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Woody vegetation within semi-abandoned olive groves: species-area relationships and minimum area values

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Abstract. The species-area relationship is among the most important patterns in ecology, and is an important tool in conservation. However, research into the species-area and minimum area dynamics of Mediterranean vegetation remains scarce, and this is particularly concerning since the heterogeneity of Mediterranean mosaic systems is being threatened by widespread land abandonment. This study investigates the woody vegetation at three semi-abandoned olive groves in the Sierra Morena de Córdoba, Southern Spain. We determined the mathematical nature of the species-area curves, and obtained minimum area values as a threshold patch size to target in terms of efficiently maximising species richness conservation. Power models proposed by Arrhenius could represent the species-area relationship of all three sites, yet Gleason's exponential model performed better at one of the groves. Surrounding habitat quality and vegetation history impacted the nature of the species-area relationship, and this was reflected in significant differences among the minimum area values. This study provides one the first descriptions of woody plant communities at partially and intermittently managed groves in the Mediterranean region, and gives insight into the potential impacts of partial abandonment on landscape conservation. Enlarging patches up to the minimum area threshold could promote plant diversity whilst maintaining an open landscape, although researchers should give special care into adequately modelling the species-area relationship, in order to obtain appropriate minimum area values.

Keywords: vegetation patches, species richness, generalised additive models, ecological restoration, natural regeneration, field colonisation.

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Introduction

One of the most documented patterns in ecology is the relationship between area and species richness, describing a pattern of increasing species richness with increasing area (Arrhenius, 1921; Gleason, 1922; Preston, 1960; MacArthur & Wilson, 1967; MacArthur, 1972; Simberloff, 1974; Rosenzweig, 1995). The species-area relationship is an important tool in conservation, allowing managers to design reserves that retain enough diversity, or to predict the loss of species due to the reduction of habitat (Lomolino, 2000). Species richness is heavily influenced by processes relating to habitat variability (Hart & Horwitz, 1991). Larger areas have higher habitat diversity because there are stronger environmental gradients, evident edge effects and mosaic succession patterns, meaning species with different tolerances and requirements can survive and establish (Paine & Levin, 1981; Wilcove, 1985; Triantis *et al.*, 2012). Many studies have focused on the mathematical nature of the relationship, and species-area curves have been described by different functions (Tjørve, 2012). Arrhenius (1921) proposed that species-area curves could be described by the power function $S = cA^z$, or $\log(S) = \log(c) + z\cdot\log(A)$, where S is species richness, A is area, and c and z are constants. Alternatively, Gleason (1922) concluded that the exponential model, where $S = c + b\cdot\log(A)$, was the best approximation for species-area relationships (Figure 1). Since then, numerous other functions have been proposed (Williams *et al.*, 2009), but most observed species-area curves can be described with either the power or exponential models (Triantis *et al.*, 2012).

Few studies have focused on determining the mathematical nature of species-area relationships of Mediterranean vegetation. Californian shrublands, post-fire herbs in Eastern Iberia and fire-managed fynbos have shown power species-area relationships (Schwilk *et al.*, 1997; Pausas *et al.*, 1999; Keeley, 2003; Keeley & Fotheringham, 2003). Alternatively, curves for Australian heathlands and Eastern Iberian woody vegetation appear to follow the exponential model (Pausas *et al.*, 1999; Keeley, 2003; Keeley & Fotheringham, 2003), whilst those for plants within the Guadalentín Floodplain could

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be assigned to either power or exponential functions (Pardo *et al*., 2003). Other studies focusing on species-area relationships within Mediterranean ecosystems have used power curve functions without substantially justifying that decision (Eugenio & Lloret, 2006; Cowling *et al*., 2015; Cristaudo *et al*., 2015; Chiarucci *et al*., 2017; D'Antraccoli *et al*., 2019). Differences in the shape of the species-area relationship have important consequences for conservation and management, since the curve function will determine the point at which increases in area stop yielding meaningful or economically sustainable changes in richness. The point at which the species-area curve becomes approximately horizontal can be defined by the minimum area value (Braun-Blanquet, 1932). Specifically, the minimum area represents the point at which an increase in 10% of the sampling area yields only a 10% increase in the total number of recorded species (Müeller-Dombois & Ellenberg, 1974; Cristaudo *et al*., 2015). The lack of research investigating minimum area values for species richness in Mediterranean ecosystems is concerning, given that Mediterranean vegetation systems are characterised by high landscape heterogeneity due to the existence of mosaic patches of variable sizes (Pinto Correia, 1993).

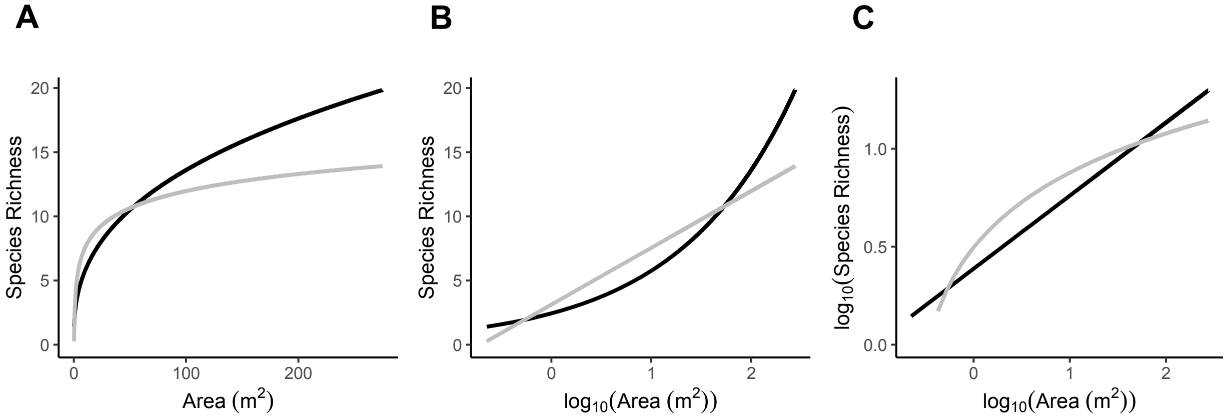

Figure 1. Graphical representation of typical power (black) and exponential (grey) species-area relationships. A, untransformed scales; B, semilog space - log-transformed area, and untransformed richness; C, log-log space - log-transformed species richness and log-transformed area. Curve functions are derived from the linear models in Table 2.

