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Ecosystemic structural–functional approach of the state and transition model

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Keywords
Dynamic equilibrium; Rangeland ecology; Resilience; Resistance; Thresholds

Abbreviations
KIRP = key individuals recruitment process; RUE = rain-use efficiency; SFSTM = Structural–Functional State and Transition Model; STM = State and Transition Model

Nomenclature
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Abstract

Objective: To contribute to the integration of key ecological concepts such as dynamic equilibrium, critical threshold, resistance and resilience to the 'State and Transition Model' (STM), in order to apply them in a more feasible way for rangeland management.

Methods: Review and discussion of conceptual models and applied literature, including examples of rangeland dynamics.

Results and Conclusions: We propose to enhance the STM considering two principal axes: (a) the x axis determined by structural ecosystem changes (vegetation and soil) and (b) the y axis determined by ecosystem functions and/or processes (recruitment, rain use efficiency). These axes define what we will call Structural–Functional State and Transition Model (SFSTM). Both axes of SFSTM make it possible to determine and quantify states and transitions, critical thresholds and to evaluate the resistance and resilience of an ecosystem to a given disturbance. The critical threshold is identified by structural and functional thresholds (x and y axes), thus defining the point where the ecosystem loses its resilience. Furthermore, in the supplementary file we provide examples with field data from Patagonia to illustrate the SFSTM. The proposed SFSTM has large implications for rangeland research and management, facilitating the understanding and integration of key concepts to enhance the STM. The identification of variables to assess structure and processes makes the model more useful.

Introduction

One of the most challenging issues of rangeland ecology is to build models and tools to enable sustainable management of natural resources. In the 20th century, rangeland management was mainly based on the range model (continuous and reversible vegetation dynamics) (Dyksterhuis 1949). However, early in the 1980s, evidence showing that the range model was not applicable to all rangelands began to accumulate (Westoby 1980). The concept and the succession model have suffered criticism and constant revisions. The main points that have been under constant analysis are the state of equilibrium and linear succession (Tansley 1939; Egler 1954; Allen-Diaz & Bartolomé 1998; Fernández-Gimenez & Allen-Diaz 1999; Briske et al. 2003, 2005, 2008; Hein 2006). In this sense, emphasis was focused on building models that represented multidirectional vegetation dynamics, sometimes irreversible, to ease the identification of key processes and factors of good functioning and management for the system under study (Naveh & Lieberman 1994).

The State and Transition Model (STM) (Westoby et al. 1989) was proposed as an alternative and flexible tool. According to this model, for a determined system, there are different alternatives of vegetation states with different transitions between them. The transition into a different state is triggered by a natural event (e.g. abundant rain or extreme drought) by a disturbance and/or management action (e.g. grazing, fire) or by the interaction of any of these factors. Transitions may occur in different directions and generally, may not be linear,

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occurring by different pathways. There are negative transitions of rangeland degradation (e.g. structure changes, decreasing forage species and productivity) and positive transitions of ecosystem recovery. Negative transitions have higher occurrence probability than positive transitions, and often are irreversible (Westoby et al. 1989). This conceptual model has had very important consequences for rangeland management, because there may be a broad variety of vegetation states characterized by a particular dynamics in the same site.

The STM includes concepts with different degrees of consensus about its basic definitions and empirical relevance for ecosystem management, such as: states, equilibrium and non-equilibrium, thresholds, ecosystem resilience and resistance (Briske et al. 2003, 2005, 2006, 2008; Stringham et al. 2003; Bestelmeyer et al. 2004, 2009). Our main objective is to enhance the STM and to increase its explanation power, encompassing the complexity of dynamic ecosystems. Therefore, in this review we propose a set of structural and functional variables to evaluate rangelands upon which we enhance the STM, allowing us to define and/or to quantify the states and transitions of an ecosystem more precisely. Considering this approach, we include the dynamic equilibrium concept to approach the steady state definition. Finally, we integrate the critical threshold, ecosystem resistance and resilience to the STM. To illustrate the integration and application of these concepts we supply three examples with field data from Patagonian steppes (see the Supporting Information). For that purpose, we focus on grazing of domestic animals as the main disturbance affecting natural rangelands.

