

1 **Water availability and species identity control shrub colonization in abandoned semiarid**  
2 **steppes<sup>1</sup>**

3 Short title: Patch dynamics in drylands

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5 Victor Rolo<sup>1,2\*</sup>, Beatriz Amat<sup>3</sup> and Jordi Cortina<sup>3</sup>

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7 <sup>1</sup>Department of Silviculture, Faculty of Forestry and Wood Technology, Mendel University,  
8 Brno, Czech Republic

9 <sup>2</sup>Current address: Conservation Ecology Research Unit, University of Pretoria, Pretoria, South  
10 Africa

11 <sup>3</sup>Department of Ecology and IMEM, University of Alicante, Ap. 99, 03080 Alicante, Spain

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13 \*Corresponding author: [victorroloromero@gmail.com](mailto:victorroloromero@gmail.com)

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17 **Abstract**

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

35

36 **Keywords:** Shrub encroachment, long-term plant dynamics, aerial photography, standardized  
37 precipitation index, drylands, *Stipa tenacissima*

38 **1. Introduction**

39 The proliferation of woody species is a common phenomenon in drylands worldwide (van  
40 Auken, 2009). Information derived from time series of aerial photographs has advanced our  
41 knowledge of the dynamics and extent of shrub encroachment (Briggs et al., 2002; Peters et al.,  
42 2006). However, research on the drivers of shrub colonization has mostly focused on the effect  
43 of physical factors, particularly soil properties and topographic features such as aspect and  
44 elevation (Browning et al., 2008; Davies et al., 2010; Levick and Rogers, 2011) or grazing  
45 (Bartolomé et al., 2005; Roques et al., 2001; Ward et al., 2014). In contrast, the identity of the  
46 colonizing shrub species as major driver of shrub expansion has seldom been studied. This is  
47 despite the strong relationship between climate, morphological/-functional traits and shrub  
48 dynamics (Eldridge et al., 2011; Pueyo et al., 2010).

49

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

59

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

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

70

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

87

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

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

105

## 106 **2. Material and Methods**

### 107 **2.1 Study sites**

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

117

### 118 **2.2 Biotic and abiotic attributes of the environmental units**

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

122 transect, we quantified plant cover and rock cover by visual estimation in 14 consecutive 1.5 x  
123 1.5 m quadrats. Total plant cover was estimated as the sum of all species present in the transect.  
124 Rock cover was estimated as the sum of the cover of unconsolidated rocks as well as the cover  
125 of bedrock that appeared at the surface of the ground.

126

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

134

135 Additionally, we georeferenced all shrub patches present in each EU in 2009 to calculate shrub  
136 patch density. Shrub patch density was calculated in each EU by dividing the total number of  
137 shrub patches by EU surface area. Field measurements of shrub patch density were used to  
138 assess the accuracy of aerial photograph interpretations (see below). We recorded species  
139 composition and the presence of dominant species (6 species in total) in 30 randomly selected  
140 patches (450 patches in total). We considered as dominant species those shrubs that form clearly  
141 defined patches, because of their large size and their ability to create new microhabitats. The six  
142 dominant species were *Pistacia lentiscus* L., *Quercus coccifera* L., *Rhamnus lycioides* L.,  
143 *Juniperus oxycedrus* L., *Ephedra fragilis* Desf. and *Osyris lanceolata* Hochst. & Steud (Amat,  
144 2015). Species richness was recorded as the total number of species per EU. We measured soil  
145 depth by inserting a 1-cm diameter iron rod into the soil and recording the maximum depth  
146 attained. Average soil depth under a shrub patch was estimated by measuring 6-10 points  
147 beneath their canopy. Average soil depth in each EU was estimated from the soil depth  
148 measured in 30 randomly chosen locations within each catchment.

149

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

162

### 163 **2.3 Aerial photography interpretation**

164 Aerial photos were obtained from public and commercial flights launched in 1956, 1978, 1985,  
165 1998 and 2009 (Table 1). Digitized images of 1998 and 2009 were acquired, georeferenced and  
166 orthorectified. Photos from 1956, 1978 and 1985 were digitized by scanning on an A3 flatbed  
167 scanner (HP Deskscan, HP Co., Palo Alto, USA) at 1200 dpi, using an 8-bit grey-scale. Images  
168 were geometrically corrected, resampled to a common spatial resolution (1 m) and registered to  
169 the UTM projection by performing and image-to-image registration on 40 points from 2009  
170 images (Fig. A2).