Indeed, the huge ecological diversity of Mediterranean landscapes is generated by complex geography and topography, by the convergence of tropical and temperate zones (López-Villalta, 2016) and by diverse human management and fire disturbances (Pinto Correia, 1993). However, since the mid 20th century, European countries have become urbanised (Blasi *et al*., 2000). Demographic change has been particularly evident in olive-producing regions of Southern Spain, where the rural population is aging and traditional olive cultivation has almost disappeared (Rallo, 2007). As olive groves are abandoned, they become indistinguishable from the surrounding shrubland (Blasi *et al*., 2000). The recently forested areas provide helpful ecosystem services such as increased carbon sequestration and habitat provision for wildlife, but they also become less accessible, limiting the chances of future agricultural or recreational exploitation (Allen *et al*., 2006). Fire risks can increase due to fuel build-up, and soil erosion can intensify if terraces are not adequately maintained (Duarte *et al*., 2008). Whilst the impact of olive grove abandonment on biodiversity is largely unknown, a decrease in landscape heterogeneity increases the rate at which vulnerable ground flora is being lost (Sala *et al*., 2000; Allen *et al*., 2006). To avoid complete land abandonment, some landholders in the Sierra Morena de Córdoba (Southern Spain) have been actively maintaining an open vegetation structure in marginal mountain olive groves. Agricultural management is minimal, but the open habitat structure is maintained by ploughing the spaces between the olive trees and by introducing grazers. Ploughing and grazing are the most popular weed-control methods in olive agriculture, as they allow managers to remove competing plants in a cost-efficient way, whilst grazing can even provide additional economic returns (Pastor *et al*., 2001; Carbonero Muñoz *et al*., 2013). Ploughing and grazing pressure has been moderate, and patches of vegetation have developed around the olive trees (Figure 2).

The existence of distinct vegetation patches within semi-abandoned olive groves therefore provides a unique chance to study the plant community within these semi-abandoned landscapes, as well as an opportunity to examine key ecological concepts such as species-area relationship. Determining the nature of species-area curves within the olive groves allows us to predict what patch size maximises biodiversity (Triantis *et al*., 2012), and whether it is feasible to obtain significant increases in species richness above a threshold such as the minimum area value. Thus, in this study, we aimed to investigate the species-area relationship of woody plants within three semi-abandoned olive groves in the Sierra Morena de Córdoba, Southern Spain. We examined the species-area relationships at the three groves, and determined if they followed the power or exponential curve functions. We also aimed to determine the minimum area value for each species area curve, since this allowed us to outline the main management implications of fitting different functions. We hypothesised that richness of woody plants should increase with patch size. Larger patches receive more incoming dispersal from adjacent areas and can sustain a wider range of microhabitats, being more likely to support more species than smaller patches (Hart & Horwitz, 1991). We predicted that the species-area curves at the three groves would follow the power curve model, and would show statistical similarity. The sites have similar environmental conditions and management history, and power species-area relationships appear to be more common within Mediterranean ecosystems.

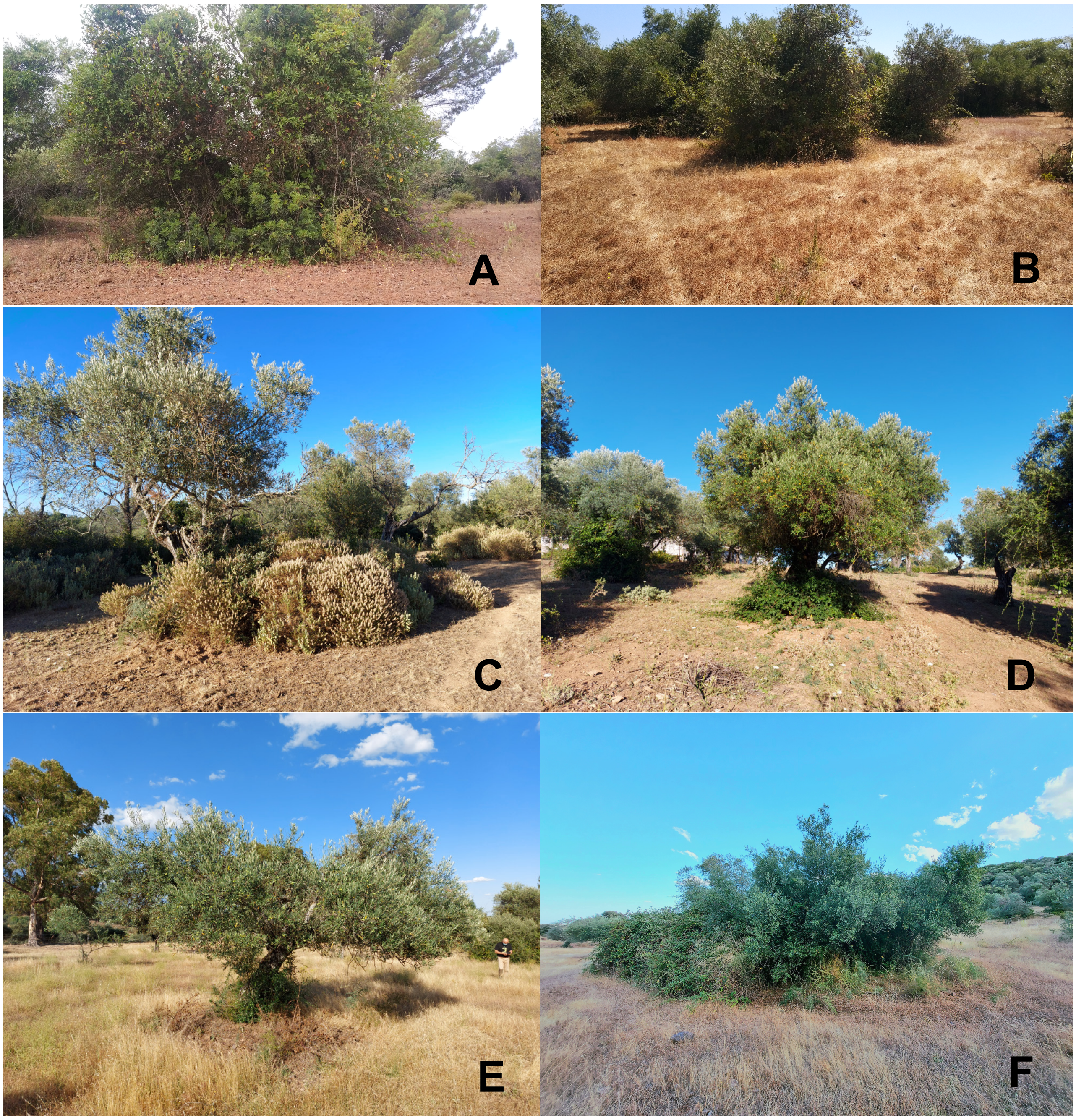

Figure 2. Vegetation patches surrounding olive trees at semiabandoned groves in Sierra Morena de Córdoba, Southern Spain (July 2021). A-B, La Soledad; C-D, Las Niñas; E-F, Piquín.

