



Review

## Exotic herbivores as drivers of plant invasion and switch to ecosystem alternative states

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### Abstract

This paper discusses the evidence of the way in which coupled herbivore and plant invasions altered the structure and functioning of ecosystems in central Chile, and compares these patterns to results from other Mediterranean ecosystems around the world. In pre-Columbian times, sclerophyllous 'matorral' forests largely covered mediterranean Chile. Remnants of the original, continuous matorral can now be found only on relatively humid slopes of the Coastal Range. In the Intermediate Depression, a long central valley, it has been replaced by extensive savannas dominated by the exotic *Acacia caven*, whereas the matorral remains on dry slopes as isolated shrub clumps. Experimental work suggests that introduced cattle have played a major role in promoting the shift to *Acacia* savanna, whereas introduced European rabbits prevent the recolonization of clearings by matorral on the slopes. As in other regions of the world, the loss of woodlands in Chile is likely to have resulted in reduced carbon storage capacity and nutrient recycling, and in increased erosion and climatic aridity within the region. Numerous exotic herbs and grasses now dominate the open areas, and experiments indicate that the dry conditions in the absence of woodland cover in combination with loss of soil fertility and severe grazing by introduced mammals has pushed the competitive balance from native to exotic species. These changes are probably very difficult to reverse. Even if grazing is drastically reduced, drought may prevent the recovery of matorral species in much of the region. However, recent theoretical work suggests that if such grazer reduction is timed to coincide with wet El Niño episodes, recovery of the original woodlands may be triggered.

### Introduction

Although it is known that exotic species can substantially influence the composition and structure of plant and animal communities, alter nutrient and water cycles, and change disturbance regimes (e.g. Parker et al. 1999; Mack et al. 2000), most of our understanding of the ecological effects of invaders is still concentrated at the population levels (Parker et al. 1999). Here, I review evidence of the way in which coupled herbivore and plant invasions altered the structure and functioning of ecosystems in central Chile, and compare these patterns to results from other Mediterranean systems.

Mediterranean ecosystems offer a good opportunity to study the mechanisms of biological invasions. We have a good understanding of these ecosystems because ecologists have long been interested in the similarities and differences between the five Mediterranean regions around the world (California, central Chile, the Mediterranean Basin, southwest Australia, and southwest Africa). These regions have been recognized as global biodiversity hotspots (Myers et al. 2000), but they all face conservation problems caused by biological invasions among other things. The five Mediterranean regions have exchanged plant and animal species in different degrees. An early primary invasion brought mainly aggressive annual plants and

herbivores from the Mediterranean Basin to the other regions, which was followed by secondary species exchanges between the four regions and sometime back to the Mediterranean Basin (Fox 1990).

In the mediterranean region of central Chile, almost one-half of all native vascular plant species are endemic (Arroyo and Cavieres 1997). However, the species-rich matorral forests and other native vegetation types that we find today are likely to be only a small fraction of what was once present. Since the mid-sixteenth century, central Chile has been heavily impacted by anthropogenic disturbance. Native plant communities have been reduced by woodcutting, burning, and grazing, or completely replaced by intensive agriculture or plantation forestry. These activities, coupled with the introduction of European rabbits and the invasive success of some exotic keystone plants have radically changed the landscape of central Chile (Fuentes 1991, Fuentes and Muñoz 1995). A recent comprehensive review of plant invasion patterns in Chile reports that 690 alien plant species have become naturalized in continental Chile since colonial times. Most species are herbaceous (92%). They are often annuals (50.6%) and originate mainly from Eurasia and North Africa (71%). The mediterranean area of central Chile contains 73% of this alien flora, of which 74.4% has this Eurasian–North African origin (Arroyo et al. 2000).

