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

3
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26 **Abstract**

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

48

49 **Keywords:** arrested succession; Chile; disturbance; evergreen; invasion; shrubland

50

51 **Introduction**

52 Mediterranean type-ecosystems cover only 5% of the earth's surface but house about 20% of
53 all plant species, many of which are endemic to these ecosystems (Cowling et al. 1996; Myers
54 et al. 2000). A long history of human disturbances has strongly influenced ecosystem
55 functioning and species composition in the five Mediterranean regions around the world
56 (Aschmann, 1973; Conacher and Sala, 1998), i.e. California (Stylinksi and Allen, 1999;
57 Franklin, 2010), the European Mediterranean Basin (Barbero et al., 1990; Acácio et al., 2009;
58 2010; Pulido et al., 2010), central Chile (Fuentes et al., 1989; Holmgren, 2002; Figueroa et al.,
59 2004; Armesto et al., 2010), southwest South Africa (Brown and Van Staden, 1997; Alston and
60 Richardson, 2006), and southwest Australia (Hobbs and Huenneke, 1992; Dixon et al., 1995).

61 Regeneration of the original vegetation in these regions has traditionally been conceived
62 as a relatively linear and predictable process. However, evidence from several Mediterranean-
63 type ecosystems indicates that succession can be halted under certain circumstances and that
64 successional stages can become notoriously persistent (Fuentes et al., 1984; Westoby et al.,
65 1989; Holmgren, 2002; Acácio et al., 2009). Understanding the mechanisms responsible for
66 arrested succession and their relative importance across ecosystems will not only contribute to
67 ecological theory but will be also highly relevant for the development of conservation and
68 restoration strategies of these diverse ecosystems. In socio-ecological systems this requires the
69 combined knowledge of ecological and social factors affecting disturbance regimes and the
70 response of ecological communities (Acácio et al., 2010; Westley et al., 2010).

71 In South America, Mediterranean-type ecosystems are concentrated in central Chile.
72 **The vegetation is characterized by multispecific sclerophyllous shrub clumps of various sizes**
73 **(Fuentes et al., 1984). On dry sites and equator-facing slopes clumps tend to be small, but on**
74 **wet sites and south facing slopes they tend to be large often forming a fairly continuous shrub**
75 **matrix (Fuentes et al., 1986).** The original evergreen sclerophyllous vegetation that once

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

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

113 In central Chile, exotic herbivores have been major drivers of vegetation change (Jaksic
114 and Fuentes, 1980; Holmgren, 2002; Del Pozo et al., 2006). Experimental evidence indicates
115 that introduced herbivores (rabbits, hares and livestock) are the strongest limiting factor in the
116 regeneration of evergreen shrublands and forests (Fuentes et al., 1984; Holmgren, 2000b;
117 Gutiérrez et al., 2007). Domestic livestock also facilitates the dispersion of exotic herbs and
118 trees (Gutiérrez and Armesto, 1981) and has stronger negative effects on native plant species
119 than on exotic ones (Fuentes et al., 1989; Holmgren et al., 2000b). Unlike other Mediterranean
120 regions, fires in central Chile are not ignited by natural lightning but mostly produced by
121 humans and therefore they are a relatively recent type of disturbance in evolutionary terms
122 (Aschmann and Bahre, 1977). Although native tree species of the sclerophyllous forest are able
123 to recolonize burned patches by resprouting (Fuentes et al., 1994), their seed bank is very
124 sensitive to fire intensity (Muñoz and Fuentes, 1989; Segura et al., 1998). Most sclerophyllous
125 forest species are unable to survive even to low intensity fires (Segura et al., 1998), **which**

126 suggests that even small increases in fire occurrence can have strong effects on vegetation
127 change. Fires have promoted exotic plant invasions in other Mediterranean ecosystems (Dixon
128 et al., 1995; Franklin, 2010) and may have contributed to the expansion and persistence of
129 *Acacia* savannas as well.

