probabilistic networks and probabilistic cause effect models). Forest or silvopastoral management decision support tools can be developed that maintain the benefits of STMs (such as diagrammatic, low cost, flexible) whilst providing scenario analysis capabilities, adaptive management capabilities and the ability to accommodate uncertainty (Nicholson & Flores 2011).

Conclusions

The SFSTM developed for ñire forests in Southern of Patagonia that provides a quantification of thresholds (and its indicators) can be a useful tool to explain the changes affecting these systems under different types and regimens of disturbances factors and guide the decision-making for sustainable management. However, a monitoring system using exclosures is needed in order to identify and validate the threshold responses among degraded states and to generate more information related to identify more phases/communities in other states (e.g. S-II to the S-VII). Furthermore, for forest management at regional scale, it is necessary the mapping of ecological sites and its states, and begin to assess the interactions at the landscape level to determine the magnitude of changes that each ecological site – and the whole landscape– can support before losing its ecosystem functionality.

Acknowledgement

The research leading to these results has received funding from the European Commission's Seventh Framework Programme (OpenNESS project, grant agreement no. 308428).

Disclosure statement

No potential conflict of interest was reported by the authors.

ORCID

Dardo Rubén López http://orcid.org/0000-0001-9709-0070
Guillermo Martínez Pastur http://orcid.org/0000-0003-2614-5403

References

Allen CR, Cumming GS, Garmestani AS, Taylor PD, Walker BH. 2011. Managing for resilience. Nebraska Cooperative Fish & Wildlife Research Unit – Staff Publications. Paper Available from: 130.http://digitalcommons.unl.edu/ncfwrustaff/130

Bahamonde H, Peri PL, Monelos L, Martínez Pastur G. 2013. Regeneración por semillas en bosques nativos de *Nothofagus antarctica* bajo uso silvopastoril en Patagonia Sur, Argentina. Bosque. 34:89–101.

Bahamonde HA, Peri PL, Martínez Pastur G, Monelos L. 2015. Litterfall and nutrients return in *Nothofagus antarctica* forests growing in a site quality gradient with different management uses in Southern Patagonia. Eur J For Res. 134:113–124.

Bestelmeyer BT, Briske DD. 2012. Grand challenges for resilience-based management of Rangelands. Rangeland Ecol Manag. 65:654–663.

Bestelmeyer BT, Goolsby DP, Archer SR. 2011. Spatial perspectives in state-and-transition models: a missing link to land management? J Appl Ecol. 48:746–757.

Bestelmeyer BT, Moseley K, Shaver PL, Sanchez H, Briske DDFernandez-Gimenez ME. 2010. Practical guidance for developing state-and-transitionmodels. Rangelands. 32:23-30.

Bestelmeyer BT, Tugel AJ, Peacock GL, Jr, Robinett DG, Shaver PL, Brown JR, Herrick JE, Sanchez H, Havstad KM. 2009. State-and-transition models for heterogeneous landscapes: a strategy for development and application. Rangeland Ecol Manag. 62:1–15.

Briske DD, Bestelmeyer BT, Stringham TK, Shaver PL. 2008. Recommendations for development of resilience-based state-and-transition models. Rangeland Ecol Manag. 61:359–367.

Briske DD, Fuhlendorf SD, Smeins FE. 2005. State-and transition models, thresholds and rangeland health: a synthesis of ecological concepts and perspectives. Rangeland Ecol Manag. 58:1–10.

Briske DD, Fuhlendorf SD, Smeins FE. 2006. A unified framework for assessment and application of ecological thresholds. Rangeland Ecol Manag. 59:225–236.

Burkhard B, Kroll F, Nedkov S, Müller F. 2012. Mapping ecosystem service supply, demand, and budgets. Ecol Indic. 21:17–29.

Cavallero L, López DR, Raffaele E, Aizen MA. 2015. Structural-functional approach to identify post-disturbance recovery indicators in forests from northwestern Patagonia: a tool to prevent state transitions. Ecol Indic. 52:85–95.

Clements WH, Vieira NKM, Sonderegger DL. 2010. Use of ecological thresholds to assess recovery in lotic ecosystems. J Am Benthological Soc. 29:1017–1023.

Collado L. 2009. Clasificación de los ñirantales de Tierra del Fuego. In: Peri PL, editor. Relevamiento de los bosques nativos de ñire (*Nothofagus antarctica*) de Tierra del Fuego (Argentina) como herramienta para el manejo sustentable. Buenos Aires (Argentina): Editorial Instituto Nacional de Tecnología Agropecuaria (INTA); p. 10–27.

Convention on Biological Diversity. 2008. Decisions adopted by the conference of the parties to the convention on biological diversity. Available from: http://www.cbd.int/doc/decisions/cop-09/full/cop-09-dec-en.pdf.