The introduction of much of the alien flora coincided with the introduction of exotic herbivores. Introduced domestic livestock (cows, horses, and goats) and leporids (rabbits and hares) from the Mediterranean Basin have become very common. European rabbits and hares were introduced as recently as the 19th century and have become abundant and widespread (Jaksic and Fuentes 1991) probably due to the lack of natural enemies (Jaksic and Soriger 1981). In this paper I argue that perhaps more than in most other Mediterranean regions, introduced herbivores have paved the way to plant invasion in central Chile and that the loss of extensive woodlands in this region may be interpreted as shifts to two different, alternative, stable ecosystem states (*sensu* Scheffer et al. 2001) that are extremely difficult, but not impossible to reverse.

### The loss of Chilean matorral forests

The Chilean vegetation structure has changed profoundly since pre-Columbian times (Figure 1, upper panel). In the pre-Columbian landscape, a shrubland

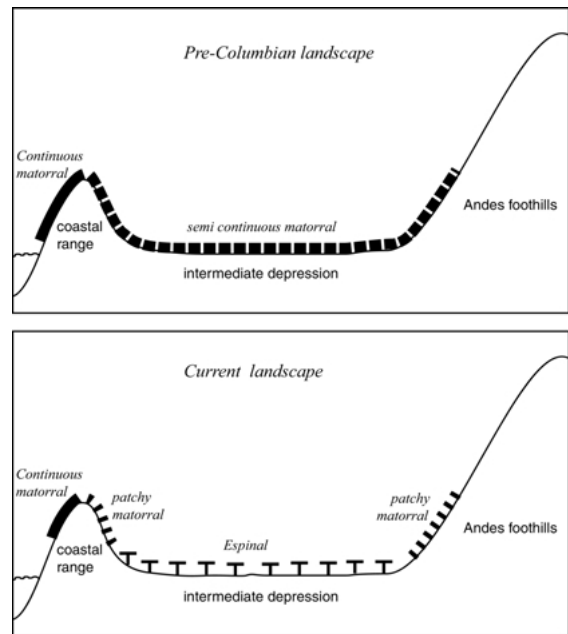


Figure 1. Schematic representation of the pre-Columbian (upper panel) and the current (lower panel) distribution of dominant vegetation structures in the central Chilean landscape.

vegetation called matorral probably covered most of the central Chilean landscape (Muñoz-Schick 1975), with the most dense and continuous forest presumably covering the more mesic sites, such as polar facing slopes or coastal ranges. Today, remnants of continuous matorral can only be found on the most mesic mountainous sites, whereas, on drier sites, such as equatorial facing slopes or the foothills of the Andean Mountains, the matorral consists of small remnant, multispecific clumps surrounded by a seasonal matrix of herbaceous plants dominated by exotic species (Fuentes et al. 1984, 1986). Within the extensive areas of the long Intermediate Depression, the matorral has been completely replaced by a savanna of *Acacia caven* (Ovalle et al. 1990, 1996) (Figure 1, lower panel). The following sections describe the mechanisms thought to be responsible for these transitions.

#### From matorral to *Acacia* savannas

The original vegetation in much of central Chile was probably matorral combined with *Prosopis chilensis* woodlands, especially towards its northern range (Arroyo et al. 1995). *Prosopis chilensis*, locally known as algarrobo, used to form dense forests (Looser 1962). While for some authors these

*Prosopis* woodlands represent climax vegetation formations, others consider them as secondary stages, remnants of a previously more diverse vegetation (see Fuentes et al. 1989). Indeed, the archeological botanical remains in El Carrizo Cave showed low abundance of *P. chilensis* seeds, indicating a minor role for this species in a landscape dominated by matorral species (Henriquez 2000). In any case, the *Prosopis* forests have disappeared and where this species is left it is represented mainly by some older trees sparsely distributed throughout the landscape. Comparisons of aerial pictures between 1954 and 1980, in representative areas of the Intermediate Depression, have shown a decrease of about 50% of *Prosopis* trees, indicating that the decline continues (Fuentes et al. 1989).

