The weight of the past: land-use legacies and recolonization of pine plantations by oak trees

Irene Navarro-González,[1,3] Antonio J. Pérez-Luque,[1] Francisco J. Bonet,[1] and Regino Zamora[1,2]

[1]*Laboratorio de Ecología (iEcolab), Centro Andaluz de Medio Ambiente (CEAMA), Universidad de Granada,*
Avenida del Mediterráneo s/n, Granada 18006 Spain
[2]*Departamento de Ecología, Facultad de Ciencias, Universidad de Granada, Avenida Fuentenueva s/n, Granada 18071 Spain*

Abstract. Most of the world's plantations were established on previously disturbed sites with an intensive land-use history. Our general hypothesis was that native forest regeneration within forest plantations depends largely on in situ biological legacies as a source of propagules. To test this hypothesis, we analyzed native oak regeneration in 168 pine plantation plots in southern Spain in relation to land use in 1956, oak patch proximity, and pine tree density. Historical land-use patterns were determined from aerial photography from 1956, and these were compared with inventory data from 2004–2005 and additional orthophoto images. Our results indicate that oak forest regeneration in pine plantations depends largely on land-use legacies, although nearby, well-conserved areas can provide propagules for colonization from outside the plantation, and pine tree density also affected oak recruit density. More intense land uses in the past meant fewer biological legacies and, therefore, lower likelihood of regenerating native forest. That is, oak recruit density was lower when land use in 1956 was croplands (0.004 ± 0.002 recruits/m² [mean $\pm$ SE]) or pasture (0.081 ± 0.054 recruits/m²) instead of shrubland (0.098 ± 0.031 recruits/m²) or oak formations (0.314 ± 0.080 recruits/m²). Our study shows that land use in the past was more important than propagule source distance or pine tree density in explaining levels of native forest regeneration in plantations. Thus, strategies for restoring native oak forests in pine plantations may benefit from considering land-use legacies as well as distance to propagule sources and pine density.

Key words: biological legacies; historical vs. ecological factors; land-use change; land-use legacies; pine density; pine plantations; Quercus *regeneration; seed dispersal.*

INTRODUCTION

The study of relationships between landscape changes and subsequent species replacement is valuable to clarify the factors regulating species distribution and abundance. Thus, knowledge of site history of an ecosystem is often crucial for understanding current ecological processes. Under this paradigm, time-lag effects of land use (i.e., land-use legacies) have gained attention, and various studies have highlighted the long-term impact of former land use on the current composition and dynamics of ecosystems (e.g., Koerner et al. 1997, Compton and Boone 2000, Goodale and Aber 2001, Foster et al. 2003). In view of the widespread prevalence of land use and the ubiquity of land-use legacies, Foster et al. (1998, 2003) recommend addressing human activity as a fundamental ecological process and applying lessons from land-use history to landscape conservation and management.

Forest plantations are an example of widespread intensive and extensive land-use change that can

significantly shape terrestrial \ecosystems (Hobbs et al. 2006, Chazdon 2008). Forest plantations are usually characterized by higher stand density, lower tree diversity, and different species composition than occur in natural forests (Hartley 2002, FAO 2006). The area covered by forest plantations has increased dramatically in recent decades, currently representing approximately 140 million hectares worldwide (FAO 2006). Mountainous areas of Mediterranean Europe were planted with trees following the abandonment of croplands and pastures during the last 50 years (Gerard et al. 2010). In Spain, 3.8 million hectares were converted to plantations between 1945 and 1986 (Ortuño 1990). These plantations were established mainly on highly degraded, extensive agricultural landscapes. There has been increased interest in recent decades to restore native forests, in an effort to manage for biodiversity, carbon storage, and greater resiliency in the face of changing climates (Maestre and Cortina 2004, Brockerhoff et al. 2008, Pejchar et al. 2008).

The potential of plantations to facilitate native forest regeneration has previously been explored in a variety of types, including tropical (Parrota 1992, 1995, Brown and Lugo 1994, Lugo 1997, Tubelis et al. 2007), temperate (Hewitt and Kellman 2002*a*, *b*) and Mediter-

ranean forests (Lookingbill and Zavala 2000, Pausas et al. 2004, Gómez-Aparicio et al. 2009, Zamora et al. 2010). These studies indicate that natural regeneration depends on the degree of site degradation, proximity to native-forest seed sources, availability of zoochorous vectors, and characteristics of the plantations such as stand density. In a context of long-term human management, legacies may greatly influence the restoration potential in Mediterranean forest ecosystems (Dambrine et al. 2007). However, to date, no studies have explicitly analyzed the simultaneous influence of both historical land-use legacies and ecological factors, such as proximity to propagule sources and pine tree density, influencing the forest regeneration potential in forest plantations.