171

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

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

191

## 192 **2.4 Data analysis**

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

198

199 Shrub patch dynamics was analyzed in different ways. Firstly, we used generalized linear mixed  
200 models to assess the relationship between temporal dynamics of shrub patch density (i.e.  
201 dependent variable) and biotic, climatic, topographical and geomorphological attributes (i.e.  
202 independent variables). Moreover, we included year in the model as an independent variable to  
203 test for differences in shrub patch density between time steps. We included precipitation and  
204 SPI as the averaged value in the decade prior to each aerial photograph. We did not include  
205 temperature because of the lack of complete data. We included site scores of the first two axes



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

216

217 Secondly, the rate of shrub colonization was analyzed by fitting non-linear functions to shrub  
218 patch density increment ratios. Shrub patch density increment ratios ( $PD_r$ ) (adapted from Gale  
219 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  
220 patch density in 1956,  $t_f$  is shrub patch density in 2009, and  $t_i$  is shrub patch density at  
221 successive time steps ( $i = 1956, 1978, 1985, 1998, 2009$ ). A set of non-linear models (i.e.  
222 monomolecular, logistic and exponential) was fitted to the data to model the relationships  
223 between  $PD_r$  values against time. In each site, we selected the function showing the best fit  
224 based on the coefficient of determination to observational data (see Table A2 for a summary of  
225 these analysis). Then, we solved each equation at  $PD_r(t) = 0.5$  to estimate the time needed to  
226 reach a 50% change in  $PD_r$  ( $t_{50}$ ; sensu Gale and Grigal, 1987). Thirdly, we calculated the total  
227 change in shrub patch density in each EU from 1956 to 2009 (hereafter density change).

228

229 Linear mixed models containing  $t_{50}$ , density change and detection probability as dependent  
230 variables and biotic, climatic and physical attributes were fit to the data, including catchment as  
231 a random effect. We included RDA1 and RDA2 in the model to test the effect of species  
232 identity, and initial patch density to test density-dependent effects. We could not include SPI  
233 values in these models because its mean is zero when considering the whole precipitation time

234 series. Alternatively, we categorized each SPI values per year according to the National Drought  
235 Mitigation Center of the USA (<http://droughtmonitor.unl.edu>) as: 0 ( $+0.5 \leq \text{SPI} \leq -0.5$ ); -1  
236 ( $-0.5 < \text{SPI} > -0.8$ ); and -2 ( $-0.8 \leq \text{SPI} > -1.3$ ). We only included the first three categories of  
237 this classification scheme because our database did not contain values of  $\text{SPI} < -1.3$ . We  
238 included the mean values of the new categorization per catchment in these models.  
239 Additionally, we related averaged SPI values between two consecutive aerial photographs to  
240 mean  $t_{50}$  values per catchment, to test if  $t_{50}$  values per catchment corresponded to periods of  
241 higher water availability.

242

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

256

### 257 **3. Results**

#### 258 **3.1 Association of shrub patch species with biotic and abiotic attributes**

259 Redundancy analysis showed that 55% of the variance in species abundance was explained by  
260 northness, soil depth, patch area, temperature and precipitation (Table 2). The first two  
261 canonical axes explained 86% of the total variance, and were statistically significant ( $P = 0.005$

262 for both axes after 999 permutations). Temperature and precipitation played an important role in  
263 EU dispersion along the first axis (Fig. 1). *Osyris lanceolata* abundance was positively  
264 correlated with precipitation, soil depth and northness. In contrast, the abundance of *Rhamnus*  
265 *lyciodes* and *Ephedra fragilis* were positively correlated with temperature. Resource sink area  
266 was weakly correlated with *Quercus coccifera* abundance. The position of other species in the  
267 space defined by the two axes was intermediate.

