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Contents lists available at SciVerse ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Nucleated regeneration of semiarid sclerophyllous forests close to remnant vegetation

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ARTICLE INFO

Article history:

Received 14 October 2011

Received in revised form 14 February 2012

Accepted 19 February 2012

Keywords:

Chile
Facilitation
Mediterranean
Nurse plant
Positive interaction
Succession

ABSTRACT

Natural regeneration of mediterranean plant communities has proved difficult in all continents. In this paper we assess whether regeneration of sclerophyllous forests shows nucleated patterns indicative of a positive effect of vegetation remnants at the landscape level and compare the regeneration patterns between sites with distinctive climate conditions. We studied the spatial patterns of vegetation change during 52 years in central Chile using remotely-sensed images to test the predictions that (1) regeneration of sclerophyllous vegetation expands from patches of remnant vegetation; and (2) regeneration is more dependent on remnant vegetation in drier sites. Our results show that the regeneration of the sclerophyllous vegetation in central Chile is a slow process that may be possible under certain conditions. We found that the fraction of regenerated vegetation increases with the proximity to remnant sclerophyllous forest in an aggregated pattern. Especially in drier sites, vegetation remnants have a facilitative role on the regeneration of mediterranean-type ecosystems. These results have important implications for the management and conservation of these ecosystems.

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1. Introduction

The regeneration of mediterranean-type ecosystems has proved to be difficult and irregular in all continents, including southeast Australia (Westoby et al., 1989), California (Laycock, 1991), central Chile (Fuentes et al., 1984, 1986), the Mediterranean Basin (Kéfi et al., 2007; Acácio et al., 2009) and southwest South Africa (Vlok and Yeaton, 2000). Understanding the conditions under which natural regeneration may be possible is highly relevant for restoration planning since active restoration attempts can be notoriously unsuccessful and costly (Rey-Benayas et al., 2008). Natural regeneration may represent an opportunity for the conservation of these global hotspots of biodiversity, characterized by high levels of floristic richness and endemism (Myers et al., 2000; Olson and Dinerstein, 2002), and suppliers of provisioning, regulating and cultural services for human populations (Millennium Ecosystem Assessment, 2005).

Regeneration of the original mediterranean-type forests and evergreen shrublands is mostly slowed down by limited seedling establishment (Fuentes et al., 1984; Retana et al., 1999; Holmgren et al., 2000), and the persistence of pioneer vegetation stages that maintain the ecosystem in a condition of arrested succession (Vicente and Ales, 2006; Acácio et al., 2009; Van de Wouw et al., 2011). Experimental evidence indicates that tree seedling recruitment is generally limited by multiple ecological factors affecting seed predation and dispersion, as well as germination, growth and survival of seedlings (Fuentes et al., 1986; Retana et al., 1999; Acácio et al., 2007), which interact with land use and management practices to further difficult vegetation change (Acácio et al., 2010).

One of the most important lessons learnt from the restoration of mediterranean-type ecosystems has been the recognition of shade availability as a crucial condition for enhancing seedling establishment. In a comprehensive assessment of the experiences in Spain, Gómez-Aparicio et al. (2004) concluded that shrubs act as nurse plants enhancing the recruitment of tree seedlings in reforestation programs. Under the nurse canopy, the microclimate is cooler and often also moister, ameliorating plant thermal and water stress (Holmgren et al., 1997). This positive effect of the nurse canopy is often essential for seedlings to survive the summer drought that

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characterizes all mediterranean-type ecosystems (Fuentes et al., 1984; Holmgren et al., 2000; Gómez-Aparicio et al., 2004). In addition, nurse plants can increase soil nutrients (Holmgren et al., 1997; Padilla and Pugnaire, 2006) or protection from herbivores (Baraza et al., 2006). Nurse plants can also enhance seed availability by attracting seed dispersers, such as birds or mammals (Debussche et al., 1982; Pausas et al., 2006), amplifying the effects of environmental stress amelioration.

Since the net effect of the interaction between plants is an unavoidable interplay of positive and negative effects, plant interactions can switch from facilitation to competition if stress amelioration under the nurse shade is insufficient to compensate for the limitation in light availability (Holmgren et al., 1997). This can happen under very stressful conditions when resources, as soil water, are too limiting (Maestre et al., 2009), or when the capacity of nurse plants to change environmental conditions is insufficient to ameliorate stress in a significant way (Holmgren and Scheffer, 2010). For instance, in some very dry Mediterranean systems, positive interactions become neutral or negative if competition for soil water overrides the positive effects of the canopy on reducing thermal stress (Maestre and Cortina, 2004). These empirical results have inspired current theoretical models predicting either a linear increase in facilitation as environmental stress becomes more stressful (Bertness and Callaway, 1994) or a maximum effect of facilitation at intermediate conditions of abiotic stress (Maestre et al., 2009; Holmgren and Scheffer, 2010). These experimental findings and theoretical models suggest therefore that natural regeneration of mediterranean-type vegetation should be particularly dependent on nurse plants under dry sites, but indicate also potential limits to the role of positive interactions under very stressful conditions. At a landscape level, regeneration should be then characterized by a patchy spatial pattern of vegetation growth expanding from remnant vegetation patches, especially at drier sites.

