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Persistent *Acacia* savannas replace Mediterranean sclerophyllous forests in South America

Paul Van de Wouw^{a,b}, Cristian Echeverría^c, José María Rey-Benayas^d, Milena Holmgren^{a,*}

^a Resource Ecology Group, Wageningen University, P.O. Box 47, 6700 AA Wageningen, The Netherlands

^b Department of Aquatic Ecology and Environmental Biology, Radboud University Nijmegen, P.O. Box 9701, 6500 GL Nijmegen, The Netherlands

^c Departamento de Manejo de Bosques y Medio Ambiente, Facultad de Ciencias Forestales, Universidad de Concepción, Casilla 160-C, Concepción, Chile

^d Departamento de Ecología, Edificio de Ciencias, Universidad de Alcalá, 28871 Alcalá de Henares, Spain

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ABSTRACT

Mediterranean ecosystems are global hotspots of biodiversity threaten by human disturbances. Growing evidence indicates that regeneration of Mediterranean forests can be halted under certain circumstances and that successional stages can become notoriously persistent. The Mediterranean sclerophyllous forest in central Chile is been largely transformed into savannas dominated by the invasive legume tree *Acacia caven* as result of interacting management and ecological factors. We used multi-temporal satellite imagery to study the transition dynamics of these major vegetation types over the last four decades (1975–2008). Vegetation changes were related to indicators of resource availability (topography, water availability, solar radiance), potential propagule availability (distance to forest remnant patches) and disturbance regimes (grazing, fire occurrence and distance to roads and cities). During this study period, forests were mostly converted into *Acacia* savannas (46.1%). *Acacia* savanna was the most persistent natural vegetation type. The probability of sclerophyllous forest degradation into *Acacia* savanna increased on drier northern-exposed slopes, close to roads and further away from forest remnants. In contrast, forest regeneration from *Acacia* savanna was higher on moister southern-exposed slopes and closer to forest remnants. *Acacia* savannas are increasingly being converted into cultivated land on the moister locations or switching into a bare soil state in locations close to cities and further away from forest remnants. These results highlight the vulnerability of diverse sclerophyllous forests and its increasing conversion into persistent *Acacia* savannas in the Mediterranean region of central Chile and identify the ecological conditions for successful conservation and restoration of the native sclerophyllous forest vegetation that can be used for sensible land use planning.

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1. Introduction

Mediterranean type-ecosystems cover only 5% of the earth's surface but house about 20% of all plant species, many of which are endemic to these ecosystems (Cowling et al., 1996; Myers et al., 2000). A long history of human disturbances has strongly influenced ecosystem functioning and species composition in the five Mediterranean regions around the world (Aschmann, 1973; Conacher and Sala, 1998), i.e. California (Stylinski and Allen, 1999; Franklin, 2010), the European Mediterranean Basin (Barbero et al., 1990; Acácio et al., 2009, 2010; Pulido et al., 2010), central Chile (Fuentes et al., 1989; Holmgren, 2002; Figueroa et al., 2004; Armesto et al., 2010), southwest South Africa (Brown and Van Staden, 1997; Alston and Richardson, 2006), and southwest Australia (Hobbs and Huenneke, 1992; Dixon et al., 1995).

* Corresponding author. Tel.: +31 317 48 52 84; fax: +31 317 48 48 45.

E-mail address: Milena.Holmgren@wur.nl (M. Holmgren).

Regeneration of the original vegetation in these regions has traditionally been conceived as a relatively linear and predictable process. However, evidence from several Mediterranean-type ecosystems indicates that succession can be halted under certain circumstances and that successional stages can become notoriously persistent (Fuentes et al., 1984; Westoby et al., 1989; Holmgren, 2002; Acácio et al., 2009). Understanding the mechanisms responsible for arrested succession and their relative importance across ecosystems will not only contribute to ecological theory but will be also highly relevant for the development of conservation and restoration strategies of these diverse ecosystems. In socio-ecological systems this requires the combined knowledge of ecological and social factors affecting disturbance regimes and the response of ecological communities (Acácio et al., 2010; Westley et al., 2010).

In South America, Mediterranean-type ecosystems are concentrated in central Chile. The vegetation is characterized by multi-specific sclerophyllous shrub clumps of various sizes (Fuentes et al., 1984). On dry sites and equator-facing slopes clumps tend