Methods

Study Site

Three traditional mountain olive groves (La Soledad, Las Niñas and Piquín) were selected within Sierra Morena de Córdoba, in Central Southern Spain (Figure 3). The three groves are located about 6 km northwest of the city of Córdoba, in the southermost edge of the Sierra Morena hills. All three groves were historically dedicated to olive oil production and agriculturally managed up to the beginning of the 21st century (Cantizani Oliva & Córdoba Estepa, 2006; Moriana Elvira *et al*., 2020). In the last 20 years, the groves have become semi-abandoned. The groves have been intermittently ploughed and grazed by sheep and cattle, to remove herbaceous vegetation from the spaces between the olive trees. However, ploughing and grazing have intensity has been moderate, allowing vegetation patches to develop around the olive trees as woody plant species spread from the surrounding scrub and woodland habitats.

All three study sites are located on areas with flat topography (500 m asl) within a broader, topographically complex area characterised by steep south-eastern slopes towards the Guadalquivir Valley (IGN, 2021). The area is dominated by dolomite and limestone rock from the Lower Cambrian and has neutral to alkaline soils (Moriana Elvira *et al.*, 2020; IGME, 2021). The climate is Mediterranean, with cool rainy winters and hot dry summers. Mean annual temperature is 18.2ºC and mean annual rainfall is 605 mm (AEMET, 2021).

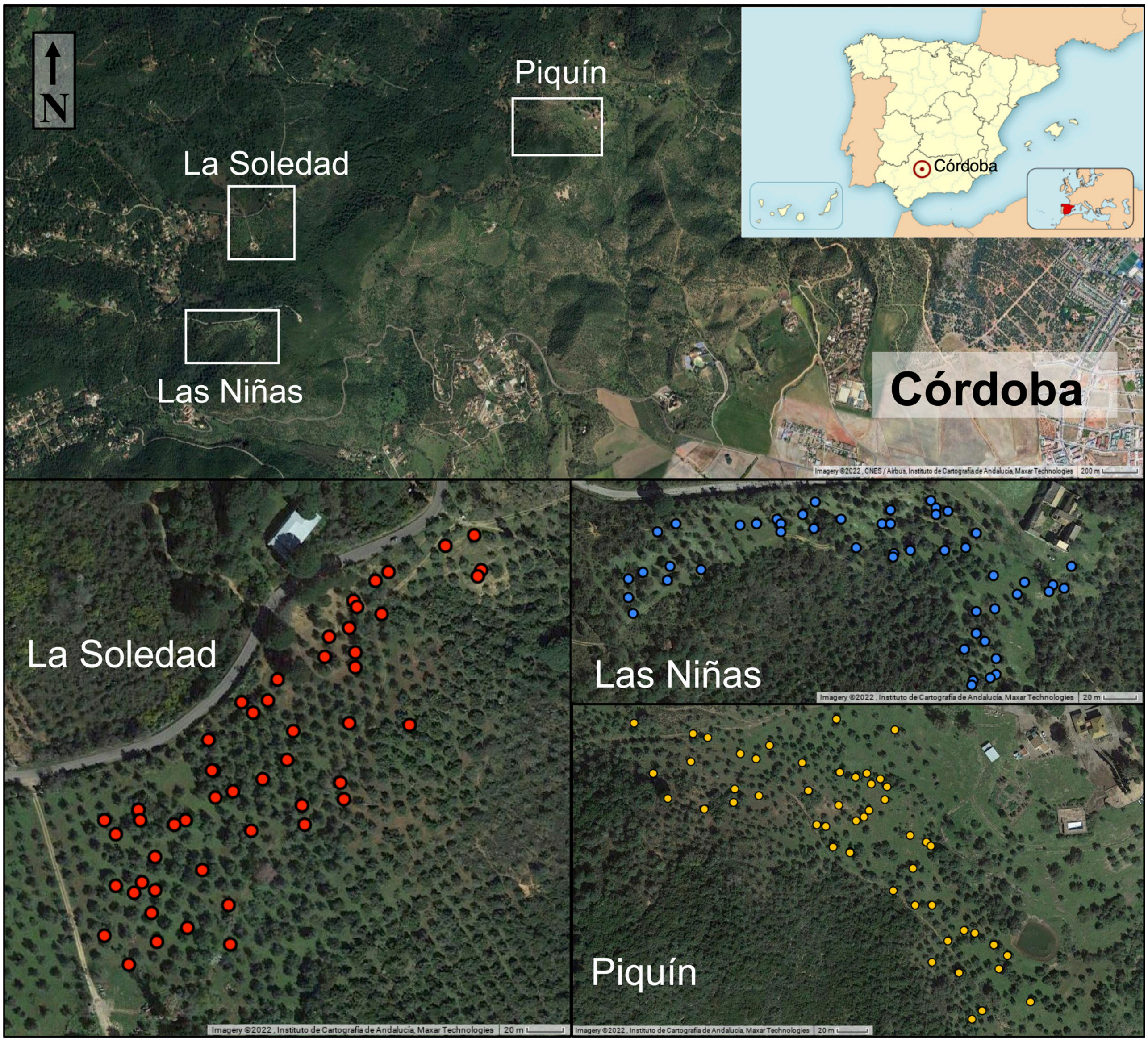

Figure 3. Location of the study sites with respect to the city of Córdoba in Southern Spain (top) and distribution of the sampled vegetation patches within each of the groves (bottom). The map images were obtained from Google Maps (2021), and Wikimedia Commons (2010). Aerial images and coordinate locations for each grove were obtained using Maps.co (2021).

