Water availability and species identity control shrub colonization in abandoned semiarid steppes

Short title: Patch dynamics in drylands

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Highlights

- Shrub cover has increased in former agricultural lands worldwide.
- Colonization rates are explained by the identity of shrub species.
- Species idiosyncratic effects are contingent on water availability.
- Abiotic attributes, such as aspect or rock cover, played a lesser role.

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Abstract

The increase in shrub cover and density is a widespread phenomenon in drylands worldwide. Its causes and consequences are complex and strongly idiosyncratic. Detailed knowledge of the rate of shrub colonization, and its abiotic and biotic drivers is crucial to fully understand and manage these areas. We used a set of aerial photographs (1956, 1978, 1985, 1998 and 2009) and field data to relate shrub patch dynamics, and abiotic and biotic properties of 27 abandoned steppes in SE Iberian Peninsula. Shrub patch density in 2009 ranged from 11 to 143 patches ha^{-1}, and increased by an average of ~ 180% between 1956 and 2009. Temporal changes in shrub patch density followed non-linear functions (monomolecular, logistic and exponential) describing early, gradual and late recruitment, respectively. Differences in shrub patch colonization rate were related to the identity of patch-forming species, but contingent on water availability. Total increases in shrub patch density were larger when patches were dominated by late colonizer species. Overall shrub patch dynamics was mostly related to the identity of patch-forming species and climatic conditions, and to a lesser extent physical factors such as aspect and rock cover. Given the sensitivity of patch-forming species to climatic conditions, new challenges for steppe management will emerge over the next decades. Species able to thrive under harsh conditions may increase their dominance at the expense of species adapted to less demanding conditions.

1. Introduction

The proliferation of woody species is a common phenomenon in drylands worldwide (van Auken, 2009). Information derived from time series of aerial photographs has advanced our knowledge of the dynamics and extent of shrub encroachment (Briggs et al., 2002; Peters et al., 2006). However, research on the drivers of shrub colonization has mostly focused on the effect of physical factors, particularly soil properties and topographic features such as aspect and elevation (Browning et al., 2008; Davies et al., 2010; Levick and Rogers, 2011) or grazing (Bartolomé et al., 2005; Roques et al., 2001; Ward et al., 2014). In contrast, the identity of the colonizing shrub species as major driver of shrub expansion has seldom been studied. This is despite the strong relationship between climate, morphological/-functional traits and shrub dynamics (Eldridge et al., 2011; Pueyo et al., 2010).

Different shrub assemblages, which are the result of long-term processes such as habitat filtering and niche differentiation (Gross et al., 2013), may exhibit contrasting colonization dynamics. Differences in life-history traits among species (e.g. age at maturity or number of offsprings) may generate different sequences of shrub colonization (e.g. Iannone et al., 2014). Different sequences may also result from contrasting survival strategies among co-occurring shrub species to disturbances such as fire (e.g. Hodgkinson, 1998). However, most studies addressing the drivers of shrub cover change in drylands consider the encroaching vegetation as a single functional group (e.g. D'Odorico et al., 2012), overlooking potential species-specific effects of shrubs on colonization dynamics.

Variable colonization dynamics can also result from changes in climatic conditions, such as water availability during the colonization process (Browning et al., 2008). Thus, coupling species-level information on colonization with data on past climatic events may provide further insights into the linkages between climate and vegetation and, therefore, on the mechanism behind shrub colonization (Munson et al., 2015). This is especially relevant for dryland environments where climate projections predict increased variability in precipitation as well as

increased frequency of extreme events, such as drought (IPCC, 2007). Clarifying how drought intensity mediates species-specific effects of shrub colonization can be of great help to predict future trends in shrub population dynamics, and assess the consequences of future global change regimes on the provision of ecosystem services (Ruppert et al., 2015).

Knowledge of the drivers of shrub colonization is of major importance in those ecosystems where planting woody species has become a major priority in restoration programs (Cortina et al., 2011; Maestre et al., 2001; Padilla et al., 2009b). For instance, open steppes dominated by *Stipa tenacissima* L. are conspicuously distributed in the semiarid regions of the western Mediterranean basin. For centuries, the provision of *S. tenacissima* fiber was the main management priority in these steppes. Large shrubs were removed to favor *S. tenacissima* production (Maestre et al., 2007). Over the last decades, an increase in shrub cover has been reported in southern European steppes, probably as a result of the abandonment of traditional agricultural practices (Alados et al., 2004; Maestre et al., 2007) and linked to desertification reversal (Maestre et al., 2009). However, managers perceive that shrub colonization of abandoned *S. tenacissima* steppes is often absent or too slow and that this delay may compromise the delivery of ecosystem services and ecosystem stability. In this context, an increased understanding of the endogenous and exogenous factors controlling shrub colonization may therefore help to clarify the relationship between biotic/abiotic and structural/functional ecosystem components (sensu Turnbull et al., 2008), and prioritize restoration efforts in semiarid steppes.

The aim of the present study is to relate long-term shrub dynamics with biotic and abiotic ecosystem attributes. We used a set of aerial photographs (1956, 1978, 1985, 1998 and 2009) and field data to relate shrub patch dynamics to biotic, climatic, topographic and geomorphological properties of 27 abandoned steppes in SE Iberian Peninsula. The use of aerial photographs has several advantages over other methodological approaches (Morgan et al., 2010) and has been widely used in studies of shrub colonization (Hellesen and Levin, 2013; Hudak

and Wessman, 1998; Laliberté et al., 2004; Ward et al., 2014). We hypothesized that the effects of species identity and climate may be more influential in shaping long-term processes of shrub colonization than other factors related to the physical context of each abandoned steppe. Specifically, we expect that the rate and intensity of shrub colonization may depend on the identity of the colonizing species, and also on how species respond to climate in particular physical contexts characterized by topographic and geomorphological features. Describing shrub dynamics in abandoned steppes can be of great help to identify species with high and low ability to colonize under present and future climatic conditions. Furthermore, disentangling how long-term shrub dynamics are mediated by biotic and abiotic ecosystem attributes is crucial to prioritize management interventions because it provides evidences of suitable and unsuitable areas for establishment.