Structural and functional axes to enhance the STM

We propose two principal axes over which the STM can be optimized: (a) the *x* axis determined by structural ecosystem changes (vegetation and soil) and (b) the *y* axis determined by ecosystem functions and/or processes (Fig. 1). These axes determine what we will call the Structural–Functional State and Transition Model (SFSTM). The adoption of these axes is based on the assumption that a disturbance such as overgrazing negatively affects the ecosystem composition, structure, productivity and functioning (Soriano & Movia 1986; Paruelo & Sala 1992; Paruelo et al. 1992; Noy-Meir 1995; Fernández-Gimenez & Allen-Diaz 1999; Hein 2006). High grazing pressures produce loss of plant cover, litter, organic matter and surface soil layer (owing to erosion), drastically changing the ecosystem structure. These changes result in a potential loss of soil water storage, water loss by superficial run-off and deep percolation, and great changes in the matter and energy interchange with the environment (Soriano & Movia 1986; Paruelo & Sala 1992; Bertiller 1994; Aguiar et al. 1996; Whitford 2002; Barger et al. 2004; Yong-Zhong et al. 2005; Chartier & Rostagno 2006). As a consequence, water-use efficiency of an ecosystem decreases under high grazing pressure (Hein 2006); the micro-environmental conditions also become more unstable and extreme, producing a loss of safe sites for seedling germination and implantation (Bertiller 1994; Snyman 2004). Thus, each alternative state of an ecosystem has different characteristics of structure–function feedback (Bestelmeyer et al. 2009).

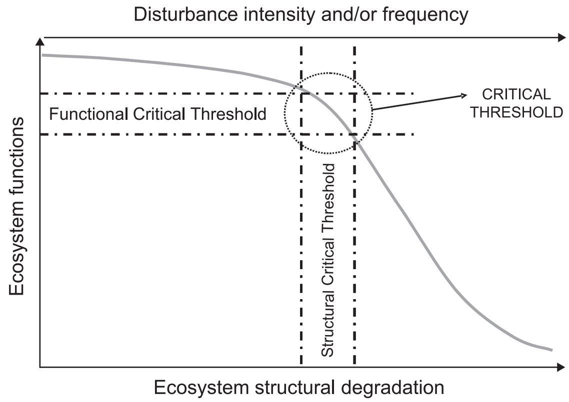

Fig. 1. Loss of ecosystem functions (*y* axis) and structural degradation (*x* axis) produced by a determined disturbance (e.g. grazing), adapted from Tongway & Hindley (2000, 2004).

Although a disturbance simultaneously affects not only the structure, but also the ecosystem functioning, factors such as grazing act directly on the vegetation structure (above-ground biomass consumption). If grazing intensifies and turns into a disturbance (overgrazing), the ecosystem structure is drastically changed, thereby producing significant losses of plant cover and soil erosion. The structure of an ecosystem (*x* axis, Fig. 1) is defined mainly by physiognomy, relative species composition and growth forms, diversity, vegetation spatial distribution, soil characteristics (depth, organic matter, structure and fertility) and the percentage of bare soil (Briske et al. 2006). This degradation process substantially affects fundamental ecosystem functions.

The ecosystem functions are the ecological processes that maintain the functioning and resilience of the ecosystem (Gunderson & Holling 2002). The ecosystem functioning is mainly determined by the amount of water and nutrients retained. The loss of ecosystem functions occurs when the amount and the spatial distribution of soil cover has been modified enough to accelerate water, nutrients and soil run-off through the landscape (Briske et al. 2006). This situation mainly affects the rain-use efficiency (RUE) of an ecosystem (Hein 2006) and the key individuals recruitment process (KIRP) of the plant community (Bertiller 1994), compromising its continuity and maintenance in time. Therefore, RUE and KIRP are defined as fundamental ecosystem functions and processes (*y* axis, Fig. 1). The RUE shows how the main resource utilization of an ecosystem is modified by a disturbance (water and nutrient availability), and depends on different factors (e.g. state of vegetation and soil). The KIRP includes several processes and factors (e.g. plant vigor, pollen and seed production and dispersal, germination and seedling survival in safe sites), related to the ability of the ecosystem to maintain its original community composition.

Dynamic equilibrium of natural systems

The range model and the STM are conceptually related to the equilibrium and non-equilibrium models respectively. The equilibrium model is based on the assumption that ecosystems have the capacity of internal regulation through negative feedback mechanisms such as intraspecific and interspecific competition and plant–animal interactions (Wu & Loucks 1995; Briske et al. 2003). In contrast, the non-equilibrium model is based on the assumption that ecosystems have a limited capacity for internal regulation owing to the fact that they are more vulnerable to external factors (Briske et al. 2003). According to this model, major changes in vegetation are associated with periodic and stochastic climate events (event-driven vegetation dynamics) (Westoby et al. 1989).