Our general hypothesis is that native forest recolonization in forest plantations depends largely on biological legacies prior to the plantation establishment. Land-use legacies at a given site include surviving organisms (residuals), organic materials, and environmental patterns that persist in time and serve as foci for regeneration and re-colonization of a disturbed site (Swanson et al. 2011). Understanding both the influence of history (land-use legacies) and current ecological factors (proximity to seed sources of propagules and pine density) is vital to explain vegetation changes through time in pine plantations. That is, these factors may provide insights into why some plantations have high levels of oak recruitment and others with seemingly similar current environmental characteristics lack oak recruits. Our objective is to understand their importance, in both relative and absolute terms in influencing oak regeneration in the plantations. In other words: to what extent does the past help us understand what we see in the present?

To answer this question, we analyzed the density of native oak regeneration in 168 pine plantation plots in southern Spain in relation to land-use type in 1956, oak patch proximity, and pine tree density. Specifically, we make the following predictions: (1) Current native oak forest regeneration in pine plantations is negatively correlated with land-use intensity in the recent past, as well as with distance to propagule sources and pine density. 2) Effect of land use, prior to plantation establishment, on native oak regeneration is greater than effect of propagule source distance or pine density. By incorporating the temporal dimension, our approach analyzes how both historical and current aspects of ecosystems influence the likelihood of regenerating native forests in humanized Mediterranean environments.

METHODOLOGY

Study site

This study was conducted in Sierra Nevada National Park (Andalusia, southeast Spain; Fig. 1a and b), a mountainous region with an altitudinal range between 860 m and 3482 m above sea level (m a.s.l.) and a surface area of more than 2000 km^2. The climate is Mediterranean, characterized by cold winters and hot summers, with pronounced summer drought (July–August). The annual average temperature decreases in altitude from 12° to 16°C below 1500 m to 0°C above 3000 m a.s.l., and the annual average precipitation is around 600 mm. The forested area in the National Park includes ~40 000 ha of pine plantations, which were planted with several species, including *Pinus halepensis* and *P. pinaster* Ait Mill. in the low-altitude plantations (<1500 m a.s.l.), and *P. nigra* Arnold. subsp. *salzmannii* (Dunal) Franco and *P. sylvestris* L. at high altitudes (1500–2200 m a.s.l.). Native *P. sylvestris* L. var. *nevadensis* Christ forests can also be found at localized points at high altitudes with a characteristic sparse tree cover. Our study was conducted in pine-dominated plantations, excluding small native pine patches and mixed oak–pine forest. These plantations were established mainly during the period 1950–1980 on highly degraded, extensive agricultural landscapes abandoned after the Spanish Civil War (1936–1939). The density of the plantations currently ranges from 100 to 2100 pines/ha (Bonet García et al. 2009). The main native forests of Sierra Nevada are dominated by the evergreen oak *Quercus ilex* subsp. *ballota* (Desf,) Samp. (which currently represents about 13% of forest cover of the national park). All oak stands are native, and they have different structure and diversity depending on land-use management. The altitudinal range of distribution for *Q. ilex* is from 400 m to 1900 m a.s.l. The European Jay (*Garrulus glandarius*) is the major acorn disperser species, its behavior in this sense depending heavily on the spatial configuration of the vegetation (Gómez 2003, Pons and Pausas 2007). Acorns require a mild microclimate to germinate in order to avoid seed dehydration (Broncano et al. 1998), these microclimatic conditions being common in the understory of plantations (Mendoza et al. 2009).