130 The different response of native and invasive plant species to exotic herbivores and fire
131 might have triggered a vegetation shift towards *Acacia* savannas in central Chile (Fuentes et al.,
132 1989; Holmgren, 2002). In this study we used multi-temporal remotely sensed data to estimate
133 the rates and trajectories of change in *Acacia* savannas and sclerophyllous forest vegetation
134 during the last four decades (1975-2008) and to assess the role of disturbance and landscape
135 features associated with resource availability on the probability of vegetation changes. Based
136 on what has been learnt from field experiments, we predict larger forest persistence and a faster
137 regeneration of sclerophyllous forests in moister locations especially under lower disturbance
138 and closer to remnant forest patches. In contrast, we expect *Acacia* savannas to be more likely
139 to invade and persist in drier and more disturbed locations. Vegetation change and the potential
140 factors explaining it have rarely been assessed at large scales in central Chile. Our regional
141 assessment will provide a better understanding of the driving forces in Mediterranean
142 vegetation dynamics, emphasizing the factors important for landscape vegetation change and
143 the prevailing dominance of *Acacia* savannas. The results will be useful for land use planning
144 and effective ecosystem restoration measures, and pinpoint the locations where the chances for
145 successful ecosystem restoration are best.

146

147 **Methods**

148 *Study region*

149 The study region covers 1,265,204 ha. between 33°51'00"-34°07'55" S and 71°22'00"-
150 71°00'48" W (Figure 1). The climate is Mediterranean with dry summers and rainy winters.

151 Annual precipitation averages ca. 530 mm but inter-annual variability is high (Montecinos et
152 al., 2000, 2003). The region is listed as a world biodiversity hotspot for conservation priority
153 (Myers et al., 2000; Funk and Fa, 2010) containing about 2400 different plant species, of which
154 23% are endemic (Cowling et al., 1996).

155

156 *Vegetation cover and spatial data*

157 A series of four thematic maps generated **and validated** by Schulz et al. (2010) based on
158 Landsat satellite images (MSS 1975, TM 1985, ETM+ 1999 and TM 2008) was used to analyze
159 land cover changes over a 33 year period. These images were originally classified into eight
160 land cover categories (Table 1) and the classified images stored in raster grids at a resolution of
161 30 m. We grouped the eight land cover categories into four categories to assess the trajectories
162 of change between sclerophyllous forests, *Acacia* savannas, bare soil, and cultivation. The land
163 cover types originally classified as ‘Crops’, ‘Pastures’ and ‘Plantations’ were grouped under
164 the new ‘Cultivation’ category to summarize the change of natural vegetation types by
165 agricultural land and forest plantations.

166 Annual rates of change between these four land cover categories were calculated for
167 each time interval (1975-1985, 1985-1999, 1999-2008). We used the Landscape Change
168 Modeler (LCM) extension of IDRISI-software (The Andes Version 15.00, ClarkLabs, 2006) to
169 create maps of persistence and transitions of forest, *Acacia* savannas and bare soil for each of
170 the three time intervals and the whole study period (1975-2008). We mapped (I) the persistence
171 of forest and the transition of forest into *Acacia* savannas, (II) the persistence of *Acacia*
172 savannas and its change into forest, and (III) the persistence of *Acacia* savannas and its change
173 into bare soil.

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

177

178 *Biophysical factors*

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

186 The DEM was also used to estimate the potential soil water availability in each grid
187 cell. We calculated the Topographic Wetness Index (TWI) according to the method of Beven
188 and Kirkby (1979). TWI is based on the contribution of local slope and upslope areas to soil
189 water availability in a particular site (Sørensen et al., 2005; Sørensen and Seibert, 2007; Pei et
190 al., 2010). We used an ArcView GIS 3.2 (ESRI 2008) script (Schmidt, 2004) to calculate the
191 TWI as $\ln(a/\tan \beta)$, where a is the upslope area from which water is directed into the
192 calculation unit, in our case a grid cell of 30x30 m, $\tan \beta$ is the slope of the ground surface, and
193 β is the slope angle. High TWI values represent relatively flat areas with a large adjacent
194 upslope area and a large water retention capacity. The DEM was further used to estimate solar
195 radiation. Solar radiation was calculated in watt*hour/m² with the ArcMap option ‘whole year’.
196 This option calculates the solar radiation for a whole year with a monthly interval, and accounts
197 for latitude, elevation, slope angle, aspect and shade effects cast by surrounding topography.

198

199 *Forest remnants*

200 We determined the distance to forest remnants as a potential driving factor of vegetation
201 change as regeneration of evergreen forests is likely dependent on seed dispersal. We used the
202 distance to the nearest forest remnant at the beginning of a time interval because these forest
203 patches may act as islets for forest regeneration in the following period (Rey Benayas et al.,
204 2008).