The dynamic equilibrium hypothesis (Huston 1979) states that both models (equilibrium and non-equilibrium) influence vegetation dynamics, operating at different spatial and/or temporal scales. Thus, communities are structured not only by internal regulation processes (e.g. herbivory and competition), but also by external regulation processes (e.g. response to external factors such as climatic variability). As a consequence, the interaction of both (equilibrium and non-equilibrium) dynamics contributes to a relatively stable species composition of a plant community at different spatial and temporal scales (Huston 1979; Briske et al. 2003; Bestelmeyer et al. 2004). This interaction between both dynamics causes certain fluctuations at structural and functional levels of an ecosystem; however, these changes do not exhibit a particular tendency and may oscillate near an average. Therefore, these fluctuations do not represent a transition to another state (Walker 1993). Nevertheless, these regulation processes do not have the same importance and the prevalence of one over the other is specific for each ecosystem. The dynamic equilibrium of some ecosystems may be regulated by internal processes (e.g. competition and recruitment) interacting also with external factors; in other ecosystems this can also be more controlled by external factors, such as climatic and/or hydrological cyclical fluctuations [e.g. ENSO (El Niño-Southern Oscillation) cycle] (Crawley & Ross 1990; Nicholls 1991; Gutiérrez et al. 2000; Holmgren et al. 2001). Therefore, the dynamic equilibrium of ecosystems is complex and depends on the interaction of internal and external regulation processes that contribute to a relatively stable species composition, with certain oscillations at structural and functional levels, characteristic of each state of an ecosystem.

To explain the concept of the structural and functional fluctuations of the state of an ecosystem in dynamic equilibrium, we will consider the patch dynamic of the Patagonian steppe (Soriano et al. 1994; Aguiar & Sala 1999) as a simplified example taking into account a community controlled mainly by internal factors and processes. This patch dynamic is composed by two main phases: building and degenerative. This dynamic would originate two main types of patches: (a) high cover patches formed by adult shrubs surrounded by a ring of perennial grasses (mature patch); and (b) low cover patches represented by perennial grasses and/or small shrubs scattered over a bare soil matrix (Fig. 2a; Soriano et al. 1994). In a community, at a given time, there can be different proportions of vegetation patches in different phases coexisting within a mosaic. There are two scale-dynamics here: one is the single patch dynamic (Fig. 2a), and the other is the mosaic dynamic composed of different patches within the community (Fig. 2b). As individual patch dynamics are not synchronized there is a mosaic with patches at different phases of their dynamics (Watt 1947). Fluctuations in the proportion of patches in different phases could occur depending on the temporal scale analysed. In the case of a Patagonian steppe, different types of patches in different phases can coexist within a mosaic. Each phase in each patch could last a different length of time, thus producing these fluctuations. This situation could be associated with internal factors or processes (topography or ecophysiological species-specific responses), external factors (cycles of wet–dry years), or the interaction of both and may accelerate or delay some phase of different patches in the community. This dynamic determines spatial heterogeneity at structural level which fluctuates in time, associated with a functional oscillation. The functional oscillation is related to processes such as vegetative growth and seedling recruitment (associated with RUE and KIRP, respectively) that occur in each patch type of the mosaic (Soriano et al. 1994). Thus, in point 1 of our example (Fig. 2b), similar proportions of patches can be found in all phases within the mosaic. In general terms, the point 1 represents the proportion of patches characteristic of the state, around which the community fluctuates. In our case, the ecosystem state has intermediate function and

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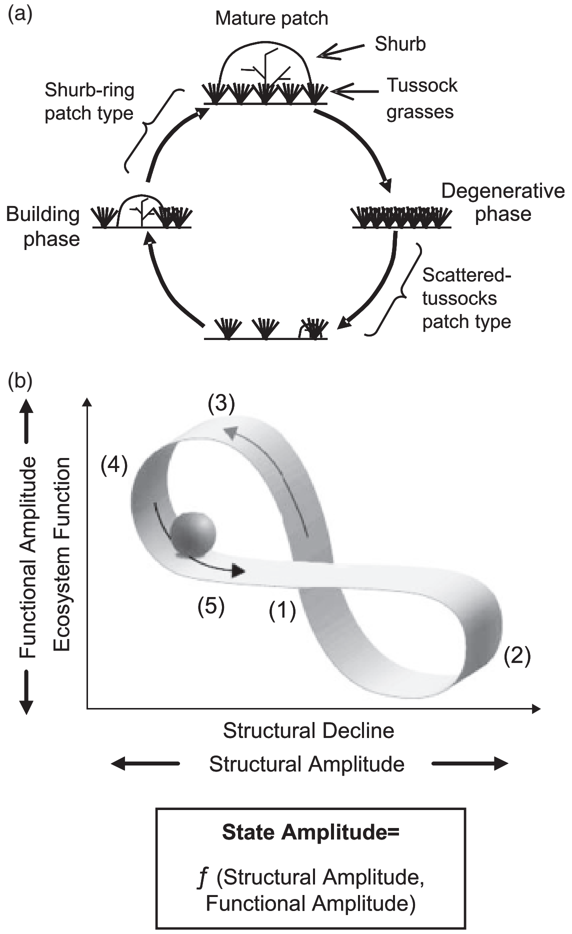