At present, *Acacia* savannas are the most widespread plant community in central Chile, covering about  $2 \times 10^6$  ha between 30°–36°S (Ovalle et al. 1996). The dominant species in this community, *A. caven*, was originally limited to the Gran Chaco, a region covering north-central Argentina, adjacent parts of Bolivia, a small portion of Brazil, and nearly half of Paraguay (Aronson 1992; Ebinger et al. 2000). However, *A. caven* is now one of the most widespread trees in South America. In central Chile, the species tends to form savannas called ‘espinales’, with a herbaceous layer dominated by exotic annuals. It has invaded most of the Intermediate Depression, a relatively flat area between the Coastal Range to the west and the Andean Range to the east. *A. caven* invades abandoned fields, open cow pastures, and clearings of the matorral where livestock is allowed to roam (Ovalle et al. 1990).

It is difficult to precisely determine the introduction date of *A. caven* to Chile. The seeds of this species are well adapted for long-distance dispersal by large vertebrates. Therefore, it has been hypothesized that they were brought through the Andes by either large Pleistocene mammals or by guanacos (*Lama guanicoe*), which were abundant in pre-Columbian times (Fuentes et al. 1989). However, botanical remains recovered from archeological sites in El Carrizo Cave in central Chile indicate a noteworthy late appearance of *A. caven* seeds (Henriquez 2000). This suggests that *A. caven* may be a relatively recent invader, which has rapidly spread to cover extensive areas. At present, domestic livestock are certainly the most important means of dispersal of *A. caven* seeds (Gutiérrez and Armesto 1981).

Fuentes et al. (1989) studied some of the ecological mechanisms that could be responsible for the

progressive transformation of *Prosopis* woodlands into *Acacia* savannas. In a combination of field studies and experiments, they showed that in the absence of introduced herbivores, the germination rate of *P. chilensis* is much higher than that of *A. caven*. However, after domestic livestock eat the fruits, the germination rate of *A. caven* is ca. five times higher than that of undigested seeds. In contrast, the germination of *P. chilensis* is reduced to about one-fifth of the germination rate of undigested seeds. Also, seedling survival is higher for *A. caven* than for *P. chilensis* in fields grazed by livestock and rabbits. Importantly, seedlings of this species are quite tolerant to drought stress, which occurs frequently in this open landscape, and *A. caven* can resprout from cut roots in lands plowed for agricultural use, which is also a common practice in central Chile.

In summary, the successful invasion of *A. caven* in central Chile is most likely due to a combination of land-clearing practices and the introduction of livestock. The over-ruling role of livestock on the invasive success of *A. caven* probably explains why this species has remained restricted to the relatively flat Intermediate Depression and did not invade the hillsides where cattle roam less frequently (Fuentes et al. 1989).

#### *From matorral to shrub islands*

Toward its drier range, the current matorral consists of small shrub clumps surrounded by a seasonal matrix of herbaceous plants. Exotic annual grasses and forbs dominate this herbaceous layer between the shrubs (Gulmon 1977; Montenegro et al. 1991). The patchy pattern occurs even on seemingly homogeneous landscapes and remains remarkably constant over time, suggesting that both the shrub as the herbaceous patches represent alternative stable states. For example, a comparison of the extension of these woody patches revealed virtually no change over a 30-year time span, indicating that both types of patches are highly resilient. Despite considerable variation in rainfall over time, none of the open herbaceous areas was invaded by shrubs or trees (Fuentes et al. 1984).