Data set

The oak regeneration variable (dependent variable), measured as the number of *Quercus ilex* recruits per sampled area, was estimated from the forest inventory of Sierra Nevada conducted during 2004–2005. This forest inventory included an extensive network of 600 plots (20 × 20 m) distributed within the three main forest units of the national park: oak forests, deciduous broadleaf forests, and pine forest. The network of the plots was a random sample stratified by land cover and altitude, covering a gradient from 974 to 2439 m a.s.l. Trees with a diameter at breast height (dbh; measured at 1.3 m height) of at least 7.5 cm were tallied by species and dbh. In each plot the number of saplings (dbh = 2.5–7.5 cm) and seedlings (dbh < 2.5 and height <1.3 m) of tree species was measured within a circle of 5 m radius. Oak regeneration within pine plantations was measured as the sum of seedlings and saplings (recruits) in the 5 m radius subplot. Our approach did not allow a clear
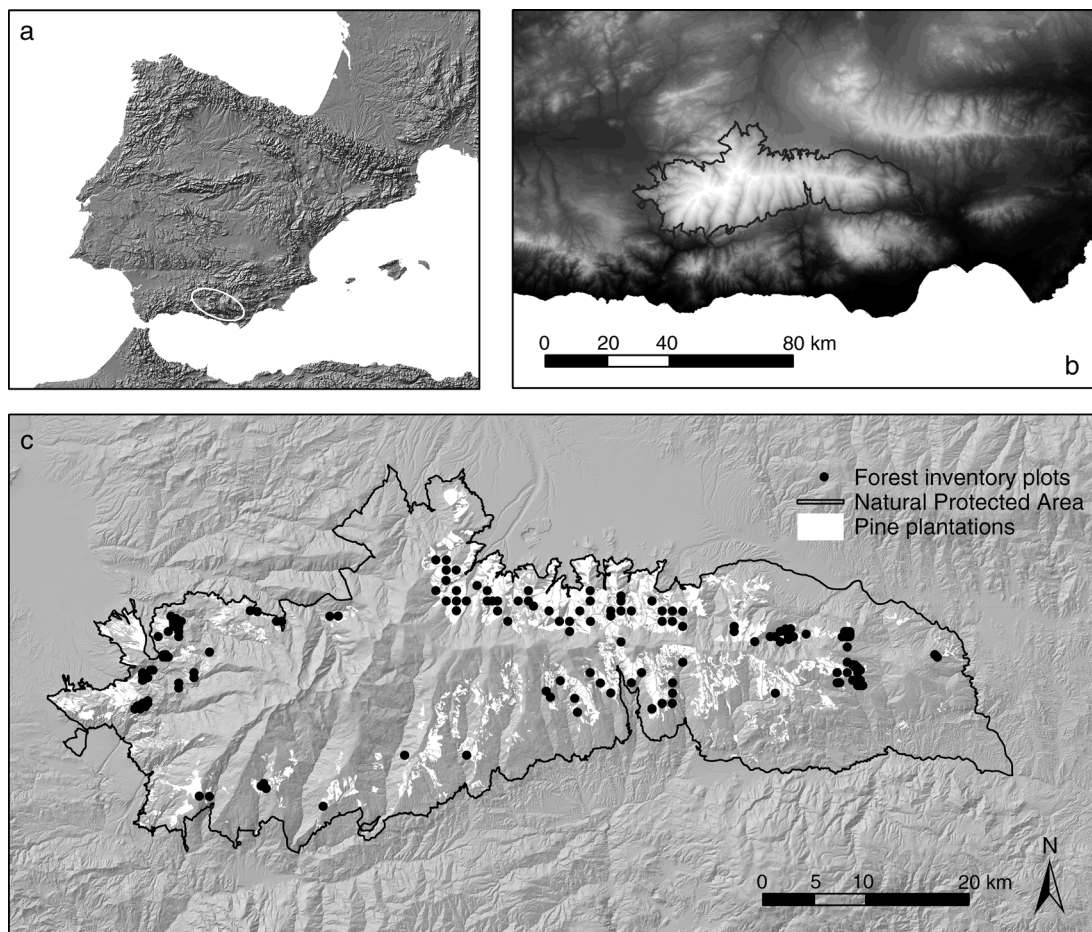
Fig. 1.   Maps showing the study area (the Sierra Nevada mountains in southern Spain) and the location of the forest inventory plots (n = 168 plots). All plots were situated within the Sierra Nevada National Park (highest level of protection), which is surrounded by an area of similar size (~91 000 ha) protected as Natural Park.

distinction between ramets and genets. This difficulty did not significantly affect the main conclusions of the study regarding regeneration patterns, which were based more on relative differences between plantation plots.

In an initial step, we selected the plots located in pine-dominated plantations. Pine-plantation distribution in Sierra Nevada National Park was delimited using the last version of the forest map of Andalusia 1:10 000 for 2005 (CMA 2009). Pine-dominated plantations were considered to be any patch with ≥50% tree cover and 75% of the tree cover being pine, excluding the remnant small fragments of native *Pinus sylvestris* forests (Molero Mesa et al. 2001). Also, we excluded mixed forests of pine plantation and oak, assuming that oak recruitment at those sites was due to the presence of mature oak trees. Then, we excluded the plots located above 1900 m a.s.l. because this altitude is a physiological limit for oak species growth (Lorite 2001). Thus, a total of 168 plots were selected from the 600 inventory plots (Fig. 1c).

Our independent variables were land cover in 1956, oak propagule source distance, and pine tree density.

1956 land cover.—Each inventory plot in pine-dominated plantations (n = 168 plots) was assigned a vegetation cover type for 1956, which was inferred by the interpretation of 1956 orthophotos at a detailed level (1:5000 to 1:10 000). Four categories were established according to vegetation type and their possible contribution to oak regeneration: oak formation, dense or open oak forest; mid-mountain shrubland, composed mainly of aromatic plants (*Rosmarinus, Thymus*) and some pyrophytes (*Ulex, Cistus*, and so on); pasture; and cropland. We considered a gradient of management intensity to classify the different 1956 vegetation covers, assuming that the highest use intensity in the past resulted in the lowest oak recruitment today (Dupouey et al. 2002, Plieninger et al. 2004, Gimmi et al. 2010). The vegetation cover was classified according to land-use intensity, from highest to lowest: cropland, pasture, mid-mountain shrubland, and oak formation. Croplands were considered the most intensive land use as

TABLE 1.   Oak regeneration (mean ± SE), distance to propagule source, and pine tree density by land-use type in 1956, with plot sample sizes (*n*) for each land-use type.