Sampling and Data Collection

We sampled the woody vegetation within different-sized patches at the three groves (La Soledad, Las Niñas and Piquín) during July 2020. We defined woody vegetation as trees and shrubs, as well as perennial forbs with above-surface woody tissues (López Tirado, 2018) since these are sometimes classified as woody plants. Patches were defined as the continuous extent of woody vegetation surrounding one or more olive trees, being distinct from the surrounding herbaceous habitat (see Figure 2). Patches were selected randomly, but following a stratified approach. There were 12 different patch size categories, based on work by Hong *et al.* (2007). The size categories were 0.25, 0.5, 1, 4, 9, 16, 25, 50, 100, 150, 200 and 250 m^2 (area was allowed to vary ±10%). Within each of the groves, patches were randomly selected until each size category had a sample size of 5. Sample size at larger areas (150 to 250 m^2) was limited, meaning we could only find one or two patches within these categories at each grove. We obtained the area of patches by adding up area of circular and polygon shapes, and recorded patch coordinates. Patches that were adjacent to paths or located on slopes were excluded to minimize confounding factors of slope, disturbances and altered environmental conditions.

All woody plants within each of the vegetation patches were identified, and the abundance of each species was recorded. Non-woody plants were excluded due to their variable temporal abundance and their progressive decline during the summer months (Simón López-Villalta, 2016). Plants with evident cotyledons or those smaller than 10 cm height and with no branches, were also excluded since seedling mortality during the first summer is disproportionately high in Mediterranean ecosystems (Rühl *et al*., 2011; Simón López-Villalta, 2016). Suckers and basal shoots were omitted. Plants were identified using the guide "Flora Vascular del Término Municipal de Córdoba" (López Tirado, 2018), upon which taxonomic nomenclature was based. Seed dispersal mechanisms of all sampled species were determined by reviewing the literature. The groves' management history was determined by interviewing site managers and by reviewing the historic database of aerial photographs at the Spanish Geographical Institute (CNIG, 2021).

Table 1. List of sampled plant species and their main characteristics. Species are classified into and (ordered by) taxonomic families (according to López Tirado, 2018) and most common mode of seed dispersal is also noted (Alday *et al.*, 2011; Bonet & Pausas, 2004; Debussche & Lepart, 1992; González-Varo *et al.*, 2015; Herrera, 1995; La Mantia *et al.*, 2019; Martín Mosquero *et al.*, 2005; Parolin *et al.*, 2014; Pemán García *et al.*, 2013; Sánchez & Peco Vázquez, 2002; Voigt *et al.,* 2011). Species presence at each site is also included (LS = La Soledad, LN = Las Niñas, P = Piquín).

SPECIES	FAMILY	MODE OF DISPERSAL	SPECIES PRESENCE		
			LS (33)	LN (38)	P (35)
Pinus pinea L.	Pinaceae	dyszoochory/barochory	✓		
Laurus nobilis L.	Lauraceae	endozoochory	✓		
Castanea sativa Mill.	Fagaceae	dyszoochory/barochory		✓	
Quercus coccifera L.	Fagaceae	dyszoochory/barochory	✓	✓	
Quercus ilex L.	Fagaceae	dyszoochory/barochory	✓	✓	✓
Quercus suber L.	Fagaceae	dyszoochory/barochory		✓	
Celtis australis L.	Ulmaceae	endozoochory	✓	✓	✓
Ulmus minor Mill.	Ulmaceae	anemochory		✓	
Ficus carica L.	Moraceae	endozoochory	✓		✓
Cistus albidus L.	Cistaceae	barochory/anemochory	✓	✓	✓
Cistus crispus L.	Cistaceae	barochory/anemochory		✓	✓
Cistus ladanifer L.	Cistaceae	barochory/anemochory	✓	✓	✓
Cistus salviifolius L.	Cistaceae	barochory/anemochory	✓	✓	
Halimium umbellatum Spach	Cistaceae	barochory/anemochory		✓	
Capparis spinosa L.	Capparaceae	endozoochory	✓	✓	✓
Arbutus unedo L.	Ericaceae	endozoochory	✓	✓	✓
Erica arborea L.	Ericaceae	barochory/anemochory	✓		✓
Crataegus monogyna Jacq.	Rosaceae	endozoochory	✓		
Prunus domestica L.	Rosaceae	endozoochory	✓		
Prunus dulcis (Mill.) Webb	Rosaceae	dyszoochory/barochory	✓		
Rubus ulmifolius Schott	Rosaceae	endozoochory	✓	✓	✓
Adenocarpus telonensis DC.	Fabaceae	barochory/ballistochory	✓	✓	✓
Coronilla juncea L.	Fabaceae	barochory/anemochory			✓
Cytisus scoparius (L.) Link	Fabaceae	barochory/ballistochory	✓	✓	✓
Genista hirsuta Vahl	Fabaceae	barochory	✓	✓	✓
Ononis spinosa L.	Fabaceae	barochory	✓		✓
Retama sphaerocarpa Boiss	Fabaceae	endozoochory		✓	✓
Daphne gnidium L.	Thymelaceae	endozoochory	✓	✓	✓
Osyris alba L.	Santalaceae	endozoochory	✓	✓	✓
Rhamnus alaternus L.	Rhamnaceae	endozoochory	✓	✓	✓
Rhamnus oleoides L.	Rhamnaceae	endozoochory		✓	✓
Pistacia lentiscus L.	Anacardiaceae	endozoochory	✓	✓	✓
Pistacia terebinthus L.	Anacardiaceae	endozoochory	✓	✓	✓

SPECIES	FAMILY	MODE OF DISPERSAL	SPECIES PRESENCE		
			LS (33)	LN (38)	P (35)
Ruta montana L.	Rutaceae	barochory		✓	✓
Melia azedarach L.	Meliaceae	endozoochory		✓	
Calamintha nepeta (L.) Kuntze	Lamiaceae	barochory/anemochory		✓	✓
Lavandula stoechas L.	Lamiaceae	barochory	✓	✓	✓
Marrubium vulgare L.	Lamiaceae	barochory/epizoochory		✓	
Origanum vulgare L.	Lamiaceae	barochory/anemochory		✓	
Phlomis purpurea L.	Lamiaceae	barochory/anemochory		✓	✓
Teucrium fruticans L.	Lamiaceae	barochory			✓
Thymus mastichina L.	Lamiaceae	barochory/anemochory	✓	✓	
Lonicera implexa Aiton	Caprifoliaceae	endozoochory	✓	✓	✓
Viburnum tinus L.	Adoxaceae	endozoochory	✓	✓	✓
Dittrichia viscosa (L.) Greuter	Asteraceae	anemochory		✓	
Helichrysum stoechas (L.) DC.	Asteraceae	anemochory	✓		✓
Phagnalon saxatile L.	Asteraceae	anemochory	✓	✓	✓
Smilax aspera L.	Smilacaceae	endozoochory	✓	✓	✓
Asparagus albus L.	Liliaceae	endozoochory			✓
Asparagus acutifolius L.	Liliaceae	endozoochory	✓	✓	✓