to be small, but on wet sites and south facing slopes they tend to be large often forming a fairly continuous shrub matrix (Fuentes et al., 1986). The original evergreen sclerophyllous vegetation that once covered the Coastal Range and Andean foothills has been replaced by fragmented patches or totally replaced by early successional plant communities dominated by exotic plant species. Diverse sclerophyllous forests have been largely transformed into savannas dominated by the invasive legume tree *Acacia caven*, locally known as 'espinales' (Fuentes et al., 1989; Ovalle et al., 1990, 1996). These *Acacia* savannas are currently the most widespread land cover type in the Mediterranean region of central Chile (Schulz et al., 2010), spreading between 30° and 36° S (Ovalle et al., 2006). Originally from the Chaco region of South America (Cabrera and Willinck, 1973), *Acacia caven* (Molina) appears to have spread relatively recently into other bio-geographical regions where it is considered invasive (Aronson, 1992). The species was first described from central Chile by Molina in 1782 and later revised by Aronson (1992) who described six varieties and concluded that probably only one (var. *caven*) was present in central Chile. *A. caven* may have been brought to Chile by guanacos (*Lama guanicoe*), a herbivore that was abundant on both sides of the Andes and domesticated by indigenous people in pre-Columbian times (Fuentes et al., 1989; Ovalle et al., 1990). The development of *Acacia* savannas was initially stimulated by the progressive clearing and fragmentation of the native sclerophyllous vegetation, especially since the 16th century, for livestock grazing and annual cropping, creating an agroforestry system that resembles the dehesas and montados in Mediterranean Europe (Ovalle et al., 2006). The further ecological success of *A. caven* expansion has been attributed to several mechanisms, including long distance seed dispersal by introduced domestic livestock and higher resprouting success after cutting, grazing and burning compared to native shrub and tree species (Fuentes et al., 1989; Muñoz and Fuentes, 1989). *Acacia* savannas are generally considered to be very persistent (Fuentes et al., 1989; Ovalle et al., 1990) and the regeneration of sclerophyllous forests to be very difficult under the prevailing environmental conditions in central Chile (Fuentes et al., 1984, 1986; Ovalle et al., 1996; Holmgren et al., 2000a; Holmgren, 2002).

In semiarid Mediterranean-type ecosystems, the interaction of resource availability and disturbances plays a key role in explaining vegetation change. Our knowledge of the processes influencing plant species composition and successional change in the Mediterranean region of central Chile is based on small scale field experiments and observations. The summer drought that characterizes Mediterranean ecosystems represents a strong limitation for seedling recruitment of evergreen forest species, often in interaction with topographical features (Fuentes et al., 1984, 1986; Holmgren et al., 2000a). South-facing slopes and ravines are cooler and moister than north-facing slopes, facilitating the establishment of evergreen forest species and the growth of a denser and continual plant cover (Armesto and Martínez, 1978; Badano et al., 2005). Also the canopy of shrubs and trees significantly ameliorates abiotic stress by providing shady microsites that facilitate tree seedling survival during the summer drought (Fuentes et al., 1984; Holmgren et al., 2000a).

In central Chile, exotic herbivores have been major drivers of vegetation change (Jaksic and Fuentes, 1980; Holmgren, 2002; Del Pozo et al., 2006). Experimental evidence indicates that introduced herbivores (rabbits, hares and livestock) are the strongest limiting factor in the regeneration of evergreen shrublands and forests (Fuentes et al., 1984; Holmgren et al., 2000b; Gutiérrez et al., 2007). Domestic livestock also facilitates the dispersion of exotic herbs and trees (Gutiérrez and Armesto, 1981) and has stronger negative effects on native plant species than on exotic ones (Fuentes et al., 1989; Holmgren et al., 2000b). Unlike other Mediterranean regions, fires in central Chile are not ignited by natural

lightning but mostly produced by humans and therefore they are a relatively recent type of disturbance in evolutionary terms (Aschmann and Bahre, 1977). Although native tree species of the sclerophyllous forest are able to recolonize burned patches by resprouting (Fuentes et al., 1994), their seed bank is very sensitive to fire intensity (Muñoz and Fuentes, 1989; Segura et al., 1998). Most sclerophyllous forest species are unable to survive even to low intensity fires (Segura et al., 1998), which suggests that even small increases in fire occurrence can have strong effects on vegetation change. Fires have promoted exotic plant invasions in other Mediterranean ecosystems (Dixon et al., 1995; Franklin, 2010) and may have contributed to the expansion and persistence of *Acacia* savannas as well.

The different response of native and invasive plant species to exotic herbivores and fire might have triggered a vegetation shift towards *Acacia* savannas in central Chile (Fuentes et al., 1989; Holmgren, 2002). In this study we used multi-temporal remotely sensed data to estimate the rates and trajectories of change in *Acacia* savannas and sclerophyllous forest vegetation during the last four decades (1975–2008) and to assess the role of disturbance and landscape features associated with resource availability on the probability of vegetation changes. Based on what has been learnt from field experiments, we predict larger forest persistence and a faster regeneration of sclerophyllous forests in moister locations especially under lower disturbance and closer to remnant forest patches. In contrast, we expect *Acacia* savannas to be more likely to invade and persist in drier and more disturbed locations. Vegetation change and the potential factors explaining it have rarely been assessed at large scales in central Chile. Our regional assessment will provide a better understanding of the driving forces in Mediterranean vegetation dynamics, emphasizing the factors important for landscape vegetation change and the prevailing dominance of *Acacia* savannas. The results will be useful for land use planning and effective ecosystem restoration measures, and pinpoint the locations where the chances for successful ecosystem restoration are best.

2. Methods

2.1. Study region

The study region covers 1,265,204 ha between 33°51'00"–34°07'55" S and 71°22'00"–71°00'48" W (Fig. 1). The climate is Mediterranean with dry summers and rainy winters. Annual precipitation averages ca. 530 mm but inter-annual variability is high (Montecinos et al., 2000; Montecinos and Aceituno, 2003). The region is listed as a world biodiversity hotspot for conservation priority (Myers et al., 2000; Funk and Fa, 2010) containing about 2400 different plant species, of which 23% are endemic (Cowling et al., 1996).