| | | Descriptive statistics by land use | | | |
1956 land cover	Units	Oak formation (*n* = 48)	Mid-mountain shrubland (*n* = 80)	Pasture (*n* = 17)	Cropland (*n* = 23)
Oak regeneration	no. recruits/5-m radius plot	24.67 ± 6.27	7.75 ± 2.46	6.41 ± 4.24	0.30 ± 0.18
	no. recruits/m^2	0.314 ± 0.080	0.098 ± 0.031	0.081 ± 0.054	0.004 ± 0.002
Oak propagule source distance	m	263.30 ± 60.95	472.59 ± 39.95	501.90 ± 173.73	687.53 ± 108.63
Pine tree density	no. trees/ha	577.47 ± 69.12	789.12 ± 47.61	1031.38 ± 124.96	992.76 ± 124.64

they involved removal of native vegetation as well as soil disturbance. Pasture was the second most intensive land use because sometimes native oak stumps and shrubs were left. A large part of the mid-mountain shrubland cover was oak coppice, used for firewood or charcoal, so the pine plantation established in these areas were being quickly re-colonized by native oak vegetation.

Oak propagule source distance.—Oak recruitment bank quantified within plantations in the forest inventory of 2004–2005 was composed of individuals of different ages that had been established during the recent decades within plantations. We hypothesized that the number of oak recruits found in pine plantations would depend on the distance of dispersion from the *Quercus ilex* patches nearest to plantations (Gómez-Aparicio et al. 2009). We calculated the oak propagule source distance as the average of the nearest oak patch distances in 1956 and 2005. The minimum size of oak patch considered was 100 m^2. We used the oak patches delimited by interpretation of the 1956 and 2005 orthophotos because these were the oldest and the most recent dates. Oak patch distances were determined by calculating the edge distance to the nearest *Quercus ilex* patch using ArcGIS 9.2 (ESRI, Redlands, California, USA). We used the land-use and land-cover map of Andalusia 1:25 000 for 1956 (CMA 2007) as a reference to delimit the oak patches in 1956. However, we performed a more detailed photographic interpretation (1:5000), correcting errors and increasing accuracy with respect to the previous map. The forest map of Andalusia 1:10 000 for 2005 (CMA 2009) served as a reference to delimit the oak patches in 2005 to check the vegetation cover in 1956 from the current oak forests. Orthophoto imagery in black and white from 1956 (1-m spatial resolution), and in color (IR) from 2005 (0.5-m spatial resolution) were used.

Pine tree density.—The density of pines, measured as the number of pine trees ≥7.5 cm dbh within the 20 × 20 m plots (*n* = 168 plots), was obtained from the forest inventory of Sierra Nevada conducted during 2004–2005 (Table 1 and Supplement).

Analysis

The effects that 1956 land use, oak propagule source proximity, and pine tree density exerted on oak recruitment in the pine plantation were analyzed at the plot level (*n* = 168 plots). Tree recruitment data are often count data with a larger proportion of zeros than expected from the pure count data (Lambert 1992, Barry and Welsh 2002). Zero-inflated Poisson distributions (ZIP) have been recommended to model these kinds of data, with an excess of zeros, which cannot be accommodated by traditional discrete probability distributions (i.e., Poisson distribution [Martin et al. 2005, Rathbun and Fei 2006, Zuur et al. 2010]). This model, which has been used in several ecological studies (Welsh et al. 1996, Cunningham and Lindenmayer 2005, Kuhnert et al. 2005, Fortin and DeBlois 2007, Gómez-Aparicio et al. 2009), has a statistical advantage over the standard count data model (i.e., Poisson and negative binomial models) in modeling the preponderance of zeros as well as the distribution of positive counts simultaneously. We used the Vuong's test (Vuong 1989) to compare the ZIP model vs. the standard Poisson model by testing the null hypothesis that both models are equally similar to the observed distribution. The resulting z value was positive and statistically significant ($z = 3.6343$; $P < 0.00013$), demonstrating that the ZIP model reflected the observed data more accurately than did the standard Poisson.

Oak regeneration was then assumed to follow a ZIP distribution and we modeled it as a result of two distinct processes: first, the occurrence of recruitment, and second, the number of recruits conditional to the occurrence of recruitment. The density function of a ZIP model has the following form:

$$f(y \mid p_z, \lambda) = \begin{cases} p_z + (1 - p_z) \times \exp^{-\lambda} & y_i = 0 \\ (1 - p_z) \times \dfrac{\lambda^{y_i} \times \exp^{-\lambda}}{y_i!} & y_i > 0 \end{cases}$$

where y_i represents the number of recruits in plot i, p_z represents a constant probability across the data set of getting zero recruits (structural zeroes), and λ is the mean of Poisson distribution. The expected number of recruits is then $E[y] = \mu = (1 - p_z)\lambda$. The two distribution parameters, λ and p_z, were linked to the three covariates (1956 land cover, average distance to propagule sources and pine tree density) using the GLM (generalized lineal model) approach. We can then express the λ and p_z

TABLE 2. Comparison of models of oak regeneration (recruit density of *Quercus ilex*) related to past land cover (land cover class from 1956 orthophoto: oak formation, mid-mountain shrubland, pasture, or croplands), propagule source distance (average distance to nearest *Quercus ilex* patch for 1956–2005 period), and pine tree density ($n = 168$ plots).