205

206 *Disturbances*

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

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

216 We used the 1997 National Agricultural Census (Instituto Nacional de Estadística,
217 1997) to gather information on the number of cows, horses, goats, mules and sheep for a subset
218 of 200 property sites randomly spread throughout the study region. Animal densities were
219 calculated for these 200 property sites for the period 1999-2008. These were the only data
220 available for the study region which could be spatially referenced.

221

222 *Statistical analysis*

223 Spatial data of the variables that may account for vegetation changes were stored in ArcMap
224 raster maps. Multivariate logistic regression models were used to assess the probability of
225 transition of sclerophyllous forest into *Acacia* savanna and *vice versa* and conversion of *Acacia*
226 savannas into bare soil. The response variable in these models was land cover change coded as
227 'persistent' (value = 0) if no change was observed in a specific grid cell or 'transition' (value =
228 1) if the vegetation of land cover type of a grid cell had changed.

229 Three sets of models were used. The first set of models included all explanatory
230 variables that were available for the entire study period, namely biophysical variables, forest
231 remnants and distance to cities and roads; this set of models did not include fire occurrence and
232 herbivore density. With this first set of models we analyzed changes in the three time intervals
233 (1975-1985, 1985-1999, 1999-2008) and the total study period 1975-2008. The second set of
234 models included also fire occurrences just for the period 1985-2008. Finally, a third set of
235 models was used on a small subset of sampling points spread across the entire study region for
236 the time interval 1999-2008 to explore the effects of all available variables but fire occurrence.
237 This set of models included also information on the density of the various herbivore species,
238 which entered the models as separate explanatory variables. We assumed that the contribution
239 of these variables to persistence or transition has operated from 1975 to 2008. All the
240 explanatory variables were converted to a raster map of 30 m x 30 m grid cells using Arc Map
241 software.

242 Regular sample point files were created for each model and for each time interval, with
243 sampling points 1000 m apart from each other. The Intersect Point Tool (Beyer, 2004) was
244 used to extract values from the raster maps of the explanatory variables. Only points that
245 intersected with locations of sclerophyllous forest or *Acacia* savannas presented in the earliest
246 maps were used for logistic regression analysis. We excluded cultivation in the analyses of
247 drivers because we were mostly interested in the environmental factors potentially explaining

248 changes between forest and savanna vegetation. The economic and social factors explaining
249 changes in cultivated land are more complicated than the set of biophysical and disturbance
250 factors explored in this paper. For each time interval, we entered the explanatory and response
251 variables of the intersected points into R statistical package to generate the logistic regression
252 models.

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

261

262 **Results**

263 *Proportions and rates of land cover change*

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

269 *Acacia* savanna was the most persistent vegetation type (44.2%) across the entire study
270 period despite the 30.8 % loss of its initial cover as a result of land cultivation (Figure 2).
271 About 15.1% of the initial *Acacia* savanna cover changed into bare soil and only 6.3% had
272 turned into sclerophyllous forest by 2008. The rates of *Acacia* savanna loss into cultivated land

273 or bare soil increased in every period, and the rate of change into cultivation was higher than
274 the rates of change into forest and bare soil (Figure 3B).

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

283

284 *Drivers of land cover change*

285 The probability of forest transition into *Acacia* savanna was consistently and positively related
286 to slope aspect in all time periods. North facing slopes were more likely to experience forest
287 loss into savanna (Table 2A). Also the proximity of roads and cities tended to increase the
288 probability that forest changed into savannas. Since 1985, increasing distance to forest
289 remnants increased the probability of forest change into savannas. Only the topographic
290 wetness index showed a consistent and negative relation with the probability of this transition
291 across time, meaning that with increasing soil water availability forests were less likely to turn
292 into savanna. Since 1999, increasing elevation became a significant variable that reduced the
293 probability of forest transition into savanna; forests at higher elevation were thus more likely to
294 persist (Table 2A).

295 The transition probability of *Acacia* savanna to sclerophyllous forest decreased in all
296 time intervals especially with increasing distances to forest remnants and on north facing slopes
297 (Table 2B). The variables elevation and distance to roads showed an inconsistent contribution

298 to the probability of this transition across time. For the time interval 1975-1985, the probability
299 was higher at higher altitudes and increasing distance to roads. However, in the following
300 period 1985-1999, the pattern reversed (Table 2B) indicating increased human ecosystem
301 pressure towards higher altitudes and further away from roads. This is also suggested by the
302 patterns of regeneration in the time interval 1999-2008, when the probability of forest
303 regeneration from *Acacia* savanna also decreased on steep slopes.