Fig. 2. Schematic representation of an ecosystem in dynamic equilibrium. (a) The model of patch dynamics for vegetation of the Patagonian steppe (extracted from Soriano et al. 1994) and (**b**) Schematic representation proposed for the state of an ecosystem in dynamic equilibrium in the framework of Structural–Functional State and Transition Model (SFSTM) (adapted from Gunderson & Holling 2002), taking into account the model proposed in (**a**). Under this scheme we postulate an alternative representation of each ecosystem state, based on the dynamic equilibrium hypothesis (Huston 1979). Point 1: the plant community (gray ball) is a mosaic with similar proportion of patches in all phases (the ecosystem state has intermediate function and process values). Point 2: the proportion of patches in degenerative phase is larger in the plant community. Point 3: the plant community has a greater proportion of patches in building phase, therefore the ecosystem state has high values at functional level. Point 4: the plant community has a greater proportion of mature patches. Although points 3 and 5 are structurally similar (similar proportions of mature patches), they differ from the functional perspective: in point 3 the community is in active growing in many patches (higher rain-use efficiency, RUE) and has a high key individual recruitment process (KIRP). In contrast, in point 5 there are proportionally more patches in degenerative phase, where the RUE and the KIRP are decreasing. The state amplitude is function of structural and functional amplitude.

process values (KIRP and RUE) at this point. Towards point 2 (Fig. 2b) the proportion of patches in degenerative phase increases. RUE and KIRP decrease towards this point and therefore the ecosystem state is declining. In contrast, towards point 3 (Fig. 2b) the proportion of patches in the building phase increases, and thus the ecosystem state has high values at functional level. Towards point 4 (Fig. 2b), the proportion of mature patches increases. Although points 3 and 5 (Fig. 2b) have similar proportions of mature patches in the mosaic (structural level), they differ from the functional perspective. In point 3 there are many patches in the building phase and the community is actively growing (high RUE) and has high KIRP. In contrast, in point 5, there are proportionally more patches in the degenerative phase, where vegetative growth and seedling recruitment are decreasing. Therefore, depending on the proportion of patches that are in degenerative or building phase, there will be certain variations in the state structure and function, but oscillating around an average.

Then, we define the state of an ecosystem as a plant community (mosaic of patches), in dynamic equilibrium, supported by a determined quantity of resources that fluctuate in space and/or time, known as ‘growing space’ (e.g. water, nutrients, light and space availability) (Oliver & Larson 1996). The growing space fluctuates owing to external and internal regulation processes. The interaction of mosaic-level dynamics with the fluctuation of the growing space maintains the state of an ecosystem in dynamic equilibrium. This is determined by structural (structural amplitude) and functional (functional amplitude) oscillations at the community level, defining the state amplitude (Fig. 2b).

Critical threshold concept in the SFSTM

The identification of ecological thresholds represents a key issue to differentiate between the multiple states of an ecosystem. It is also a management tool to prevent the occurrence of less desired states. This concept has been widely used in ecology, it extended in the 1970s under the theory of multiple stable states with the object of describing the limits between alternative stable states. The lack of understanding of ecological thresholds makes it difficult to identify them, minimizing their utility in ecosystem management (Bestelmeyer et al. 2003; Stringham et al. 2003; Briske et al. 2006).

Thresholds are limits in space and/or time between states, so one or more primary ecological processes have changed irreversibly and should be actively restored to return to the previous state (Friedel 1991). However, Groffman et al. (2006) defines a threshold as the point at which an abrupt change occurs in some property or process that is important for an ecosystem, altering not only the structure, but also the ecosystem services and functions. Many authors have addressed and contributed to the understanding of thresholds (Laycock 1991;

Aronson et al. 1993; Beisner et al. 2003; Bestelmeyer et al. 2003, 2004; Briske et al. 2003, 2005, 2006; Stringham et al. 2003; Suding et al. 2004; Geist 2005; Groffman et al. 2006), but Briske et al. (2005, 2006) offer an interesting perspective suggesting deepening the identification, quantification and interrelation of structural and functional thresholds, and its incorporation into the STM framework.

The SFSTM emphasizes on the 'critical threshold' concept (Groffman et al. 2006). The critical threshold is surpassed when a negative transition occurs, from which the probability of returning to the original state decreases significantly once the disturbance is eliminated. This situation defines a threshold where, in addition to important changes that occur at the vegetation structural level, great changes at the soil level also occur (e.g. erosion), causing substantial losses of ecosystem functions and/or processes (Fig. 1), that in our model we prioritize: RUE and KIRP.