In this paper, we assess if the long-term regeneration of sclerophyllous forests in central Chile shows nucleation patterns indicative of a positive effect of vegetation remnants at the landscape level, and compare the regeneration patterns between sites with distinctive climate conditions. Most of the original vegetation of this region has been destroyed by agricultural and urban growth (Schulz et al., 2010), or replaced by early successional plant communities (Fuentes et al., 1989; Van de Wouw et al., 2011) in a long historical process of landscape fragmentation and degradation (Armesto et al., 2010). Field experiments in central Chile have demonstrated that tree seedling survival can be extremely rare, particularly in drier sites, as result of desiccation and severe herbivory (Fuentes et al., 1984, 1986; Holmgren et al., 2000; Gutiérrez et al., 2007; Becerra et al., 2011), as well as intense and frequent fires (Fuentes and Muñoz, 1995; Segura et al., 1998). These field experimental results have been essential to understand the role of shrub patches on the regeneration of vegetation, but have been conducted at small scales and monitored for a couple of years only (but see Holmgren et al., 2000). On the other hand, remote-sensed studies have identified the drivers correlated with large scale patterns of vegetation change during the last 40 years (1975–2008; Schulz et al., 2011; Van de Wouw et al., 2011), but did not assess the role of vegetation remnants on the regeneration of sclerophyllous forests at a landscape scale. We studied the spatial patterns of vegetation change in a period of 52 years using remotely-sensed images to test the predictions that (1) regeneration of sclerophyllous vegetation expands from patches of remnant vegetation; and (2) regeneration is weaker under drier conditions (north-facing slopes, inland sites and further away from ravines).

2. Methods

2.1. Study area

The study sites were located in the Valparaíso and Metropolitan administrative regions of Chile (Fig. 1; Appendix A). The climate is Mediterranean with rainfalls concentrated in winter and dry summers. Microclimatic conditions differ strongly between coastal and inland sites as result of the influence of the cold Pacific Ocean. In the Coastal range temperatures are moderate, precipitation is higher than inland, and morning fogs are frequent (Cereceda, 1989), which most likely reduce plant heat and water stress during the dry summer months and enhance seedling survival (Fuentes et al., 1984, 1986; Holmgren et al., 2000). The vegetation of this region (locally known as 'matorral') is characterized by evergreen sclerophyllous forests (Gajardo, 1994; Luebert and Plissock, 2006) with a rather continual cover on coastal and south-facing slopes and a highly fragmented structure in the inland Andean foothills and north-facing slopes (Fuentes et al., 1984, 1986). Although species composition overlaps across the region, local plant communities respond strongly to topographical and latitudinal gradients (Villagrán, 1995) as well as to the different microclimatic conditions present in the coastal and inland sites (Luebert and Plissock, 2006).

In order to be able to detect forest regeneration, we searched for unburned sites. We used georeferenced fire occurrence data obtained from the Chilean Forest Fire Protection Department of CONAF (National Forestry Corporation) to select sites that had remained unburned since at least 1985 when the fire records started. We selected only sites with evident vegetation cover increase after comparing 1955 aerial photographs and actual Google Earth images. We found five sites meeting both criteria (Appendix A): three sites were located on the Andean foothills close to Santiago (San Carlos de Apoquindo, Cerro Blanco, and Santa Rita), and two sites were located on the Coastal range (Cachagua and Los Molles). The scarcity of sites reflects the large degree of disturbance in central Chile and agrees with the findings of large scale remote-sensed assessments (Schulz et al., 2010; Van de Wouw et al., 2011). This implies that the effect of vegetation patches we describe here is applicable to situations where anthropic effect is low (no fires) and forest regeneration has been possible. The study sites were approximately of the same size (mean 760 ha), with Haploxeroll soils (Luzio et al., 2009), and covered by a mosaic of fragmented sclerophyllous forest within a matrix of open pastures, early pioneer scrubs and bare grounds (Fig. 1; Appendix A). These sites have been probably affected by herbivory by rabbits and domestic livestock, as well as by wood extraction which are common disturbances in central Chile.

2.2. Image processing

Vegetation cover was estimated for 1955, 1983 and 2007. We used two aerial photographs taken during the Hycon and Chile-30 fly-overs in 1955 and 1983, respectively; and one Spotmaps satellite image from 2007. With these images, we evaluated the vegetation changes during two consecutive periods (1955–1983 and 1983–2007) as well as the 52 years period between 1955 and 2007. For the temporal analysis, we undertook a co-registration process for each pair of images using the geometric correction module in ERDAS 9.1. We used the Rubber Sheeting method (Doytsher and Gelbman, 1995), with a variable number of 150–200 common points in the images, and resampling in the Spotmaps georeferenced grid with 2.5 m of spatial resolution. To quantify