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

309

310 *Effects of fire and domestic herbivores*

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

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

318

319 **Discussion**

320 *Forest-Acacia savanna transitions*

321 *Acacia* savanna covered the largest part of the study region over the last 33 years being highly
322 persistent despite its overall reduction. In contrast, sclerophyllous forests were far less

323 persistent and transformed into *Acacia* savanna at increasing rates. Expansion of *Acacia*
324 savanna was the main contributor to forest loss. Our results indicate that the sclerophyllous
325 forest loss may be larger than commonly considered, with a gradual trajectory, as forest may be
326 first converted into *Acacia* savanna rather than directly cleared. This supports the idea that
327 *Acacia* savanna is an intermediate condition in a process of ongoing forest degradation that has
328 provided opportunities for exotic species to invade and become naturalized (Fuentes et al.
329 1989; Ovalle et al., 1990, 1996). Forest fragmentation has facilitated the successful expansion
330 of many exotic species, particularly herbaceous plants from the Mediterranean Basin (Arroyo et
331 al., 2000; Figueroa et al., 2004), and tree species such as *Pinus radiata* (Bustamante et al.,
332 2003). The conversion of forests into *Acacia* savannas may further increase this process. For
333 instance, whereas exotic annuals may represent 50% of the herbaceous flora of fragmented
334 sclerophyllous forests (Figueroa et al., 2004), they can reach up to 95% in *Acacia* savannas
335 (Ovalle et al., 1990). Our results also indicate that forest regeneration from *Acacia* savanna,
336 although difficult, may be possible in moister areas closer to forest remnants. This suggests that
337 *Acacia* savanna might also act as an intermediate successional stage for sclerophyllous forest
338 recovery (Armesto and Pickett, 1985; Fuentes et al., 1984, 1986). Forest regeneration from
339 former savannas seems, however, increasingly difficult since *Acacia* savannas are being
340 transformed into plantations and bare soil at increasing rates.

341 Sclerophyllous forests were less likely to be degraded into *Acacia* savannas on locations
342 with high water availability and southern expositions, and forest regeneration from *Acacia*
343 savanna was more likely to occur on south facing slopes. In Chile, northern exposed slopes are
344 drier and warmer (Armesto and Martínez, 1978). Our models emphasize the importance of
345 water availability, indicated by topography, for forest persistence and decreased probability of
346 degrading into *Acacia* savannas. Similarly, they contribute to the explanation of the distribution
347 of sclerophyllous forest remnants mostly on south facing slopes and moister ravines (Fuentes et

348 al., 1984, 1986; Schulz et al., 2010), whereas *Acacia* savannas cover the more northern exposed
349 slopes and most of the relatively dry Intermediate Depression (Ovalle et al., 1990, 1996). Once
350 established, *Acacia* savannas can be very persistent even on locations with relatively high water
351 availability where sclerophyllous forest could otherwise be expected.

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

365 Our results revealed that vegetation changes between *Acacia* savanna and
366 sclerophyllous forest are closely related to distance to forest remnants. The persistence of
367 forests as well as the probability of forest regeneration from *Acacia* savanna increased with
368 proximity to forest patches. Shultz et al. (2011) also concluded that forest regeneration in
369 central Chile was enhanced closer to forest patches, particularly in isolated areas and steeper
370 slopes. These results demonstrate the importance of mature sclerophyllous vegetation for seed
371 dispersal (Jiménez and Armesto, 1992) and seedling recruitment of sclerophyllous tree species
372 at the landscape scale (Fuentes et al., 1984, 1986; Holmgren et al., 2000a; Rey Benayas et al.,

373 2008). The persistent condition of Chilean *Acacia* savannas contrasts with the transitional
374 nature of *Quercus* savannas in the Mediterranean Basin (Mazzoleni et al., 2004; Acácio et al.,
375 2009) and resembles the role of persistent *Cistus* shrublands in arresting succession of
376 Mediterranean oak forests (Acácio et al., 2007, 2009, 2010).