Data analysis

All statistical analyses were performed using R Statistical Software version 3.6.3 (R Core Team, 2020). General linear models and generalised additive models (GAMs) were used to model the relationship between species richness and area for each of the groves. Our research focused on exponential and power species-area curves. Other models, especially those incorporating an asymptote were excluded from our analysis for two main reasons: 1) Asymptotic models assume there is a theoretical upper limit for richness (Williamson *et al*., 2001; Lomolino, 2002; Williamson *et al*., 2002), yet our sampling reveals that maximum possible richness (overall species richness across the three sites) is still much higher than the maximum observed richness in one single site, meaning patch richness has the potential to keep increasing; and 2) reduced sample sizes above 150 m^2 implies there is a large uncertainty at higher areas, meaning any estimation of an upper boundary is inherently prone to error.

Exponential models were constructed by log-transforming the area values (Gleason, 1922), and power models by log-transforming both area and species richness (Arrhenius, 1921). Zero values for species richness were included within the log-transformed data by adding 1 to all values (Borcard *et al*., 2018), allowing all observations to be used and minimising bias. Model fit was assessed using R^2 values. The suitability of power vs exponential models was also evaluated by checking for normality of residuals and heteroskedasticity.

The minimum area values for each site-specific species-area curve were calculated, both for power and exponential models, based on approaches developed by Müeller-Dombois & Ellenberg (1974) and Cristaudo *et al.* (2015). Minimum area, the point at which a 10% increase in 10% in area yields only a 10% increase in richness, was identified by taking the abscissa of the intersection between the estimated species–area curve and a tangent line that is parallel to the line connecting the origin of the axes and the maximum values for x and y (Margalef, 1951).

Site-related differences in the power species-area curves were analysed using multivariate linear regression (ANCOVA) that allows an area-site interaction. We used a GAM, fitting different intercepts and smooth functions for the species-area curve at each site, to assess whether including the three curves within a single power model is appropriate. This model was compared against another GAM that did not include separate smooth functions for each site. Indeed, GAMs provide a further to assess the suitability of the species-area functions, by testing whether the log-log power relationship is linear. Multivariate GAMs also allow us to detect site-specific deviations from linearity within the general trend, which may be masked within linear regression. The models were compared using AIC (Akaike Information Criterion) values. GAMs were fitted using smoothing via Restricted Maximum Likelihood (REML) and using the default number of basis functions (Zuur *et al*., 2009).

Results

A total of 154 vegetation patches were sampled across the three groves, with a total of 15,863 individual woody plants recorded from 50 species belonging to 22 families (Table 1). While woody species composition varied between sites, each site supported plants that belong to mature and secondary growth woodlands, as well as typical maquis and garrigue species, dwarf shrubs, woody forbs and vines (López-Villalta, 2016). Some escaped domestic species were also present at the groves.

Species-area curve functions

Species-area curves for Las Niñas and Piquín were more adequately represented by the power model, having better model fit, higher F-values, lower p-values and more normally distributed residuals (Table 2). The species-area curve at La Soledad could be modelled by both exponential and power models. However, the power model for La Soledad was heavily heteroskedastic, even if the R^2 value was high. Still, the power ANCOVA model that incorporated data from all three sites met all assumptions of linear regression, and suggested no interaction between site and area (Figure 4).

The power GAM acknowledging different intercepts and smooth functions for each site revealed that the species-area relationship at Las Niñas and Piquín was approximately linear, but that log transformed species richness at La Soledad appears to be showing a curved relationship with log-transformed area (Figure 5). It is important to note that this model only showed a statistically equivalent model fit ($R^2 = 0.829$, AIC = -117.49) compared to the GAM that did not acknowledge site-specific smooth functions ($R^2 = 0.824$, AIC = -116.65).

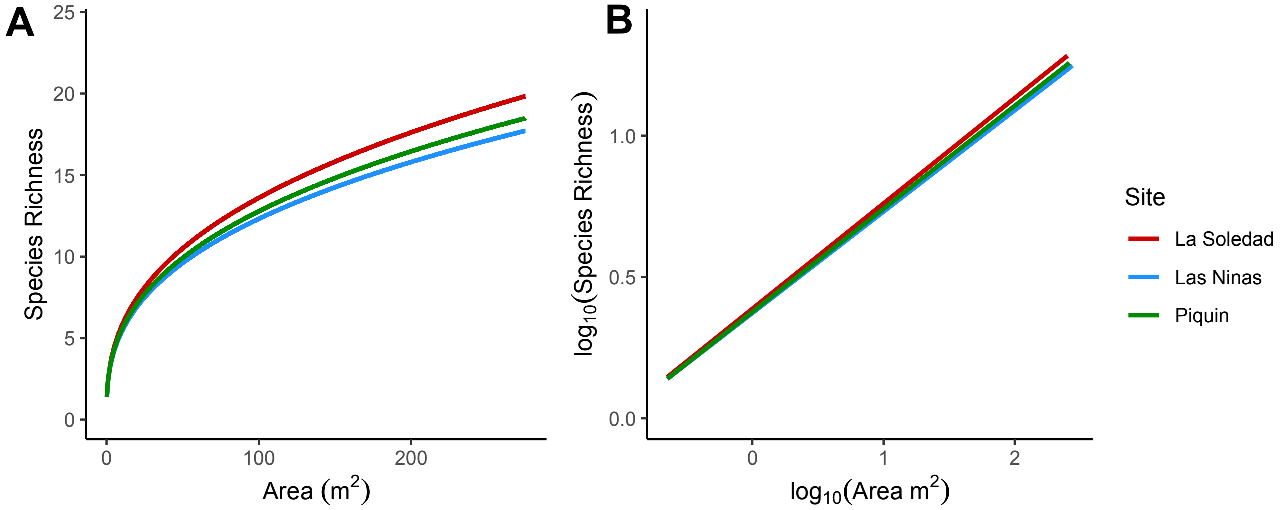

Figure 4. Representation of the power species-area curves for the woody patch vegetation within the olive groves. A, power species-area relationships on the raw scale; B, relationship between log-transformed species richness and log-transformed area at all three groves, described by a linear regression ANCOVA model interacting area with site. There is good model fit and significant effect of area (Linear regression, R^2 adj.=0.81, F=129.8, df=5.148, p<0.001) but no significant effect of site ('Las Niñas'=-0.012, t=-0.322, p<0.001; 'Piquín'=-0.011, t=-0.235, p<0.001) or interaction between site and area.