268

### 269 **3.2 Detection probability of shrub patches**

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

275

### 276 **3.3 Influence of biotic and abiotic attributes on changes in shrub patch density and** 277 **colonization rate**

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

285

286 Three contrasting patterns of change were observed when increases in shrub patch density were  
287 standardized (Fig. 2, Table A2). In 18 EUs, they followed a logistic growth curve, whereas in  
288 other EUs, the pattern was better explained by a monomolecular curve (4 EUs) or an  
289 exponential curve (5 EUs). The coefficients of all equations were strongly significant, and all

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

309

#### 310 **4. Discussion**

311 Our results conformed to the expectation that species identity and climate are important drivers  
312 of shrub colonization. Previous studies on temporal patterns of shrub colonization have mostly  
313 focused on the role of site conditions (Browning et al., 2008; Davies et al., 2010; Levick and  
314 Rogers, 2011), fire (Malkinson et al., 2011) and grazing (Roques et al., 2001). We observed  
315 that aspect and rock cover were significant predictors of shrub patch density. However, our  
316 results showed that the biotic characteristics of the colonizing species coupled with changes in  
317 climatic conditions were more influential than topographic and geomorphological features as

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

328

#### 329 **4.1 Species identity and non-linear patterns of shrub colonization**

330 Results from experimental plantations have shown that species identity can play a major role in  
331 the success of restoration efforts of semiarid areas (Padilla et al., 2009b). Our results accord  
332 with these findings and highlight the importance of species identity in the processes of shrub  
333 colonization. Differences in colonization rate may emerge soon after the end of disturbance. The  
334 way plants overcome critical bottlenecks, such as summer drought during the first stages of  
335 succession, may shape community assemblage in semiarid systems (Schulze et al., 1996). In *S.*  
336 *tenacissima* steppes, plant traits related to seed phenology, dormancy and dispersal range,  
337 vulnerability to predation, and rooting capacity may generate different sequences of shrub  
338 colonization (Barberá et al., 2006; García-Fayos and Verdu, 1998; Mendoza-Aguilar et al.,  
339 2014).

340

341 We observed that EUs with different shrub species showed different colonizing trajectories. On  
342 one hand, the positive association between  $t_{50}$  and RDA2, and the negative relation between the  
343 latter and the abundance of *Q. coccifera*, suggest that in EUs where this species was abundant,  
344 colonization was fast and maximum patch density was achieved in few years. The negative  
345 association between *Q. coccifera* and  $t_{50}$  and density change supports this finding (Fig. 3). Two

346 alternative processes may explain this pattern. On the one hand, the rapid increase in patch  
347 density may reflect the ability of *Q. coccifera* and other patch forming species to resprout. In  
348 patch-forming species, resprouters usually grow faster than mature plants and seedlings (Castell  
349 et al., 1994), which is in agreement with the fast colonization rates observed in some  
350 catchments. On the other hand, the formation of new patches dominated by *Q. coccifera* may  
351 also rely on successful acorn dispersal and the availability of safe sites (Eriksson and Ehrlén,  
352 1992). These safe sites may become saturated early, when patch density reaches an asymptote  
353 (Browning et al., 2008). However, the slow growth rate of planted *Q. coccifera* seedlings  
354 (Vilagrosa et al., 2014, 2003) suggests that seedling establishment was not the main process  
355 behind the increase in *Q. coccifera* patches.

356

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

366

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

372

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

380

#### 381 **4.2 Abiotic factors and shrub patch dynamics**

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

392

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

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

408

### 409 **4.3 Management implications**

410 Our results have clear implications for the management of *S. tenacissima* steppes. On the one  
411 hand, shrub patch density ranged from 11 to 143 patches ha<sup>-1</sup>, which is much lower than the  
412 density used in most plantation programs (Serrada, 2000). This observation should be taken into  
413 account when evaluating plantation success in semiarid steppes. On the other hand, the increase  
414 in shrub patch density in all EUs ranged from 0.1 to 2.0 new patches ha<sup>-1</sup> year<sup>-1</sup>; 75% of these  
415 were less than one patch ha<sup>-1</sup> year<sup>-1</sup>. As average shrub patch density was 67 patches ha<sup>-1</sup>, it may  
416 take more than a century to attain these values in most EUs. Thus, planting patch-forming  
417 species may help to increase the rate of patch formation. This is particularly true for patches  
418 dominated by ‘slow’ species or species located at the upper end of the RDA2 axis (e.g., *E.*  
419 *fragilis* vs. *Q. coccifera*, Fig. A4). Finally, the non-linear increase in patch density and its  
420 relationship with climatic conditions should be taken into account, as it could help identify  
421 suitable periods for planting, and for optimizing watering and moisture conservation programs.