377

378 *Further land degradation into bare soil*

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

392

393 *The role of domesticated livestock*

394 Surprisingly, the models including livestock density did not reveal any significant effect on
395 vegetation change at the landscape scale. We only had spatial data on domesticated herbivores
396 for the last ten years of the study period and for a relatively small subset of locations. These

397 may have been insufficient to reveal their effect on the landscape. Interviews to landowners
398 during our fieldwork indicate that they perceive the impact of cattle as an important contributor
399 to explain the loss of forest and the persistence of *Acacia* savanna in their properties. Also
400 earlier studies have highlighted the role of livestock as a major disturbance factor in central
401 Chile (Fuentes et al., 1989). In general, herbivores play a significant role in explaining
402 vegetation changes in all Mediterranean regions (e.g. Jaksic and Fuentes, 1980; Fuentes et al.,
403 1983; Mill, 1983, 1986; Gómez-Sal et al., 1999; Holmgren and Scheffer, 2001; Gutiérrez et al.,
404 2007; Pulido et al., 2010). **Clearly, the relative importance of drivers changes spatially and
405 temporally. New crops and forestry plantations have become the main drivers of land use
406 change in central Chile in the last 30 years (Armesto et al., 2010; Schultz et al., 2010). In
407 contrast, since the 1960s, major socioeconomic changes in Mediterranean Europe led to a
408 gradual abandonment of traditional agriculture and stimulated rural exodus (Pinto-Correia,
409 2000). Nevertheless, former cultivation and grazing left a signature in the landscape. Lack of
410 forest regeneration has been explained by former management in combination with higher
411 frequency of fire and droughts particularly on drier sites (Acácio et al., 2007, 2009, 2010).**

412

413 **Conclusions**

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

421

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672

673

674 **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
Acacia 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

675

676

677

678 **Table 2** Results of the multivariate logistic regression models that explain the probability of
679 change of (A) sclerophyllous forest into *Acacia* savanna, (B) *Acacia* savanna into
680 sclerophyllous forest, and (C) *Acacia* savanna into bare soil. Variables that did not significantly
681 improve the models were removed (n.s.). * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

(A) Forest into savanna	'75-'85		'85-'99		'99-'08		'75-'08	
	coefficient	<i>p</i>	coefficient	<i>p</i>	coefficient	<i>p</i>	coefficient	<i>p</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	***
	N=1610		N=1207		N=1146		N=1506	
(B) Savanna into forest	'75-'85		'85-'99		'99-'08		'75-'08	
	coefficient	<i>p</i>	coefficient	<i>p</i>	coefficient	<i>p</i>	coefficient	<i>p</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	***
	N=3257		N=3474		N=3072		N=2646	
(C) Savanna into bare soil	'75-'85		'85-'99		'99-'08		'75-'08	
	coefficient	<i>p</i>	coefficient	<i>p</i>	coefficient	<i>p</i>	coefficient	<i>p</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.	-	-
	N=3753		N=3236		N=3105		N=3276	

682

683

684 **Table 3** Results of multivariate logistic regression models that included the number of fires for
 685 the period 1985 to 2008. Variables that did not significantly improve the models were removed
 686 (n.s.). * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

687

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	***
	N=1144		N=3176		N=3522	

688 **Legends to the figures**

689

690 **Figure 1** Study region in central Chile. A: sclerophyllous forest. B: *Acacia* savanna. (Photo ©

691 M. Holmgren)

692

693 **Figure 2** Transitions between 1975 and 2008 among four major land cover classes. Percentages

694 are presented as the proportions of that land cover class in 1975 that changed or remained in

695 2008. Below the percentages is the corresponding number of hectares. The class ‘cultivation’

696 includes ‘agricultural crops’, ‘pastures’ and ‘plantation’ (Table 1).

697

698 **Figure 3** Annual transition rates per time interval as percentage of initial land cover type in