Minimum area values

Minimum area values (Table 2) were higher for all power law species-area models, regardless of site identity. On average, minimum area values for power curves were about twice as large as minimum area values for exponential functions. Mean species richness at the minimum area was (21%) higher for power models. The largest minimum area value was derived from the power curve at Piquín, closely followed by the power curve at La Soledad. The smallest minimum area value was derived from the exponential curve at Las Niñas, which also showed the smallest minimum area values within the power curves. It is important to remember that any reference to minimum area values for exponential curves at Las Niñas and Piquín should be taken with care, since these are derived from less suitable statistical models. The minimum area and corresponding richness values for the power model at La Soledad were about 2.5 and 1.5 times as high as the values derived from the exponential curve.

Discussion

Power models clearly approximated species-area relationships better for two out of the three groves, and the species-area relationships in all three groves could be adequately described by this function. Transformed species richness varied linearly with log-transformed area, following the function proposed by Arrhenius (1921). This pattern followed the initial expectations, being statistically similar across all three sites. The influence of alternative factors on richness is likely minimised by all three groves having similar climate, geology, soil type and management history. The results are also consistent with species-area patterns observed in the literature, both within and outside Mediterranean ecosystems. For example, power functions adequately represented species-area curves within the Californian chaparral (Keeley, 2003; Keeley & Fotheringham, 2003), for herbaceous plants within citrus groves (Cristaudo *et al.*, 2015) and for vegetation in salt steppes (Pardo *et al.*, 2003) and post-fire forests in south-eastern Iberia

(Pausas *et al*., 1999). Power models also performed best for 449/601 worldwide species-area datasets studied (Triantis *et al*., 2012).

Despite this, the species-area relationship at La Soledad was more adequately represented by Gleason's exponential model, even though it can be approximated by the power model both as a single function (showing significant heteroskedasticity), and within the general ANCOVA model. The GAM analysis reveals that the power species-area curve for La Soledad's is curved, accounting for the uneven distribution of variance within the model. However, allowing separate smooth functions for each site barely improved model fit, further supporting the fact that La Soledad's data is able to fit a power species-area relationship. Therefore, incorporating all three curves within the same power model is suitable, because La Soledad's deviation from linearity falls within the bounds of the statistical assumptions of linear regression. Using a power model with separate intercepts and gradients for all three sites represents a trade-off. It does not fully represent the true species-area relationship at La Soledad, but it allowed us to statistically test if there were any significant differences in terms of intercept and gradient.

Table 2. Output statistics and normality of residuals for linear models describing the species-area relationship at each site. It includes both exponential (log-transformed area, species richness) and power (log-transformed area, log-transformed richness) models, as well as minimum area values (and corresponding species richness, S) for the respective species-area curves in the real scale. The table also includes the output for Bartlett tests revealing variance in richness and log-transformed richness is homogeneous across the site categories. Exponential: Bartlett's K-squared = 0.044635, df = 2, p-value = 0.9779; Power: Bartlett's K-squared = 2.7953, df = 2, p-value = 0.2472.

	Linear Regression				Shapiro-Wilk Test		Minimum Area	
	R^2 adj.	F-value	DF	p-value	W	p_w-value	A (m^2)	S
Exponential								
La Soledad	0.8301	250.1	1.50	<2.2e-16	0.96541	0.13430	32.2	7.8
Las Niñas	0.6997	115.2	1.48	2.377e-14	0.91815	0.00202	27.9	9.3
Piquín	0.6896	114.3	1.50	1.612e-14	0.94471	0.01747	40.3	10.6
Power								
La Soledad	0.8172	229.0	1.50	<2.2e-16	0.98955	0.92680	77.4	12.4
Las Niñas	0.7879	183.1	1.48	<2.2e-16	0.98360	0.71030	46.1	9.3
Piquín	0.8232	238.5	1.50	<2.2e-16	0.97738	0.42140	79.9	11.8

Being able to apply both power and exponential functions is also consistent with the literature, since species–area relationships often tend to fit both Arrhenius' and Gleason's functions (Tjørve, 2012). Keeley (2003) found that species-area relationships in Australian shrublands were better represented by exponential functions, while Pardo *et al.* (2003) acknowledged that exponential curves fitted their data almost as well as power models.

The fact that the species-area relationship at La Soledad follows the exponential function means species richness levels-off at higher areas, and this eventual reduction in the rate of increase of richness could be explained by factors relating to seed dispersal and land use history. A large part of the land directly surrounding the sampled area at La Soledad is composed of semi-abandoned olive groves on steeper slopes, whereas Piquín and Las Niñas are surrounded by a greater proportion of fully encroached scrub. Forest or shrubland habitats cover 92% of the surface within 40 m of the grove at Las Niñas (Figure S1). This proportion falls to 46% at Piquín (Figure S2), and 27% at La Soledad (Figure S3), meaning the habitat quality around La Soledad is less natural. This has direct consequences on the dispersal of plant species into the groves because colonisation of woody species is mainly influenced by the quantity of nearby mother plants (Debussche & Lepart, 1992; Rühl, 2007). Thus, richness of plants that disperse into vegetation patches at La Soledad should be smaller because the site is father away from seed sources. Similarly, Las Niñas and Piquín were partially encroached by scrub between 1976 and 1983 (CNIG, 2021), which could mean that a more diverse seed bank was able to establish within the patches before the groves were re-cleared and separated from the surrounding scrub.

Las Niñas and Piquín support a higher proportion of barochorous/anemochorous species (Table 1), which are primarily dispersed by gravity and by wind. These species have small propagules that rely on their small size in order to be blown away, meaning they are usually dispersed over short distances (Vittoz & Engler, 2007). Thus, the absence of species like *Ruta montana* L. and *Coronilla juncea* L. within vegetation patches at La Soledad could be explained by limits to seed dispersal processes.