422

### 423 **4.4 Conclusions**

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



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

432

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443

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617 Table 1. Main features of the different sets of aerial photographs included in the time series  
618 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

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

624

	df	F	<i>P-value</i>
625 Aspect (northness)	1	2.6	0.035
626 Soil depth	1	4.3	0.001
Patch area	1	2.3	0.056
627 Mean annual air temperature	1	10.9	< 0.001
Mean annual precipitation	1	5.2	< 0.001

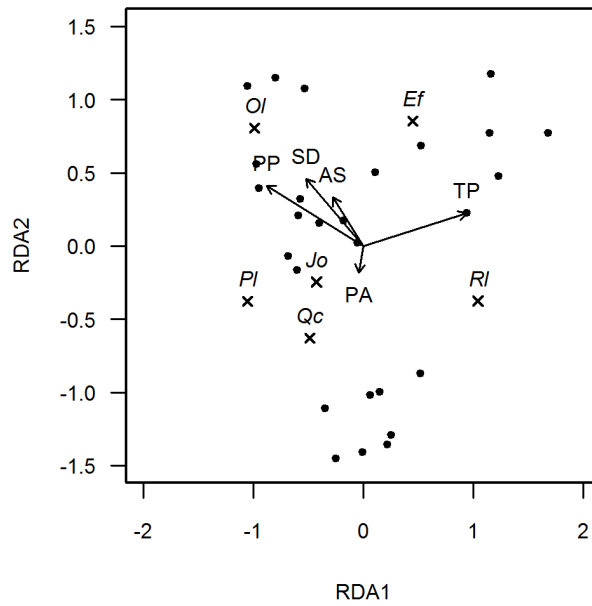
628

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

635

		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 <sub>50</sub>	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