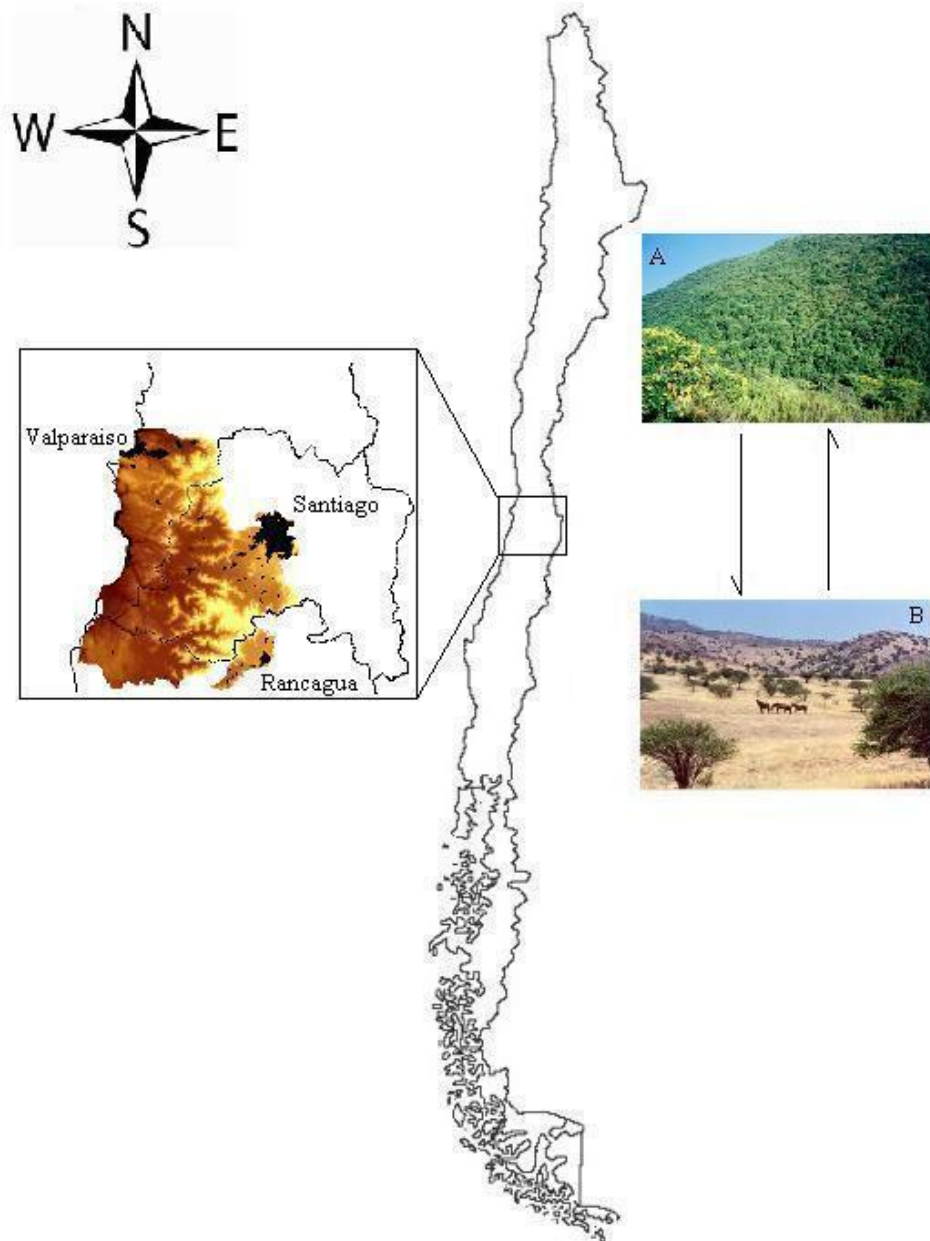
699 each time interval.

