Chapter 2

Trade-offs in High Mountain Conservation

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Abstract High mountain ecosystems present features that determine their conservation: isolation, harsh environmental conditions and steep gradients. The vulnerability of ecological systems to disruptive agents can be addressed by considering exposure to these agents and the sensitivity of the system. Conservation management usually offsets trade-offs of resources allocated to minimise exposure with strategies designed to reduce sensitivity. Although exposure to human action may be reduced in high mountains by isolation, this effect is offset by disruptive agents operating at global or regional scales, such as pollution and climate change. In the long term, climate change can be expected to have a strong impact on alpine habitats, as the dispersal of their native species is severely constrained. Alternatively, high mountains may provide refuges for threatened species currently populating lower altitudes. When reducing exposure is not a feasible strategy, the alternative is to reduce sensitivity, which in high mountains would focus on improving connectivity, preserving habitat quality and controlling antagonistic interactions such as grazing. Lowering vulnerability to climate change requires interventions in various contributing drivers. Cost-effective models make help to optimise the outcome of different goals subject to trade-offs, and they can also be useful for allocating alternative actions over time. The application of ecological trade-off concepts helps to frame conservation from a functional perspective. This approach should also take into account the fact that the functional properties of ecological entities are multifactorial and interactive. This concept is recognised in ecosystem services that present negative correlations—trade-offs—as well as positive ones—synergies.

Keywords Climate change • Conservation • Ecosystem services • Ecosystem management • Exposure • High mountain • Sensitivity • Trade-off

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2.1 Introduction

Conservation involves the allocation of limited resources to actions aimed at preserving the diversity of natural heritage and the properties and functions of ecosystems, particularly if these actions are expected to provide outcomes beneficial to significant portions of human society (i.e. ecosystem services).

The managed subjects (belonging to different organisation levels: species, population, ecosystem) compete for the resources allocated to conservation. Furthermore, conservation strategies may differ according to whether they focus on minimising exposure to human-driven impact or on reducing the sensitivity of the exposed biological system. These two strategies thus also compete for conservation resources. This situation is made even more complex by the fact that conservation goals compete, in their turn, with other objectives of human societies closely related to economic well-being. Competition for shared resources between different functions, as exemplified by trade-offs, constitutes a basic principle of economics that is shared by ecological systems. Here I use a framework based on the ecological concept of trade-offs to analyse conservation issues relevant to high mountain ecosystems.

2.2 Distinctive Features of Conservation in High Mountain Ecosystems

High mountain ecosystems present several distinctive ecological features that have important consequences for conservation (Beniston 2003) (Fig. 2.1). First, they experience a remarkable degree of isolation, due to their topographic location and the presence of summits which limit both biotic flux and human access. While genetic and demographic flux is restricted in mountain populations, the latter also

Fig. 2.1 Ecological characteristics of high mountain ecosystems (grey boxes) and their effects on components of vulnerability (exposure, sensitivity). Solid and broken arrows indicate negative and positive consequences for conservation, respectively (see text). Arrow body shows relevance of the relationship

benefit from greater protection from pathogens, pests and widespread disturbances than populations in well-connected areas. However, this isolation is not sufficient to protect them from global processes such as climate change and pollution, as these are transmitted through the atmosphere. Significantly, high mountains are usually situated in sparsely populated areas, due to their low accessibility, in contrast with lowlands and coastal areas, where the most human population is concentrated, all over the world. The human-driven impact on high mountain areas is, therefore, lower in comparison with these densely populated regions. Nevertheless, historically human presence has played an important role in configuring mountain ecosystems. For instance, in the Alps and Pyrenees, human activity has been regularly recorded since Neolithic times (Tinner et al. 2005; Gassiot Ballbè et al. 2017), and it has profoundly modified the landscape over the last centuries (Colombaroli et al. 2010; Pélachs et al. 2017). Isolation and low population density also provide high mountains with emotional and aesthetic values that are often idealised. These habitats commonly play host to sanctuaries, or an entire mountain system can be seen as a sanctuary in itself. This perception coincides with the concept of preservation and may contribute to the conservation of natural systems. Interestingly, low accessibility may imply fewer resources for conservation. On the other hand, these remote areas may experience looser control by centres of decision over the conservation practices carried out there.