2. Material and Methods

2.1 Study sites

We selected fifteen catchments covered by *Stipa tenacissima* L. steppes in a semiarid area in Alicante, SE Spain (38º 20' 50''N, 0º 29' 29'' W), where winters are mild and summer drought is intense. Mean annual precipitation ranges between 282 and 525 mm, and mean annual air temperature between 15ºC and 18ºC (Ninyerola et al., 2005). Most soils are Lithic Calciorthid (Amat, 2015). Catchment surface area ranged between 3-11 ha, and were located within a 60-km NE-SW transect. Each catchment was divided into 3-6 environmental units (EU) on the basis of their aspect, topography, plant cover and previous land use. We identified 27 EUs in total based on the analysis of aerial photographs and field validation during a survey conducted in 2009.

2.2 Biotic and abiotic attributes of the environmental units

We measured biotic, climatic, topographical and geomorphological attributes in one to three 15 x 21m plots set in each EU, depending on its surface area. In each plot we established two 21m transects, 8 m apart, parallel to the maximum slope. In total we sampled 106 transects. In each

transect, we quantified plant cover and rock cover by visual estimation in 14 consecutive 1.5 x 1.5 m quadrats. Total plant cover was estimated as the sum of all species present in the transect. Rock cover was estimated as the sum of the cover of unconsolidated rocks as well as the cover of bedrock that appeared at the surface of the ground.

In each 21m transect, we estimated indicators of ecosystem function, such as patch area (hereafter resource sink area), and the average "inter-patch" length (hereafter fetch length), following Landscape Functional Analysis approach (LFA; Tongway and Hindley, 2004). In this method, a patch is every long-lived feature that acts as a sink for resources by obstructing or diverting water flow and thus collecting and filtering water, nutrients, seeds (e.g., grass tussocks, large rock fragments, branches and litter). Accordingly, "inter-patches" are gaps between resource sinks, as bare soil, gravels, and plants whose structure is unable to retain resources.

Additionally, we georeferenced all shrub patches present in each EU in 2009 to calculate shrub patch density. Shrub patch density was calculated in each EU by dividing the total number of shrub patches by EU surface area. Field measurements of shrub patch density were used to assess the accuracy of aerial photograph interpretations (see below). We recorded species composition and the presence of dominant species (6 species in total) in 30 randomly selected patches (450 patches in total). We considered as dominant species those shrubs that form clearly defined patches, because of their large size and their ability to create new microhabitats. The six dominant species were *Pistacia lentiscus* L., *Quercus coccifera* L., *Rhamnus lycioides* L., *Juniperus oxycedrus* L., *Ephedra fragilis* Desf. and *Osyris lanceolata* Hochst. & Steud (Amat, 2015). Species richness was recorded as the total number of species per EU. We measured soil depth by inserting a 1-cm diameter iron rod into the soil and recording the maximum depth attained. Average soil depth under a shrub patch was estimated by measuring 6-10 points beneath their canopy. Average soil depth in each EU was estimated from the soil depth measured in 30 randomly chosen locations within each catchment.

We recorded elevation (m a.s.l.), slope (%) and predominant aspect of each EU using digital elevation models. To avoid confusion with the circular nature of aspect, we calculated the cosine of its value (hereafter northness). This transformation generates values between 1 (if the aspect is northwards) and -1 (if the aspect is southwards). We employed published records to estimate local mean annual precipitation (mm) from 1945 to 2009 (MOPREDAS database, González-Hidalgo et al., 2011), and mean annual air temperature (ºC) (Ninyerola et al., 2005). From the mean annual precipitation database, we calculated the standardize precipitation index (SPI) for each EU and year. The SPI has been widely used to estimate drought intensity, and is computed as the number of standard deviations that the average precipitation over a given period of time deviates from the long-term mean (Vicente-Serrano, 2006). The main properties of all EU's, and a schematic view of the sampling design are summarized as supplementary information (Table A1, Fig. A1).

2.3 Aerial photography interpretation

Aerial photos were obtained from public and commercial flights launched in 1956, 1978, 1985, 1998 and 2009 (Table 1). Digitized images of 1998 and 2009 were acquired, georeferenced and orthorectified. Photos from 1956, 1978 and 1985 were digitized by scanning on an A3 flatbed scanner (HP Deskscan, HP Co., Palo Alto, USA) at 1200 dpi, using an 8-bit grey-scale. Images were geometrically corrected, resampled to a common spatial resolution (1 m) and registered to the UTM projection by performing and image-to-image registration on 40 points from 2009 images (Fig. A2).

A texture layer was created from each image to enhance the difference between dark shrub canopies and the surrounding bright soil and herbaceous vegetation (Asner et al., 2003). Specifically, texture analysis consisted of passing a 3 x 3 pixel window computing the mean, variance and range within the kernel. Visual interpretation of generated images was performed to mark the presence of patches. Our sample unit was a shrub patch, defined as a woody plant

Table 1. Main features of the different sets of aerial photographs included in the time series analysis.

Year	Source	Colour	Scale	Pixel size (m)
1956	American Flight Serie B	Grey scale	1/35.000	0.5
1978	Interministerial Flight	Grey scale	1/18.000	0.5
1985	Interministerial Flight	Grey scale	1/18.000	0.5
1998	Olysat (Sig Oleicola)	Grey scale	1/40.000	1
2009	CNIG	Color (RGB)	1/5000	0.5

canopy which represents and individual or a cluster of individuals with overlapping canopies sensu (sensu Browning et al., 2008). In each texture layer, the same author (VR) marked the location of each shrub patch within the EU, to minimize observer bias. We related field measurements of shrub patch density and estimations based on aerial photographs to assess the accuracy of our approach. In addition, we estimated the detection probability of shrub patches using the double observer approach. This approach is commonly used in point count studies to provide estimates of population size and detection probability (Williams et al., 2002). It requires two independent counts of the same subjects to estimate detection probability. We used shrub patches georeferenced in 2009 field survey as a benchmark. Detection probability of the visual interpretation of aerial photographs (p) can be computed as $p = m_2/n_1$. Where m_2 is the number of shrub patches detected in both surveys (aerial photographs and field observations) and n_1 is the number of shrub patches identified on aerial photographs. We used ArcGIS v.9.3 (Environmental Science Research Institute, Redlands, California, USA) to process, quantify and classify information obtained from images.

2.4 Data analysis

The relationship between patch species composition and biotic and abiotic attributes was explored using redundancy analysis (RDA). The response variables were the abundance of the dominant shrub species recorded in the field survey, and explanatory variables were the biotic, climatic, topographical and geomorphological attributes. The significance of total canonical variation and individual eigenvalues were tested with permutation methods.