Experimental work has revealed mechanisms behind the lack of expansion of shrub islands. Seedling establishment of mature matorral shrub species appeared only possible under the canopy of large shrub clumps. This facilitative effect of the canopy on recruitment is explained by three mechanisms, two of them involving alien species. Probably the most important positive effect of the shrub canopy on seedling recruitment

is the creation of a more favorable microclimate. Under the shrub canopy, seedlings experience reduced water stress during the severe summer drought, which tends to prolong survival (Fuentes et al. 1984, 1986). Herbivory by introduced rabbits also tends to be lower under the adult shrub canopy (Fuentes et al. 1984) because rabbits feed mainly in the open areas between shrubs (Jaksic et al. 1979; Jaksic and Fuentes 1980). In addition, competition with herbaceous plants in the open patches is strong and shrub seedlings do not survive the presence of a herbaceous layer (Fuentes et al. 1989). As a result, shrub seedling establishment in open patches is practically impossible due to the combination of drought stress, increased rabbit herbivory, and increased competition with herbs.

The spatial distribution of exotic herbs in this matorral also has a characteristic pattern that has been ascribed to rabbit effects. Whereas annuals and introduced species predominate in the open spaces, perennial native herbaceous plants tend to be most abundant under the shrub canopy where rabbit grazing is less severe (Jaksic and Fuentes 1980). Holmgren et al. (2000b) studied some of the mechanisms responsible for the dominance of exotic herbaceous plants in disturbed open patches in more detail. In field studies, they found that the relative abundance of introduced herbaceous species was higher on sites grazed by livestock and on very poor soils. Through field experiments, they showed that native grasses were more sensitive than introduced grasses to rabbit grazing, but also that nutrient addition tended to increase the abundance of native grasses while decreasing introduced ones.

These results may explain why alien species invaded a landscape where introduced herbivores are abundant and soil fertility has become seriously degraded by human activities. Certainly, the introduction of most herbaceous plants was a consequence of land cultivation using seeds brought from Europe (e.g. Matthei 1995). However, the invasive success of many of these introduced species may be due to their superiority in tolerating grazing, drought and low nutrient availability. The ability to survive under grazing pressure by livestock and rabbits may well be related to the fact that most of the introduced herbs and herbivores (livestock and rabbits) originally came from the Mediterranean Basin in Europe, where they were exposed to long and intense selective pressure for coexistence with these notoriously effective grazers (e.g. Crosby 1986).

It should be noted that, in contrast to other Mediterranean regions, central Chile does not have natural

(lightning induced) fires, and there is no evidence that recurrent natural fires were ever significant there (Aschmann and Bahre 1977). One could hypothesize that the increased frequency of human-induced fires in central Chile could increase the relative abundance of European herbaceous species that have been exposed to a longer selection by fire. However, the evidence is not conclusive. Some authors find an increase in the abundance of introduced species (Avila et al. 1981) in response to fire, but others find no effects in the proportion of introduced herbaceous species (Keeley and Johnson 1977). Also, an experimental fire study showed no significant differences in the composition of herbaceous communities between burned and unburned plots (Holmgren et al. 2000b).

In summary, although various mechanisms interact to explain invasion success, the introduction of cattle and rabbits has likely been a major factor boosting the spread of introduced plants in mediterranean Chile.

### **Invasion of other mediterranean shrubland ecosystems**

#### *Australia*

As in the Chilean matorral case, regeneration of the southwestern Australian ecosystems has been strongly affected by the interactive effects of exotic plant species, and grazing by introduced European rabbits (*Oryctolagus cuniculatus*) and livestock (Specht 1972; Hobbs 2001). Plant invasion has been facilitated by livestock grazing, and the competition with herbaceous species from Mediterranean Europe and South Africa has reduced seedling establishment of native tree and shrub species (e.g. Hobbs and Atkins 1991). As in Chile, the herbivore impacts are not limited to simple grazing effects. The altered microclimate and soil structure have made the regeneration of native vegetation even more difficult (e.g. Yates 2000). The impact of rabbits became especially evident after the noticeable recovery of the native vegetation that followed the reduction in rabbit numbers due to recent virus release (Drollette 1997). Invasion by leguminous shrubs (*Cytisus scoparius*) is important in some open woodlands but the role of herbivory is still unclear. Although facilitated by disturbances, the invasion can progress in undisturbed woodlands. The shrub grows fast, creating a dense understory that outcompetes the native species and prevents their recruitment,

especially in nutrient rich soil (Fogarty and Facelli 1999). Apparently a positive feedback takes place, due to *Cytisus*' ability to fix nitrogen, which ultimately leads to the formation of monospecific stands.