Model	k	AIC_c	ΔAIC_c	w_i	Pseudo-R^2
Propagule source distance + 1956 land cover + pine density (full model)	12	2866.15	0	1	0.2110
1956 land cover + pine density	10	2939.98	73.83	9.29×10^{-17}	0.1892
Propagule source distance + 1956 land cover	10	3004.03	137.88	1.15×10^{-30}	0.1714
1956 land cover	8	3171.17	305.02	5.83×10^{-67}	0.1238
Propagule source distance + pine density	6	3195.51	329.36	3.02×10^{-72}	0.1157
Propagule source distance	4	3308.55	442.39	8.62×10^{-97}	0.0832
Pine density	4	3418.17	552.02	1.35×10^{-120}	0.0527
Null model	2	3603.87	737.72	6.40×10^{-161}	

Notes: Models are ranked from best to poorest fits. Parameters are: k, the number of estimated parameters in the model; AIC_c, Akaike's information criterion corrected for small sample sizes; ΔAIC_c, the difference between model AIC_c and the model with the lowest AIC_c; w_i, the Akaike weight for each of the competing models; and pseudo-R^2 (McFadden's), a measure of goodness-of-fit.

values as a function of a set of explanatory variables:

$$\text{logit}\left(p_z(x_i)\right) = \alpha_0 + \boldsymbol{\beta}_0(x_i)$$

$$\log\left(\lambda(z_i)\right) = \alpha_1 + \boldsymbol{\beta}_1(z_i)$$

where the parameters α_0 and α_1 represent constant terms in each regression component, x_i and z_i represent the predictor variables (explanatory variables) in plot i, and $\boldsymbol{\beta}_0$ and $\boldsymbol{\beta}_1$ are vectors, representing the coefficients estimated for each explanatory variable fitted in the model. The parameters were estimated by maximum likelihood estimation. The significance of covariates was tested using the likelihood ratio test (LRT), and odds ratios for each covariate were estimated.

Three different models were tested to determine how oak regeneration was affected by 1956 land cover, propagule source distance, and pine tree density. First, we computed three univariate models: one with 1956 land cover as the explanatory variable, one with average distance to the propagule source, and a third with pine tree density; and the bivariate models resulting from the corresponding combinations. Then we computed a model in which the oak regeneration was modeled as a function of the three explanatory variables considered: the 1956 land cover, the average distance to propagule source and the pine tree density. We compared the different models using Akaike's information criterion corrected for small sample size (AIC_c; Burnham and Anderson 2002). Each model was ranked on the basis of its difference from the model with the lowest AIC_c (ΔAIC_c). Then, ΔAIC_c values were used to derive the Akaike weights (w_i) for the three alternate models. The Akaike weight of model i can be interpreted as the expected probability of that model being selected as the best when repeated independent samples are taken for the same population. The best model is considered to be clearly superior to the other candidate models when its $w_i \geq 0.9$ (Burnham and Anderson 2002). The model accuracy was tested by McFadden's pseudo-R^2, used as a measure of goodness of fit. All analyses were

performed using R version 2.12.2 (R Development Core Team 2011) and the pscl version 1.03.5. package (Zeileis et al. 2008, Jackman 2012).

RESULTS

The oak regeneration model including all independent factors (1956 land use, average distance to propagule sources, pine tree density; i.e., full model) showed higher strength of empirical support than did models for each of the three independent factors separately and the combinations, i.e., the full model had the lowest AIC_c value and $w_i > 0.9$, making it the best model (Table 2). The bivariate 1956 land-cover and pine density model was the next best model with the second-lowest AIC_c value. The 1956 land-cover and pine density model and the average propagule distance and 1956 land-cover model were stronger by far than the average propagule distance and pine density model, which showed a much lower pseudo-R^2. The strongest univariate model for predicting oak regeneration was the one using 1956 land cover.

The oak formation land cover in 1956 significantly affected (zero model; $P < 0.05$; Table 3) the probability of finding oak regeneration (structural zero) in current pine plantation plots. Holding average propagule distance and pine density constant, the odds of finding no regeneration were higher in plots with mid-mountain shrubland, pasture, and croplands 1956 land covers than in plots with oak formation 1956 land cover. There was a likelihood of finding no regeneration gradient by 1956 land cover, from highest to lowest: pasture, croplands, mid-mountain shrubland, and oak formation (Table 3).