2.2. Vegetation cover and spatial data

A series of four thematic maps generated and validated by Schulz et al. (2010) based on Landsat satellite images (MSS 1975, TM 1985, ETM+ 1999 and TM 2008) was used to analyze land cover changes over a 33 year period. These images were originally classified into eight land cover categories (Table 1) and the classified images stored in raster grids at a resolution of 30 m. We grouped the eight land cover categories into four categories to assess the trajectories of change between sclerophyllous forests, *Acacia* savannas, bare soil, and cultivation. The land cover types originally classified as 'Crops', 'Pastures' and 'Plantations' were grouped under the new 'Cultivation' category to summarize the change of natural vegetation types by agricultural land and forest plantations.

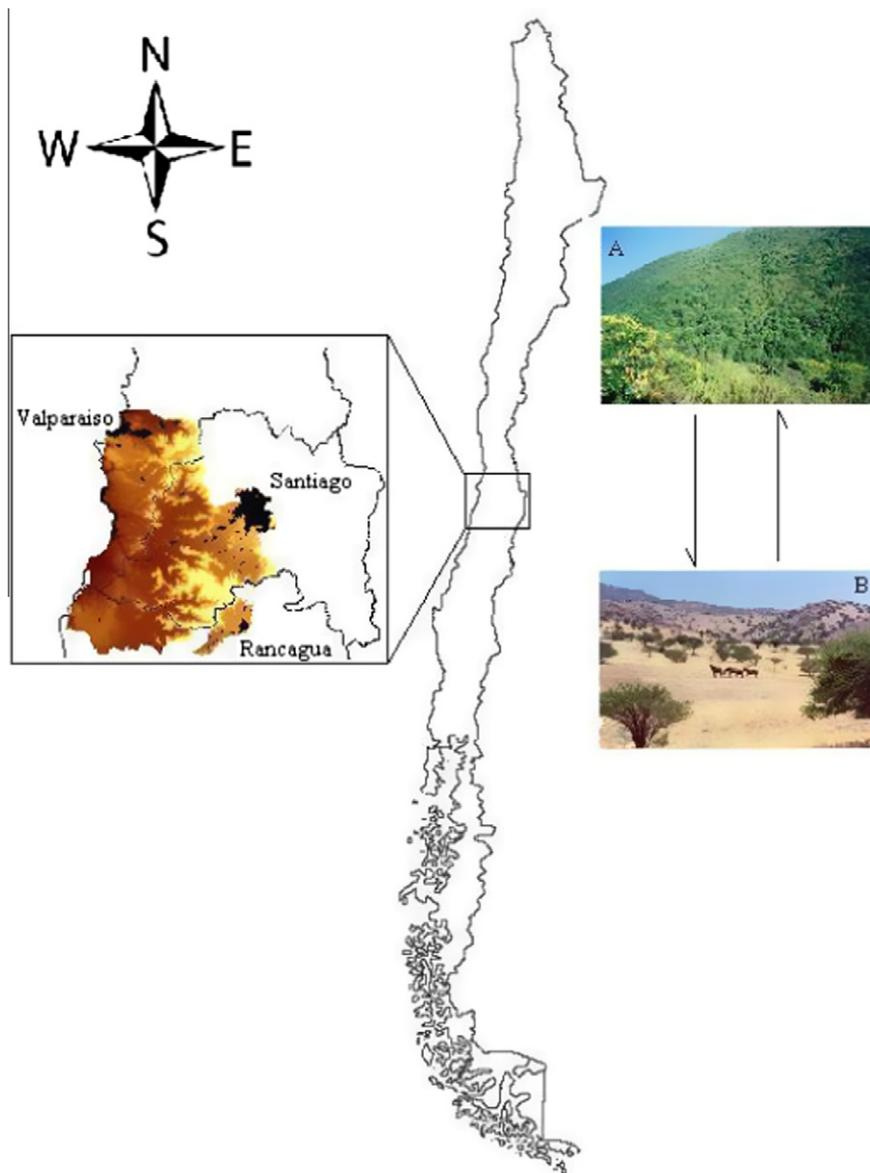


Fig. 1. Study region in central Chile. (A) Sclerophyllous forest, (B) *Acacia* savanna. (Photo© M. Holmgren)

Table 1

Classification of land cover types.