Therefore, the concept of threshold becomes really important when rangeland functions are affected and when the ability of the ecosystem to return to its original state is severely diminished or lost, defining a critical threshold. While Tongway & Hindley (2000, 2004) do not define thresholds in their approach of landscape functions loss, we adapted this model to explain the concept of critical threshold (Groffman et al. 2006). Thus, a critical threshold can be identified when a significant change (increase) in the rate of loss of ecosystem functions is registered, while at the same time the disturbance intensity increases (Fig. 1). Thus, the critical threshold is defined by a structural threshold and a functional and/or process threshold, thereby identified by structural and functional indicators, respectively (Fig. 1). Therefore, the ecosystem has overcome the critical threshold when it has severely diminished or lost its resilience, because core functions that determine and regulate the ecosystem dynamics have been significantly affected. In this sense, it is of practical importance to define and integrate concepts such as ecosystem resilience and resistance, because they are relevant from the perspective of sustainable rangelands management (Stringham et al. 2003).

Resistance and resilience: relationship with the SFSTM

The main objective of sustainable management is to assess the ecosystem resistance and resilience, preserving its ability to respond and adapt to future disturbances and/or changes (Convention on Biological Diversity 2008). In this context, to develop the SFSTM we adopt two complementary concepts: resistance and resilience (Holling 1973, 1996; Westman 1978; Dell et al. 1986; Scheffer et al. 1993, 2001; Suding et al. 2004; Briske et al. 2006; Groffman et al. 2006). Although these concepts have undergone many revisions (Carpenter & Cottingham 1997; Carpenter et al. 1999; Lavorel 1999; Gunderson 2000; Gunderson & Holling 2002; Scheffer & Carpenter 2003), it is necessary to integrate them to the SFSTM with clear definitions to be able to apply and evaluate ecosystem resistance and resilience. Therefore, we consider resistance as the ability of an ecosystem to tolerate a determined disturbance without suffering significant changes in its structure and functioning (Westman 1978; Dell, Hopkins & Lamont 1986; Stringham et al. 2003). This concept is associated with the speed at which the ecosystem state can pass to another state under a determined disturbance and the magnitude of structural–functional degradation (degradation speed and rate). By contrast, resilience is defined as the capacity of an ecosystem to return to the condition before a perturbation once the disturbance is suppressed (Holling 1973; Westman 1978; Pimm 1984; Dell et al. 1986; Fox & Fox 1986; Keeley 1986). Holling (1973) also defines ecological resilience as the amount of disturbance that is needed to change the state of an ecosystem. Thus, we will consider the Holling (1973) and Westman (1978) resilience definitions. These authors analyse, from our point of view, two important and useful concepts: (a) ecosystem elasticity (the speed at which the more degraded state of an ecosystem returns to its previous and/or original state once the disturbance is suppressed); and (b) ecosystem amplitude (the interval of states under which an ecosystem can move before crossing the 'critical threshold', beyond which, it cannot return by itself to its previous and/or original state once the disturbance is suppressed; Figs 1 and 3). If a determined amount (intensity and/or frequency) of disturbance is needed to cross the critical threshold, we can assume that it corresponds to the definitions of Holling (1973), Westman (1978) and Briske et al. (2008). Therefore, ecosystem resilience is defined by the ecosystem elasticity and amplitude. Thus, the greater the elasticity and amplitude of an ecosystem, the greater will be its resilience. Furthermore, it is necessary to consider that a given resilience is regarded as being specific to a determined disturbance; for example, resilience to fire does not imply resilience to grazing (Williams et al. 1993).

Integration of the main concepts to the SFSTM

To integrate the above exposed concepts we propose a new way to represent the STM based on the x and y axes already defined: SFSTM (Fig. 3). The top left corner refers to the less degraded states whereas in the bottom right are the most degraded states. When the disturbance intensity and frequency are strong enough to alter the dynamic