Second, high mountain habitats provide harsh living conditions. The altitudinal gradient implies a decrease in temperature and a prolonged duration of snow cover, which combine to shorten the periods of growth. Moreover, strong winds, low water availability at high altitudes and the scanty soil development associated with steep slopes and erosion result, overall, in a pronounced abiotic stress. In consequence, vegetation cover is reduced, leading to mutually reinforcing feedback (for instance, between vegetation cover, water retention and soil erosion). Also, high altitude favours the passage of pollutants from the troposphere to the ground (Camarero 2017b) and a loss of atmospheric protection against ionising radiation. Therefore, only relatively few species are able to persist in these extreme conditions. These species typically present low growth rates and life cycles adapted to the short duration of favourable conditions (Laiolo and Obeso 2017). The environmental conditions specific to high mountains, along with their geographic isolation, have forged an adaptive landscape that has shaped the characteristic functional and compositional traits of its biota. Another consequence is a noticeable fragility in these ecosystems, as the resident species are often pushed to their limits of eco-physiological tolerance. Nevertheless, selective pressure may have favoured adaption to these environments. Simultaneously, species tolerant of a broad range of conditions are often found here, far from the competition withstood by other species. Also, importantly, low growth rates and short periods of growth limit population recovery after disturbances or harsh environmental conditions, thus reducing resilience.

Another characteristic of high mountain ecosystems is that they tend to exhibit steep environmental gradients over relatively short distances. These gradients are largely determined by topography and aspect, which determine the radiation

balance and the hydrological system, including water run-off and freshwater courses and reservoirs. Moreover, poorly structured soils make these gradients more dependent on the chemical and physical properties of bedrock, thereby enhancing the role of this source of environmental heterogeneity. Overall, high mountains tend to offer significant environmental heterogeneity (i.e. microhabitats) in combination with strong seasonal fluctuations. In fact, to some extent this heterogeneity associated with steep gradients counterbalances isolation, favouring the existence of altitudinal corridors and stepping stone routes that allow dispersal. The result is that we expect relatively low levels of biodiversity, although this is highly idiosyncratic and has a substantial spatial turnover.

All three ecological characteristics (isolation, harsh environment, steep environmental gradients) are the consequences of mountain topography and they interact mutually. Strong environmental changes over small distances, together with harsh abiotic conditions, may constrain a population's expansion by limiting its size, but they may also permit effective dispersal by saving relatively close barriers or allow populations to migrate across the altitudinal range in search of suitable conditions. Harsh conditions, in their turn, are a major component of pronounced gradients—in fact, mountains tend to correspond to the extremes of many abiotic gradients at the regional level—and they contribute to isolation (Fig. 2.1).

2.3 Conservation, Vulnerability and Trade-offs

One major goal of conservation is to deal with the vulnerability of natural systems (species, populations, habitats, ecosystems) in the face of risks associated with human activity, by maintaining or increasing the values related to the persistent functioning of such systems. The concept of vulnerability may be approached from different perspectives; in the ecological context, and particularly when assessing climate change vulnerability is defined as the degree to which a system is able to cope with adverse effects, being a function of (1) the exposure of the system in question to agents that can potentially diminish these values, (2) the system's sensitivity to subsequent changes, and (3) its eventual resilience or adaptability to the new context (Turner et al. 2003; Parry et al. 2007; Chapin et al. 2010). Let us concentrate on the two first components, exposure and sensitivity, which are affected by the immediate impact of environmental hazards: any situation involving an increase in exposure or sensitivity will result in greater vulnerability and should thus require conservation action. Similarly, conservation management could maintain a given degree of vulnerability by reducing exposure when sensitivity is increased (e.g. because populations become too small). Therefore, as a first approach vulnerability would result from the product of exposure and sensitivity. Given that vulnerability is defined in relation to a disruptive agent, if no such agent exists, exposure and vulnerability equal zero.

The ecological characteristics of high mountain ecosystems have different consequences on vulnerability (Fig. 2.1). Isolation reduces exposure to human

intervention and the resulting loss of habitat and alteration of biogeochemical cycles, including those caused by local pollution. In contrast, environmental harshness explains the high sensitivity of these systems, particularly their difficulties in recovering from disturbances. In fact, this high sensitivity is reinforced by isolation, due to the limitations imposed on genetic and demographic flux through dispersal, and by the resulting small populations. Furthermore, steep gradients contribute to small population size as the habitat area is limited. In contrast, isolation can diminish exposure to deleterious biotic agents—pests, pathogens—at the landscape scale, although the high heterogeneity promoted by steep gradients may favour the dispersal of these agents. The spread of other disturbances, such as wildfires, can also be constrained by the low degree of connectivity, although rough topography may also enhance the propagation of fire uphill.