Minimum area values

Our results imply that higher diversity of woody plants could be obtained by enlarging the size of the current patches. According to the power species area curves (Figure 4), patches of 250 m² will support about 5.5 times more richness than patches of 2.5 m². Enlarging patches whilst maintaining patch structure should promote plant diversity, and this could enhance seed dispersal and floral availability for pollinators (Carpio *et al.*, 2018), as well as provide a wide range of vegetation microhabitats that will encourage patch occupancy by larger animals (Carpio *et al.*, 2016; Assandri *et al.*, 2017). Maintaining and enlarging patch structures could also provide increased grazing sustainability, as there will be higher quantities of fodder resource, and because grazing pressure will be relieved due to the presence of a wide range of shrubs with different palatabilities and defence mechanisms (Papanastasis *et al.*, 2008).

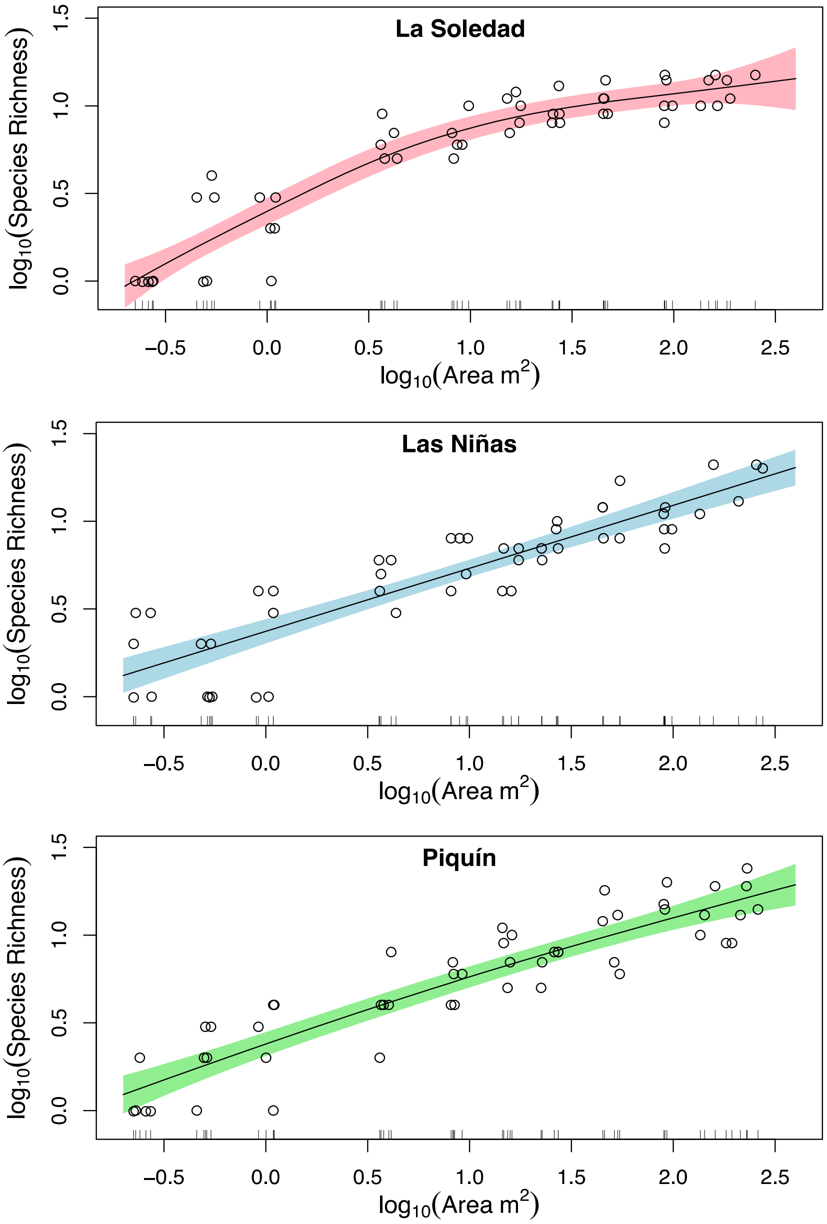

Figure 5. Assessing non-linear species-area relationships in the log-log space. The data is described by a generalised additive model allowing different intercepts and smoothing functions for each site (GAM, R^2adj=0.829, AIC=-117.49; La Soledad: EDF=2.82, F=76.7, p<0.001; Las Niñas: EDF=1.00, F=221.81, p<0.001; Piquín: EDF=1.656, F=125.08 p<0.001).

However, it is important to acknowledge that patch area should not be increased indefinitely, and that landholders will be constrained by limitations in total land area, budget and resources. Therefore, patches should be enlarged up to a point where increases in area stop being meaningful: the minimum area threshold (which is approximately 63 m² on average for olives groves exhibiting power species-area relationships, 46 m² for Las Niñas and 80 m² for Piquín). Up to this point, patch size increases of 10% will always translate to >10% increases in richness. This is an attainable strategy, since minimum areas derived from power species-area model are more than three times smaller than maximum patch sizes. Minimum area patches will also hold significant richness: 44 and 49% of the maximum richness observed within single patches at Las Niñas and Piquín.

These results fit within the range of values obtained by previous studies focusing on the vegetation Mediterranean and temperate climates. Cristaudo *et al.* (2015) sampled the herbaceous vegetation within Sicilian citrus groves, and found that minimum area for each grove ranged from 33 to 56 m^2. Alternatively, minimum area for temperate oak-laurel forests in Chile was 110 m^2 (Ramírez *et al.*, 1997), whilst temperate woodlands in Europe usually presented minimum area values of above 200 m^2 (Knapp, 1984). Obtaining moderate minimum area values reflects our study's scope, which focused on plants, woody shrubs and trees, of intermediate sizes and area requirements.

Our results also reveal that the species-area relationships are spatially variable, and that increase in richness at larger patch areas could be inhibited by site-related factors like surrounding habitat quality and land-use history. Moreover, estimates of minimum area values are sensitive to the modelling approach used, with (Table 2) exponential curves estimating steeper declines in gradient at larger areas (Figure 6). This has important implications for the effectiveness of the minimum area threshold as a conservation strategy, since applying the incorrect species-area function will lead to a very different minimum area estimate, limiting the strategy's effectiveness. Assigning a power function to the species-area curve at La Soledad might be statistically appropriate but will mean minimum area (77.7 m^2) and corresponding richness (12.4) are much larger. Meanwhile, managers will not obtain significant increases in richness above a threshold of 32.2 m^2 if they follow an exponential model, which would lead to different management decisions, potentially with monetary consequences. Appropriate minimum area values (those derived from the appropriate relationship at each site) are also quite variable, ranging from 32 to 80 m^2 and averaging at 53 m^2. We therefore stress the importance of taking appropriate steps for assigning the correct function to the species-area relationships at different locations, as well as of replicating the study at more groves to obtain more reliable estimates.