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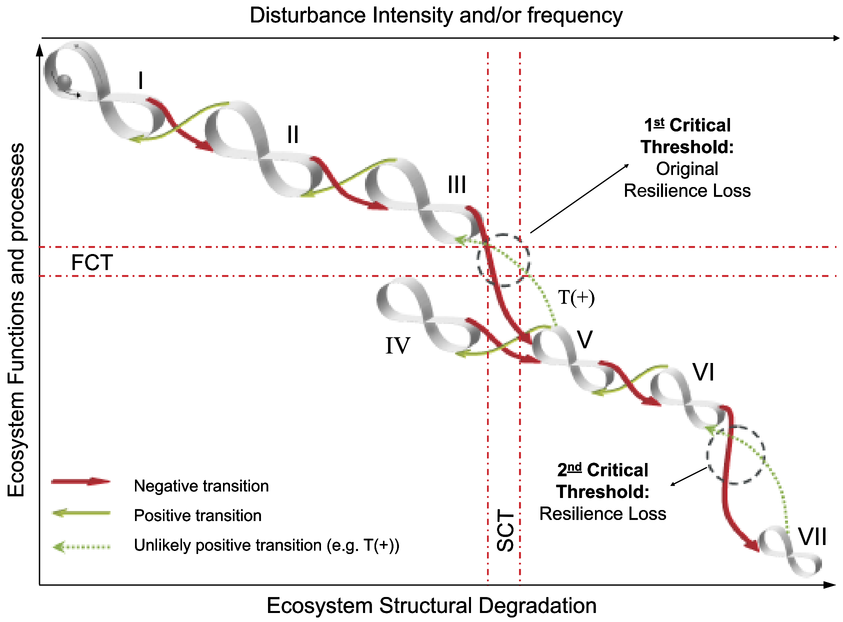

Fig. 3. Schematic representation of the Structural–Functional State and Transition Model (SFSTM): *x* axis represents ecosystem structural degradation and *y* axis represents ecosystem functions and processes. The gray ball represents the plant community which fluctuates in dynamic equilibrium of the ecosystem state. Different states are identified by roman numerals (the highest value identifies the more degraded situation). The likelihood of a transition is reflected by the width and the filling of the arrow. Negative transitions are more feasible than positive transitions and are represented by thicker and filled arrows. In contrast, positive transitions (more unlikely than negative) are represented with thin arrows. When positive transitions are improbable, they are represented with dotted arrows. As disturbance intensity and/or frequency increase (e.g. grazing), the transition from one state to another is produced and is shown by the movements toward the right of the *x* axis and to the lowest part of the *y* axis. If a disturbance produces an important decrease in an ecosystem functions and/or process and produces an abrupt change on the *y* axis (increase in the rate of loss of functions and processes), the critical threshold is defined. SCT = Structural Critical Threshold; FCT = Functional Critical Threshold.

equilibrium of a state, a change of greater magnitude than the state amplitude is produced, triggering a negative transition. This change should produce a directional displacement in the *x* and/or *y* axes of ecosystem degradation. These changes are persistent in time and are reflected in a ‘transition’ from one state towards another state in dynamic equilibrium. The transition likelihood depends on the disturbance applied to the system and on the moment at which the state is found within the dynamic equilibrium. For example, if the plant community is found at point 2 (Fig. 2b), the probability that a given disturbance (e.g. overgrazing and/or extreme drought) will force a negative transition is greater than if it is found at point 3 (Fig. 2b).

If an ecosystem is disturbed (e.g. overgrazing) and a negative transition is produced, we hypothesize that more degraded states would have less state amplitude. Although the way in which the state amplitude changes as an ecosystem degrades should be evaluated, we believe the decrease in state amplitude is associated with a reduction of functions and processes that can be performed by the ecosystem. At structural level, a decrease in state amplitude could be associated with changes in the spatial heterogeneity (Hutchings et al. 2000; Adler et al. 2001; Alados et al. 2007). Some authors (Paruelo et al. 1993; Aguiar et al. 1996) have registered a lower productivity range for most degraded states. This would suggest a decrease in the state amplitude as the ecosystem degrades. Similarly, the decrease in the state amplitude could be associated with a reduced occurrence probability of a positive transition, (e.g. the transition between state VII and VI would be less unlikely than the transition between state V and III; Fig. 3).

Environmental disturbances, such as extraordinary drought (Briske et al. 2008), differ from human-induced disturbances such as domestic grazing because the former occur in relatively short periods of time (weeks to months) and the latter maintain their intensity through time (years). The environmental triggers are extraordinary events that would negatively affect the ecosystem structure and functions, directly (fire: burning the vegetation) or indirectly (drought: decreasing the growing space), modifying the dynamic equilibrium of a state. Thus, the probability of a negative transition would increase.

Considering the intermediate disturbance theory (Paine 1966), in some ecosystems, low and intermediate grazing pressures could produce an increase in the species diversity and heterogeneity of a community (Paine 1966; Adler et al. 2001; Cingolani et al. 2005, 2008), probably increasing the state amplitude. This situation may be caused not only by a differential grazing in palatable and non-palatable species, but also by the heterogeneity of the grazing area (e.g. vicinity of water source) (Adler et al. 2001; Morici et al. 2003; Oesterheld et al. 2005; Cingolani et al. 2008). Therefore, in the initial states (states I and II, Fig. 3), the ranges of state amplitude (structural and/or functional amplitude) could be maintained, or even a small increase could occur. Everything will depend not only on intrinsic ecosystem factors (community type, species and topography), but also on extrinsic factors (grazing or disturbance type).