Corlett RT. 2016. Plant diversity in a changing world: status, trends, and conservation needs. Plant Divers. 38:10–16.

Costanza R, d'Arge R, de Groot R, Farberk S, Grasso M, Hannon B, Limburg K, Naeem S, O'Neill RV, Paruelo J, et al. 1997. The value of the world's ecosystem services and natural capital. Nature. 387:253–260.

de Groot RS, Wilson MA, Boumans RMJ. 2002. A typology for the classification, description and valuation of ecosystem functions, goods and services. Ecological Econ. 41:393–408.

Duncan DH, Wintle BA. 2008. Towards adaptive management of native vegetation in regional landscapes. In Pettit C, Cartwright W, Bishop I, Lowell K, Pullar D, Duncan D, editors. Landscape analysis and visualisation. Spatial models for natural resource management and planning. Berlin: Springer Verlag.

Franklin JF, Shugart HH, Harmon ME. 1987. Tree death as an ecological process. The causes, consequences, and variability of tree mortality. BioScience. 37:550–556.

Gargaglione V, Peri PL, Rubio G. 2013. Partición diferencial de nutrientes en árboles de *Nothofagus antarctica* creciendo en un gradiente de calidades de sitio en Patagonia Sur. Bosque. 34:291–302.

Gargaglione V, Peri PL, Rubio G. 2014. Tree-grass interactions for N in *Nothofagus antarctica* silvopastoral systems: evidence of facilitation from trees to underneath grasses. Agroforestry Syst. 88:779–790.

Ghazoul J, Burivalova Z, Garcia-Ulloa J, King LA. 2015. Conceptualizing forest degradation. Trends Ecol Evol. 30:622–632.

Haines-Young R, Potschin M. 2013. Common international classification of ecosystem services (CICES): consultation on version 4; 2012 Aug–Dec. UK: European Environment Agency.

Ivancich H, Martínez Pastur G, Peri PL. 2011. Modelos forzados y no forzados para el cálculo del índice de sitio en bosques de *Nothofagus antarctica* en Patagonia Sur. Bosque. 32:135–145.

Legendre P, Legendre L. 1998. Numerical ecology. 2a ed. Amsterdam: Elsevier Science B.V.

López DR, Brizuela MA, Willems P, Aguiar MR, Siffredi G, Bran D. 2013. Linking ecosystem resistance, resilience, and stability in steppes of North Patagonia. Ecol Indic. 24:1–11.

López DR, Cavallero L, Brizuela MA, Aguiar MR. 2011. Ecosystemic structural–functional approach of the state and transition model. Appl Vegetation Sci. 14:6–16.

Martínez Pastur G, Lencinas MV, Cellini JM, Peri PL, Soler Esteban R. 2009. Timber management with variable retention in *Nothofagus pumilio* forests of Southern Patagonia. For Ecol Manage. 258:436–443.

Nicholson AE, Flores MJ. 2011. Combining state and transition models with dynamic bayesian networks. Ecol Modell. 222:555–566.

Peri PL, Bahamonde H, Lencinas MV, Gargaglione V, Soler R, Ormaechea S, Martínez Pastur G. 2016b. A review of silvopastoral systems in native forests of *Nothofagus antarctica* in southern Patagonia, Argentina. Agroforestry Syst. 90:933–960.

Peri PL, Dube F, Varella A. 2016a. Chapter 1, Silvopastoral systems in the subtropical and temperate zones of South America: an overview. In: Peri PL, Dube F, Varella A, editors. Silvopastoral systems in Southern South America. Switzerland: Advances in Agroforestry, Springer International Publishing; p. 1–8.

Peri PL, Gargaglione V, Martínez Pastur G, Lencinas MV. 2010. Carbon accumulation along a stand development sequence of *Nothofagus antarctica* forests across a gradient in site quality in Southern Patagonia. For Ecol Manage. 260:229–237.

Peri PL, Hansen N, Rusch V, Tejera L, Monelos L, Fertig M, Bahamonde H, Sarasola M. 2009a. Pautas de manejo de sistemas silvopastoriles en bosques nativos de *Nothofagus antarctica* (ñire) ñire en Patagonia. In: Peri PL, INTA, editors. Actas Primer Congreso Nacional de Sistemas Silvopastoriles. Posadas (Misiones): Ediciones INTA; p. 151–164, 14 al 16 de Mayo 2009].

Peri PL, Hansen NE, Bahamonde HA, Lencinas MV, Von Müller AR, Ormaechea S, Gargaglione V, Soler R, Tejera LE, Lloyd CE, Martínez Pastur G. 2016d. Chapter 6, Silvopastoral systems under native forest in Patagonia Argentina. In: Peri PL, Dube F, Varella A, editors. Silvopastoral systems in Southern South America. Switzerland: Advances in Agroforestry, Springer International Publishing; p. 117–168.