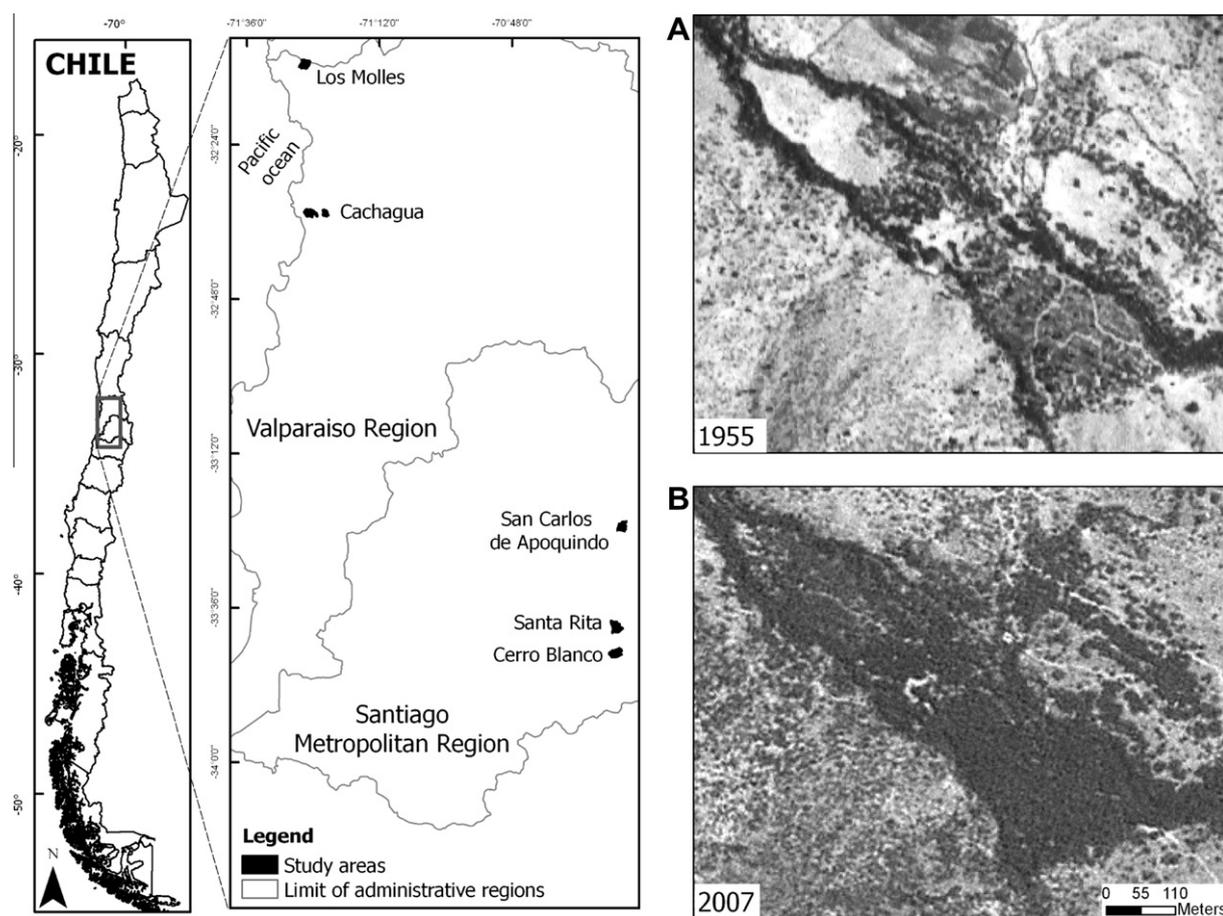


Fig. 1. Study sites in central Chile: Los Molles, Cachagua (Coastal slopes), San Carlos de Apoquindo, Santa Rita and Cerro Blanco (Andean slopes). Right panels illustrate the increase of evergreen vegetation between (A) 1955 and (B) 2007 detected in Cerro Blanco.

forest cover and spatial distribution, we used a supervised classification developed in ERDAS 9.1 with the maximum likelihood algorithm. In order to do this, we visited each study site to recognize the different vegetation types and compare them with the landscape composition patterns in the 1955 and 1983 aerial photos. We selected patches that had remained unchanged in all periods and used them for training areas in the supervised classification analysis. In each image, we identified two thematic classes: class 0 (i.e. bare soil and pasture lands with early pioneer scrubs) and class 1 (i.e. woody cover with sclerophyllous evergreen forest and dense pioneer species). Because of the image spectral resolution, it was impossible to distinguish between early and late successional woody plant communities.

The supervised classification of the 2007 image for each site was validated through an accuracy assessment (Congalton and Green, 1999) using 20 ground control points for each thematic class (i.e. 40 points in total for each site). The ground control point distribution was originally developed by generating a random point set. However, the difficult accessibility of some areas forced us to choose for accessible sampling points representative of each thematic class and suitable for subsequent fieldwork. Finally, the accuracy assessment calculation was made by building a confusion matrix for each study area, which consists in comparing the field observation with thematic classification. The accuracy of each thematic classification was determined by the overall Index of Accuracy expressed by the percentage of pixels that had been correctly assigned to each thematic class (Story and Congalton, 1986). The accuracy assessment of each thematic classification

was fairly high: San Carlos de Apoquindo (89%), Cerro Blanco (95%), Santa Rita (93%), Cachagua (92%) and Los Molles (95%).

2.3. Landscape variables and forest regeneration

We related vegetation change to six landscape variables which could potentially influence forest regeneration: exposure, elevation, distance to ravines, solar radiation index (Fu and Rich, 2000), topographic wetness index (TWI) (Beven and Kirkby, 1979; O'Loughlin, 1981), and distance from remnant forest patches at the start of the study period (1955 or 1983). Each variable was presented as a 5×5 m spatial resolution in a Geographic Information System (GIS).

We obtained a Digital Elevation Model (DEM) with 5×5 m spatial resolution for each study site using the Orthobase module of ERDAS 8.6 and used it to derive the landscape variables. The TWI variable is an indicator of potential water availability and is calculated as $\ln(a/\tan \beta)$, where β is the local slope of the ground surface and a is the upslope area per unit contour length, computed as $a = A/L$, where A (in m^2) is the upslope area and L (in meters) is the contour length. A high TWI value is assigned to relatively flat locations with a large upslope area, which are expected to have relatively higher water availability than sloping locations with a small upslope area, with a low TWI value (Beven and Kirkby, 1979; O'Loughlin, 1981; Wilson and Gallant, 2000).

The solar radiation index was calculated using the Solar Radiation module of ArcGIS 9.2 to estimate the total solar radiation during one year in each location of the digital elevation maps. This

index takes into account atmospheric effects, latitude, elevation, slope and aspect, and effects of shadows cast by surrounding topography.

To evaluate vegetation change in each time interval (period 1: 1955–1983, period 2: 1983–2007 and total: 1955–2007), we assigned as class “1” those transitions from open patch conditions (bare soil, grassland or scrub) to evergreen vegetation and as class “0” if the open condition remained unchanged until the end of a given period (i.e. transition 0–0 and 0–1). Any other transition was discarded from the analysis. This means that we studied only the vegetation changes towards forest regeneration.