Recruit density in plots with oak regeneration varied strongly among different types of 1956 land cover (count model; $P < 0.001$; Table 3). The oak regeneration model predicted an expected regeneration gradient depending on 1956 vegetation cover. Expected regeneration, when average distance to oak patch was zero and the mean pine density was 750 trees/ha (optimum pine tree density for oak regeneration [Gómez-Aparicio et al. 2009]), was 0.57 recruits per 5 m radius plots (0.01 recruits/m^2) with croplands in 1956, 8.49 recruits per 5 m radius plots

TABLE 3. Summary of parameters for full oak regeneration zero-inflated Poisson model including all variables using 1956 land cover, propagule source distance, and pine tree density ($n = 168$ plots).

Model term	Estimate	SE	Wald statistic	P	CI, 2.5%	CI, 97.5%	Odds ratio
Zero model (logit)							
Oak formation	-0.9326	0.4102	-2.274	0.0229	-1.7366	-0.1287	0.3935
Mid-mountain shrubland	0.5639	0.4020	1.403	0.1606	-0.2240	1.3519	1.7576
Pasture	1.1352	0.6480	1.752	0.0798	-0.1349	2.4053	3.1119
Croplands	1.1106	0.7886	1.408	0.1590	-0.4349	2.6562	3.0362
Propagule source distance	1.17×10^{-3}	4.79×10^{-4}	2.454	0.0141	2.36×10^{-4}	2.11×10^{-3}	1.0012
Pine tree density	1.68×10^{-4}	3.98×10^{-4}	0.423	0.6719	-6.12×10^{-4}	9.50×10^{-4}	1.0002
Count model (Poisson)							
Oak formation	3.3281	0.0529	62.818	<0.0001	3.2243	3.4319	
Mid-mountain shrubland	-0.5819	0.0531	-10.953	<0.0001	-0.6861	-0.4778	
Pasture	-0.7471	0.1083	-6.901	<0.001	-0.9593	-0.5349	
Croplands	-3.4645	0.4901	-7.039	<0.0001	-4.4251	-2.5039	
Propagule source distance	-7.18×10^{-4}	8.37×10^{-5}	-8.581	<0.0001	-8.83×10^{-4}	-5.54×10^{-4}	
Pine tree density	5.73×10^{-4}	3.90×10^{-5}	14.658	<0.0001	4.96×10^{-4}	6.49×10^{-4}	

Note: Abbreviations are: SE, standard error; CI, confidence interval.

(0.11 recruits/m^2) with pastures in 1956, 13.41 recruits per 5 m radius plots (0.17 recruits/m^2) with mid-mountain shrubland in 1956, and 29.62 recruits per 5 m radius plots (0.38 recruits/m^2) with oak formation in 1956 (Fig. 2).

The average oak patch distance to pine plantation plots affected both the probability of getting zero oak recruits (zero model; $P = 0.0141$; Table 3) and the recruit abundance in plots with oak regeneration (count model; $P < 0.0001$; Table 3). The pine tree density did not affect the probability of getting zero oak recruits (zero model; $P > 0.05$; Table 3) but it affected the recruit abundance in plots with oak regeneration (count model; $P < 0.0001$; Table 3). Predicted regeneration values from our model showed a decreasing exponential trend when the oak patch average distance increased; and an increasing exponential trend when the pine density increased (Fig. 2).

DISCUSSION

In our study, native forest regeneration in plantations depended more on land use in the past than distance to propagule source or pine tree density. This result, reflected in the difference of explained variance percentages by the propagule distance model, the pine density model, and 1956 land-use model (Table 2), is of special interest because it indicates the resilience of "natural" forest ecosystems, as they sometimes retain some biological legacies even below pine plantations, when past management was not too intense.

Different past land-use intensities affected the available oak recruit bank; higher degradation levels associated with more intense land uses in 1956 modulated the biological legacies in current pine plantations. As a result, pine plantations established in areas where vegetation cover in 1956 was *Quercus ilex* had the largest recruit bank compared with other past uses (Table 3). The presence of oak recruits allow the potential conversion of pine plantations into a mixed forest, because a large number of Mediterranean woody species (including oak) have a comparatively higher probability of persisting in the understory of plantations, benefiting from the mild microclimate generated by the canopy (Gómez-Aparicio et al. 2009, Mendoza et al. 2009, Zamora et al. 2010; see also Parrota 1992, 1995, Brown and Lugo 1994, Keenan et al. 1997, Lugo 1997, Tubelis et al. 2007 for tropical forests, and Hewitt and Kellman 2002a, b for temperate forests).

According to our first prediction, the results show a potential native oak regeneration in pine plantation strongly related to previous land-use intensity (cropland, pasture, mid-mountain shrubland, and oak formation). This finding underlies the importance of the temporal links in recolonization processes of native vegetation in forest plantations. The higher land-use intensity in the past, the smaller reserve of biological legacies would be and, therefore, the lower current native forest regeneration, and vice versa (Fig. 2). These results are consistent with other studies: Plieninger et al. (2004) reported negative consequences of cultivation for *Q. ilex* demography, showing higher recruitment levels in shrubby sites than in grazed or cultivated rangelands, and Dupouey et al. (2002) demonstrated that species richness and plant communities varied according to the intensity of ancient land uses in limestone plateaus of northeastern France.