Peri PL, Lencinas MV, Bousson J, Lasagno R, Soler R, Bahamonde H, Martínez Pastur G. 2016c. Biodiversity and ecological long-term plots in Southern Patagonia to support sustainable land management: the case of PEBANPA network. J Nat Conservation. 34:51–64.

Peri PL, Martínez Pastur G, Lencinas MV. 2009b. Photosynthetic and stomatal conductance responses to different light intensities and water status of two main *Nothofagus* species of south Patagonian forest. J For Sci. 55:101–111.

Peri PL, Martínez Pastur G, Rusch V, López D, Rusch G. 2015. Un marco ecológico para establecer márgenes de manejo de sistemas silvopastoriles. In: Peri PL, editors. El caso de ñirantales de Patagonia Sur, Argentina. Actas VIII Congreso Internacional de Sistemas Agroforestales y III Congreso Nacional de Sistemas Silvopastoriles . Iguazú (Misiones): Ediciones INTA; p. 641–645; 2015 Mayo 7–9.

Peri PL, Ormaechea S, Martinez Pastur G, Lencinas MV. 2013. Inventario provincial del contenido de carbono en bosques nativos de ñire en Santa Cruz. Actas 4to Congreso Forestal Argentino y Latinoamericano; 23 al 27 de Septiembre de 2013; Iguazú (Misiones): Misiones, Asociación Forestal Argentina (AFOA); 10 pp.

Peri PL, Ormaechea S. 2013b. Especies invasoras exóticas en ñirantales de Santa Cruz: *hieracium praealtum* e *Hypochoeris radicata*. In: Peri PL, editor. Proceedings II Jornadas Forestales de Patagonia Sur y 2do Congreso Internacional Agroforestal Patagónico. El Calafate (Santa Cruz): INTA-Instituto Forestal de Chile-UNPA-CONICET; p. 103; 16 al 18 de Mayo de 2013.

Peri PL, Ormaechea SG. 2013a. Relevamiento de los bosques nativos de ñire (*Nothofagus antarctica*) en Santa Cruz: base para su conservación y manejo. Buenos Aires: Ediciones INTA; 88 pp.

Rumpff L, Duncan DH, Vesk PA, Keith DA, Wintle BA. 2011. State-and-transition modelling for Adaptive Management of native woodlands. Biol Conserv. 144:1224–1236.

Rusch V, López D, Cavallero L, Rusch G, Peri PL, Cardozo A, Hansen N, Von Müller A, Garibaldi L, Sarasola M. 2015. Un marco ecológico para establecer márgenes de manejo de sistemas silvopastoriles. 1- El caso de ñirantales del norte de la Patagonia, Argentina. Actas VIII Congreso Internacional sobre Sistemas Agroforestales para la Producción Pecuaria y Forestal Sostenible- Tercer Congreso Nacional de Sistemas Silvopastoriles. Ediciones INTA; Peri P.L., INTA; 7 al 9 de Mayo 2015; Iguazú (Misiones).

Rusch V, Roveta R, Peralta C, Márques B, Vila A, Sarasola M, Todaro C, Barrios D. 2004. Indicadores de sustentabilidad en sistemas silvopastoriles. In: Alternativas de Manejo Sustentable para el Manejo Forestal Integral de los bosques de Patagonia. Informe Final del Proyecto de Investigación Aplicada a los Recursos Forestales Nativos (PIARFON), Dirección de Bosques de la Secretaría de Ambiente y Desarrollo Sustentable de Nación (SAyDS). Buenos Aires (Argentina): Dirección de Bosques de la Secretaría de Ambiente y Desarrollo Sustentable de Nación (SAyDS); p. 681–797.

Seppelt R, Dormann CF, Eppink FV, Lautenbach S, Schmidt S. 2011. A quantitative review of ecosystem service studies: approaches, shortcomings and the road ahead. J Appl Ecol. 48:630–636.

Steege HT, Pitman NCA, Killeen TJ, Laurance WF, Peres CA, Guevara JE, Salomao RP, Castilho CV, Amaral IL, De Almeida Matos FD, et al. 2015. Estimating the global conservation status of more than 15,000 Amazonian tree species. Sci Adv. 1:e1500936.

Steinke LR, Premoli AC, Souto CP, Hedrén M. 2008. Adaptive and neutral variation of the resprouter *Nothofagus antarctica* growing in distinct habitats in northwestern Patagonia. Silva Fennica. 42:177–188.

Westoby M, Walker B, Noy –Meir I. 1989. Opportunistic management for rangelands not at equilibrium. J Range Manag. 42:266–274.