2.4. Plant species composition

In the spring of 2010, we conducted vegetation surveys to identify which species were responsible of the changes in vegetation patch condition at each site. We sampled the three types of transitions; 0–1 (increased evergreen cover), 1–1 (evergreen cover unchanged) and 0–0 (open condition unchanged). We chose 10 sampling points for each type of transition detected between 1955 and 2007. The coordinates of each point were considered as the center of a circle with a diameter able to include the unavoidable errors of the image-resolution and GPS location. We established a 10-m diameter circle with two perpendicular transects crossing through the center (north–south and east–west transects). Along these transects, we used the line-transect technique to estimate the relative cover of each adult woody species, grasses, and bare soil (Canfield, 1941). In addition, we counted and identified all seedlings of woody species (<20 cm tall) along each transect increasing the area 0.5 m at each side of it, to calculate seedling density in a 19 m² area per sampling point.

2.5. Statistical analysis: drivers of forest regeneration

We subdivided the area of each site using a grid of 250 × 250 m per cell, resulting in about 147 ± 19 cells per site (mean ± SD). In each cell, we calculated the fraction of patches (5 × 5 m) that switched to an evergreen forest condition during each study time interval as a measure of forest regeneration, and used it as response variable on statistical modeling.

We used three types of models to analyze the relationship between forest regeneration and the landscape variables: multiple linear regression, autoregressive model (AR), and simultaneous autoregressive model (SAR). To assess which of the three regression models best fitted the data, we selected the model with the lowest value of AIC (akaike information criterion) (Johnson and Omland, 2004).

Prior to fitting the multiple regression models, we assessed if all model assumptions were met. To meet the assumption of residuals normally distributed (Legendre and Legendre, 1998) we logit transformed the response variable (i.e. $\text{logit}(p) = \ln[p/(1-p)]$), where p is the fraction of 5 × 5 m patches that recovered sclerophyllous forest in the 250 × 250 m cell (Fox, 2002). To assess the linearity of the explanatory variables we used generalized additive models (GAM; Wood, 2001), and to evaluate the degree of correlation between explanatory variables we conducted a multicollinearity analysis with variance inflation factor (VIF; Fox, 2002), as result, we removed the solar radiation index because it was highly correlated with the topographic wetness index (TWI). To verify the assumption of spatially independent observations, we evaluated the spatial autocorrelation of the residuals using Moran's correlograms (Moran, 1950). Correlograms were constructed at regular distance intervals (250 m). For each distance class (d), we performed 1000 permutations to verify if autocorrelation level was significantly different from random and tested with sequential Bonferroni correction (Legendre and Legendre, 1998).

We used two autoregressive spatial regression models that model the spatial dependence of variables (Legendre, 1993; Keitt et al., 2002): the autoregressive model (AR) models spatial autocorrelation of the dependent variable, and the simultaneous autoregressive model (SAR) models the spatial autocorrelation of residuals (Legendre and Legendre, 1998; Keitt et al., 2002; Overmars et al., 2003). In the AR model, the autocorrelation function reveals an endogenous spatial process (e.g. limited seed dispersion of matorral plant species), whereas in the SAR model, the autocorrelation function reflects an exogenous spatial process (e.g. aggregated favorable microclimatic or soil conditions) (Keitt et al., 2002).

2.6. Statistical analysis: plant species composition

We used generalized linear models to evaluate how the number of seedlings of sclerophyllous evergreen species was affected by site location (Andean or Coastal) and the type of vegetation transition recorded. We used a negative binomial distribution because seedling distribution was aggregated in few points.

For all statistical analyses we used R software, version 2.10.1 (R Development Core Team, 2009) and associated packages: car (Fox, 2002), MASS (Venables and Ripley, 2002), mgcv (Wood, 2001) and spdep (Bivand, 2001).

3. Results

3.1. Spatial patterns of woody cover increase

The multi-temporal image analysis showed an increase of woody vegetation cover in all study sites and periods analyzed. However, vegetation regeneration was lower between 1955 and 1983 than between 1983 and 2007 in at least three sites (Cachagua, San Carlos de Apoquindo, Cerro Blanco; Fig. 2).

We found a positive spatial autocorrelation in the first lag distance (250 m), indicating that the regeneration of woody vegetation in areas adjacent to each cell was more similar and aggregated than expected by random (Moran Indexes I_m , $p < 0.05$, see Appendix B). Woody cover increase was more likely to occur in areas immediately adjacent to regenerating patches as expected by a nucleation model of vegetation change.

Unlike the linear regression models, spatial regression models removed the positive spatial autocorrelation of the residuals and improved the overall fit in all analysis (lower AIC and higher R^2 , Table 1), indicating that cover increase was best explained by landscape features that are autocorrelated in space. The spatial model most frequently selected was SAR (9 of 13 times, Table 1). This effect reveals that areas with environmental conditions that favor vegetation regeneration are spatially aggregated (Keitt et al., 2002; Overmars et al., 2003). We found that the regeneration of sclerophyllous vegetation increases close to remnant patches of forest (negative relationship with “distance to forest” variable), on south-facing slopes (negative relationship with northing), higher altitude (positive relationship with “elevation”) and increased exposure towards the west (negative relationship with easting). On the other hand, evergreen vegetation regeneration decreased with the proximity to ravines (positive relationship with “distance to ravine”). In the sites with ravines, the fraction of forest regenerated was significantly larger at 15 m or more from the ravines (T test = 2.716, d.f. = 137, $p = 0.0075$).