### *California*

The effects of introduced herbs and herbivores in Californian chaparral seem to have been less than those observed in the Chilean and Australian ecosystems. Mature Californian chaparral has few introduced species (Kruger et al. 1989). Most introduced herbs are found in mechanically disturbed habitats (e.g. Knops et al. 1995), or during the first post-fire years (Keeley et al. 1981). Exotic shrubs have not invaded the chaparral (Kruger et al. 1989). The relatively small role of invasions in the chaparral may be related to the fact that lagomorph grazers are among the native mammals within the chaparral, where they have a strong impact on vegetation dynamics (e.g. Quinn 1986). In contrast, most mammalian herbivores presently dominating the Chilean and Australian shrublands were introduced. Rabbits and hares were introduced as recently as the nineteenth century into Chile and southwestern Australia, and can maintain very large populations because they lack natural enemies (Jaksic and Soriger 1981; see also references in Hobbs 2001).

### *South Africa*

One of the major threats to the conservation of the South African mediterranean fynbos is the invasion by exotic trees. Large areas of lowland fynbos have been invaded by two *Acacia* species of Australian origin (*A. saligna* and *A. cyclops*). These species have a large impact in reducing species richness (e.g. Holmes and Cowling 1997a), modifying the habitat (through nutrient enrichment, reduced light availability, and reduced water availability) (e.g. Musil 1993 and accompanying citations), and changing fire regime (e.g. Richardson and Cowling 1992). In contrast to the Chilean case, where livestock activity is the main driving force promoting *Acacia* invasion, *Acacia* species invade the fynbos by colonizing burned stands more effectively than native competitors, which are also adapted to fire. *Acacia* species regenerate both from resprouts and soil-stored seeds, grow rapidly and shade out native species. In addition, they produce seeds abundantly that accumulate in a persistent soil seed bank until the next fire (Richardson and Cowling 1992).

Native species that can only regenerate from stored seeds, especially serotinous shrubs with seeds stored in woody infructescences, are unable to cope with *Acacia*, which becomes increasingly dominant after each fire. Restoration of the native vegetation in *Acacia* invaded stands does not seem to be easily feasible from surrounding native vegetation because some native species have short seed-dispersal distances (e.g. Manders 1986). Nonetheless, some native species show rather long-term persistence in the soil seed bank and may be restored by promoting seed germination after *Acacia* removal (e.g. Holmes and Cowling 1997b). In general, grazing by introduced herbivores has not played an extraordinarily role in plant invasion in the South African fynbos (Kruger et al. 1989), probably due to the failure of several exotic species in establishing feral populations (Bigalke and Pepler 1991).

## **Discussion**

### *Role of herbivores*

The emerging picture is that due to their different history, the Mediterranean systems of the world differ profoundly in their susceptibility to exotic plant invasions. The absence of natural fires in central Chile suggests that man-made fires could be the main disturbance to which native plants are less adapted than invaders. However, experimental evidence indicates that the introduction of exotic mammalian herbivores has probably been the dominant factor paving the way for numerous exotic plants to invade central Chile. Livestock has greatly favored *Acacia*, turning the Intermediate Depression into a savanna, while rabbits have prevented the recolonization of clearings by woody matorral species on hillsides where livestock densities are lower (Fuentes et al. 1984, 1989). In general, native shrub and herbs simply seem to have been more sensitive to the effects of introduced herbivores than exotic plants either in terms of germination and seedling survival (e.g. *Prosopis* vs. *Acacia*), or in their ability to cope with the combined effects of drought and herbivory in the more open landscapes (matorral shrubs vs. introduced herbs), or due to the fact that they are preferentially eaten or less successful in replacing the lost biomass (e.g. native vs. introduced herbs). At first sight, the substantial effect of exotic herbivores in Chile and Australia may be surprising, as both communities evolved in the presence of native herbivores.