The concept of ecological trade-offs provides a useful framework for understanding and designing the allocation of resources devoted to conservation goals, such as the management of exposure and vulnerability. In organisms, the allocation of limited resources to different purposes or functions implies a negative relationship between these resources. However, the configuration of this relationship is not an easy task, first because it is essential to establish a common currency that accounts for the various functions (Reekie and Bazzaz 1987). A negative correlation between estimators of different functional properties is not in itself a proof of trade-off unless the mechanisms connecting functional properties can be properly determined and converted to this common currency. Another key issue is the fact that these functions are essential for the overall persistence of the system in question, which in its original ecological sense corresponds to organisms. Consequently, the product of the estimators of the different functions, after conversion to a common currency (e.g. biomass), should be a constant other than zero, as a zero value would mean that the system does not exist. One typical case of ecological trade-off describes the allocation of resources to seed production in plants (Harper et al. 1970). Assuming a constant amount of resources allocated to each seed set, seed size and seed number reveal different functions: small seed size and a large number of seeds would optimise dispersal, while large seed size—in detriment to number—would favour seedling survival. Obviously, the reality is much more complex since small seed size may contribute to other functions, such as minimising genotype losses by predation. Alternatively, a given function usually determines the involvement of different resources, generating a complex network of interacting functions and resources that are used to different degrees.

Conservation practice can be considered as analogous to the allocation of limited resources, and trade-offs would correspond to different management actions. While natural selection would be the main driver of resource allocation at the species level, in conservation this role would be performed by environmental managers involved in decision-making processes. Conservation has an economic component associated with the allocation of limited funding to different goals (i.e. economic trade-off). But this funding allocation is intrinsically associated with ecological properties, which are also subjected to trade-offs.

2.4 Conservation Management of Exposure and Sensitivity in High Mountains

According to the application of trade-off principles to conservation management, resources allocated to a reduction in the exposure of conserved systems would often be detrimental to those assigned to decreasing sensitivity (Fig. 2.2). The conservation of endangered species, such as grizzly and brown bears in mountain areas, illustrates the application of these principles (Martin et al. 2012; Braid and Nielsen 2015). The presence of these species in a landscape reflects a trade-off between food resources and human presence, which roughly correspond to the components of these species' vulnerability—sensitivity and exposure, respectively—in the territory. GIS techniques allow these properties of habitat quality and exposure to disturbance to be combined in spatially explicit contexts to determine areas of prioritised use at the regional level (e.g. road development or habitat restoration) (Braid and Nielsen 2015) (Fig. 2.3a). Such analyses can achieve a notable degree of detail when existing populations are recorded. They can, therefore, support conservation management by promoting the use of attractive sink-like habitats (with good food quality but also proximity to human structures) that connect segmented populations, provided disturbances of human origin are actively curtailed (i.e. reducing exposure). In contrast, in areas that are attractive sink-like habitats but are located far from pre-existing populations, the vulnerability of the brown bear may be reduced by discouraging bears to use these habitats (e.g. by allowing forest logging, building electrified barriers near potential food resources or minimising rubbish). Similarly, refuge habitats (with poor food quality but far from human exposure) can be managed to decrease the sensitivity of their populations by

Fig. 2.2 Trade-off between conservation resources allocated to manage the two components of ecological vulnerability (exposure, sensitivity) by reducing human frequentation or enhancing ecological integrity

Fig. 2.3 Different cases of trade-off applied to conservation. **a** Maps of sensitivity ((a) habitat productivity) confronted to exposure ((b) road-based mortality risk) to identify sink (c) and refuge areas (d) for bear populations in Alberta, Canada (Braid and Nielsen 2015). **b** Solution for a reserve model considering the trade-off between owl populations (x-axis) and timber harvest (y-axis) (CM, current management scenario) in Oregon, USA (Nalle et al. 2004). **c** Trade-off among provisioning service (meat) and regulating services (carbon sequestration and water conservation) in alpine grasslands of Tibet, China (Pan et al. 2014). **d** Maps of modelled outputs of fire management considering a trade-off between fuel reduction by prescribed fires and limited resources: expected tree density (A) fire intensity (flame height) (B), and predictions after wildfire with and without previous fuel reduction treatments (Ager et al. 2013)

Fig. 2.3 (continued)

favouring the production of resources (e.g. by increasing forest hard mast species) (Martin et al. 2012). Because these actions involve spending money, a rationale based on using GIS, models and simulations to identify the distribution of trade-offs over space and time becomes a powerful tool for managers. These models may also incorporate the shifting balance of the trade-offs between services provided at the landscape level, such as food supply and shelter for vertebrates, over the course of seasons and life stages (May et al. 2010).