The spatial regression models explained a higher percentage of variance in the Andean foothill sites (65% on average) than in the coastal sites (46% on average) suggesting that the nucleating pattern of woody cover expansion is stronger in the inland sites (Table 1). In the drier Andean sites, vegetation regeneration was positively correlated with moister areas as suggested by higher TWI

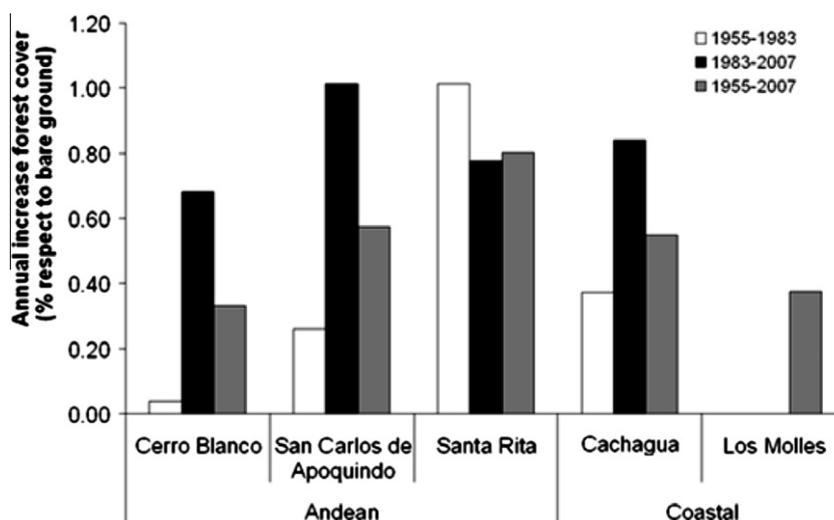


Fig. 2. Annual increase in forest cover (% respect to bare ground) during each study period for each study site (Data for 1983 is not available for Los Molles).

Table 1
Selected variables in the best regression models describing increase in evergreen vegetation cover in each study site and period. Variables were ordered by descending contribution to final model. The signs before each variable indicate whether the relationship was positive or negative. Note that the best fit (by lower values of AIC) was always obtained with spatial regression models.

Zone	Study site	Period (years)	Variables selected	Non spatial model		Spatial model			
				AIC	R ²	Best fit	AIC	R ²	N
Coastal	Cachagua	55–07	– Distance to forest – northing + elevation	429.12	0.49	SAR	408.15	0.60	177
Coastal	Cachagua	55–83	– TWI – northing – easting	713.25	0.24	SAR	710.33	0.29	177
Coastal	Cachagua	83–07	– Distance to forest + elevation	530.43	0.31	AR	525.72	0.37	178
Coastal	Los Molles	55–07	– Distance to forest – northing – TWI	474.52	0.51	SAR	471.03	0.57	132
Andean	Cerro Blanco	55–07	– Distance to forest + distance to ravines + twi	535.91	0.50	AR	493.60	0.69	131
Andean	Cerro Blanco	55–83	– Distance to forest + twi	666.73	0.36	AR	656.17	0.46	131
Andean	Cerro Blanco	83–07	– Distance to forest + distance to ravines	482.25	0.57	SAR	472.26	0.64	131
Andean	Santa Rita	55–07	– Distance to forest + elevation + twi – northing	342.48	0.51	SAR	314.16	0.64	136
Andean	Santa Rita	55–83	– Distance to forest + distance to ravines	407.08	0.35	AR	360.68	0.59	136
Andean	Santa Rita	83–07	– Distance to forest – easting + elevation	370.6	0.41	SAR	358.86	0.49	136
Andean	San Carlos	55–07	– Distance to forest – northing	367.76	0.67	SAR	304.86	0.83	150
Andean	San Carlos	55–83	– Distance to forest – northing – easting	362.62	0.61	SAR	341.01	0.70	150
Andean	San Carlos	83–07	– Distance to forest – northing – easting	306.71	0.80	SAR	297.54	0.82	152

values, whereas the opposite trend was observed in the coastal sites.

3.2. Plant species composition and vegetation change

The proportion of bare soil in patches that had remained not colonized by woody species during the 52-year study period (patch transition 0–0) was larger in the Andean (23.4%) than in Coastal sites (11.2%) (Table 2). In the Andean sites where woody cover had increased (transition 0–1), the patches were currently dominated by drought tolerant sclerophyllous species such as *Lithrea caustica* (48.6%) and *Quillaja saponaria* (11.1%) and pioneer species such as *Acacia caven* (16.7%) and *Trevoa trinervis* (10.4%). Drought sensitive evergreen species such as *Cryptocarya alba* and *Kagenecia oblonga* were less common (Table 2). In the patches where sclerophyllous vegetation remained (transition 1–1), we found a larger diversity of native species typical of evergreen sclerophyllous forests such as *L. caustica* (56.9%), *C. alba* (20.1%), *Q. saponaria* (12.5%), *K. oblonga* (3.1%) and *Persea lingue* (1.6%) (Table 2).

In the coastal sites, patches colonized by woody species (transition 0–1) were dominated by species common to early successional stages such as *T. trinervis* (15.6%) and *Baccharis concava* (11.2%), as well as late successional ones such as *Schinus latifolius* (23.4%), *C. alba* (15.7%), *Lithraea caustica* (9.7%), *Azara celastrina*

(5.5%) and *Peumus boldus* (3.5%) (Table 2). In the forest patches that had persisted during the entire study period, we found the most common tree and shrub species native to the sclerophyllous forests of the coastal range, such as *C. alba* (73.8%) and *S. latifolius* (16.7%) (Table 2).

We found a significantly lower number of sclerophyllous tree and shrub seedlings in the Andean than Coastal sites (GLM negbin $\chi^2 = 13.38$, d.f. = 1, $p = 0.0003$). Also species diversity (especially of late successional species) among seedlings colonizing new open places was generally low in the Andean foothills and doubled in the coastal sites (Table 2).