Shrub patch dynamics was analyzed in different ways. Firstly, we used generalized linear mixed models to assess the relationship between temporal dynamics of shrub patch density (i.e. dependent variable) and biotic, climatic, topographical and geomorphological attributes (i.e. independent variables). Moreover, we included year in the model as ann independent variable to test for differences in shrub patch density between time steps. We included precipitation and SPI as the averaged value in the decade prior to each aerial photograph. We did not include

temperature because of the lack of complete data. We included site scores of the first two axes of the RDA (hereafter RDA1 and RDA2) to account for the effect of species composition on shrub patch density. Site scores are the coordinates of the sites expressed in the space generated by the species abundance matrix, without the influence of independent variables included in the RDA (Borcard et al., 2011). To account for differences in surface area between EUs, these values were included in the model as an offset (Zuur et al., 2009). We included the random effect of catchment and year in a varying intercept and slope model, to account for repeated measures of patch density over time (Bates, 2010). To account for the differences in image quality between aerial photographs (Table 1), we categorized scale as small-scale (1/35.000 and 1/40.000), mid-scale (1/18.000) and large-scale (1/5.000) and include it as a random effect in the model.

Secondly, the rate of shrub colonization was analyzed by fitting non-linear functions to shrub patch density increment ratios. Shrub patch density increment ratios (PD_r) (adapted from Gale and Grigal, 1987) at each time step were calculated as: $PD_r = (t_i - t_o)/(t_f - t_o)$, where t_o is shrub patch density in 1956, t_f is shrub patch density in 2009, and t_i is shrub patch density at successive time steps (i = 1956, 1978, 1985, 1998, 2009). A set of non-linear models (i.e. monomolecular, logistic and exponential) was fitted to the data to model the relationships between PD_r values against time. In each site, we selected the function showing the best fit based on the coefficient of determination to observational data (see Table A2 for a summary of these analysis). Then, we solved each equation at $PD_r(t)= 0.5$ to estimate the time needed to reach a 50% change in PD_r (t50; sensu Gale and Grigal, 1987). Thirdly, we calculated the total change in shrub patch density in each EU from 1956 to 2009 (hereafter density change).

Linear mixed models containing t_{50}, density change and detection probability as dependent variables and biotic, climatic and physical attributes as independent variables were fit to the data, including catchment as a random effect. We included RDA1 and RDA2 in the model to test the effect of species identity, and initial patch density to test density-dependent effects. We

could not include SPI values in these models because its mean is zero when considering the whole precipitation time series. Alternatively, we categorized each SPI values per year according to the National Drought Mitigation Center of the USA (http://droughtmonitor.unl.edu) as: 0 $(+0.5 \leq \text{SPI} \geq -0.5)$; -1 $(-0.5 < \text{SPI} > -0.8)$; and -2 $(-0.8 \leq \text{SPI} > -1.3)$. We only included the first three categories of this classification scheme because our database did not contain values of SPI < -1.3. We included the mean values of the new categorization per catchment in these models. Additionally, we related averaged SPI values between two consecutive aerial photographs to mean t_{50} values per catchment, to test if t_{50} values per catchment corresponded to periods of higher water availability.

To evaluate which predictor variables contributed consistently across each model per response variable (shrub patch density, t_{50}, density change and detection probability) we followed a model averaging approach following Grueber *et al.,* (2011). For this, regression coefficients of each explanatory variable were averaged across all competing models where ΔAICc < 2. For each competing model, Akaike Information Criterion weight (AICc-wi), which represents the likelihood of a given model relative to all other models, was generated. An importance value of each explanatory variable was calculated by adding the AICc-wi values of the competing models in which the predictor was present. Importance values vary between zero (low importance) and one (high importance). Competing models were based on the combination of explanatory variables whose variance inflation factor was below four, to avoid collinearity. All analyses were carried out with R v3.0.1 (R Development Core Team, 2013). We employed *vegan* (RDA), *SPEI* (SPI), *minpack.lm* (non-lineal fitting), *lme4* (GLMM), and *MuMln* (multimodel inference) packages.

3. Results

3.1 Association of shrub patch species with biotic and abiotic attributes

Redundancy analysis showed that 55% of the variance in species abundance was explained by northness, soil depth, patch area, temperature and precipitation (Table 2). The first two

Table 2. Final set of significant descriptors included in the RDA analysis to describe the relationship between biotic and abiotic attributes and species composition in shrub patches.

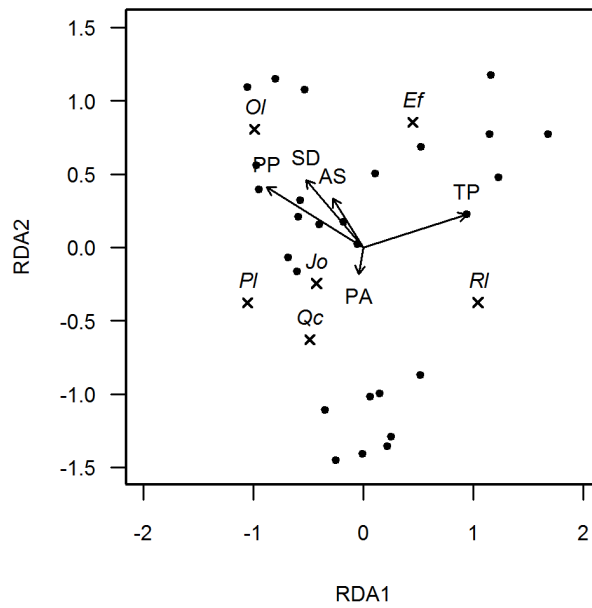|	df	F	*P-value*
Aspect (northness)	1	2.6	0.035
Soil depth	1	4.3	0.001
Patch area	1	2.3	0.056
Mean annual air temperature	1	10.9	< 0.001
Mean annual precipitation	1	5.2	< 0.001

Figure 1. RDA triplot depicting the abundance of the dominant patch forming shrub species as a function of biotic [resource sink area (PA)] and abiotic [aspect as standardized as northness (AS), soil depth (SD), precipitation (PP) and temperature (TP)] ecosystem attributes. Circles and crosses represent environmental units and dominant patch forming species, respectively. Codes for species names are as follows: *Ephedra fragilis* (Ef), *Rhamnus lycioides* (Rl), *Quercus coccifera* (Qc), *Juniperus oxycedrus* (Jo), *Pistacia lentiscus* (Pl) and *Osyris lanceolata* (Ol).

canonical axes explained 86% of the total variance, and were statistically significant ($P = 0.005$ for both axes after 999 permutations). Temperature and precipitation played an important role in EU dispersion along the first axis (Fig. 1). *Osyris lanceolata* abundance was positively correlated with precipitation, soil depth and northness. In contrast, the abundance of *Rhamnus lyciodes* and *Ephedra fragilis* were positively correlated with temperature. Resource sink area was weakly correlated with *Quercus coccifera* abundance. The position of other species in the space defined by the two axes was intermediate.