Land classification	Description
Bare soil	Cleared land, degraded land, river beds, dunes, beaches, rocks
Agricultural crops	Fruit plantations, vineyards, rain fed and irrigated agricultural land
<i>Acacia</i> savannas	25–75% covered mainly by <i>Acacia caven</i> and other species such as <i>Prosopis chilensis</i> , <i>Maytenus boaria</i> , <i>Trevoa trinervis</i> , <i>Colliguaja odorifera</i>
Forest	50–100% canopy cover, advanced succession of evergreen sclerophyllous forest
Pasture	Grassland, less than 25% shrub cover
Forest plantation	Industrial forest plantations of exotic species such as Eucalypt and Pine species
Urban area	Urban and industrial area
Water	Rivers, lakes, water catchments

Annual rates of change between these four land cover categories were calculated for each time interval (1975–1985, 1985–1999, 1999–2008). We used the Landscape Change Modeler (LCM) extension of IDRISI-software (The Andes Version 15.00, ClarkLabs, 2006) to create maps of persistence and transitions of forest, *Acacia* savannas and bare soil for each of the three time intervals and the whole study period (1975–2008). We mapped

(I) the persistence of forest and the transition of forest into *Acacia* savannas, (II) the persistence of *Acacia* savannas and its change into forest, and (III) the persistence of *Acacia* savannas and its change into bare soil.

The persistence/transition of target land cover types was explored in relation to biophysical factors, distance to forest remnants, and disturbances that may explain the vegetation changes.

2.3. Biophysical factors

Topographic features were used as indicators to derive ecologically relevant biophysical factors. A 30-m resolution Digital Elevation Model (DEM) was used to determine elevation, slope angle, aspect and solar radiation of each grid cell. The DEM was obtained from the Chilean governmental institute for geology and mining (Servicio Nacional de Geología y Minería, 2007). Aspect was calculated in degrees, with 0° facing perfectly north. Subsequently, aspect was categorized into six classes (0–5; where 5 was north, 4 was northeast–northwest, 3 was flat areas, 2 was east or west, 1 was southeast or southwest, and 0 was south).

The DEM was also used to estimate the potential soil water availability in each grid cell. We calculated the Topographic Wetness Index (TWI) according to the method of Beven and Kirkby (1979). TWI is based on the contribution of local slope and upslope areas to soil water availability in a particular site (Sørensen et al., 2005; Sørensen and Seibert, 2007; Pei et al., 2010). We used an ArcView GIS 3.2 (ESRI, 2006) script (Schmidt, 2004) to calculate the TWI as $\ln(a/\tan \beta)$, where a is the upslope area from which water is directed into the calculation unit, in our case a grid cell of 30×30 m, $\tan \beta$ is the slope of the ground surface, and β is the slope angle. High TWI values represent relatively flat areas with a large adjacent upslope area and a large water retention capacity. The DEM was further used to estimate solar radiation. Solar radiation was calculated in $W \cdot h/m^2$ with the ArcMap option 'whole year'. This option calculates the solar radiation for a whole year with a monthly interval, and accounts for latitude, elevation, slope angle, aspect and shade effects cast by surrounding topography.

2.4. Forest remnants

We determined the distance to forest remnants as a potential driving factor of vegetation change as regeneration of evergreen forests is likely dependent on seed dispersal. We used the distance to the nearest forest remnant at the beginning of a time interval because these forest patches may act as islets for forest regeneration in the following period (Rey-Benayas et al., 2008).

2.5. Disturbances

The frequency and intensity of human disturbances are likely to be higher in areas close to where human activities are concentrated. We related vegetation persistence and change to the minimum distance to a city >2000 inhabitants (i.e. which are substantially large) at the beginning of a time interval and the distance to the nearest road. We also explored the potential effect of property size on the probability of vegetation change, as human pressure may be stronger and the effects on vegetation more severe in small properties compared to larger ones.

We related the number of fires to vegetation changes during the period 1985–2008. Spatial data on fire occurrence was only available since 1985 from the Chilean Forest Service (CONAF) as the total number of fire incidents that had occurred in that period.

We used the 1997 National Agricultural Census (Instituto Nacional de Estadística, 1997) to gather information on the number of cows, horses, goats, mules and sheep for a subset of 200 property sites randomly spread throughout the study region. Animal densities were calculated for these 200 property sites for the period 1999–2008. These were the only data available for the study region which could be spatially referenced.

2.6. Statistical analysis

Spatial data of the variables that may account for vegetation changes were stored in ArcMap raster maps. Multivariate logistic

regression models were used to assess the probability of transition of sclerophyllous forest into *Acacia* savanna and *vice versa* and conversion of *Acacia* savannas into bare soil. The response variable in these models was land cover change coded as 'persistent' (value = 0) if no change was observed in a specific grid cell or 'transition' (value = 1) if the vegetation of land cover type of a grid cell had changed.

Three sets of models were used. The first set of models included all explanatory variables that were available for the entire study period, namely biophysical variables, forest remnants and distance to cities and roads; this set of models did not include fire occurrence and herbivore density. With this first set of models we analyzed changes in the three time intervals (1975–1985, 1985–1999, 1999–2008) and the total study period 1975–2008. The second set of models included also fire occurrences just for the period 1985–2008. Finally, a third set of models was used on a small subset of sampling points spread across the entire study region for the time interval 1999–2008 to explore the effects of all available variables but fire occurrence. This set of models included also information on the density of the various herbivore species, which entered the models as separate explanatory variables. We assumed that the contribution of these variables to persistence or transition has operated from 1975 to 2008. All the explanatory variables were converted to a raster map of 30×30 m grid cells using Arc Map software.