4. Discussion

4.1. Aggregated spatial patterns of forest regeneration

Our statistical models indicate that patches where sclerophyllous forest regenerated are spatially autocorrelated, meaning that vegetation growth occurred in an aggregated way. The processes that could generate this spatial pattern are diverse. Two main types of spatial autocorrelation might be distinguished depending on whether endogenous or exogenous processes generate the spatial structure of the observations (Legendre and Legendre, 1998). Spatial pattern can be generated by factors that are an inherent

Table 2

Woody species composition in patches with different vegetation transitions between 1955 and 2007 in central Chile. Vegetation transitions are: (0–0) open patches with no recovery of sclerophyllous vegetation, (0–1) open patches with increase woody cover, and (1–1) patches where sclerophyllous vegetation remained. Data shows the abundance of adult shrubs (A; percent of cover) and seedlings (S; number of seedlings per m²) in Andean ($n = 30$ transects per transition) and Coastal ($n = 20$ transects per transition). Classification of species in early and late successional stages follows Hoffmann (1989).

Plant species	Andean						Costal					
	0–0		0–1		1–1		0–0		0–1		1–1	
	A	S	A	S	A	S	A	S	A	S	A	S
<i>Late successional stage</i>												
<i>Lithrea caustica</i>	0.2	0	48.6	0.004	56.9	0	0	0	9.7	0.01	5.2	0.01
<i>Quillaja saponaria</i>	0	0	11.1	0.002	12.5	0	0	0	1.3	0.003	2.2	0
<i>Cryptocarya alba</i>	0	0	3.7	0.002	20.1	0.09	0	0	15.7	0.1	73.8	0.1
<i>Peumus boldus</i>	0	0	0	0	0	0	0	0	3.5	0.1	1.5	0.04
<i>Schinus latifolius</i>	0	0	0	0	0	0	0	0	23.4	0.02	16.7	0
<i>Azara celastrina</i>	0	0	0	0	0	0	0	0	5.5	0.1	0	0.01
<i>Escallonia pulverulenta</i>	0	0	0	0	0	0	0	0	2.1	0.003	0.1	0
<i>Azara petiolaris</i>	0	0	0	0	0	0	0	0	0	0	0	0.01
<i>Luma chequen</i>	0	0	0	0	0	0	0	0	0.2	0	0	0
<i>Proustia pyrifolia</i>	0	0	0	0	0	0	0	0	0.9	0	0	0
<i>Maytenus boaria</i>	0	0	0.2	0	0	0	0	0	1.5	0.01	0	0
<i>Myrceugenia exsucca</i>	0	0	0	0	0	0	0	0	0.6	0	0	0.003
<i>Adesmia sp.</i>	0	0	0	0	0	0	0	0	0	0	0.5	0
<i>Kageneckia oblonga</i>	0	0	0.7	0	3.1	0	0	0	0	0	0	0
<i>Azara dentata</i>	0	0	0.8	0	0	0	0	0	0	0	0	0
<i>Persea lingue</i>	0	0	0	0	1.6	0	0	0	0	0	0	0
<i>Early successional stage</i>												
<i>Trevoa trinervis</i>	0	0	10.4	0	0	0	0	0	15.6	0	0	0
<i>Cestrum parqui</i>	0.8	0	0	0.1	0	0.04	0	0	0	0	0	0
<i>Baccharis linearis</i>	0	0	0.3	0	0	0	1.5	0	0	0	0	0
<i>Baccharis concava</i>	0	0	0	0	0	0	0	0	11.2	0	0	0
<i>Baccharis sp.</i>	0	0	0	0	0	0	5.3	0	0	0	0	0
<i>Eupatorium saliva</i>	0	0	0	0	0	0	0	0	6.1	0.01	0	0
<i>Muehlenbeckia hastulata</i>	0	0	0	0	0	0	0	0	0.5	0.01	0	0
<i>Lepechinia chamaedryoides</i>	0	0	0	0	0	0	0	0	0.2	0	0	0
<i>Flourensia thurifera</i>	0	0	0	0	0	0	0.3	0	0	0	0	0
<i>Colliguaja sp.</i>	0.5	0	5.3	0.01	3.6	0.004	0	0	0	0	0	0
<i>Adenopeltis serrata</i>	0	0	0	0	0	0	0	0	0	0	0	0.02
<i>Acacia caven</i>	0	0	16.7	0	0.3	0	0	0	0	0	0	0
<i>Rubus ulmifolius</i>	0	0	0	0	0.6	0	0	0	0	0	0	0
<i>Open patches</i>												
Pasture	75.1	0	2.1	0	0	0	81.7	0	2	0	0	0
Bare soil	23.4	0	0.1	0	1.3	0	11.2	0	0	0	0	0
Total	100	0	100	0.1	100	0.1	100	0	100	0.3	100	0.2

property of the response variable itself, such as biotic processes that are distance related (e.g. dispersal). Exogenous processes, on the other hand, can also induce spatial autocorrelation when factors independent to the response variable vary spatially as well, for example, vegetation growth may respond to geomorphological attributes that are spatially aggregated in the landscape. The ecological interpretation of statistical models is not trivial, and the distinction between the endogenous or exogenous nature of the processes involved can be challenging (Austin, 2002).

