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LANDSCAPE IN MOTION: REVISITING THE ROLE OF KEY DISTURBANCES IN THE PRESERVATION OF MOUNTAIN ECOSYSTEMS

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ABSTRACT. *The history of the planet is an ever-changing story. Nowadays, managers of the natural environment face the challenge of dealing with a dynamic landscape that is at a turning point due to the global change (climate and land use change) brought about by human actions in recent centuries. This article discusses the traditional concept of conservation of the natural environment, analyses the role played by key disturbances in the functioning and dynamics of ecosystems over time, and offers a new management approach derived from this knowledge. Combined practices of controlled fire and guided grazing (pyric herbivory) as environmental tools for the preservation of valuable mountain ecosystems are justified, as well as the need to consolidate them by combining traditional expertise with scientific and technical knowledge in order to maximize their positive effects and minimize the potential negative impacts on the natural environment.*

El paisaje dinámico: revisando la función de perturbaciones clave en la preservación de ecosistemas de montaña

RESUMEN. *La historia del planeta es una historia dinámica, de continuo cambio. Los responsables de la gestión del medio natural se enfrentan actualmente ante un paisaje muy cambiante debido a las condiciones de cambio global (cambio climático y de usos del suelo) provocadas por la acción humana en los últimos siglos. La dimensión temporal es un aspecto clave en la gestión del medio natural, y conocer la historia de los agentes que han esculpido el paisaje permite entender los nuevos escenarios impulsados por el cambio global. Este artículo discute el concepto tradicional de conservación del medio natural, analiza el papel de determinadas perturbaciones en el funcionamiento y la dinámica de los ecosistemas y ofrece un nuevo enfoque de gestión derivado de este conocimiento. Las prácticas combinadas de fuego controlado y pastoreo guiado (herbivorismo pírico) emergen como valiosas herramientas de conservación de los ecosistemas de montaña, que deben consolidarse aunando experiencia y conocimiento científico-técnico para maximizar sus efectos positivos y minimizar los potenciales impactos negativos.*

Key words: preservation, mountain landscape, disturbance regime, fire, pyric herbivory.

Palabras clave: conservación, paisaje de montaña, régimen de perturbaciones, fuego, herbivorismo pírico.

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1. The new paradigm: Towards the preservation of ecosystem processes

Earth is dynamic, and so are the natural ecosystems developing on it. Terrestrial communities, in the absence of limiting factors, are a succession of pastures, scrublands and forests. Succession implies progressive changes in the dominance of groups of species which, in turn, drive to environmental changes that lead to the development of new plant communities with a differentiated functioning. The climax theory, developed in the early 20th century (Clements, 1936), stated that terrestrial ecosystems progressed to culminate to the climax, mature forests in most of the cases, which were considered the most valuable ecosystems to preserve. In the last decades, the ecological conception of succession has radically changed and a dynamic, cyclical view of the process prevails. Since communities replace each other continuously, one particular ecosystem is not considered more pristine or valuable than other.

The cyclical conception of succession has important implications for preservation since compels to manage ecosystems that evolve continuously. In the last centuries, nature conservation promoted the development of climax wooded communities, as an unmistakable sign of an optimal ecosystem. Nowadays, the new paradigm in conservation focuses on the safeguarding of the processes (i.e. the capacity for change) rather than the particular outcomes (i.e. a static picture of a mature forest).

The perpetuation of the natural processes is the essence of conservation (Suding *et al.*, 2004; Suding and Hobbs, 2009), but it entails many difficulties. Often, natural processes and their resulting outcomes occur on a time scale that humans are unable to perceive. The protection of valuable environmental assets (biodiversity, soil fertility, nutrients and water cycle, etc.) entails safeguarding the evolutionary capacity of change and response to the environment. Ecosystems evolved according to an historical abiotic and biotic environment and a prevailing regime of disturbances, operating at different scales, recurrences and intensities (Pickett and White, 1985). Dominant disturbances shaped species and promoted a wide variety of plant adaptations that left its imprint on the characteristics of the whole community. Besides, disturbances played a key role in the creation of landscape by affecting the course of plant community successions (Svenning, 2002; Vera, 2000). While some disturbances (forest fires, floods, plagues...) caused intense damages in the original communities and fostered processes of secondary succession, other low-intensity disturbances, such as herbivory (selective removal of biomass), affected specific functions of the communities (regrowth, nutrient cycle...) and slowed down successional processes, favoring the maintenance of particular successional stages (i.e. park-grass landscapes before hominids expansion in the European continent, Vera, 2000) (Table 1).