If grazing pressure increases and the ecosystem only moves along the *x* axis, without passing beyond the critical threshold, there can be a gradient of possible states according to grazing pressure (Fig. 3). Between these states (states I, II and III, Fig. 3) it is difficult to identify thresholds and therefore it is not practical from a management perspective. However, it is important to define these possible states (e.g. between state I and III, Fig. 3) in order to determine how far the rangeland is from crossing the critical threshold. This will provide decision-makers of rangeland management with a fundamental tool.

A marked displacement along the *y* axis indicates that a disturbance drove significant changes at vegetation and soil levels causing significant losses in functions and/or processes (increase in the rate of loss of functions and/or processes) which compromise the rangeland sustainability. In other words, the ecosystem has crossed the critical threshold, beyond which it loses or significantly decreases its resilience (Fig. 3). At this point, positive transitions become more unlikely and stochastic factors, such as favorable climate events (series of wet years) (Westoby et al. 1989; Briske et al. 2008) or active restoration actions, gain importance as triggers of positive transitions (Friedel 1991). This type of event produces an increase in the growing space available for a community and therefore, in the state functional and/or structural amplitude, increasing the probability of a positive transition (Westoby et al. 1989) (Fig. 3, e.g. T(+)). A restoration action can also involve an increase in the growing space (fertilization, watering) or enhancements at a structural level (artificial revegetation).

Although, the response of other variables to disturbances should be evaluated, we propose two functions and/or processes as indicators for the *y* axis in order to determine the critical threshold: RUE and KIRP. These must be evaluated in each ecosystem whether both have the same relative importance or if any one of them is more important than the other in the maintenance resilience. We consider that if a disturbance causes a significant decrease in any of these variables, this situation determines that the critical threshold has been crossed.

In the SFSTM, the resistance of an ecosystem state defines the dynamics of the negative transition (magnitude and speed of change) to another state, from the top left to the lower right of the graph (Fig. 3). Conversely, ecosystem resilience defines how (ecosystem elasticity) and how much (ecosystem amplitude) the movement is between the states of an ecosystem on the *x* axis toward its previous and/or original state once the disturbance is suppressed. If negative transitions occur toward lower levels on the *y* axis, (e.g. state III to IV, Fig. 3), the critical threshold has been surpassed and the ecosystem begins to have another structure and function. This new position on the *y* axis redefines a second critical threshold and a new resilience of this new ecosystem state (Fig. 3). The second critical threshold is defined by their specific structural and functional critical thresholds in the *x* and *y* axes, respectively (Fig. 3). In our case (Fig. 3), this new resilience defines the recovery capacity between states VI and IV once the disturbance that maintained the ecosystem in state V or VI is suppressed. Some critical thresholds can be associated with local extinction of key species. If this were the case for the threshold between states III and V, the removal of the disturbance that maintained the ecosystem in state V would just produce a positive transition to state IV (Fig. 3). This state would be structurally similar to state III, but without some key species (relevant in ecosystem functioning).

Finally, it must be said that the model components will depend on the ecosystem under study and management. It is worth noting that Fig. 3 is a basic scheme to illustrate and explain the model simply. This scheme shows only two critical thresholds, following two simple degradation pathways (between state I to V, and state IV to VII). In more complex systems, there may be more than one degradation pathway for one state; for example, in addition to having a critical threshold between state III and V, there may be another between state III and IV (with their associated negative and positive transitions).

In summary, the proposed SFSTM integrates several concepts in order to increase application of the theory to understand current ecosystems and develop management tools, considering the following issues: (a) The states and transitions of an ecosystem are defined by structural (*x* axis) and functions and/or processes (*y* axis) changes (Fig. 3); (b) the plant community is a mosaic of patches that follows an internal cyclic dynamic in interaction with the environment maintaining it in dynamic equilibrium, defining the state amplitude (Figs 2b and 3); (c) the critical threshold is defined by a structural threshold (in *x* axis) and a functional threshold (in *y* axis); (d) The axes *x*

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and *y* allow us to evaluate the resistance and resilience of an ecosystem. Specifically, the critical threshold defines the ecosystem amplitude (Fig. 3).

In the Supporting Information we present three case studies supporting the state amplitude concept and the main premises of the SFSTM with field data, providing an application and integration of the concepts expressed in this review. Based on the structural and functional and/or processes axes, we approach and evaluate the different states of degradation of a shrubby-grassland steppe of *Mulinum spinosum* and *Poa ligularis* of North Patagonia, defining and quantifying the structural and functional thresholds associated with ecosystem resilience (critical threshold). Finally, we present another example of a grassland steppe of *Festuca pallescens* of south-west Patagonia, to better illustrate the SFSTM applied to a more complex system with two different degradation pathways.