3.2 Detection probability of shrub patches

The mean value of detection probability across EUs was 0.73 ($\pm$ 0.03). Rock cover, plant cover and fetch length showed positive model coefficient estimates of detection probability (Table 3). However, coefficient estimates of the three attributes were not different from zero. Estimated shrub patch density from aerial photographs was positively and linearly related to shrub patch density measured in the field ($P < 0.001$, $r^2 = 0.77$) (Fig. A3).

3.3 Influence of biotic and abiotic attributes on changes in shrub patch density and colonization rate

Aerial photograph interpretation showed that shrub patch density increased from 24 ± 3.2 to 67 ± 7.4 patches ha^{-1} (average $\pm$ SE) over the 53-years period. Shrub patch density increased significantly in each time step as compared to the reference value in 1956 (Table 3). The best set of predictors for shrub patch density included year, precipitation, northness, rock cover, resource sink area and plant cover in 2009 (Table 3). We observed a negative association between shrub patch density and precipitation, northness, rock cover, and resource sink area. Plant cover was positively associated with shrub patch density.

Three contrasting patterns of change were observed when increases in shrub patch density were standardized (Fig. 2, Table A2). In 18 EUs, they followed a logistic growth curve, whereas in other EUs, the pattern was better explained by a monomolecular curve (4 EUs) or an
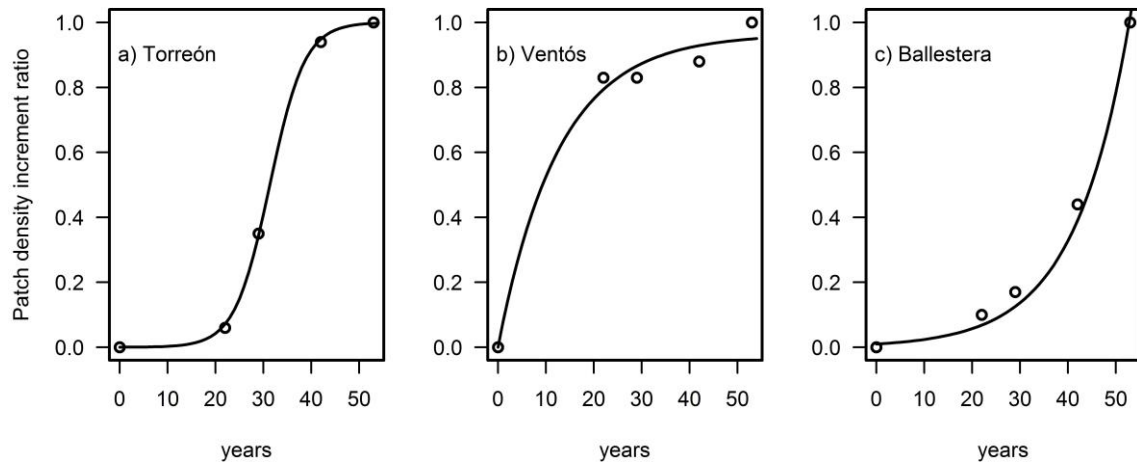
Figure 2. Examples of non-linear curve fitting of patch density increment ratio as a function of time of three EUs. The three non-linear response found were logistic a), monomolecular b) and exponential c).

Table 3. Coefficient estimates, adjusted standard errors (SE) and confidence intervals (95%) describing shrub colonization after model averaging of GLMMs. Estimates represent standardize values and, therefore, they are in a comparable scale. Shrub patch density in 1956 is the reference level for the factor year in the shrub patch density model. The relative importance of predictor variables was calculated as the sum of AICc-wi values of the competing models in which the predictor was present.

|		Estimate	SE	Conf. Interval (5 - 95%)	Importance
Patch density	Intercept	17.10	5.4	8.24, 25.95	
	Resource sink area	-4.47	1.91	-7.63, -1.31	1.00
	Year 1978	16.06	3.67	9.97, 22.16	1.00
	Year 1985	17.77	4.6	10.13, 25.42	1.00
	Year 1998	32.08	5.5	23.61, 42.01	1.00
	Year 2009	43.98	6.65	32.96, 54.99	1.00
	Precipitation	-5.41	2.23	-9.11, -1.72	0.79
	Plant cover	3.14	1.28	1.02, 5.26	0.67
	Aspect (northness)	-2.74	1.19	-4.72, -0.76	0.42
	Rock cover	-2.68	1.14	-4.57, -0.79	0.33
t_{50}	Intercept	28.53	1.67	25.82, 31.25	
	Precipitation	5.27	2.02	1.98, 8.56	0.70
	RDA2	3.75	2.01	0.49, 7.02	0.60
	SPI	3.42	1.74	0.60, 6.24	0.44
	Rock cover	2.89	1.73	0.09, 5.69	0.36
	Plant cover	4.58	2.06	1.22, 7.93	0.27
	Resource sink area	3.17	1.82	0.22, 6.12	0.26
	Fetch length	3.2	1.95	0.05, 6.35	0.04
	Temperature	-3.54	1.75	-6.37, -0.69	0.03
Density change	Intercept	46.33	6.83	35.17, 57.48	
	Plant cover	15.21	3.22	9.99, 20.43	1.00
	SPI	14.8	4.71	7.13, 22.46	1.00
	Temperature	25.67	5.07	17.4, 33.94	1.00
	Resource sink area	-9.84	4.32	-16.88, -2.79	0.61
	Initial density	-0.48	0.23	-0.85, -0.10	0.28
Detection probability	Intercept	0.55	0.02	0.51, 0.59	
	Plant cover	0.02	0.01	-0.01, 0.04	0.24
	Rock cover	-0.01	0.01	-0.02, 0.01	0.18
	Fetch length	-0.01	0.01	-0.03, 0.01	0.18
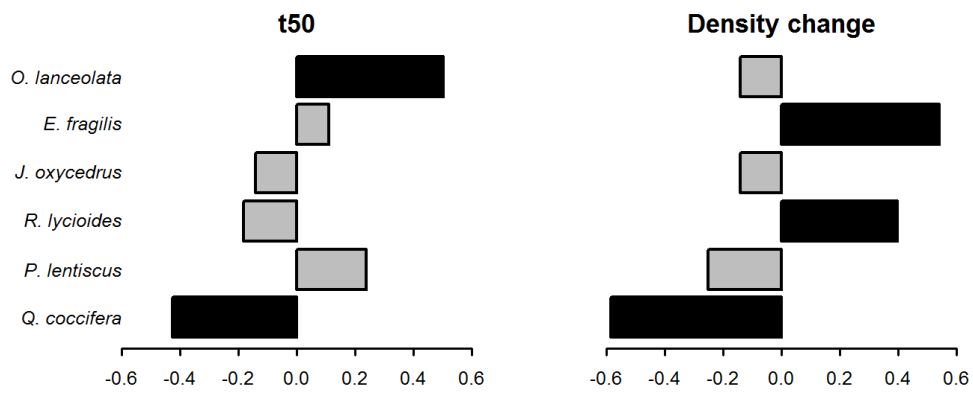
Figure 3. Spearman rank correlations between abundance of dominant species and variables of shrub colonization dynamics (t_{50} and density change). Dark bars depict significant associations at $P < 0.05$.