Table 1. Studies revisited and main current conclusions of Vera (2000) dissertation.

Revisited studies	Current conclusions
Review of fossil pollen studies conducted in the early 20th in Europe concluding that mature forests constituted the most abundant habitats before human intervention	- Previous pollen studies considered tree species as a whole. Current revisions elucidate among species, which allows a better understanding of particular habitats requirements (i.e. species from border forests such as hazel). - Modeling techniques have improved. Sedimentation spectra of modern pollens show that non-arboreal pollen does not relate linearly with the degree of habitat opening. - Current patterns of pollen sedimentation in open landscapes are very similar to those in fossil pollen spectra.
Historical analysis of ancient forest use regulations through Europe	In the Middle Ages, there was a strict regulation for the use of shrubs as firewood. Restrictions were based on the idea that the greatest regeneration of trees occurred in open spaces (not in closed forests as believed in latter centuries), and that bushes (thorny, toxic, with high phenolic contents...) protected young trees and promoted regeneration in grazed areas.
Tree regeneration research in valuable European mature forest reserves: Neuenburger Urwald (Germany), Bialowieza Forest (Poland), Krakovo Primeval Forest Reserve (Slovenia) and Dalby Söderskog (Sweden).	Nowadays, there is no natural oak regeneration in these reserves. Old oaks date from periods when herbivory existed. Reduced herbivory has not led to oak regeneration but to the development of species such as beech, elm and hornbeam.

The knowledge of the ecological history of the planet has made great progresses in recent years due to the development of paleoecology, a science that encompasses and nourishes from disciplines such as paleobotany, sedimentology, evolutionary biology, dendrology and biostatistics, among others. Paleoecological knowledge is of great interest for ecosystems conservation and restoration, since allows to discover how the past was like, identifies ancestral modelling agents and tracks until the present-day situation (Galop and Catto, 2014; Pérez-Díaz *et al.*, 2015).

The combination of the information derived from ancient charcoal and fossil pollen sediments and the study of the strategies and adaptations developed by plants throughout the evolution to respond to the effects of the dominant modelling agents, permit to reconstruct the history of the planet and the historical landscape (Conedera *et al.,* 2009; Fuhlendorf *et al.,* 2001; Keeley *et al.*, 2011).

2. History of fire in the natural environment

Fire needs oxygen, fuel and a source of ignition to occur, three elements present in Earth since remote times (Pausas, 2012). The rise of photosynthetic organisms –firstly in marine environments, 2.5 billion years ago, and later, colonizing the terrestrial environment, 450 million years ago– fostered the oxygenation of the primitive atmosphere. The plant biomass accumulated in the earth's crust provided the fuel, and thunderstorms and volcanism the ignition sources. The fossil charcoal record reconstructing the planet's incendiary history, reports the high variability of fire regimes that occurred over time, depending on the prevailing climate, the atmospheric oxygen concentrations, the volcanism and the herbivorism (Pausas and Keeley, 2009; Gil-Romera *et al.*, 2014).

Pyne (2001) review defines three periods of fire regime in relation to the hominids development in earth: natural, anthropogenic and industrial. In the first period, ignition sources were natural and hominids influence was insignificant. In the anthropogenic period, hominids learned to manage fire in the landscape with different objectives (i.e. hunting, transit...) and intensified its use since the Neolithic with agricultural purposes (i.e. creation of fields and pastures, improvement of soil fertility, pest control...), promoting new cultural landscapes and a diversity of land uses. The industrial period set off a stage of fire avoidance, to protect human beings and their settlements and resources from destructive fires. At the first stages of the latter period, wildfires significantly declined due to the intense use of the territory by agriculture, livestock and forestry (Marlon *et al.,* 2008; Montiel, 2013). Nowadays, many lands and traditional uses have been abandoned while human efforts put in fire avoidance have largely increased.