700

701

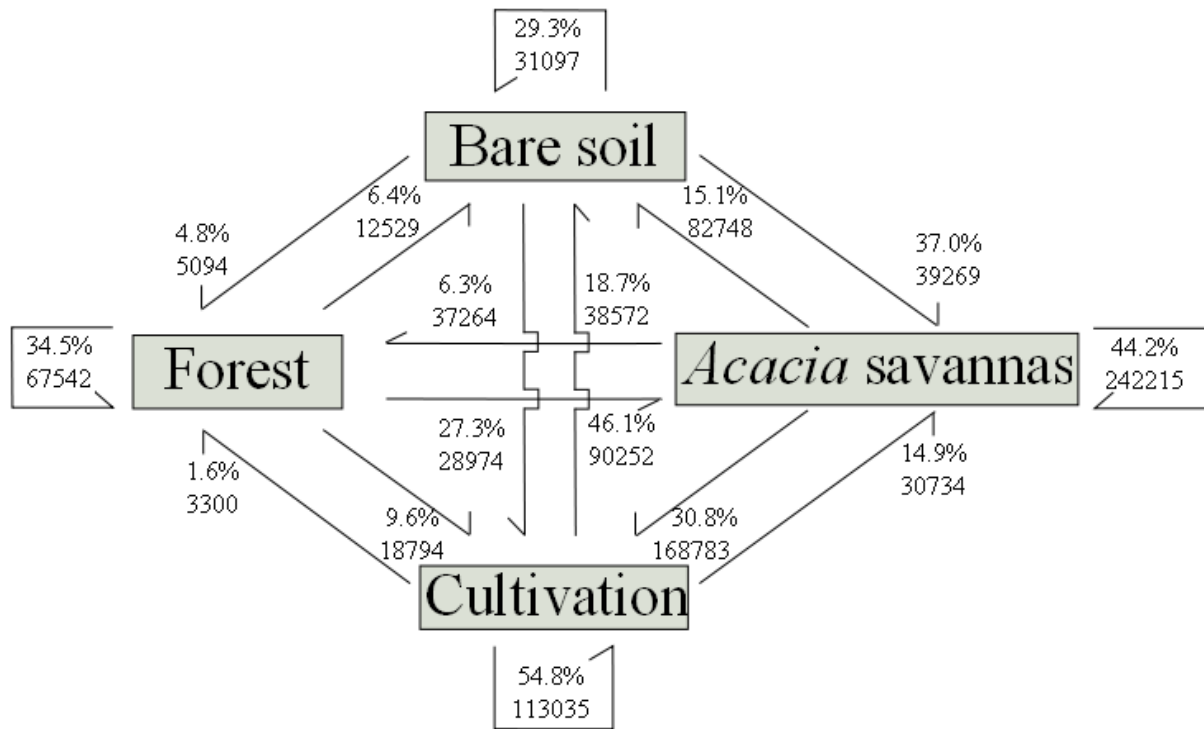
702

703 **Figure 1**



704

705 **Figure 2**

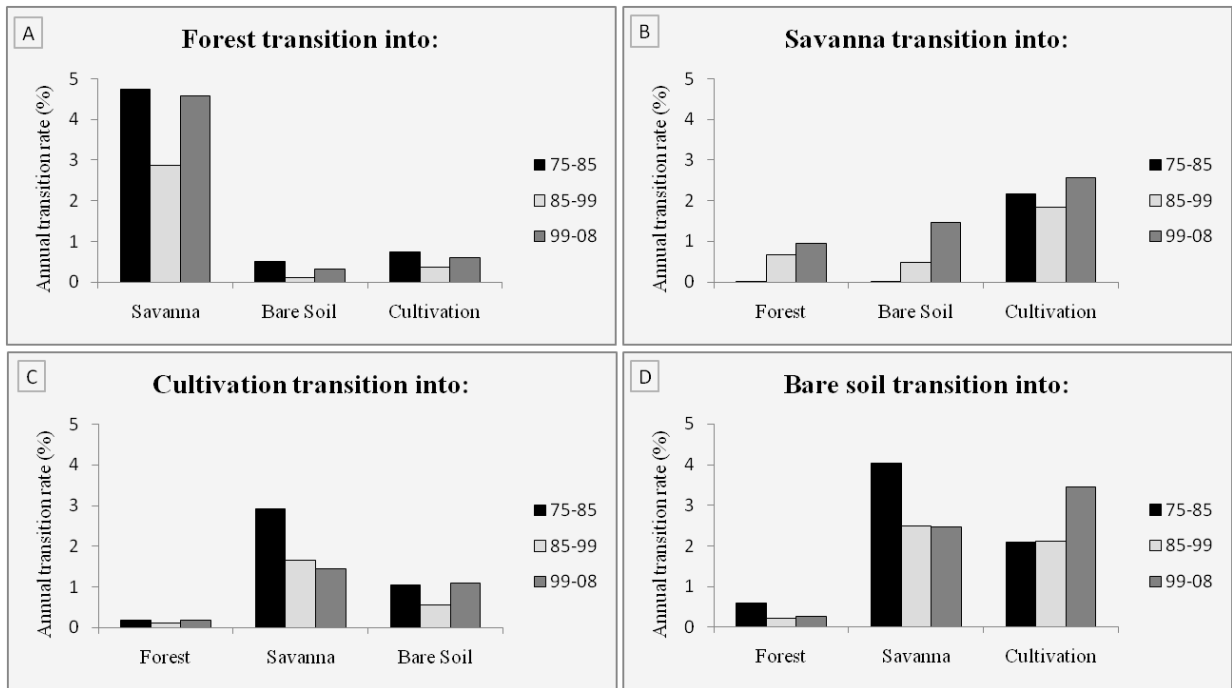


706

707

708 **Figure 3**

709



710