Regular sample point files were created for each model and for each time interval, with sampling points 1000 m apart from each other. The Intersect Point Tool (Beyer, 2004) was used to extract values from the raster maps of the explanatory variables. Only points that intersected with locations of sclerophyllous forest or *Acacia* savannas presented in the earliest maps were used for logistic regression analysis. We excluded cultivation in the analyses of drivers because we were mostly interested in the environmental factors potentially explaining changes between forest and savanna vegetation. The economic and social factors explaining changes in cultivated land are more complicated than the set of biophysical and disturbance factors explored in this paper. For each time interval, we entered the explanatory and response variables of the intersected points into R statistical package to generate the logistic regression models.

To avoid multicollinearity between different variables, either by their synergetic nature or by false accidental correlations (Graham, 2003), correlation matrixes of all variables were created for all models. Highly correlated variables (Spearman's Rho > 0.5) were excluded from entering the models. The lowest average correlation coefficient of a variable was used as a selection criterion for exclusion of correlated variables (Mitchell-Olds and Shaw, 1987). Variables that were not correlated were also entered in the multivariate logistic regression models. We assessed spatial autocorrelation using Moran's I correlograms for the final model residuals (Dormann et al., 2007). No autocorrelations were found.

3. Results

3.1. Proportions and rates of land cover change

Only 34.5% of the initial sclerophyllous forest cover persisted during the entire study period. Forests were mainly converted into *Acacia* savannas (46.1%) and to a lesser extent into cultivated land (9.6%) and bare soil (6.4%) (Fig. 2). The annual transition rate by which forest was lost into *Acacia* savanna was much higher than the rates of change into bare soil and cultivation (Fig. 3A).

Acacia savanna was the most persistent vegetation type (44.2%) across the entire study period despite the 30.8% loss of its initial cover as a result of land cultivation (Fig. 2). About 15.1% of the ini-

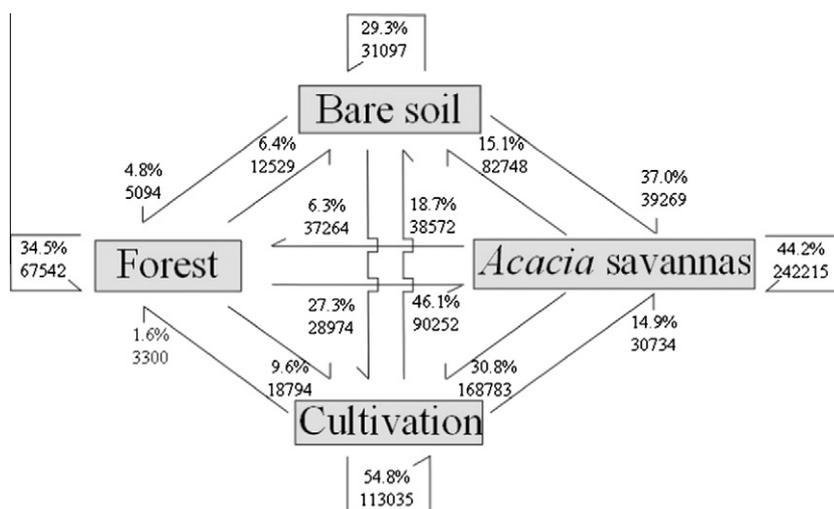


Fig. 2. Transitions between 1975 and 2008 among four major land cover classes. Percentages are presented as the proportions of that land cover class in 1975 that changed or remained in 2008. Below the percentages is the corresponding number of hectares. The class 'cultivation' includes 'agricultural crops', 'pastures' and 'plantation' (Table 1).

tial *Acacia* savanna cover changed into bare soil and only 6.3% had turned into sclerophyllous forest by 2008. The rates of *Acacia* savanna loss into cultivated land or bare soil increased in every period, and the rate of change into cultivation was higher than the rates of change into forest and bare soil (Fig. 3B).

Cultivated land was very persistent (54.8%) and changed mostly into bare soil (18.7%) and *Acacia* savanna (14.9%) (Fig. 2). Only 1.6% of the cultivated land in 1975 developed into forest by 2008 (Fig. 2). Bare soil was also very persistent (29.3%, Fig. 2). A relatively high proportion (37%) of bare soil in 1975 was converted into *Acacia* savanna by 2008, and the highest transition rate was observed between 1975 and 1985 (Fig. 3D). Of the initial bare soil area, 27.3% was cultivated by 2008 (Fig. 2) at increasing rates during each time interval (Fig. 3D). The proportion of bare soil that changed into forest was small (4.8%, Fig. 2) and exhibited a decreasing rate across time (Fig. 3D).

3.2. Drivers of land cover change

The probability of forest transition into *Acacia* savanna was consistently and positively related to slope aspect in all time periods.

North facing slopes were more likely to experience forest loss into savanna (Table 2A). Also the proximity of roads and cities tended to increase the probability that forest changed into savannas. Since 1985, increasing distance to forest remnants increased the probability of forest change into savannas. Only the topographic wetness index showed a consistent and negative relation with the probability of this transition across time, meaning that with increasing soil water availability forests were less likely to turn into savanna. Since 1999, increasing elevation became a significant variable that reduced the probability of forest transition into savanna; forests at higher elevation were thus more likely to persist (Table 2A).