exponential curve (5 EUs). The coefficients of all equations were significant, and all curves showed good fit (Table A2). The average time to achieve 50% of the maximum shrub patch density (t_{50}) was 10.3 ± 1.4, 28.2 ± 1.2, and 44.4 ± 0.1 years ($\pm$ SE) in EUs following monomolecular, logistic and exponential increases, respectively. The abundance of *Q. coccifera* was negatively related to t_{50} indicative of early recruitment patterns (Fig. 3). By contrast, *O. lanceolata* was positively related to t_{50}, indicative of late recruitment. Mean annual precipitation, SPI, and species composition were important predictors of t_{50} (Table 3). All three explanatory variables were positively associated with t_{50}. For a given combination of precipitation and species identity, t_{50} was lower (i.e., colonization faster) in EUs where average SPI values were lower. The change in the sign of the relationship between SPI and t_{50} along the studied period further confirmed the control of water availability on colonization rate (Fig. 4). SPI and t_{50} showed a negative relationship before 1978. Conversely, between 1998-2009, this relation was positive (Fig. 4). Rock cover, plant cover, resource sink area and fetch length were positively related to t_{50}. Temperature showed a weak negative effect on t_{50}. The intensity of colonization of each EU, defined as the absolute density change in the entire study period, was negatively influenced by resource sink area and initial shrub patch density, and positively affected by plant cover, SPI, and temperature (Table 3). Although composition was not a significant predictor of density change, we observed that the abundance of *Q. coccifera* was negatively associated with density change, whereas *E. fragilis* and *R. lyciodes* were positively related (Fig. 3).

4. Discussion

Our results conformed to the expectation that species identity and climate are important drivers of shrub colonization. Previous studies on temporal patterns of shrub colonization have mostly focused on the role of site conditions (Browning et al., 2008; Davies et al., 2010; Levick and Rogers, 2011), fire (Malkisnon et al., 2011) and grazing (Roques et al., 2001). We observed that aspect and rock cover were significant predictors of shrub patch density. However, our results showed that the biotic characteristics of the colonizing species coupled with changes in
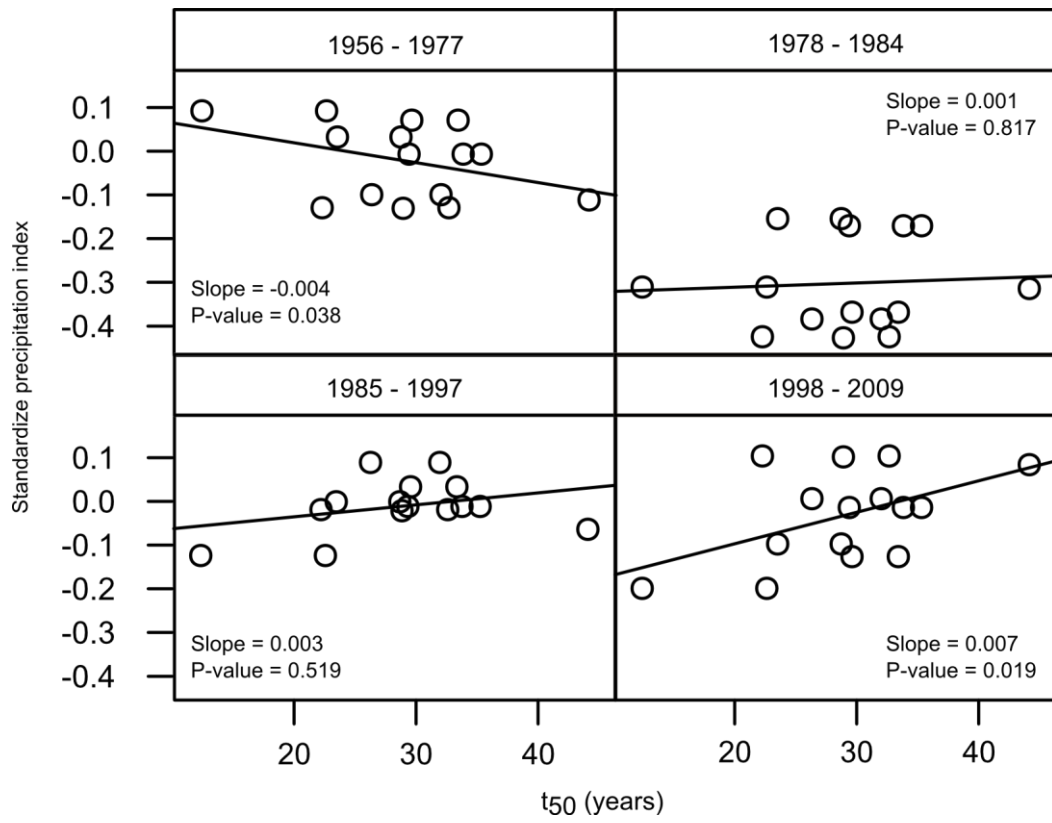
Figure 4. Relation between average values of SPI and t_{50} per catchment at time steps defined between two consecutive aerial photographs.

climatic conditions were more influential than topographic and geomorphological features as rock cover and aspect. Indeed, we found that shrub patch colonization in these semiarid steppes was very sensitive to climatic conditions. We observed that colonization was limited along periods of low water availability (low SPI). Thus, catchments with low t_{50}, showed high values of SPI early after abandonment, and low values of SPI at the end of the study period. We observed the opposite pattern in catchments with high t_{50} (Fig. 4). In addition, we found that mean annual precipitation and mean annual temperature appeared in most models of patch dynamics. These results are in accordance with the major limit that water availability imposes on the functioning and persistence of Mediterranean vegetation (Peñuelas et al., 2001), and suggest that the topographic and geomorphological factors may only affect shrub colonization once climatic filters are overcome.