European mountains encompass suitable features for the study of fire history. Highlands have experienced a low level of human disturbance compared to lowlands, and the presence of peat bogs and lakes of glacial origin provides deep strata of sedimentary columns which offer an opportunity for paleoecological studies of fossil carbons and pollens. Stratigraphic records of natural deposits and archaeological studies have been done in the Alps (Ascoli and Bovio, 2013; Valese *et al.,* 2014) and in the Pyrenees (Galop *et al*., 2011; Rius *et al*., 2012; González Samperiz *et al*., 2017) with similar results. Pyrenean records show evidence of a very old anthropization of the territory, even in high-altitude areas (Gassiot *et al.*, 2014). In Western and Eastern Pyrenees, the impact of humans on highland vegetation dates back to first hunter-gatherer societies at the end of the Early Holocene (8800-6500 BC), and to agricultural-livestock societies in the Middle Holocene (5500-4500 BC) (Miras *et al.*, 2010; Galop and Catto, 2014). In Central Pyrenees, human influence on vegetation started later, at the Bronze and Iron Ages, and was less intense (González-Sampériz *et al.*, 2017). While the impacts of human activities in the Early Neolithic were local and focused on the eastern and western edges of the massif, mining activities and agro-pastoralism during the Metal Ages impacted the landscape at a larger, regional scale, through a significant decrease of forested areas (Rius *et al*., 2012; Pérez-Díaz *et al.*, 2015). Once in the Ancient Ages, the use of fire to manage the landscape generalized throughout the Pyrenees, and intensified in the Middle Ages, peaking about 800 years ago (González-Sampériz *et al*., 2017). Anthropization was still intense due to the high population rates until the mid 20th century (Vicente-Serrano *et al.*, 2004). During these periods, grasslands increased at the expense of forests by the planned use of fire and the domestic stock (Galop *et al.,* 2011).

Nowadays, the traditional use of fire for grassland amelioration purposes (pastoral fires) has prevailed in some areas of the Pyrenean massif. Burnings are carried out in winter or early spring, with moist soils, dry vegetation and cold temperatures –which ensure a low intensity of flames– and affect relatively small and discontinuous areas (i.e. applying flames *shrub-to-shrub,* Coughlan, 2014; San Emeterio *et al.*, 2016). The use of fire in other mountain regions of Europe is variable, and the practices are maintained in some regions with different purposes, while in others have lost or are banned (Lázaro and Montiel, 2010). Figure 1 summarizes the main landscape changes observed in grazed heathlands in uplands of Western Pyrenees and Great Britain when traditional burning practices are abandoned or applied at a different regime (changing the recurrence and intensity). In some upland regions, the traditional use of fire carried out by farmers and herders coexists with modern burning practices, with different levels of success (Múgica *et al.*, 2018), and modernization has been achieved by defining specific regulations and protocols that decrease wildfire hazard in controlled burnings, and by the creation of specialized burning teams (Vélez, 2010). But more work is still ahead. Fire management has to be incorporated into the regional policies by an integrative approach that encompasses fire suppression as well as fire promotion, according to the objectives of environmental conservation and safety for human life (Montiel and Kraus, 2010; Silva *et al*., 2010).