Moreover, the spatial distribution of native oak patches influenced the arrivals of off-site oak propagules to pine plantations between 1956 and the present. In relation to our second prediction, we found a trend showing that the greater the distance to oak patches the lesser the oak colonization was and, therefore, the lower the likelihood of regeneration of native forest ($P < 0.0001$; Table 3 and Fig. 2). This result was consistent with the general theory that seed fall is inversely related to distance from the seed source (Hewitt and Kellman 2002b) and corroborated by field studies (Kunstler et al. 2007, Gómez-Aparicio et al. 2009). In contrast, oak proximity indicates a stronger probability that these
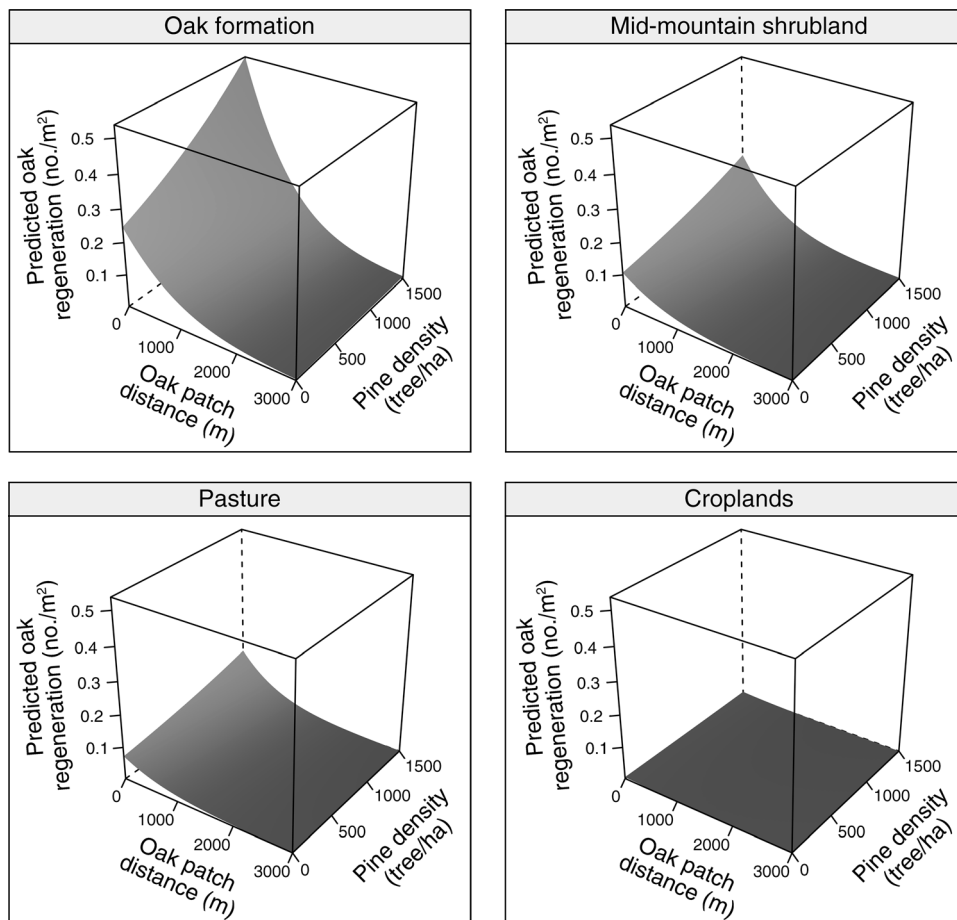
FIG. 2. Predicted variation in expected oak regeneration along two gradients: average distance to the nearest oak patch and pine tree density, by the past land-use categories considered (oak formation, mid-mountain shrubland, pasture, and croplands; see *Methodology: Data set*).

sites were occupied by native oak forest before historical uses developed in those areas. Also, stand density affected oak recruitment (Table 2 and Table 3). A highly dense stand structure is probably a direct obstacle to seed dispersal by seed disperser birds (Vallauri et al. 2002, De la Montaña et al. 2006). Moreover, oak species (such as *Q. ilex*) were able to recruit some seedlings in high-density plantations, probably as a result of its much higher shade tolerance than pine species (Retana et al. 1999, Niinemets and Valladares 2006, Gómez-Aparicio et al. 2009). However, the transition of these seedlings to the sapling stage seems to collapse at such high densities, as a result of increasing light requirements with ontogeny (Retana et al. 1999). In fact, densities over 1500 pines/ha represent a true biotic constraint to the recruitment process in the understory of pine plantations (Gómez-Aparicio et al. 2009).