4.1 Species identity and non-linear patterns of shrub colonization

Results from experimental plantations have shown that species identity can play a major role in the success of restoration efforts of semiarid areas (Padilla et al., 2009b). Our results accord with these findings and highlight the importance of species identity in the processes of shrub colonization. Differences in colonization rate may emerge soon after the end of disturbance. The way plants overcome critical bottlenecks, such as summer drought during the first stages of succession, may shape community assemblage in semiarid systems (Schulze et al., 1996). In *S. tenacissima* steppes, plant traits related to seed phenology, dormancy and dispersal range, vulnerability to predation, and rooting capacity may generate different sequences of shrub colonization (Barberá et al., 2006; García-Fayos and Verdu, 1998; Mendoza-Aguilar et al., 2014).

We observed that EUs with different shrub species showed different colonizing trajectories. On one hand, the positive association between t_{50} and RDA2, and the negative relation between the latter and the abundance of *Q. coccifera*, suggest that in EUs where this species was abundant, colonization was fast and maximum patch density was achieved in few years. The negative

association between *Q. coccifera* and t_{50} and density change supports this finding (Fig. 3). Two alternative processes may explain this pattern. On the one hand, the rapid increase in patch density may reflect the ability of *Q. coccifera* and other patch forming species to resprout. In patch-forming species, resprouters usually grow faster than mature plants and seedlings (Castell et al., 1994), which is in agreement with the fast colonization rates observed in some catchments. On the other hand, the formation of new patches dominated by *Q. coccifera* may also rely on successful acorn dispersal and the availability of safe sites (Eriksson and Ehrlén, 1992). These safe sites may become saturated early, when patch density reaches an asymptote (Browning et al., 2008). However, the slow growth rate of planted *Q. coccifera* seedlings (Vilagrosa et al., 2014, 2003) suggests that seedling establishment was not the main process behind the increase in *Q. coccifera* patches.

We found the opposite situation in other EUs, particularly where *E. fragilis* was abundant. In those EUs, shrub patch density increased slowly after abandonment, and showed no signs of stabilization after 54 years. Exponential colonization curves probably reflect the dominance of seeding vs. resprouting strategies, and the presence of limiting factors for early establishment, such as a lack of seeds and absence of suitable nurse species or safe-sites for dispersal (Reisman-Berman et al., 2006). *Ephedra fragilis* withstands harsh environmental conditions, although its ability to grow fast and root depth is less than those of other semiarid shrubs as *Salsola oppositifolia* Desf., *Retama sphaerocarpa* (L.) Boiss. and *Olea europaea* L. (Padilla et al., 2009a; Padilla and Pugnaire, 2007, 2009).

Finally, colonization in most EUs followed a logistic curve, which suggests a mixture of seeding and resprouting strategies. Briggs *et al.,* (2002) reported similar responses when analyzing encroachment in northeast Kansas grasslands, and found that maximum woody cover was reached after 40 years. Interestingly, we did not find bimodal patch recruitment curves or other curve types that would suggest consecutive phases of colonization.

As discussed above, early colonization may be favored by higher availability of seeds and buds and suitable environmental conditions. In contrast, the absolute change in patch density may be limited by other factors such as biotic interactions. The negative relationship between total density change and initial patch density suggests that as shrub patch density increased, intra- and inter-specific interference became increasingly intense. These results are in accordance with density-dependent processes observed in other semiarid environments, and may control ecosystem structure and dynamics (Skarpe, 1991; Wiegand et al., 2006).

4.2 Abiotic factors and shrub patch dynamics

In areas subjected to harsh environmental conditions, colonization started later, but total changes in shrub patch density were larger than in less demanding areas. This was corroborated by the negative association found between precipitation and shrub patch density. Climatic conditions will likely change in the next decades. Air temperature will increase and precipitation will decline and be concentrated in fewer events (IPCC, 2007). Considering the trends observed in our retrospective study, we hypothesize that the abundance of patches dominated by *E. fragilis* will increase at the expense of those dominated by *P. lentiscus*. In this line, according to field evidences and our own results, future climatic and disturbance regimes may have contrasting effects for the persistence of some patch-forming species leading to changes in the composition of species of the studied system (Delitti et al., 2005; Peñuelas et al., 2001).

Nevertheless, the consistent increase in patch density suggests that shrub recruitment was not impaired, and degraded steppes were capable of self-recovery (Maestre et al., 2007). Experimental planting of late-successional shrubs have shown that shrubs can establish in steppes with reduced capacity to capture and hold water, sediments and nutrients, i.e., reduced catchment functionality. Indeed, short-term seedling performance can be negatively related to catchment functionality (Maestre et al., 2006), which is consistent with the interference exerted by *S. tenacissima* tussocks on shrub establishment under severe drought (Maestre et al., 2001). The observed positive effect of plant cover on shrub colonization dynamics is consistent with an

interference effect of pre-existing vegetation on shrub establishment. Woody patches in *S. tenacissima* steppes, and particularly those dominated by species with dense canopies as *Q. coccifera*, facilitate the establishment of new individuals (Amat et al., 2015). Additionally to the observed positive effect of plant cover, the effect of resource sinks suggests that catchment functionality can also affect shrub colonization. Overall, our results suggest that the studied sites had not previously crossed a biotic resilience threshold (Cortina et al., 2012; Mayor et al., 2013; Whisenant, 1999).