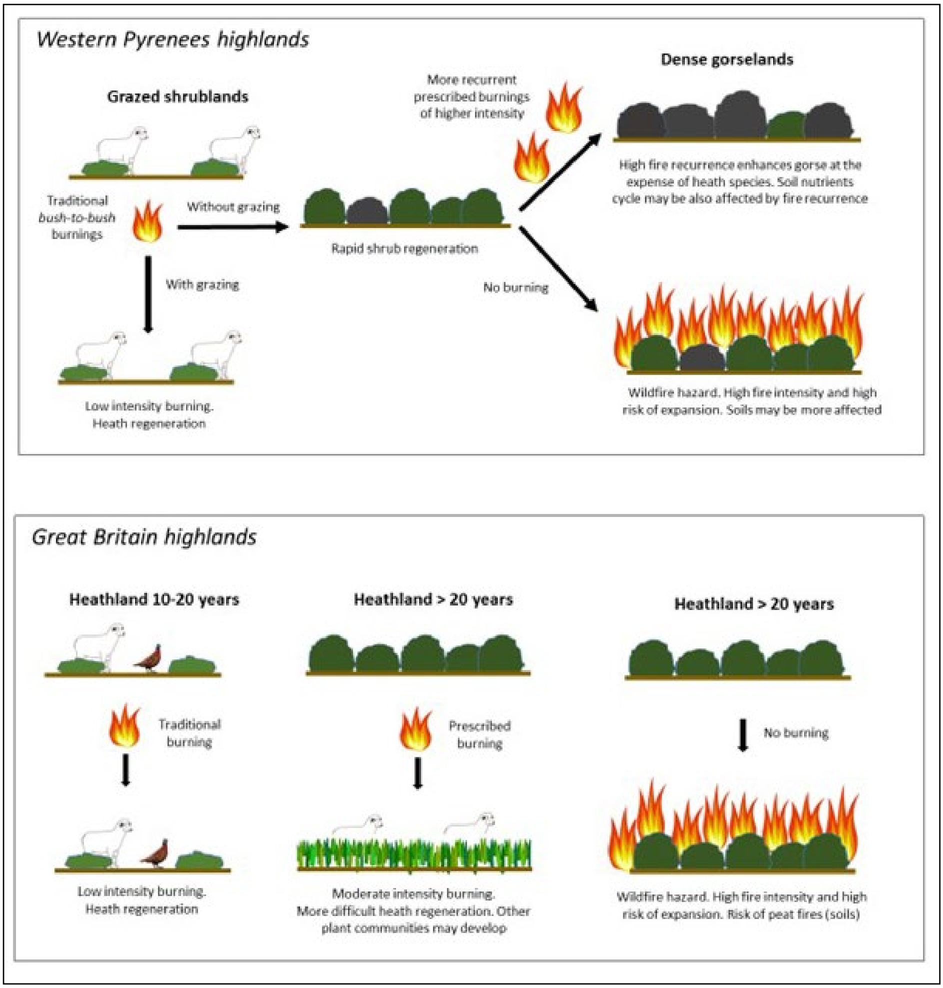

*Figure 1. ABOVE: Traditional bush-to-bush burnings for the preservation of open heathlands (*Erica spp., Calluna vulgaris, Daboecia cantabrica, Ulex spp.*) in Western Pyrenees. At present, a high recurrence and intensity of burnings to control shrub encroachment is leading to the development of dense gorselands (*Ulex spp.*) which are highly pyrophytic and fire-adapted. BELOW: Traditional burning regime for the preservation of open* Calluna vulgaris *heathlands used for hunting (*Lagopus lagopus scoticus *and* Cervus elaphus*) and grazing (wild and domestic herbivores). Nowadays, in Great Britain, wildfires in dense shrublands are much frequent than in forests. Source: Author's compilation and adaptation based on Legg* et al. *(2006), Bruce* et al. *(2010) and Múgica* et al. *(2018).*

3. History of herbivorism on earth ecosystems

At a particular point in the evolution, the history of fire on earth began to be strongly associated to the history of herbivores. Paleoecology and evolutionary ecology show the insights of this ancient relationship. According to the fossil carbon record, Paleogene (early Cenozoic) was a period of large planetary fires driven by high levels of atmospheric oxygen and high accumulation of fuels (Scott *et al.,* 2014). The preceding K/Pg extinction event had led to the disappearance of most dinosaurs, including herbivores, and the loss favored vegetation build-ups. Although catastrophic for many species, the K/Pg event (66 million years ago) provided an opportunity for the evolution and diversification of mammals. First mammals had evolved 210 million years ago and were small size, nocturnal and mostly insectivorous. The empty niches left by the dinosaur extinction upheld the evolution of daytime mammal species of large body size and new digestive and dental systems, adapted to the consumption of cellulose, the main organic component of vegetables (Christensen, 2012). Millions of years later, after the last glaciation at the end of the Pleistocene (20,000 years ago), the extinction of large herbivorous mammals began. This extinction, fostered by a changing climate and an increasing hunting activity, reproduced the large accumulations of fuels, and the planetary fire regime was again modified (Pausas and Keeley, 2009).