The transition probability of *Acacia* savanna to sclerophyllous forest decreased in all time intervals especially with increasing distances to forest remnants and on north facing slopes (Table 2B). The variables elevation and distance to roads showed an inconsistent contribution to the probability of this transition across time. For the time interval 1975–1985, the probability was higher at higher altitudes and increasing distance to roads. However, in the following period 1985–1999, the pattern reversed (Table 2B) indicating increased human ecosystem pressure towards higher altitudes and further away from roads. This is also suggested by the

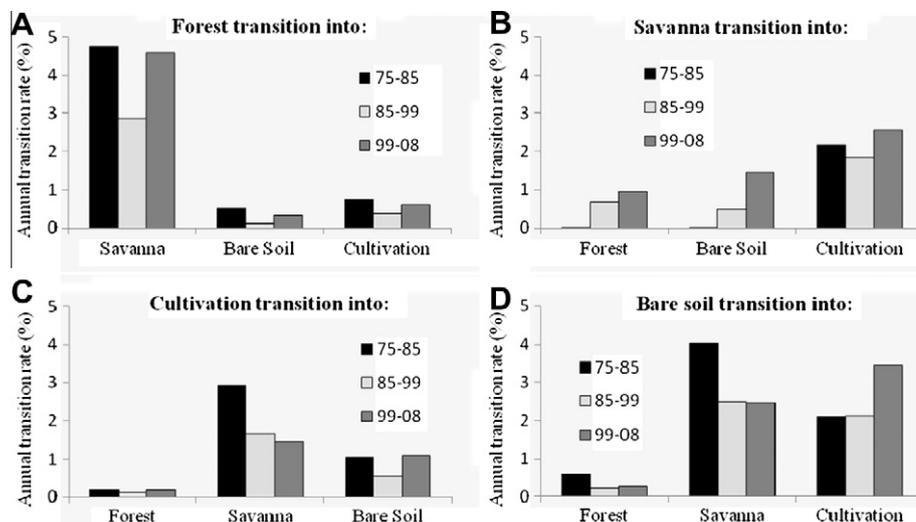


Fig. 3. Annual transition rates per time interval as percentage of initial land cover type in each time interval.

Table 2

Results of the multivariate logistic regression models that explain the probability of change of (A) sclerophyllous forest into *Acacia* savanna, (B) *Acacia* savanna into sclerophyllous forest, and (C) *Acacia* savanna into bare soil. Variables that did not significantly improve the models were removed (n.s.).

	1975–1985		1985–1999		1999–2008		1975–2008	
	Coefficient	<i>p</i>	Coefficient	<i>p</i>	Coefficient	<i>p</i>	Coefficient	<i>p</i>
<i>(A) Forest into savanna</i>								
Intercept	0.90188	*	1.65546	**	3.60613	***	2.64300	***
Distance to city	–	n.s.	–0.00002	*	–	n.s.	–	n.s.
Topographic wetness index	–0.18066	**	–0.32934	***	–0.47779	***	–0.36016	***
Slope	–	–	–	–	–	–	–	–
Solar radiation	–	–	–	–	–	–	–	–
Elevation	–	n.s.	–	n.s.	–0.00187	***	–0.00096	***
Property size	–	n.s.	–	n.s.	–	n.s.	–	n.s.
Distance to roads	–0.00007	**	–	–	–0.00005	*	–0.00001	**
Distance to forest	–	–	0.00140	**	0.00195	**	–	–
Aspect	0.25585	***	0.17905	***	0.24339	***	0.30581	***
	<i>N</i> = 1610		<i>N</i> = 1207		<i>N</i> = 1146		<i>N</i> = 1506	
<i>(B) Savanna into forest</i>								
Intercept	0.25949	–	–0.82719	***	0.38924	*	–0.66805	***
Distance to city	–	n.s.	0.00002	**	0.00001	–	–	n.s.
Topographic wetness index	–0.13562	*	–	n.s.	–	n.s.	–	n.s.
Slope	–	n.s.	–	–	–0.02124	***	–0.01543	*
Solar radiation	–	–	–	–	–	–	–	–
Elevation	0.00048	**	–0.00052	**	–	–	–	–
Property size	–	n.s.	–	n.s.	–	n.s.	–	n.s.
Distance to roads	0.00007	*	–0.00012	***	–	n.s.	0.00013	***
Distance to forest	–0.00762	***	–0.00651	***	–0.01121	***	–0.00514	***
Aspect	–0.23781	***	–0.25710	***	–0.12539	***	–0.27562	***
	<i>N</i> = 3257		<i>N</i> = 3474		<i>N</i> = 3072		<i>N</i> = 2646	
<i>(C) Savanna into bare soil</i>								
Intercept	–1.82319	***	–5.62894	***	–1.77373	***	–0.72185	***
Distance to city	–0.00003	***	–0.00001	–	–0.00004	***	–0.00003	***
Topographic wetness index	–	–	0.37930	***	0.10155	*	–	–
Slope	–0.00981	*	–	–	–	n.s.	–0.01193	**
Solar radiation	–	–	–	–	–	–	–	–
Elevation	0.00079	***	0.00164	***	–	–	–	–
Property size	0.00006	***	–	n.s.	–	n.s.	–0.00002	*
Distance to roads	–	n.s.	–	n.s.	–	n.s.	–	–
Distance to forest	0.00048	***	0.00044	*	0.00063	***	0.00044	**
Aspect	–	n.s.	–	n.s.	–	n.s.	–	–
	<i>N</i> = 3753		<i>N</i> = 3236		<i>N</i> = 3105		<i>N</i> = 3276	

* *p* < 0.05.