In all our models, vegetation remnants had a positive effect in forest regeneration at the landscape level. These patterns could be explained by higher seed availability or enhanced seedling survival. Most of the woody species found to be dominant in the Andean and Coastal sclerophyllous forests have fleshy fruits, which can be dispersed by many bird species (Reid and Armesto, 2011), native foxes (*Pseudalopex culpaeus*; Silva et al., 2005), and even European rabbits (*Oryctolagus cuniculus*; Castro et al., 2008). The use of vegetation patches by seed dispersers clearly contributes to the aggregation of seedlings around present shrubs, amplifying the facilitating role of nurse shrubs and accelerating the speed of plant succession. This phenomena has also been found in other mediterranean-type ecosystems (Debussche et al., 1982; Debussche and Isenmann, 1994; Pausas et al., 2006). However, the stronger nucleation at the drier Andean sites suggests an increasing positive effect of vegetation in facilitating the recruitment of other

shrubs when abiotic stress increases. Experimental studies in central Chile have demonstrated that seedlings growing under shrubs experience lower water stress and overheating, and often survive longer than in open places (Fuentes et al., 1984, 1986; Holmgren et al., 2000).

Correlative studies like this one cannot discard the possibility that the environmental conditions close to remnant forest patches are intrinsically better for plant growth, regardless of the effect of vegetation on the environmental conditions that affect seedling establishment. The only way to assess that is by conducting field experiments in which seedlings are planted at different distances from the forest patches and the factors that may affect seedling survival are manipulated. However, vegetation patches in arid and semiarid ecosystems are known to strongly affect the environmental conditions in their surroundings. These ecosystems often show mosaic vegetation patterns, with patches that have a relatively high plant biomass dispersed in a matrix of poorly vegetated land. Several mechanisms can play a role in the maintenance of these patchy patterns, including overgrazing, fire, plant-soil interactions and plant-plant facilitation (e.g. Aguiar and Sala, 1999). Vegetation patches tend to accumulate soil and water, becoming "islands of fertility" with the most favorable conditions for plant growth (Schlesinger et al., 1990). This patchiness of resources and plant biomass is self-reinforcing, resulting in persistent patchy patterns (Schlesinger et al., 1990). The sclerophyllous vegetation in

central Chile is also characterized by a patchy configuration (Fuentes et al., 1984, 1986). The aggregated pattern in forest regeneration closer to remnant forest is most likely explained by the positive effects of shrub patches on seed dispersal, as well as seedling growth and survival.

Shrubs have proved to facilitate the active restoration of ecosystems in the Mediterranean Basin by enhancing the establishment of planted tree seedlings (Gómez-Aparicio et al., 2004). Our results show that remnant vegetation patches can also improve the natural regeneration of sclerophyllous forests. The role of forest remnants in enabling secondary succession by ameliorating harsh microclimate conditions and improving soil structure, fertility, and biota is becoming increasingly recognized (Rey-Benayas et al., 2008).

4.2. Topographical effects on forest regeneration

After 52 years, we found enhanced natural regeneration on south-facing slopes, in topographical locations with potentially moister soils, and at higher elevation. These landscape features are associated with lower abiotic stress and human accessibility, and have been found to be important in studies conducted at larger spatial scales in central Chile (Schulz et al., 2011; Van de Wouw et al., 2011) as well as in other Mediterranean ecosystems (Kéfi et al., 2007; Acácio et al., 2009).

We found lower regeneration very close to ravines (less than 15 m from the ravine). Ravines are characterized by dense forests as result of moister conditions, difficult access, and legal protection by Chilean environmental laws. This result seems paradoxical at a first glance, since one would expect the moister and cooler microclimatic conditions of the ravines to enhance seedling establishment in dry ecosystems. Earlier studies suggested that the turnover of vegetation in closed secondary forests of mesic sites in central Chile is low (Armesto and Pickett, 1985; Armesto et al., 1995). Using a combination of field experiments, Holmgren et al. (2000) concluded that the main reason for the low turnover in existing mesic forest is related to poor seedling growth and survival (and not to seedling germination and emergence). Indeed, in their experiments, seedlings from planted seeds emerged in high numbers under the deep canopy of the forest but died faster there than in large open patches. They also suggested that low light availability restricts successful seedling establishment to only very shade tolerant species such as *C. alba*. Drought sensitive species often find a refuge in the moist and shady conditions of the ravines (Hoffmann, 1989), and may be unable to expand into the surrounding drier areas. A comparable condition was recently studied by Van Zonneveld et al. (2012) in north-central Chile, where relict temperate rainforest patches grow on the coastal mountain tops and are surrounded by arid scrub communities. They found that forest species were unable to recruit in the dry scrublands, maintaining a sharp boundary between the two plant communities.

These patterns of vegetation establishment in the mesic ravines contrast strongly with those found in drier sites. Our spatial analysis and earlier experimental results (Fuentes et al., 1984) demonstrate the importance of remnant forests for successful regeneration especially in drier areas. In recent meta-analyses of the published experiments on the interactive effects of shade and drought on plant performance, Holmgren et al. (2011) concluded that the positive effects of shade tend to be non-linear reaching a maximum at intermediate irradiance conditions.

4.3. Forest regeneration in Andean and Coastal sites

Our vegetation surveys indicate that the regeneration of the species composition of the sclerophyllous forests can be very slow and probably dependent on overall climate conditions. In the Andean foothills, tree and shrub cover expansion into open patches

was dominated by early successional (*T. trinervis*, *A. caven*) and drought tolerant species (*Lithrea caustica*, *Q. saponaria*). After five decades, the relative abundance of species more sensitive to water stress was much lower in recolonized patches compared to those that had remained as forests during the same period. For instance, *C. alba* represented less than 4% of the plant cover of recolonized patches whereas it covered more than 20% of those patches where forest had remained (Table 2).

Regeneration of the sclerophyllous vegetation seems to progress more easily in coastal sites but also there drought intolerant species (*C. alba*) seem to recover more slowly than drought tolerant ones (*L. caustica*, *Q. saponaria*) and early successional species (*T. trinervis*, *B. linearis*) remain notoriously abundant. These results indicate that despite positive changes in tree and shrub cover, the regeneration of the original plant species composition may be difficult in these semiarid ecosystems. Particularly in dry sites, the successional trajectories of disturbed mediterranean-type ecosystems may be arrested in persistent stages dominated by early successional species (Fuentes et al., 1989; Holmgren, 2002; Acácio et al., 2007, 2009; Van de Wouw et al., 2011). The much lower seedling density found in the Andean sites suggests that resprouting and lateral growth from remnant shrubs into open patches may be an important component of the regeneration of sclerophyllous forest, especially in drier sites.