In general, the reduction of exposure in protected areas is a more common practice than the reduction of sensitivity. One major reason for this is the fact that it is easier and more operative to regulate on a territorial basis, for instance by controlling access, than to intervene in ecosystems and populations, where accurate knowledge of their functioning is often lacking. This strategy is particularly appropriate in high mountain areas due to their low accessibility for humans, which makes it possible to effectively control use by visitors and locals. Another example of exposure reduction is the control of exotic species by minimising their presence through limitations on their introduction and reinforcement of their eradication.

disturbances and pollution) that threaten natural systems, in concordance with the desire of societies to preserve their collective memory of natural heritage. This passive attitude to conservation is challenged by strategies focused on adaptive conservation that take the insufficiency of our current knowledge as the starting point for the development of more effective practices (Holling 1978; Armitage et al. 2008). Exposure reduction may obtain remarkable results at a local scale, particularly in the face of changes in land use, which represent a major threat to high mountain ecosystems (Theurillat and Guisan 2001; Spehn et al. 2006), but it clearly proves inefficient against exposure to agents that operate at global or regional levels, such as pollution and climate change. The capacity of local managers to reduce exposure to these agents is very limited. For instance, high mountain lakes are particularly exposed to airborne chemical loadings (see Camarero 2017b), and in this case reducing the sensitivity of these ecosystems involves the preservation of biodiversity and food webs (Ventura et al. 2017).

High mountain areas are particularly exposed to climate change due to their position at the extreme of regional climatic gradients. Accordingly, at the global scale, vulnerability to the vegetation shifts associated with climate change is considered particularly high in alpine biomes (Gonzalez et al. 2010). Isolation and habitat specialism contribute to this vulnerability (La Sorte and Jetz 2010). In Europe, alpine and Mediterranean mountain environments are projected to decline dramatically in comparison with other climatically defined environments (Metzger et al. 2008). Thus, we expect a significant loss of habitat for many plant species particularly as a result of decreased precipitation (Engler et al. 2011). This loss of habitat may not be exclusively due to a decline in a species' climatic suitability, but rather to the improvement in conditions for species such as trees, which can modify the habitat and competitively exclude current populations of high mountain specialists (Dirnböck et al. 2011). Nevertheless, at the species level, at least until now in Europe, mountain areas seem to exhibit a substantial inertia in the face of modifications to biodiversity caused by climate change (Theurillat and Guisan 2001). In fact, mountains may constitute a shelter for many species on account of their topographic characteristics, which provide altitudinal corridors (Loarie et al. 2009). Furthermore, high mountains may become a refuge for species threatened by global changes in their current distribution at lower altitudes (Sergio and Pedrini 2007), thereby emphasising the importance of preserving large-scale elevation gradients (Moritz et al. 2008).

Given local managers' inability to directly influence climatic trends, conservation trade-offs should focus on reducing sensitivity to climate change, in many cases by acting on co-drivers that produce deleterious synergies in combination with climate change (Hulme 2005; Mawdsley et al. 2009), or alternatively by enhancing mechanisms of stabilisation and resilience (Lloret et al. 2012). Nowadays, this strategy of reducing sensitivity to climate change has established a place on agendas for conservation. This issue is becoming particularly relevant and challenging in high mountain ecosystems, due to the harshness and distinctiveness of their habitats, but also due to the frequent involvement of small populations that have experienced directional selection for generations. Specifically, management focused

on reducing sensitivity should consider connectivity and genetic flux (Moritz et al. 2008), preservation of microhabitat quality (Marini et al. 2011) and control of grazing (Nagy and Grabherr 2009). Similarly, reductions in the risk of disturbance may favour the preservation of habitats and small populations against the adverse effects of climate change (Millar et al. 2007). In fact, the management of sensitivity often comes to focus on population-level processes involving the enhancement of genetic variability (Maudet et al. 2002) and population size, as well as the control of antagonists (predators, pathogens, pests, parasites) (McKinney et al. 2009). Nevertheless, some of these actions may in themselves involve trade-offs: for instance, disturbance often contributes to species co-existence, giving rise to a complex picture that we shall discuss below.

Forest die-off clearly illustrates the difficulties in managing ecosystems, even locally, when the major threats are global. Forest die-off accompanied by tree mortality is increasingly being reported in many biomes across the world, including mountain areas of North and South America and Europe (Suarez et al. 2004; Bigler et al. 2006; van Mantgem et al. 2009; Allen et al. 2010; Smith et al. 2015) (see also Camarero 2017a). Many factors, such as the capacity of soils to store water, antagonistic biotic interactions and stand structure can significantly contribute to this phenomenon (Raffa et al. 2008; Galiano et al. 2010; Bell et al. 2014). In many cases climate, and more particularly drought and heat episodes, is closely associated with this decline (Suarez et al. 2004; Bigler et al. 2006; Allen et al. 2010, 2015; Anderegg et al. 2013; Williams et al. 2012; Smith et al. 2015). Importantly, the trend towards warming is increasingly accompanied by climatic variability, which results in pulses of extreme weather. This feature reveals a major component of the new abiotic environment of the next future (Easterling et al. 2000). Reducing exposure to this global threat is thus far beyond the scope of local managers. However, they probably can reduce forest's vulnerability to drought by acting on drivers that amplify tree mortality. In such forests, the vulnerability could be decreased by controlling antagonists (Sturrock et al. 2011) or by managing forest composition and structure (Grant et al. 2013). However, these practices, although common in forests managed for commercial purposes, could clash with the criteria for intervention in preserved areas. This conflict is particularly acute when adaptive management, which involves learning from experimental settings, is proposed as a rational alternative for improving the future health of forests (Millar et al. 2007). This controversy can only be solved by a straightforward definition and prioritisation of conservation goals by social agents. The transcendental values of forests as sanctuaries or social icons can support the effort to identify these goals and formulate specific local decisions. In any case, even in today's humid mountains in temperate regions, managers will probably have to come to terms with the management of water availability in the near future (Grant et al. 2013).