Complementing the fossil carbon record, evolutionary biology demonstrates that many traits and strategies developed by plants are adaptive responses of tolerance or avoidance to the impacts of fire and herbivory and, in many cases, it is difficult to discern which has been the key driver at a particular stage of the evolution (Christensen, 1985; Briske and Hendrickson, 1998; Pausas *et al.*, 2016). Both disturbances, fire and herbivory, despite their very different nature, exert a strong regulation over the accumulations of plant biomass and, consequently, they are closely related. High levels of herbivory reduce plant biomass, limiting the size and intensity of the fires, and low herbivory increases the amount of plant material available for burning (Gil-Romera *et al*., 2014; Canals, 2016).

The domestication of some wild herbivores began in the Neolithic, 8500 years ago. The process of domestication was biased, since mostly affected a particular group of herbivores, the grass and roughage eaters. Hofmann (1989) classified world ruminants in three morphophysiological feeding types, concentrate selectors (40% of species), intermediate feeders (35% of species) and grass and roughage eaters (25% of species). The latter constitute large herds of animals with predictable movements (from winter to summer pastures and *vice versa*), that stay most of the time in open areas, and may be attracted (and caught) in recently burned areas due to the tender grass growing in (pyric herbivory, defined by Fuhlendorf *et al.,* 2009). Presumably, domestication of grass roughage eaters was easier compared to other types of herbivores (i.e. concentrate selectors or browsers such as red, fallow and roe deers, among others) whose populations remain undomesticated. In a few thousand years, the ancestors of the current sheep, cows (ruminant digestive system) and horses (caecal digestive system) -the eastern mouflon, the uro and the tarpan- were reduced or extinguished, and replaced in the landscape by herds of domesticated animals that carried out most of the herbivorism in open spaces.

At present, the extensive management of livestock is being replaced by an increasingly intensive system, less diversified in terms of species and breeds, in which animals remain stabled most of the time, with a null or low outdoor grazing. The lack of profitability of the extensive farming activity, and the occurrence of many socio-economic constraints, is leading to a sharp decrease of farms and livestock censuses in traditional, extensive livestock-risen areas, as illustrated in Figure 2 for the Pyrenean valley of Roncal.

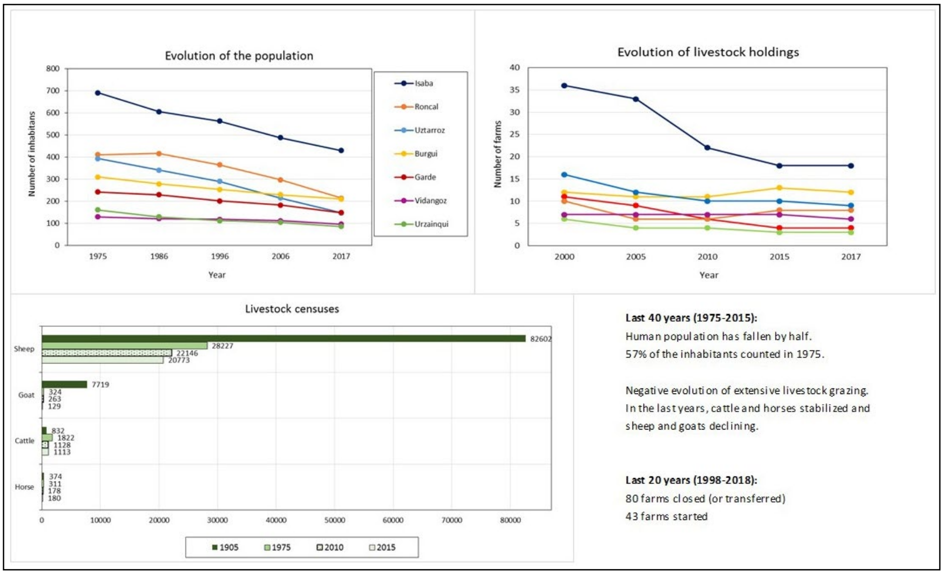

Figure 2. Evolution of human population, farms registrations and livestock censuses in Roncal valley (SW Pyrenees). The valley, constituted by seven municipalities, has been characterized by an ancient and intense use of upland grasslands by extensive livestock. The data showed can be generalized to other valleys of the massif. Source: Author compilation based on information supplied by Gobierno de Navarra, Junta del Valle de Roncal and Belardi consultoría.