However, impacts of native herbivores may be quite different from those of introduced ones, as exemplified by specific experiments comparing effects of introduced herbivores with those of their closest functional relatives from the native fauna in Chile (Simonetti and Fuentes 1983).

#### *Related loss of ecosystem function*

The alteration of the structure and composition of the native plant communities is likely to have had major consequences for the carbon and nutrient cycling processes and for the local climate. Although most of these aspects have not been explicitly studied in central Chile, they may be inferred from analyses of the consequences of loss of forest and vegetation cover in other parts of the world (e.g. Shachak et al. 1998). Certainly, the loss of woodland cover in the matorral has reduced carbon accumulation and increased soil erosion. These consequences have likely been most dramatic on slopes. The transformation of a matorral-*Prosopis* community into an *Acacia* savanna has probably been less severe, at least in terms of nutrient cycling. Since both *Acacia* and *Prosopis* are nitrogen fixers, *Acacia* will have taken over this functional role from the replaced, dominant native species. Nevertheless, the loss of the original diverse and evergreen matorral forest seems likely to have meant a net loss of carbon and nutrients from the ecosystem.

The loss of woodland cover in central Chile must also have affected the local climatic conditions as shown for other regions, where loss of forest has been associated with increased temperatures, reduced humidity, and lower water availability due to increased runoff, reduced cloud formations, and reduced regional precipitation (e.g. Zheng and Eltahir 1997). Although it is uncertain whether forest loss has resulted in less precipitation in Chile, reduced cloud formation seems a plausible consequence of forest loss in this region (Patricio Aceituno, personal communication). This may have a significant effect on plant-water relations, as illustrated by the fact that irrigation needs are reduced by 50% on cloudy days in central Chile (Fernando Santibañez, personal communication). Obviously, an increase in climatic aridity with woodland loss will have added to the irreversibility of the vegetation changes, as drought has been identified as a major problem for recolonization of open areas by the original woodland species. We do not know the magnitude of this climatic feedback in central Chile, but should not discard its

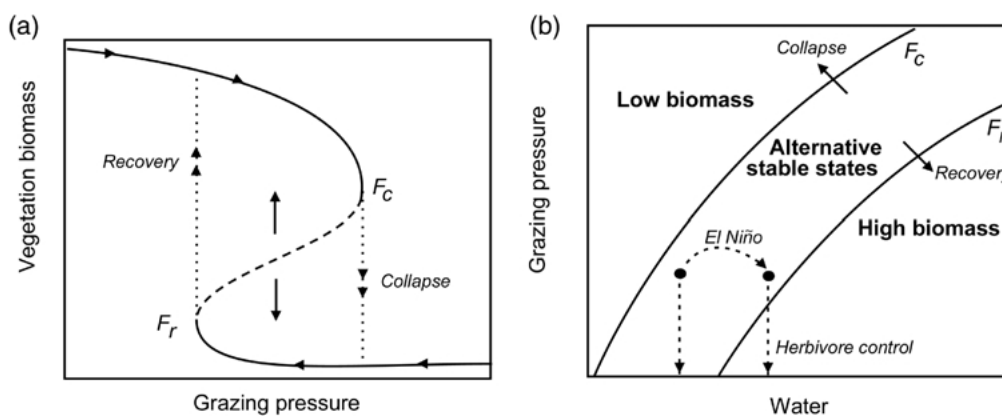
potentially important role. In other regions, it has been shown how deforestation can disrupt this feedback, make the climate drier, and beyond a certain threshold could cause an entire collapse of forest ecosystems and their replacement by savannas (e.g. Da Silveira and Sternberg 2001), which in turn can produce a further disruption of the rainfall system (e.g. Zheng and Eltahir 1997).