** *p* < 0.01.

*** *p* < 0.001.

patterns of regeneration in the time interval 1999–2008, when the probability of forest regeneration from *Acacia* savanna also decreased on steep slopes.

The probability of *Acacia* savannas degrading into bare soil decreased primarily when distance to a city became larger in all time intervals, and also on steep slopes for the time interval 1975–1985 (Table 2C). In all time intervals, this transition was more likely to occur when distance to forest remnants increased. Between 1975 and 1999, this transition was also more probable to occur at higher elevations.

3.3. Effects of fire and domestic herbivores

The second set of models, which included the number of fires as an explanatory variable, was largely in accordance with the above explained models. Fires only proved to be of positive significance for the transition of *Acacia* savanna into bare soil; a higher fire occurrence resulted in *Acacia* savanna loss (Table 3).

The third set of models, which included the density of horses, cows, mules, sheep and goats as explanatory variables of change between 1999 and 2008, did not show any significant effect of these domesticated herbivores.

4. Discussion

4.1. Forest-*Acacia* savanna transitions

Acacia savanna covered the largest part of the study region over the last 33 years being highly persistent despite its overall reduction. In contrast, sclerophyllous forests were far less persistent and transformed into *Acacia* savanna at increasing rates. Expansion of *Acacia* savanna was the main contributor to forest loss. Our results indicate that the sclerophyllous forest loss may be larger than commonly considered, with a gradual trajectory, as forest may be first converted into *Acacia* savanna rather than directly cleared. This supports the idea that *Acacia* savanna is an intermediate condition in a process of ongoing forest degradation that has provided opportunities for exotic species to invade and become naturalized (Fuentes et al. 1989; Ovalle et al., 1990, 1996). Forest fragmentation has facilitated the successful expansion of many exotic species, particularly herbaceous plants from the Mediterranean Basin (Arroyo et al., 2000; Figueroa et al., 2004), and tree species such as *Pinus radiata* (Bustamante et al., 2003). The conversion of forests into *Acacia* savannas may further increase this process. For instance, whereas exotic annuals may represent 50% of the herbaceous flora of fragmented sclerophyllous forests (Figueroa et al.,

Table 3
Results of multivariate logistic regression models that included the number of fires for the period 1985–2008. Variables that did not significantly improve the models were removed (n.s.).

1985–2008	Forest → Savanna		Savanna → Forest		Savanna → Bare soil	
	Coefficient	<i>p</i>	Coefficient	<i>p</i>	Coefficient	<i>p</i>
Intercept	1.26433	**	−1.50191	***	−1.06245	***
Distance to city	–	n.s.	–	n.s.	–	n.s.
Topographic wetness index	−0.17648	*	–	n.s.	−0.04043	***
Slope	–	–	–	–	−0.01877	***
Solar radiation	–	–	–	–	–	–
Elevation	−0.00119	***	–	–	–	–
Property size	–	n.s.	–	n.s.	–	n.s.
Distance to roads	−0.00007	*	0.00018	***	–	n.s.
Distance to forest	0.00121	*	−0.00146	***	0.00018	***
Aspect	0.22908	***	−0.24589	***	–	n.s.
Number of fires	–	n.s.	–	n.s.	0.02967	***
	<i>N</i> = 1144		<i>N</i> = 3176		<i>N</i> = 3522	

* *p* < 0.05.

** *p* < 0.01.

*** *p* < 0.001.

2004), they can reach up to 95% in *Acacia* savannas (Ovalle et al., 1990). Our results also indicate that forest regeneration from *Acacia* savanna, although difficult, may be possible in moister areas closer to forest remnants. This suggests that *Acacia* savanna might also act as an intermediate successional stage for sclerophyllous forest recovery (Armesto and Pickett, 1985; Fuentes et al., 1984, 1986). Forest regeneration from former savannas seems, however, increasingly difficult since *Acacia* savannas are being transformed into plantations and bare soil at increasing rates.

Sclerophyllous forests were less likely to be degraded into *Acacia* savannas on locations with high water availability and southern expositions, and forest regeneration from *Acacia* savanna was more likely to occur on south facing slopes. In Chile, northern exposed slopes are drier and warmer (Armesto and Martínez, 1978). Our models emphasize the importance of water availability, indicated by topography, for forest persistence and decreased probability of degrading into *Acacia* savannas. Similarly, they contribute to the explanation of the distribution of sclerophyllous forest remnants mostly on south facing slopes and moister ravines (Fuentes et al., 1984, 1986; Schulz et al., 2010), whereas *Acacia* savannas cover the more northern exposed slopes and most of the relatively dry Intermediate Depression (Ovalle et al., 1990, 1996). Once established, *Acacia* savannas can be very persistent even on locations with relatively high water availability where sclerophyllous forest could otherwise be expected.