4. Going onwards: Facing environmental preservation in a changing scenario

Mountain systems are particularly influenced by, and are very sensitive to the global change, which encompasses the change in the land use and in the climate (Pauchard *et al.*, 2009). Human depopulation and the abandonment of traditional uses in mountain areas of Europe is fostering a rapid shrub and tree encroachment (Davies *et al.,* 2008). In the Pyrenean range, landscape diversity is decreasing and forest connectivity increasing at the expense of open grassy areas (Garcia Ruiz *et al.,* 1996; Vicente-Serrano *et al.,* 2004; Komac *et al.*, 2013) (Fig. 3). In addition, climate change manifestS by a decrease of frost periods and a rise of temperatures, which extends the growing period and enhances the expansion of the treeline in altitude (Camarero and Gutiérrez, 2004). The combination of these processes leads to an accumulation of lignified biomass and involves crucial changes in the atmosphere-soil-plant interaction and the ecosystem function (Fig. 4), with important consequences for the provision of ecosystem services (some of them detailed in Table 2).

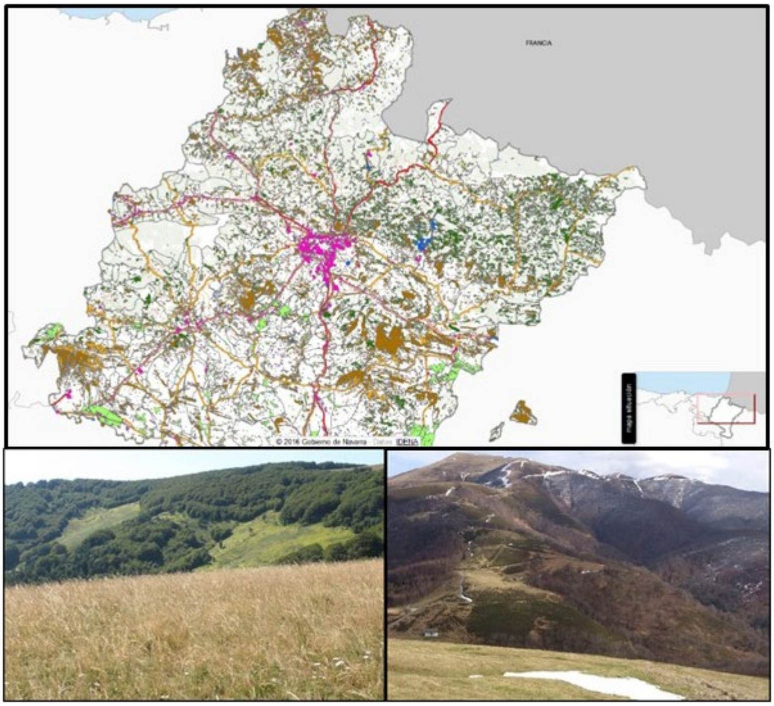

Figure 3. Cartography of land use changes in N Navarra county in the last 50 years (comparison of 1956 and 2008 flights). Dark green indicates forested surfaces developed from grasslands, shrublands and unproductive lands. Source: IDENA (Government of Navarre). Pictures below illustrate the processes of tree and shrub encroachment in open communities in Western Pyrenees (left side: Roncal valley; right side: Roncesvalles). Photographs of the author.