#### *Restoration perspectives*

The loss of matorral cover seems extremely difficult to reverse, especially in the drier regions. Experimental shrub seedlings planted in open gaps on the Andes foothills around Santiago have been unable to survive even when protected from herbivorous mammals (Fuentes et al. 1984), and even in very small gaps (1 m<sup>2</sup>) (M. Holmgren et al., unpublished results). Although seedlings planted in the shade of adult shrubs and protected from small herbivorous mammals were found alive after 10 years (M. Holmgren et al., unpublished results), even they may not be able to survive very dry summers (Fuentes et al. 1984). On more mesic sites, long-term observations indicate that matorral can regenerate more easily (Fuentes 1994) and seedlings may survive in relatively large open gaps, especially when the herbaceous layer is removed (Holmgren et al. 2000a).

If matorral recovery is at all possible, chances will obviously be best in relatively humid sites. Nonetheless, it may require intermediate stages including either *A. caven* or *Baccharis* spp. (Armesto and Pickett 1985; Fuentes et al. 1986; Armesto et al. 1995) and a close proximity to mature matorral that may act as the seed provider. The restoration of the matorral from the extensive *Acacia* savanna state will probably be extremely difficult (Aronson et al. 1993; Ovalle et al. 1996), due to a lack of seeds and reduced seedling survival caused by water stress and livestock grazing.

It has recently been suggested that the restoration of the matorral could be triggered by herbivore control in conjunction with interannual variability in precipitation (Holmgren and Scheffer 2001). In normal years, herbivore control will not invoke seedling establishment, as conditions are too dry in most areas. Also, increased rainfall during winter and spring in El Niño years alone is not enough to lead to matorral recovery, as herbivory remains a crucial problem. However, the idea is that grazer control precisely in El Niño years may trigger a recovery of the matorral woodlands,



**Figure 2.** The response of semi-arid vegetation to increased grazing pressure may be discontinuous due to the presence of alternative stable states (panel a). In the absence of grazing vegetation, biomass is relatively high. The effect of a gradual increase in grazing is minor until a critical threshold ( $F_c$ ) is reached, at which time the vegetation biomass collapses to a low level. Recovery from this state is difficult because the low-biomass state and the high-biomass state (upper and the lower branches of the curve) represent alternative attractors for intermediate grazing pressures. Only when grazing pressure is reduced below another low critical level ( $F_r$ ) does the high-biomass state recover. To see how effects of grazing and water availability may interact, the position of the two bifurcation points ( $F_c$  and  $F_r$ ) is plotted as a function of water availability (panel b). Under drier conditions, critical grazing rates for collapse ( $F_c$ ) and for recovery ( $F_r$ ) of vegetation are assumed to be lower. An implication is that not only a reduction in grazing pressure, but also a rainy El Niño event may potentially trigger vegetation recovery provided that it enhances water availability sufficiently to pass the critical level ( $F_r$ ). The dotted arrows illustrate that exclusion of herbivores coinciding with an increase in water availability due to an El Niño event may bring the system over the critical threshold to induce vegetation recovery, even if those two factors by themselves would be insufficient to trigger the switch. (Reproduced, with permission, from Holmgren and Scheffer 2001, © Springer-Verlag.)

which once re-established will persist as an alternative stable state (Figure 2). Several observations support the idea that long-lasting recovery of woody vegetation in semi-arid ecosystems may indeed result when the easing of grazer pressure and rainy conditions, such as the ones associated with ENSO events, simultaneously occur (e.g. Austin and Williams 1988; Bowers 1997; Gutiérrez et al. 1997; Holmgren et al. 2001). Nonetheless, the feasibility of this idea as a restoration tool for matorral forest has yet to be demonstrated.

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