4.3 Management implications

Our results have clear implications for the management of *S. tenacissima* steppes. On the one hand, shrub patch density ranged from 11 to 143 patches ha^{-1}, which is much lower than the density used in most plantation programs (Serrada, 2000). This observation should be taken into account when evaluating plantation success in semiarid steppes. On the other hand, the increase in shrub patch density in all EUs ranged from 0.1 to 2.0 new patches ha^{-1} year^{-1}; 75% of these were less than one patch ha^{-1} year^{-1}. As average shrub patch density was 67 patches ha^{-1}, it may take more than a century to attain these values in most EUs. Thus, planting patch-forming species may help to increase the rate of patch formation. This is particularly true for patches dominated by 'slow' species or species located at the upper end of the RDA2 axis (e.g., *E. fragilis* vs. *Q. coccifera*, Fig. 3). Finally, the non-linear increase in patch density and its relationship with climatic conditions should be taken into account, as it could help identify suitable periods for planting, and for optimizing watering and moisture conservation programs.

4.4 Conclusions

We conclude that shrub patches have colonized and expanded in abandoned *S. tenacissima* steppes in the southeastern Iberian Peninsula. This process is likely to continue in some areas, but not in those where shrub patch density has remained stable over the last decade. Colonization trajectories are largely controlled by the identity of patch-forming community and climatic conditions, particularly precipitation. Species-specific responses to climatic conditions

should be taken into account when selecting new areas for planting in restoration programs. Given the sensitivity of patch-forming species to climatic conditions, new challenges for the management of *S. tenacissima* steppes will likely emerge under the influence of climate change.

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Supplementary data

Table A1. Location and summary of main characteristics of the studied environmental units.

ID	LOCATION	X	Y	PT56	PT09	ALTI	ASPE	PREC	TEMP	SLDP	IPL
1	Aigües	731647	4267457	6	11	418	200	352	16.9	24.8	64.6
2	Aigües	731544	4267467	23	47	428	119	351	16.9	23.4	68.6
3	Aspe3	697518	4242944	49	134	280	226	290	18.7	18.5	54.6
4	Aspe3	697532	4242999	70	143	295	259	288	18.7	19.5	73.4
5	Aspe5	696395	4242605	52	128	258	122	291	18.5	15.3	77.7
6	Ballestera1	728165	4259775	26	53	105	177	319	17.3	14.4	78.4
7	Ballestera1	728165	4259880	36	80	132	164	319	17.3	19.2	62.2
8	Ballestera2	728286	4259966	28	56	143	150	319	17.3	26.4	59.9
9	Campello	733879	4263094	19	36	110	166	335	17.1	28.8	50.7
10	Colmenar2	715625	4242743	26	128	67	129	283	17.9	13.9	62.5
11	Colmenar2	715561	4242747	26	130	62	178	283	17.9	12.9	76.0
12	Colmenar3	714928	4242775	12	55	84	193	279	17.9	14.6	47.0
13	Colmenar3	714846	4242697	8	50	85	80	283	17.9	15.6	39.9
14	Crevillente	685700	4241450	16	62	476	124	291	17	17	62.7
15	Vila	745899	4271561	17	41	276	180	544	16.8	19.2	53.6
16	Vila	745714	4271425	16	80	291	74	544	16.8	27.3	25.0
17	Vila	745894	4271396	5	51	236	68	545	16.8	22.9	65.3
18	Orihuela	678238	4242403	21	39	532	147	293	17	12	71.7
19	Porxá	730152	4260435	62	109	211	115	319	17.3	25.5	61.8
20	Porxá	730031	4260496	20	108	192	57	319	17.3	30.7	56.1
21	Torreón	731607	4260298	19	49	106	84	319	17.3	24.1	73.5
22	Torreón	731667	4260313	19	55	74	148	319	17.3	34.1	33.1
23	Torreón	731474	4260406	21	27	51	283	321	17.3	30.1	59.5
24	Ventós1	708073	4260759	19	44	642	230	292	17.3	9.4	72.0
25	Ventós3	707528	4260745	12	33	595	156	291	17.3	19.6	80.4
26	Ventós3	707596	4260695	15	32	579	188	291	17.3	22.2	78.8
27	Ventós3	707619	4260658	7	30	567	166	291	17.3	13.9	60.5

ID = number of environmental unit, LOCATION = nearest town, X = northing UTM, Y= easting UTM, ED1950, PT = patch density, patches ha^{-1} estimated from aerials photographs in 1956 (PT56) and 2009 (PT09), ALTI = altitude above sea level (m), ASPE = aspect (º), PREC = averaged annual precipitation 1950-2009 (mm), TEMP = averaged annual temperature 1950-2007 (ºC), SLDP = soil depth (cm), IPL = inter-patch length.

Table A2. Non-lineal fit parameters and confidence intervals of the functions describing temporal changes in patch density increment ratio. The three types of non-linear functions that showed the best fit were: (1) logistic, (2) monomolecular and (3) exponential.

$$PD_r(t) = \frac{e^{a+bt}}{1+e^{a+bt}} \qquad (0 < PD_r(t) < 1) \qquad \text{(Eq. 1)}$$