These reinforcing co-drivers may interact with climate and with each other in complex ways involving feedbacks (either positive or negative) and trade-offs (McDowell et al. 2011; Jactel et al. 2012). For instance, Scots pine is experiencing high mortality rates in some mountain areas in the Pyrenees due to a combination of increasing drought, poorly developed soils and mistletoe infestation

(Galiano et al. 2010). Stand density also appears to be a contributing factor since competition for scarce water is to be expected. Moreover, bark beetle proliferation, a common driver of conifer mortality in association with drought, has been detected in damaged Scots pine stands in the Alps (Dobbertin et al. 2007) and it is one of the main causes of forest dieback in Western North America (Hart et al. 2014). A parallel die-off is occurring in silver fir forest in the Pyrenees, associated with logging in the past (Camarero et al. 2011; Camarero 2017a). The primary or contributing role of pests and pathogens versus drought is also often hard to elucidate, as they can establish mutually reinforcing feedback (Hart et al. 2014; Oliva et al. 2014). Such multiple interactions between factors that contribute to the decline of forests are common in many mountain areas of the world and must be taken into account by conservation managers in the new climatic scenarios (Allen et al. 2015).

2.5 Managing Conflicting Goals

The allocation of resources to competing goals represents a clear example of the application of trade-offs to conservation issues. The paradigmatic case involves the economic benefits obtained from the harvesting of natural resources, which in the mountains usually correspond to timber, grass and fish, versus values associated with biodiversity, often exemplified by key or charismatic species, by species diversity or by ecosystem functioning. This approach, which can be spatially and temporally explicit, makes it possible to develop cost-effective models that optimise the outcome of different goals subject to trade-offs, after combining functions that share a common currency (e.g. economic value). These models have, for instance, been widely used to assess wildlife and timber production in mountain forest regions (Nalle et al. 2004) (Fig. 2.3b), and to assess the relationship between forage production and the abundance of particular plant species that denote environmental quality in mountain grasslands (Loucougaray et al. 2015). Another case is the trade-off between the financial income produced by the introduction of non-native fish to lakes and streams and the environmental costs (Ventura et al. 2017); in this case, the focal entity corresponds to the whole watershed ecosystem. These cost-effective models also allow us to simulate outcomes by applying alternative management actions at different times—i.e. spreading the investment of resources over time (Lampert et al. 2014). Nevertheless, one major challenge for such quantitative analyses is the parameterisation of the current common currency for the various alternative management actions.

Although functions subject to trade-off show a negative relationship of their estimators, not all negative correlations are the result of resource allocation for the overall maintenance of a system. Recent changes in land use in European mountain areas (Pèlachs et al. 2017), provide an interesting case for illustrating the complexity of this approach. In these areas, the human-induced transformation of the landscape has led to the loss of most woodland while agricultural and grazing areas have increased. Since the mid-twentieth century, however, significant depopulation

resulting from profound socio-economic transformations is fomenting substantial afforestation (Roura-Pascual et al. 2005; MacNeill 2003; Lasanta-Martínez et al. 2005). This afforestation, in turn, results in loss of the grasslands and open habitats that play host to major elements of biodiversity. Managers can consider taking actions focused on enhancing some of these habitats: this situation could be interpreted as a trade-off. In these cases, the surface area occupied by different human activities—commercial exploitation, provisioning and regulation services, biodiversity conservation—represents a limiting resource that is likely to be promoted by management decisions. A negative correlation between different uses just reflects, however, that their sum, rather than their product, is constant (i.e. the whole territory), without any particular functional meaning. In contrast with an organism that requires different essential functions that compete for resources to persist, a territory will remain over time, regardless of whatever land cover it may support. For a proper application of the trade-off concept, the abundance of a given land use should be associated with any functional property of an upscaled, comprehensive ecological system. We can establish trade-offs between different land uses if they correspond to different conflicting benefits: for example, logging in forest areas—with direct financial revenues—as opposed to the preservation of open habitats for some species—a conservation goal. Similarly, different land uses may be associated with distinct components of the species' niche, such as foraging in open areas and refuge in forest lands (May et al. 2010; Martin et al. 2012). This concept is important because it highlights the fact that the conservation of ecological processes is not based solely on the patterns of abundance of categorical entities (species, land uses) but also on the functional properties with which they are associated. The application of the ecological trade-off concept to conservation issues helps to frame this functional perspective.