Indeed, despite the positive effect of nurse shade, seedlings may fail to establish under very dry conditions. One of our study sites included the experimental area of Fuentes et al. (1984) in the dry Andean foothills of San Carlos-Apoquindo, where earlier field experiments reported no seedling survival and aerial image analysis no significant woody patch growth in the 30-year period between 1956 and 1980. Our results suggest that shrub recolonization in these sites may occasionally occur. Plant recruitment in semiarid ecosystems like these ones can be highly episodic during rainy events. In this region, periodic rainy years associated to ENSO (El Niño Southern Oscillation) events roughly double the average precipitation (Montecinos and Aceituno, 2003) and could potentially increase shrub seedling establishment as has been found in other regions (Holmgren and Scheffer, 2001; Holmgren et al., 2006a,b; Sitters et al., 2012), especially when the response of plant communities to the rainfall pulse is faster than the response of herbivores (Holmgren and Scheffer, 2001; Scheffer et al., 2008). Field experiments in Chile have showed that water levels comparable to strong ENSO events can increase seedling survival up to 10%, but mostly for species with fast growth rates and deep roots (e.g. *Prosopis chilensis*, *Senna cumingii*) and only when protected from herbivores (Gutiérrez et al., 2007; Squeo et al., 2007; León et al., 2011).

5. Conclusions

Our results highlight the importance of forest remnants for the regeneration of semiarid sclerophyllous vegetation. The aggregated pattern of vegetation recovery close to forest remnants, especially in drier Andean sites, indicate that they facilitate the regeneration of forests. Restoration efforts could aim at generating nucleated patterns of plant recruitment around forest remnants in order to increase the success of reforestation programs.

Acknowledgements

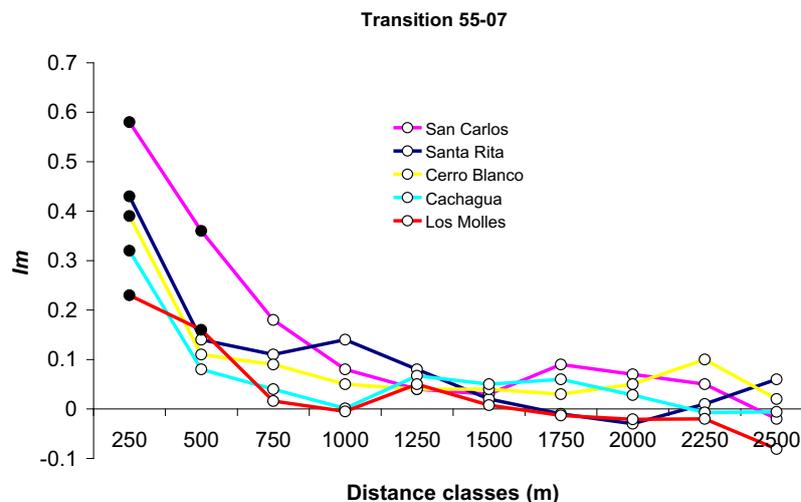
We thank Juan Armesto for facilitating this work, Cristian Delpiano for field assistance and Rodolfo Gajardo and Patricio Pliscoff for suggestions. Two anonymous reviewers provided constructive suggestions that improved the manuscript. This research was partly funded by the EU-REFORLAN (EU INCO-CT-2006-032132) and Chilean CONICYT – (RUE 33) projects.

Appendix A. Study sites in central Chile and their absolute increase in evergreen forest

Study site	Zone	Location	Area (ha)	Altitude	Vegetation cover (ha)			Absolute increase (ha)		
					1955	1983	2007	1955–1983	1983–2007	1955–2007
Cerro Blanco	Andean	33°44'S; 70°30'W	709	1150	122.8	129.1	223.8	6.3	94.7	101.0
San Carlos de Apoquindo	Andean	33°24'S; 70°29'W	824	940	265.4	306.0	432.1	40.6	126.1	166.7
Santa Rita	Andean	33°40'S; 70°30'W	712	850	426.6	507.7	545.7	81.1	38.0	119.1
Cachagua	Coastal	32°34'S; 71°25'W	911	280	326.0	387.0	492.7	61.0	105.7	166.7
Los Molles	Coastal	32°11'S; 71°25'W	631	130	377.7	–	427.2	–	–	49.5

Appendix B. Moran Index (I_m) for the first distance lag (250 m) at each study site and period (NA, not available)

Study site	1955–1983		1983–2007		1955–2007	
	I_m	p-Value	I_m	p-Value	I_m	p-Value
Cerro Blanco	0.21	0.044	0.27	0.001	0.39	1.06E-06
Santa Rita	0.50	3.43E-09	0.27	0.0057	0.43	1.08E-06
San Carlos de Apoquindo	0.36	1.85E-05	0.24	0.016	0.58	3.04E-13
Cachagua	0.37	1.77E-09	0.30	1.74E-06	0.32	3.84E-07
Los Molles	NA	NA	NA	NA	0.23	0.0027



Correlogram of the Moran Index (I_m) for the residuals of the linear regression for the transition 1955–2007 (comparable patterns found in the other two study periods, 1955–1983, and 1983–2007). The black circles indicate significant I_m values. In all sites the first lag (250 m) is significant and positive, indicating aggregated pattern. In Los Molles and San Carlos de Apoquindo, the second lag (500 m) is also significant.

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