$$PD_r(t) = a(1-e^{-bt}) \quad (0 < PD_r(t) < 1) \qquad \text{(Eq. 2)}$$

$$PD_r(t) = e^{at} \qquad\qquad (0 < PD_r(t) < 1) \qquad \text{(Eq. 3)}$$

| ID	LOCATION	Type of fit	a (5 - 95% CIs)	b (5 - 95% CIs)	r^2
1	Aigües	Logistic	-4.68 (-6.78, -2.58)	0.19 (0.11, 0.27)	0.99
2	Aigües	Logistic	-2.57 (-4.31, -0.83)	0.13 (0.07, 0.19)	0.99
3	Aspe3	Logistic	-2.29 (-3.87, -0.71)	0.1 (0.04, 0.16)	0.98
4	Aspe3	Logistic	-3.83 (-4.85, -2.81)	0.13 (0.09, 0.17)	0.99
5	Aspe5	Logistic	-3.25 (-4.89, -1.61)	0.1 (0.06, 0.14)	0.98
6	Ballestera1	Monomolecular	0.05 (0.03, 0.07)	0.07 (0.03, 0.11)	0.94
7	Ballestera1	Exponential	0.09 (0.07, 0.11)	-	0.99
8	Ballestera2	Logistic	-6.46 (-7.3, -5.62)	0.18 (0.16, 0.2)	0.99
9	Campello	Logistic	-7.06 (-11.32, -2.8)	0.22 (0.08, 0.36)	0.98
10	Colmenar2	Logistic	-3.15 (-4.25, -2.05)	0.14 (0.1, 0.18)	0.99
11	Colmenar2	Logistic	-3.82 (-4.38, -3.26)	0.15 (0.13, 0.17)	0.99
12	Colmenar3	Logistic	-3.27 (-5.21, -1.33)	0.1 (0.04, 0.16)	0.97
13	Colmenar3	Logistic	-3.51 (-5.11, -1.91)	0.14 (0.08, 0.2)	0.99
14	Crevillente	Logistic	-4.37 (-5.79, -2.95)	0.15 (0.11, 0.19)	0.99
15	Vila	Exponential	0.09 (0.07, 0.11)	-	0.93
16	Vila	Exponential	0.09 (0.07, 0.11)	-	0.93
17	Vila	Exponential	0.09 (0.07, 0.11)	-	0.94
18	Orihuela	Logistic	-7.93 (-9.33, -6.53)	0.24 (0.2, 0.28)	0.99
19	Porxá	Logistic	-3.72 (-5.2, -2.24)	0.11 (0.07, 0.15)	0.99
20	Porxá	Logistic	-3.64 (-5.6, -1.68)	0.11 (0.05, 0.17)	0.97
21	Torreón	Exponential	0.09 (0.07, 0.11)	-	0.96
22	Torreón	Logistic	-8.59 (-9.27, -7.91)	0.27 (0.25, 0.29)	0.99
23	Torreón	Monomolecular	1.09 (0.81, 1.37)	0.06 (0.02, 0.10)	0.98
24	Ventós1	Logistic	-3.83 (-4.35, -3.31)	0.17 (0.15, 0.19)	0.99
25	Ventós3	Monomolecular	0.96 (0.86, 1.06)	0.08 (0.04, 0.12)	0.97
26	Ventós3	Logistic	-4.08 (-6.04, -2.12)	0.20 (0.12, 0.28)	0.99
27	Ventós3	Monomolecular	1.02 (0.96, 1.08)	0.09 (0.05, 0.13)	0.99
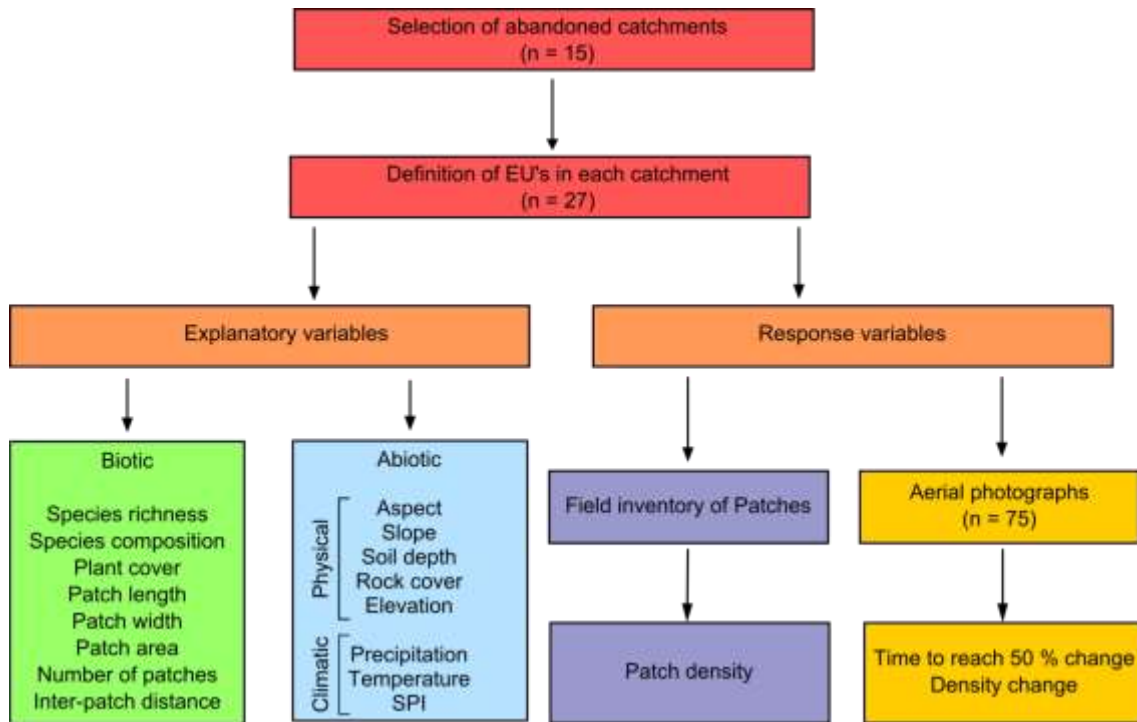
Figure A1 Flow chart depicting the design followed to obtain the dependent and independent variables included in the study. The term "patch" in patch length, patch width and inter-patches distance correspond to every long-lived feature that obstructs or diverts water flow and collects/filters out material from runoff (e.g., grass tussocks, stones, branches and litter).

Figure A2. Aerial photo of a microchatchment located near Aspe (Alicante, SE Spain) covered by *S. tenacissima* steppe, where woody patches can be identified as scattered dark spots (red arrow) and two selected EU are delimited by the red line.
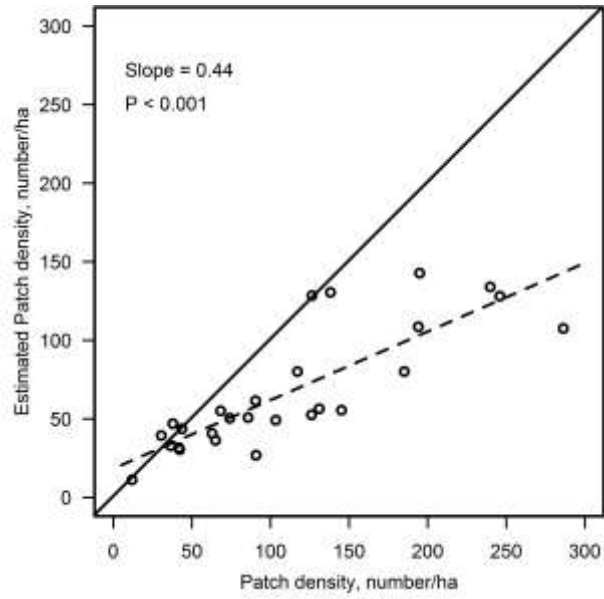
Figure A3. Relation between field measurements and estimations based on aerial photographs of patch density. Solid and dashed lines correspond to a 1:1 slope and regression lines respectively.