In short, our study provides strong evidence that management strategies should take into account that restoration of plantations depends heavily on *both* history (availability of land-use legacies) and current ecological attributes (distance to native vegetation and

stand density). Accordingly, forest policy and practice should consider both stand density and the spatial arrangement of plantation stands with respect to nearby native vegetation patches as a source of propagules (see also Gómez-Aparicio et al. 2009, Zamora et al. 2010, González-Moreno et al. 2011), as well as land-use history.

Implications for management

The goal of restoring pine plantations into more natural forests, with active regeneration better adapted to environmental variables is widely recognized around the world (Maestre and Cortina 2004, Brockerhoff et al. 2008, Pejchar et al. 2008). Plantations can be considered "emerging ecosystems" (Hobbs et al. 2006), that is, human-created ecosystems that often need active human management to avoid arrested succession, high fire and pest-infestation risks, and intense decay processes. Two management tools frequently used to help restore native species in plantations include thinning in highly dense pine plantations (>1500 pines/ha; Gómez-Aparicio et al. 2009) and oak planting to add biodiversity to planta-

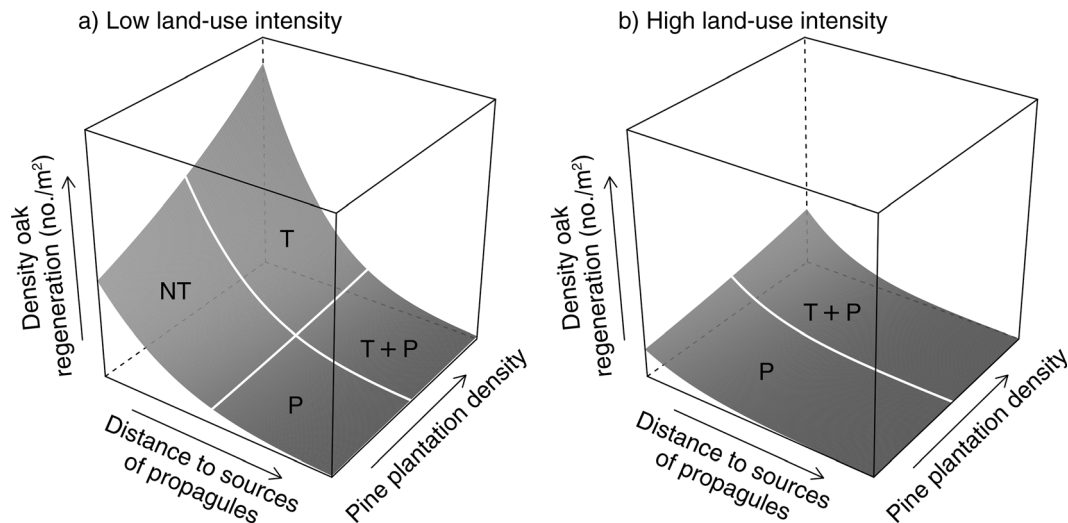a) Low land-use intensity

b) High land-use intensity

Fig. 3. Proposed management pathways. (a) Pine plantations where past land-use intensity was low. When pine stands are close to oak patches and pine density is low, then no treatment is recommended (NT). Conversely, if pine density is high, then thinning treatments (T) are recommended. When pine stands are far from oak patches and pine density is low, then planting with oak (P) is recommended. On the other hand, if pine density is high, then thinning and planting (T + P) treatments are recommended. (b) Pine plantations where past land-use intensity was high. When pine density is low, planting with oak (P) was recommended. Finally, when pine density is high, thinning and planting (T + P) treatments are recommended.

tions. Both treatments are quite expensive (US$4000/ha; Maestre and Cortina 2004, TRAGSA 2011) and are not affordable on a large scale.

Our study indicates that the weight of the past land uses is a major determinant of oak regeneration beneath the pine canopy apart from other factors widely studied such as abiotic conditions, landscape structure, and vegetative composition (Utsugi et al. 2006, Gómez-Aparicio et al. 2009, González-Moreno et al. 2011). Land-use legacy matters because the intensity of previous land management influences the supply of oak propagules that are highly valuable in the naturalization process. The final implication of our results is that consideration of previous land-use intensity may reduce the total cost of treatments designed to restore oak trees into pine plantations.

Thus, our results have several implications for management that can be translated into two different, but complementary pathways (Fig. 3): (1) Pine plantations situated at sites where there had been oaks (and/or close to seed sources) will transition back into *Quercus–Pinus* forests without intervention or with thinning if plantations are very dense. (2) Plantations located on sites with intensely managed 1956 land-cover types (and/or far from seed sources) will require planting with oaks and other woody species. These two pathways incorporate the three key factors (past land use, distance to source of propagules, and pine density) into forest management practices (Aspizua et al. 2012). These basic lessons could be applied to other regions that share two main features with our study area: a gradient of land-use history and the presence of pine plantations.

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SUPPLEMENTAL MATERIAL

Supplement

Data on oak recruit density, 1956 land cover, propagule source distance, and pine tree density (*Ecological Archives* A023-065-S1).