636



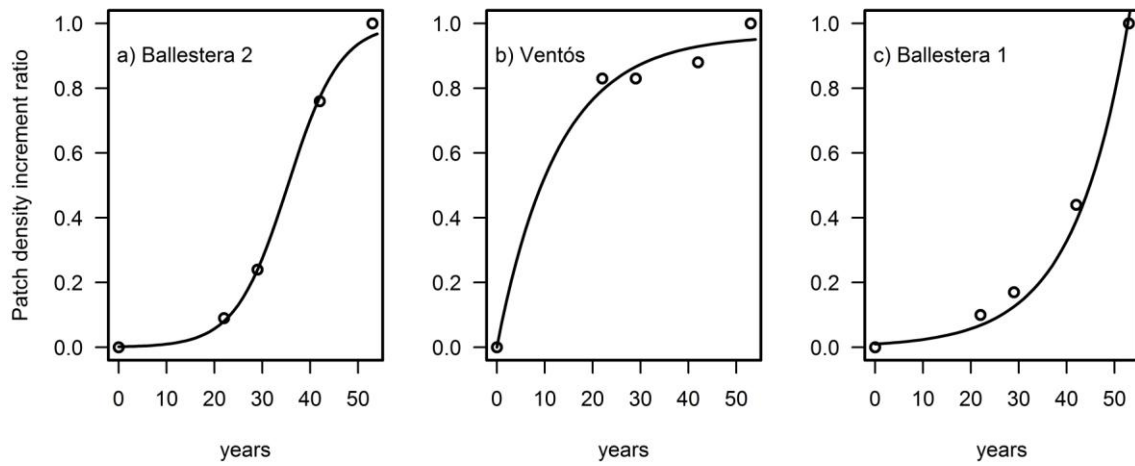
637

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

644

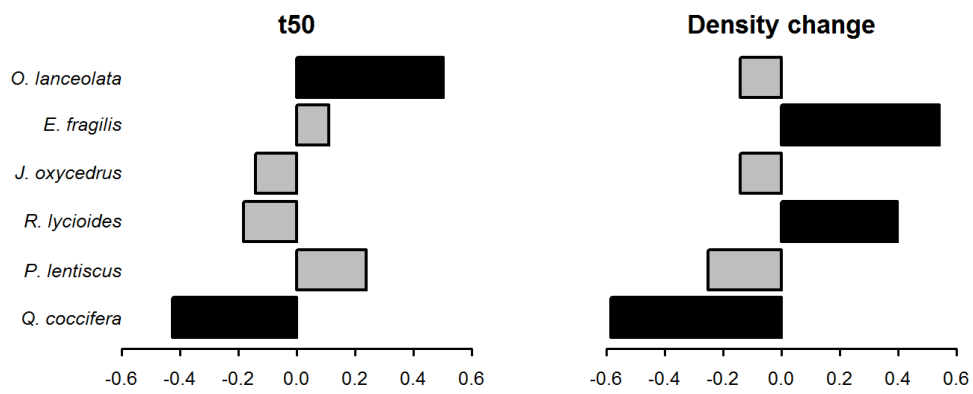
645





646

647 Figure 2. Examples of non-linear curve fitting of patch density increment ratio as a function of  
 648 time of three EUs. The three non-linear response found were logistic a), monomolecular b) and  
 649 exponential c).



650

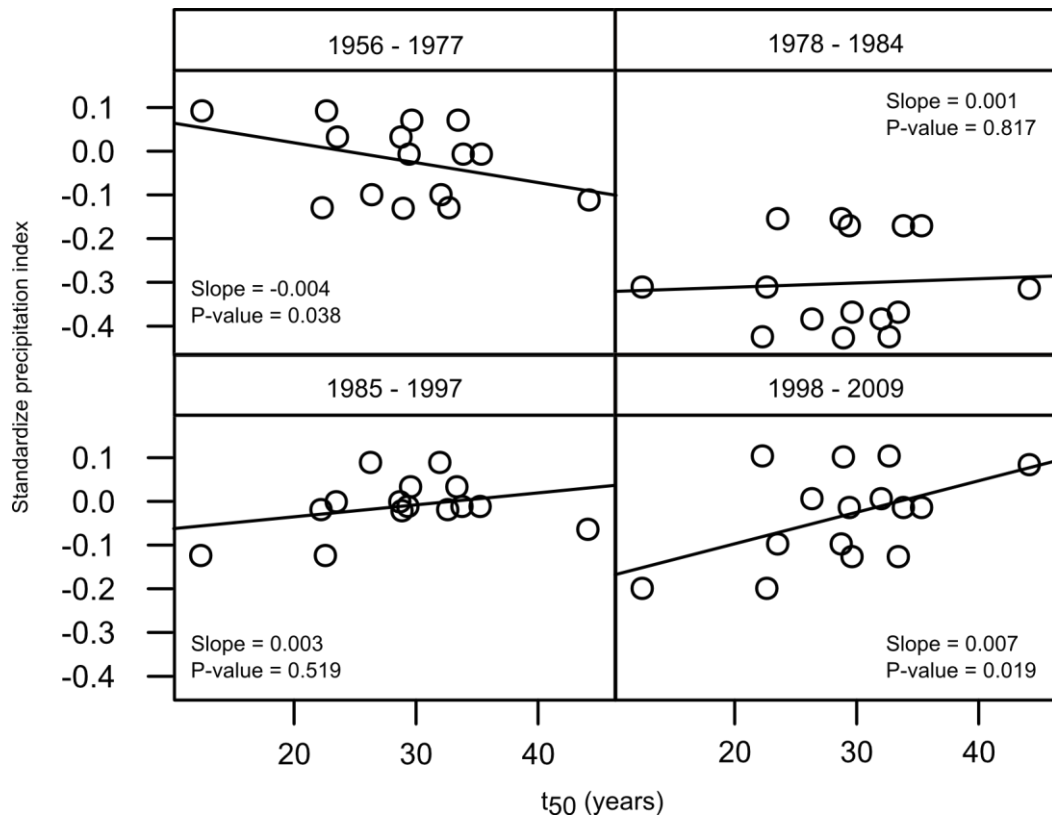
651

652 Figure 3. Spearman rank correlations between abundance of dominant species and variables of

653 shrub colonization dynamics ( $t_{50}$  and density change). Dark bars depict significant associations

654 at  $P < 0.05$ .

655



656

657 Figure 4. Relation between average values of SPI and  $t_{50}$  per catchment at time steps defined

658 between two consecutive aerial photographs.