Final thoughts

Although one of the advantages of the original STM was its simplicity and flexibility, this allowed very broad interpretations which led to a lack of consensus on some points of view, as indicated by the different structuring of graphic schemes (e.g. schemes of Paruelo et al. 1993; Bestelmeyer et al. 2003; Stringham et al. 2003). While in recent decades there has been a major theoretical development of key concepts such as resilience and thresholds (Scheffer et al. 2001; Gunderson & Holling 2002), we believe this development has brought about greater complexity, which has not allowed its integration to the STM. In this context, the SFSTM adds little complexity to the STM, and the key concepts mentioned can be incorporated and reconciled with the inclusion of only two axes (structural and functional) to the model.

The STM define the states only from a structural–floristic viewpoint. The SFSTM maintains the initial idea of a scheme in a plane, but with the advantage of sorting the information based on two axes: one structural and one functional. This allows us to see how far is a state of another (structural and/or functionally), facilitating the identification and visualization of critical thresholds (as the degradation slope among states). Thus, the SFSTM provides a very useful tool for identifying indicators (structural and/or functional) associated with resilience.

Although the proposed SFSTM should continue to be tested and further studies should be carried out in this regard (e.g. to assess the best functions to be measured in each ecosystem and the response curves between structure and function), we consider that it has profound implications in rangeland ecology and management. We believe that the SFSTM enhances a framework to understand in a simple way the ecosystem dynamics and their interaction with the use of natural resources, considering its complexity and providing an essential tool for rangeland research and management.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Fig. S1. State and Transition Model (STM) scheme proposed by Bonvissuto et al. (1993) for a subshrubby–grassland steppe of *Mulinum spinosum* and *Poa ligularis* of the Occidental District of Patagonia, Argentina.

Fig. S2. Relationship between of Structural Declination Index (SDeI) and mean seedling number per m^2 of patch in State I (S-I) of a shrubby-grassland steppe of *Poa ligularis* and *Mulinum spinosum* (Bonvissuto et al. 1993). The dotted arrows suggest the trajectory of the dynamics in the sampled communities based on the proposed axes, being similar to the trajectory proposed for the schematic representation of *state amplitude* (Fig. 2b). S-I_1 = two ha without livestock grazing for 30 yr; S-I_2 = one ha without livestock grazing for 15 yr; S-I_3 = 35 ha without livestock grazing for 30 yr.

Fig. S3. Average and standard error seedling density per m^2 in States (S) I, II, III_g and III_{wg} on autumn 2007. Different letters indicate significant differences among states ($P \leq 0.05$). g = grazing; wg = without grazing.

Fig. S4. Application of the Structural–Functional State and Transition Model (SFSTM), based on an *x* axis of ecosystem structural degradation and on a *y* axis of ecosystem functions and/or processes, for a subshrubby–grassland steppe of *Mulinum spinosum* and *Poa ligularis* of the Occidental District of Patagonia. The grey dashed line represents the trajectory of functions and/or processes loss with the structural degradation of the ecosystem while grazing pressure increases. SCT = Structural Critical Threshold; FCT = Functional Critical Threshold. Roman numerals inside gray balls indicate different states.

Fig. S5. State and Transition Model (STM) scheme proposed by Bertiller & Bisigato (1998) for a grassland steppe of *Festuca pallescens* of the SW of the Chubut, Argentina.

Fig. S6. Application of the SFSTM, based on an *x* axis of Ecosystem Structural Degradation and on a *y* axis of Ecosystem Functions and/or Processes, for a grassland steppe of *Festuca pallescens* of the SW of Chubut, Argentina. The black and grey dashed lines represent two trajectories of functions and/or processes loss with the ecosystem structural degradation while grazing pressure increases. SCT = Structural Critical Threshold; FCT = Functional Critical Threshold. Roman numerals inside gray balls indicate different states.

Table S1. Mean ± standard error of vegetation variables of three States I (S-I) of shrubby-grassland steppe in the Occidental District of Patagonia (70° 35′ 21″ W and 41° 01′ 42″ S). S-I_1: 2 ha without livestock grazing for 30 yr, S-I_2: 1 ha without livestock grazing for 15 yr and S-I_3: 35 ha without livestock grazing for 30 yr). The variables were not different between the sampled communities ($P > 0.05$).

Table S2. States (S) I, II, IIIg and IV description of shrubby-grassland steppe in the Occidental District of Patagonia (70° 35′ 21″ W and 41° 01′ 42″ S) based on main characteristics of vegetation, soil depth and forage biomass production. Mean ± standard error is shown for vegetation cover and soil variables. Different letters indicate differences among the states within each variable analysed ($P \leq 0.05$).

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