Alternatively, conservation can prioritise some categories (forests or open land, particular species) irrespective of their functional properties but according to social preferences, including rarity or aesthetic and iconic perceptions. This conservation approach is based more on heritage preservation than on functionality or market utility. Heritage diversity is high in mountain areas, given the particularities of these environments and the associated evolutionary processes that are enhanced by isolation. The heritage perspective of conservation can easily lead to efforts to increase species or habitats, especially if these have some distinctive value. So, in the face of the dilemmas arising from the allocation of different land uses in a territory, the obvious solution is to increase the total protected area, following a strategy of accumulating heritage. According to this approach, the goal will be to include the smallest surface of each land use that provides a plateau of diversity, according to the asymptotic relationship between diversity and area. Alternatively, if the territory's area is limited, one preliminary solution would be to find the optimal combination of the land use surfaces—according to the same asymptotic relationships for each land use—and then consider those elements (species or habitats) that are common to the different uses. Obviously, the procedure becomes much more complicated when the relationship between diversity and area is dependent on the spatial context, i.e. influenced by the proximity of other land uses (Bennett et al. 2006).

This approach, based on the complementarity of territories for determining total diversity, concurs with “gap analysis” techniques, which have been effectively developed in conservation practice (Flather et al. 1997). An important issue is that apart from the intrinsic value of biodiversity, the contribution of diversity to ecosystem functioning—productivity, water, C and nutrient cycling—should also be strongly emphasised, particularly because of its contribution to stability and resilience (Hooper et al. 2005).

2.6 Complex/Interacting Controls of Trade-offs

The functional properties of any ecological entity are multifactorial, and they often interact. At the ecosystem level, conservation benefits from a framework that recognises multiple services, which are equivalent to functional ecosystem properties that are relevant to humans. Ecosystem services are subjected to resource allocation, and consequently, the trade-off approach can be applied, as far as human societies invest distinctly in different ecosystem types or promote some functional properties of ecosystems. In fact, conflicts between provisioning and regulating services are common (Bennet et al. 2009), and they can be considered as trade-offs provided a common currency is regarded. Often the outcome of these services roughly corresponds to land use categories, considering the explicit spatial distribution of their properties in the territory, which in mountain regions correlates to topography and distance from settlements and roads (Grêt-Regamey et al. 2008; Paletto et al. 2015). Services that are typically provided by mountain ecosystems include revenues from forests, grasslands or watersheds, protection against natural hazards and outdoor recreation (Paletto et al. 2015; Vacchiano et al. 2015; Ventura et al. 2017) (Table 2.1).

Tourism and leisure constitute one of the most important economic activities in the mountain areas of developed countries. Despite its impact on habitats and water resources (Nagy and Grabherr 2009), this activity can potentially generate strong synergies with conservation goals. The economic value of these uses can be relatively easy to quantify in terms of consumption and investment (Paletto et al. 2015). The contribution of natural systems favouring such activity can also be estimated by various indirect methods for evaluating preferences (Grêt-Regamey et al. 2008), or from indicators of aesthetic value, (f.e. changes in the colour diversity of grasslands, Loucougaray et al. 2015). Nevertheless, the current state of uncertainty about the quantification of ecosystem services is particularly marked in high mountain regions (Grêt-Regamey et al. 2008).

The multiplicity of ecosystem services illustrates the potential existence of multiple trade-offs operating on a given ecological entity. Furthermore, a parameter used to estimate a given functional property may, in fact, respond to several functional processes. Multiple trade-offs may be explored by correlation matrix between services, highlighting the consistency of negative correlations. In contrast, positive correlations would indicate synergies between services (e.g. Raudsepp-Hearne et al. 2010).