In the Mediterranean Basin, evergreen forests tend to remain in locations with increasing slope angle and elevation (Acácio et al., 2009). These topographic features determine the accessibility of terrain and, accordingly, constrain forest logging practices. In central Chile, we found no correlation between slope angle and the probability of forest loss. Instead, the effect of terrain accessibility was expressed by the correlations with distance to cities and roads; the probability of sclerophyllous forest switching into *Acacia* savannas tended to increase as roads were nearby. The rapid conversion of *Acacia* savannas into plantations of avocado and vineyards in the last 15 years has switched land use pressure from flat areas to upward slopes; as a consequence, the persistence of *Acacia* savannas has increased with increasing distance to roads and increasing elevation. Unsustainable agricultural practices related to avocado, vineyard and other orchard products have seriously compromised the vegetation (Armesto et al., 2010) and soil condition in central Chile (Castro-Ríos and Espinosa-Toro, 2008).

Our results revealed that vegetation changes between *Acacia* savanna and sclerophyllous forest are closely related to distance to forest remnants. The persistence of forests as well as the probability

of forest regeneration from *Acacia* savanna increased with proximity to forest patches. Schulz et al. (2011) also concluded that forest regeneration in central Chile was enhanced closer to forest patches, particularly in isolated areas and steeper slopes. These results demonstrate the importance of mature sclerophyllous vegetation for seed dispersal (Jiménez and Armesto, 1992) and seedling recruitment of sclerophyllous tree species at the landscape scale (Fuentes et al., 1984, 1986; Holmgren et al., 2000a; Rey-Benayas et al., 2008). The persistent condition of Chilean *Acacia* savannas contrasts with the transitional nature of *Quercus* savannas in the Mediterranean Basin (Mazzoleni et al., 2004; Acácio et al., 2009) and resembles the role of persistent *Cistus* shrublands in arresting succession of Mediterranean oak forests (Acácio et al., 2007, 2009, 2010).

4.2. Further land degradation into bare soil

Our models showed that *Acacia* savannas are vulnerable to conversion into bare soil close to cities. But the presence of nearby forest remnants could limit the loss of *Acacia* savannas into bare soil. This again emphasizes the value of sclerophyllous vegetation in limiting vegetation loss. Additionally, the second set of models including fire data showed that fires also contributed to the loss of *Acacia* savannas into bare soil. The models also revealed that the loss of savanna into bare soil was concentrated on humid locations. This unexpected pattern may be the result of land clearing prior to the expansion of agricultural land for which these humid locations are more suitable. Fire might here be used as an effective (although illegal) tool for vegetation clearing since it is widely recognized that fires are either directly or indirectly caused by humans (Fuentes et al., 1994; CONAF, 1998). It has indeed been shown that agricultural expansion was an important contributor to savanna loss (Schulz et al., 2010) and the loss of *A. caven*, particularly on hillsides under intensive cereal-pasture rotation, contributes to significant losses of soil organic matter (Ovalle et al., 2006).

4.3. The role of domesticated livestock

Surprisingly, the models including livestock density did not reveal any significant effect on vegetation change at the landscape scale. We only had spatial data on domesticated herbivores for the last 10 years of the study period and for a relatively small subset of locations. These may have been insufficient to reveal their effect on the landscape. Interviews to landowners during our fieldwork indicate that they perceive the impact of cattle as an

important contributor to explain the loss of forest and the persistence of *Acacia* savanna in their properties. Also earlier studies have highlighted the role of livestock as a major disturbance factor in central Chile (Fuentes et al., 1989). In general, herbivores play a significant role in explaining vegetation changes in all Mediterranean regions (e.g. Jaksic and Fuentes, 1980; Fuentes et al., 1983; Mills, 1983, 1986; Gómez-Sal et al., 1999; Holmgren and Scheffer, 2001; Gutiérrez et al., 2007; Pulido et al., 2010). Clearly, the relative importance of drivers changes spatially and temporally. New crops and forestry plantations have become the main drivers of land use change in central Chile in the last 30 years (Armesto et al., 2010; Schulz et al., 2010). In contrast, since the 1960s, major socioeconomic changes in Mediterranean Europe led to a gradual abandonment of traditional agriculture and stimulated rural exodus (Pinto-Correia, 2000). Nevertheless, former cultivation and grazing left a signature in the landscape. Lack of forest regeneration has been explained by former management in combination with higher frequency of fire and droughts particularly on drier sites (Acácio et al., 2007, 2009, 2010).

5. Conclusions

Our results showed the vulnerability of sclerophyllous forests and its increasing conversion into persistent *Acacia* savannas in the Mediterranean region of central Chile and identified the ecological conditions for successful conservation and restoration of the native sclerophyllous forest vegetation. If mankind fails to appraise the vulnerability and value of the region's unique vegetation, and current unsustainable socio-economic practices continue, the highly endemic vegetation of the Mediterranean region of Chile is in jeopardy. These lessons are also valid for other Mediterranean ecosystems of the world.

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