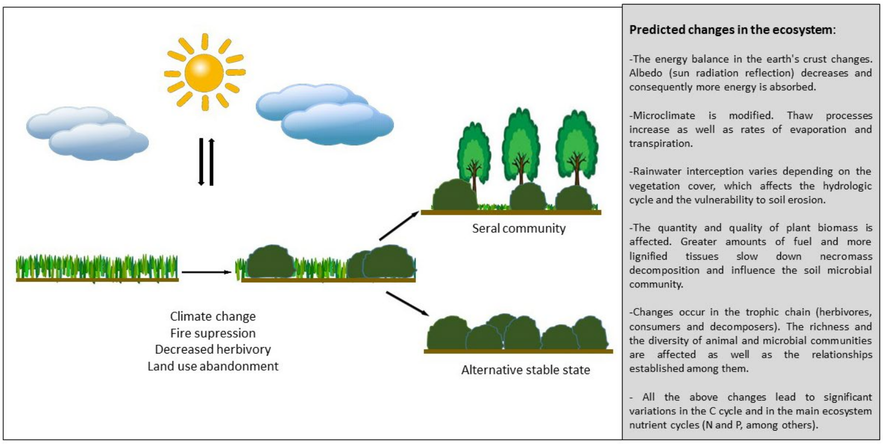

Figure 4. Factors promoting shrub encroachment and forest regeneration in mountains and predicted changes in ecosystem functions and soil-plant-atmosphere interactions. Adapted from Archer et al. *(2011).*

Table 2. Compilation of ecosystem services affected by the decrease and disappearance of open spaces in the natural environment.

Ecosystemic services negatively affected by the loss of open spaces and mosaic landscapes	
Biodiversity	Decrease of beta diversity (landscape level) due to the densification and homogenization of the vegetation. Loss of alpha diversity (community level) due to a decrease of plant and animal species from open habitats (Fuhlendorf *et al*., 2012).
Carbon sequestration	In forest stands there is a high carbon sequestration in the aboveground compartment but the risk of loss by catastrophic events is a great danger (wildfires). Wildfires may attain a high intensity in dense stands which may affect negatively the carbon compartment stored in the soil (Twidwell *et al.,* 2013).
Wildfire regime	High fire risk and greater probability of large wildfires due to 1) the accumulation of fuel, 2) the homogenization of the landscape and 3) the loss of accessibility for extinction tasks (Costa *et al.,* 2012).
Hydrological control and regulation	Outcome depends on local conditions. Forest expansion at higher altitudes may lead to earlier and faster thaws, which may originate more intense fluvial floods and affect negatively the discharge of high-mountain watersheds (Lopez-Moreno *et al.,* 2008; Lespinas *et al.,* 2010)
Food for herbivores	Less grazing surface for herbivores. Risk of disappearance of a primary sector linked to the natural environment and the sustainable use of its grazing resources (Lasanta *et al.,* 2015).

In terms of fire risk, global change is leading to a very critical situation (Bowman *et al.,* 2011). The fire regime –defined by the density (number of fires), the size (affected surface), the recurrence (return interval), the intensity (energy released), the duration, the seasonality and the severity (social, economic and environmental damages)– is undergoing intense changes, and wildfires tend to last longer, affect larger surfaces (even in cold and humid environments, Hochtl *et al.,* 2005; Valese *et al.,* 2014; Viedma *et al.*, 2015; Leys and Carcaillet, 2016) and cause more catastrophic effects than ever before (4th and 5th generation fires *sensu* Costa *et al.*, 2012). As a consequence, despite the high investments in extinction tasks and detection of fire outbreaks, an increasing number of fires become uncontrollable (Chuvieco *et al.,* 2008; San Miguel-Ayanz *et al.,* 2013). Climate changing towards warmer conditions and more unpredictable atmospheric phenomena, the accumulation of fuel biomass, the diversification of ignition sources and the increased urban-forest interface is leading to this dangerous state, which is one of the main challenges environmental management faces today (Catry *et al.,* 2010; Ganteaume *et al.*, 2013).

Although fire, like herbivory, has been a key natural agent in the generation of landscape, human growth in recent centuries has greatly altered its dynamics and behaviour patterns. Table 3 depicts the current trends of human development and their foreseeable effects in the fire regime. Both the human presence (diversified activities, urban-forest interface...) and its absence from previously inhabited habitats (rural depopulation...) may elicit deep changes in the fire regime.

Table 3. Current human influence in the natural regime of fires. Source: Adapted from Canals (2016). Both the existence of human activities and its abandonment lead to changes in the fire regime.