Table 2.1 The relative contribution of high mountains to ecosystem services (agents providing the service are shown in *italics*), indicating potential trade-offs (negative correlations) and synergies (positive correlations)

	Contribution	Trade-offs	Synergies
Provisioning services			
Food	Moderate	Raw materials, biodiversity services	Freshwater, biodiversity services
<i>Livestock, berries, mushrooms, hunting, wildlife, fish</i>			
Raw materials	Moderate	Freshwater, carbon storage, soil protection, biodiversity services, cultural services	
<i>Timber, fuelwood, hay, plant oils</i>			
Freshwater	High	Tourism	Wastewater treatment, biodiversity services, cultural services
<i>Snowpack, springs, rivers</i>			
Medicinal resources	Moderate	Biodiversity services	Cultural services
<i>Plants</i>			
Regulating services			
Local climate and air quality	Moderate		Carbon storage, biodiversity services, cultural services
<i>Forests</i>			
Carbon storage and sequestration	Moderate	Habitat for species	Soil protection
<i>Forests, soils</i>			
Moderation of extreme events	High	Habitat for species	Provisioning services, soil protection, biodiversity services, cultural services
<i>Avalanches, landslides, floods</i>			
Wastewater treatment	Low		Soil protection, biodiversity services, cultural services
<i>Wetlands</i>			
Soil protection and erosion protection	High		Biodiversity services, cultural services
<i>Soil integrity</i>			
Pollination	Low		Biodiversity services
<i>Insect biodiversity</i>			
Biological control	Low	Species and genetics diversity	Biodiversity services, recreation, tourism

(continued)

Table 2.1 (continued)

	Contribution	Trade-offs	Synergies
<i>Food webs</i>			
Biodiversity services			
Habitat for species	High	Species and genetics diversity	Species and genetics diversity, cultural services
<i>Refuges, corridors, buffers</i>			
Maintenance of species and genetic diversity	High		
<i>Species, genotypes, food webs, interaction networks</i>			
Cultural services			
Recreation and health	High	Tourism	Tourism, aesthetic appreciation, spiritual experience
<i>Hiking, picnicking, sailing</i>			
Tourism	High	Aesthetic appreciation, spiritual experience	Aesthetic appreciation, spiritual experience
<i>Skying, resorts, alpinism, trekking, hunting, fishing</i>			
Aesthetic appreciation	High		Spiritual experience
Spiritual experience	High		

Note that some services may present both trade-offs and synergies with other services depending on the intensity and characteristics of the involved processes (f.i., overgrazing often causes soil erosion while moderate grazing can promote biodiversity). Trade-offs and synergies between services are only indicated in the service appearing first in the list

For instance, in alpine grasslands, livestock provisioning services represent a trade-off with regulatory services provided by NPP, which in turn determines carbon sequestration and water and soil conservation (Pan et al. 2014; Fig. 2.3c). While trade-offs between services lead to cost-effective analyses, synergies between them represent reinforcing mechanisms that make it possible to save resources or focus investment on obtaining multiple benefits.

Another source of complexity comes from the fact that the outcomes of ecosystem services may depend on previous management. For instance, land use transformation in Andean mountains over the past decades has led to the loss of ecosystem services, due to the conversion of cloud forests and paramo grasslands in the alpine and sub-alpine stages to agricultural use; later, pine plantations were developed on open alpine grasslands and agricultural land. While pine plantations produce an adverse impact through reducing the area previously occupied by native alpine grasslands, they can improve ecosystem services when they occupy land that had been previously degraded by agriculture (Balthazar et al. 2015).

Fire management is a complex management goal that involves several of these issues: synergies between management options, interacting agents and time lags. Although weather conditions and a low fuel load overall constrain wildfires in high mountain ecosystems, their incidence is far from negligible. They can lead to the lowering of the treeline (Nagy and Grabherr 2009) and constitute a natural disturbance in the conifer forests of the mountains of western North America (Sibold et al. 2006), where fire regime has been heavily altered by active fire suppression policies over the past century (Donovan and Brown 2007). In fact, in many of the world's mountain regions, the fire has been used as a major management tool to foment grasslands, eventually determining ecotones (Nagy and Grabherr 2009). In recent decades, the loss of local population in mountain areas, at least in developed countries, is leading to encroachment onto former grasslands, and the consequences on biodiversity and ecosystem functioning have yet to be fully explored (Roura-Pascual et al. 2005; Brandt et al. 2013; Formica et al. 2014).

Fire management, and particularly fire suppression, consumes a large proportion of the resources devoted to forest management in countries with a high climatic fire risk, dense populations in the wildland–urban interface or substantial forest revenues. Fire management is therefore suited to an analysis based on trade-offs. Both actions aiming to reduce ignition—i.e. public information, regulation of access to forests, lighting restrictions—and to suppress fires share the goal of minimising burned areas. A cost-efficiency analysis in both the ecological and social contexts may help to optimise the contribution of each different action to the common goal. Paradoxically, however, the reduction of burned surface area implies further development of vegetation and subsequently the accumulation of fuel for the future, which will likely produce more intense and extensive fires (Donovan and Brown 2007; Lloret et al. 2009; Loepfe et al. 2012, but see Odion et al. 2004). This situation illustrates the temporal dimension of conservation practices and how they modify the future environment. It also reveals the existence of feedbacks regulating ecological systems; in this case vegetation growth and wildfires are mutually regulated by negative feedback. Fire suppression policies may lead the system to a structure of fire sizes that tends to be less equitable, with many small fires—which are rapidly extinguished—and very few extremely large ones, although these are usually very intense (Lloret et al. 2009). In terms of ecological trade-offs, and in the context of prolonged periods, investment in a reduction to fire exposure—limitations on lightning and fire propagation caused by humans—corresponds with increasing future fire sensitivity—associated with more intense and severe fires—. Assuming that management resources are limited, if one major goal is the minimisation of megafires of extreme extension and intensity, a strict fire extinction policy is not in itself the best long-term solution, and it may have strong consequences for the long-term structural and functional properties of ecosystems (Donovan and Brown 2007). Given that fire extinction is mandatory in some areas close to populated areas or installations, and in areas with specific conservation values, explicit geographical models can be developed to establish areas in which fuel load accumulation resulting from fire suppression should be counterbalanced by mechanical fuel reduction or by restoring