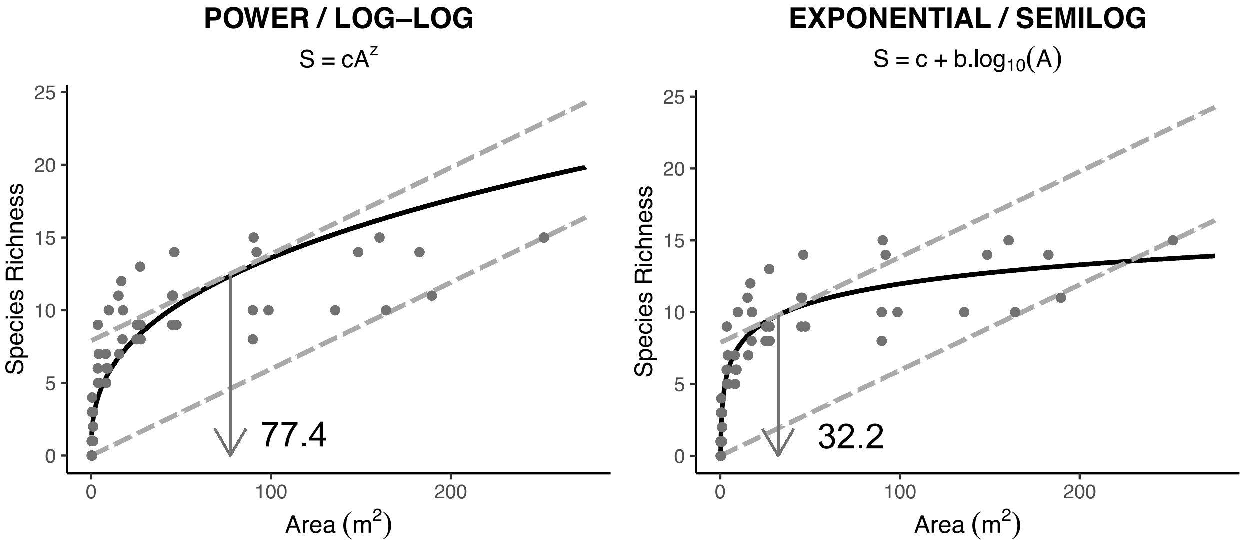

Figure 6. Power and exponential species-area curves at La Soledad, including derived values of minimum area.

Implications for management and future studies

This study suggests that encouraging the formation of vegetation patches of minimum areas within abandoned groves could provide a controlled alternative to both active restoration and natural regeneration of woody Mediterranean landscapes. Continuous-area reforestation or regeneration reduces landscape heterogeneity, which can have negative ecological and socioeconomic impacts (Blasi *et al.*, 2000; Allen *et al.*, 2006). Additionally, landholders can currently apply for reforestation and regeneration grants under the EU EAFRD scheme (Jarsky & Pulkrab, 2013), but they are often constrained due to national and regional regulations specifying that reforestation requires a minimum number of continuous hectares (Anon., 2009; Anon., 2015). Patch-mediated restoration, where land managers encourage patches of approximately 32 to 80 m^2 to develop, would allow landholders to increase the presence of natural vegetation around olive trees with reduced effort (i.e., avoiding the general practices of planting and protecting seedlings) whilst simultaneously managing patch areas and maintaining an open landscape. These practices could reduce reforestation costs, while maximising woody plant diversity and enhancing ecosystem services derived from both open and closed habitats. Patch-mediated restoration could enhance biomass production, pollination, water retention, reduction of erosion, reduction of fire risks and recreational value (Blasi *et al.*, 2000; Sala *et al.*, 2000; Allen *et al.*, 2006; Rallo, 2007; Duarte *et al.*, 2008). For example, it would allow introducing grazers into an already semi-abandoned grove, providing landholders with additional sources of income (Carbonero Muñoz *et al*., 2013).

Finally, patch-mediated restoration should consider the quality of reforested land (MAAMA, 2014). It is therefore important to study the community composition of the vegetation, rather than just focusing on species richness. Increased patch size provides a higher number of species, but could also translate into the loss of ecologically or economically important species such as *Quercus ilex* L. Subsequent studies should therefore focus on examining the relationship between area and the presence or abundance of individual species, or on investigating the community turnover across different patch areas. The establishment of patches of natural vegetation should also be encouraged in cultivated areas within more intensified landscapes, such as lowland olive and cereal agriculture, where biodiversity benefits from patch reservoirs would be greater. Yet it is also important to note that intensified agricultural landscapes are very different from those at the study area, since there is much less surrounding natural vegetation and thus our findings cannot be confidently extrapolated. We therefore encourage other experts to replicate this investigation at similar sites.

Conclusions

This study provides one the first descriptions of plant communities within vegetation patches in semi-abandoned olive groves, giving insight into the mathematical relationship between patch area and richness of woody plants. Power models could represent the species-area relationship of all three sites, yet the exponential model performed better in one of the groves. Surrounding habitat quality and vegetation history appear to have affected the nature of the species-area relationship, and this was reflected in significant differences among the minimum area values. Enlarging patches up to the minimum area threshold, from 32 to 80 m^2 depending on the site and type of relationship, could effectively promote plant diversity whilst maintaining an open landscape. However, special care should be given to adequately modelling the species-area relationship, since applying incorrect species-area functions will lead to very different minimum area estimates. Future studies should therefore emphasise the nature of species-area relationships and corresponding minimum area values, in order to propose suitable, attainable and science-based targets for land managers. This current study could be further extended to examine the vegetation within heterogeneous landscapes at other locations within Spain or other Mediterranean countries, allowing researchers to determine which locations show unique vegetation richness dynamics, and encouraging managers to design especial conservation and management strategies.

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Supplementary material

Figure S1. Encroached forest and shrubland surrounding the sampled area at Las Niñas.

Figure S2. Encroached forest and shrubland surrounding the sampled area at Piquín.

Figure S3. Encroached forest and shrubland surrounding the sampled area at La Soledad.