Increase of the fire regime	Decrease of the fire regime
Greater urban-forest interfaces (density of roads and forest tracks, residential states...) than ever before increase the risk of ignitions.	Fragmentation of the landscape may offer barriers and lead to a discontinuity of the fire.
Reduced herbivorism due to a decrease of domestic herbivores. Much lower censuses of extensive than intensive cattle ranging increase fuels build-up.	Concentration of extensive cattle in areas with livestock facilities (i.e. watering points) changes plant composition and reduces fuels build-up.
High recreational use of the forest and great risk of hazardous ignitions.	High chance of early detection of fire outbreaks due to the development of new technologies (drones...) and the surveillance of the forests.
Abandonment of agricultural lands. Landscape homogenization.	Soil tillage and establishment of crop rotations. Summer crops with high moisture contents.
The burning of stubbles and non-grazed biomass increase the risk of ignitions.	The burning of stubbles and non-grazed biomass decrease the amount of necromass accumulated in agricultural and natural areas.
Forest plantations with flammable and fast-growing tree species.	Forest harvesting and timber extraction.
Absence/decrease of traditional uses of the forest (firewood, coaling tasks...).	Development of new technologies for the use of forest biomass as a source of energy.
Absence/decrease of preventive forestry works due to the high labour costs.	Economic valorization of forest residues for energy purposes.
Climate change. Increase of heat waves and drought periods and decrease of innivation in mountains.	Climate change. Variability of the water regime, with a mean increase in rainfall in several regions.

Given the current situation and the natural history of our ecosystems, a profound reflection is necessary to undertake the task of preserving the inherited natural spaces. Some of the questions we need to ask are: What are the conservation objectives in a very dynamic landscape? Can we assume rewilding if original conditions (climatic and anthropogenic) have changed and a profound global adjustment is underway? And, essentially, are we aware about what a return to wilderness entails and do assume the risks associated with? Is it fair and makes sense rewilding a dynamic landscape without the existence of large herds of grass-roughage eaters (and their associated trophic chain) or without assuming wildfires as natural processes (which will affect valuable habitats, threatened wildlife and endanger people’s lives and properties)?

5. Conclusions and final remarks

To face the challenge of environmental preservation, an exhaustive knowledge of the factors that generated the historical landscape (its dynamics of succession and its natural regime of disturbances), and an awareness of the circumstances occurring in the last millennia and centuries (anthropization, global change), that affected the original conditions, have to be considered (Conedera *et al.*, 2009; Krebs *et al.*, 2010). At present, newly-coined and revisited terms come into view when planning the preservation of the inherited landscapes: close-to-nature management (CNS), emulation of natural disturbance regimes (ENDR), pyric herbivory, prescribed burnings… (Fuhlendorf *et al.*, 2009; Archer *et al.*, 2011; Brang *et al.*, 2014; Navarro *et al.*, 2015). In the light of these conceptions, that combine traditional and present knowledge to the objectives of conservation, different key ideas emerge to optimize the preservation of ecosystems, which are summarized below:

1. Since ecosystems are dynamic and evolve continuously, management measures must focus on the preservation of the processes. First and foremost, the ultimate goal of conservation is to guarantee the ecosystem's capability to evolve. This is a paradoxical idea given the prevailing, static perception of conservation (to keep something as it is or as it was in a particular moment).

2. The adaptive capacity of ecosystems should be promoted considering the current situation of uncertainty due to global change. Adaptive capacity depends on the resistance (ability to withstand alterations without significant changes in composition and structure) and the resilience to environmental changes (ability to recover from a disturbance, maintaining biodiversity and function) (Thompson, 2011). For this reason, it is crucial to safeguard the natural complexity of ecosystems (diversity of species and communities, diversity of functions, connectivity between habitats) to reduce their vulnerability (Lindner *et al.*, 2010).

3. Human pressure in Earth is high and will continue to be so. The preservation of the natural environment in inhabited regions has to face continuous conflicts of interests. Avoidance and intervention against natural disturbances if human goods and lives are at risk (i.e. wildfires, floodings…), social constraints (i.e. rural depopulation, social conflicts...) and economic issues (i.e. need of economic returns as a way of living, financial requirements) are important challenges to tackle with (Halme *et al.*, 2013).

4. Conservation practices, although nourished by external experiences, should be designed locally on the basis of the scientific and applied knowledge compiled. Although fire and grazing are key agents in most mountain landscapes, the historical regime of disturbances, the vegetation composition, the climate and the global change factors influencing are site-specific. Besides, the monitoring of the results is required to determine whether the measures applied are adequate or should be revised.

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