(i.e. prescribed) fire (Ager et al. 2013) (Fig. 2.3d). In many cases, the cost of mechanical fuel reduction is high and may imply a loss of commercial revenues—which can be compensated to some extent by biofuel production—or C stocks. In populated areas, these actions, therefore, tend to be concentrated in restricted, sensitive areas, often close to the wildland–urban interface (Driscoll et al. 2016). Consequently, the true trade-off regarding economic cost corresponds to fire suppression versus fuel reduction options, and the challenge is to optimise the respective actions through territory and time.

In addition to the fire–vegetation feedback, a fire-driven system is also controlled by the ambivalent effect of weather, since high temperatures and low humidity favour the ignition and propagation of fires. However, when these conditions continue over time they result in chronic drought—as in arid climates—and reduced fuel load (Loepfe et al. 2014). The increase in dry fuel after extreme drought episodes that exacerbate vegetation mortality can be considered transitory in the context of an overall fire regime, although it does represent a temporary window of opportunity for wildfires (Allen 2007). Thus, as in other ecosystems, the occurrence and severity of wildfires in mountain forests respond to a network of historical interactions involving climate, previous fires, management and other disturbances (e.g. insect outbreaks) (Bigler et al. 2005). Accordingly, a fire regime and its distribution in a landscape can be analysed by spatially explicit simulation models that include the characteristics of vegetation and management (Schumacher and Bugmann 2006; Loepfe et al. 2012). The empirical analysis of fire distribution at a regional scale reveals that in drier regions wildfires are controlled by fuel load availability, while in moist regions fire is determined by the occurrence of extreme dry periods (Loepfe et al. 2014). Therefore, the fuel vs. climate control of a fire regime can change over time, while the fuel load accumulates and climate changes (Kloster et al. 2012). In periods in which logging is intense or agricultural activity predominates, wildfires will mainly be determined by the local accumulation of fuel load; in contrast, when afforestation dominates a landscape, the limiting factors would be weather and drought (Pausas and Fernández-Muñoz 2012). In high mountains, these dynamics would often correspond to pastures and encroachment, respectively, but they have traditionally been disrupted by humans who have widely used wildfire to favour grazing (MacNeill 2003; Colombaroli et al. 2010). Thus, conservation in high mountains should come to terms with fire management, particularly because fire climatic risk is expected to increase in many regions (Moriondo et al. 2006). In addition to the financial component of the trade-off between fire suppression and fuel reduction, conservation in these areas should incorporate analysis of the trade-offs and synergies between biodiversity values and ecosystem services associated with a fire regime in terms of species composition, soil and vegetation, C stocks and erosion (García-Pausas et al. 2017). For instance, while C stock and erosion losses respond similarly to wildfires, species diversity may be favoured by moderately frequent fires (Coop et al. 2010).

2.7 General Concluding Remarks

Conservation practice involves making decisions with only a limited knowledge of complex systems, uncertainty about the future and scarcity of resources. Management decisions often reflect opportunistic reactions to urgent problems or, alternatively, routines followed without any regular evaluation or updating. I advocate that these actions will gain in consistency and effectiveness if they are designed and put into practice within a rational framework based on resource allocation, in accordance with the functional outcomes of the alternative management options that affect an integrated ecological or social entity. The application of this approach to conservation in high mountain ecosystems should take into account their particular characteristics of isolation, environmental harshness and steep gradients. Generally speaking, the minimisation of exposure to detrimental anthropogenic agents can be enhanced by the isolation of these habitats, but the latter can become particularly sensitive due to their limited extension and their legacy of selection for specific, extreme conditions. This general approach, exemplified by the concept of ecological trade-offs and associated with basic economic principles, can be developed and modelled for any specific case, incorporating the complex interactions between ecological processes and social agents, as well as the temporal dimension that takes into account both the legacy of the past and future scenarios.

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