

1 **Plant Ecology (Accepted 21/01/2020)**

2

3 **Past cover modulates the intense and spatially structured natural regeneration of woody**  
4 **vegetation in a pastureland**

5 Rafael da Silveira Bueno<sup>1,2\*</sup>, Daniel García<sup>3</sup>, Mauro Galetti<sup>2</sup> and Tommaso La Mantia<sup>1</sup>

6 <sup>1</sup> Dipartimento di Scienze Agrarie, Alimentari e Forestali, Università degli Studi di Palermo (UNIPA), Italy. <sup>2</sup>

7 Departamento de Ecologia, Universidade Estadual Paulista (UNESP), Brazil. <sup>3</sup> Departamento de Biología de

8 Organismos y Sistemas – UMIB, University of Oviedo, Spain.

9 \*Corresponding author: Rafael da Silveira Bueno. Email: [rafael.dasilveirabueno@unipa.it](mailto:rafael.dasilveirabueno@unipa.it).  
10 +393347422239

11 ORCID 0000-0001-8964-8572.

12

13 **Author contributions:** Rafael da Silveira Bueno, Tommaso La Mantia and Mauro Galetti conceived  
14 the study. Rafael da Silveira Bueno and Daniel García developed the sampling design, methodology and  
15 the analytical framework, and interpreted results. Rafael da Silveira Bueno collected and analyzed the  
16 data and wrote the first manuscript. Daniel García revised the first manuscript and all authors revised  
17 and improved the final version.

18

19 **Acknowledgments.** We thanks Giovanni Giardina for sharing helpful information regarding the history  
20 of Ficuzza and the Sicilian Dipartimento Regionale dello Sviluppo Rurale e Territoriale for the  
21 logistical support. Funding: RSB received a Ph.D. fellowship from the University of Palermo.  
22 Fieldwork and TL were funded by Italian “Ministero dell’Istruzione dell’Università e della Ricerca”  
23 (CARBOTREES - 201049EXTW). DG was supported by Spanish “Ministerio de Economía y Empresa”  
24 (FEDER CGL2015-68963- C2-2-R) and DG & MG were supported by CYTED program (Red Temática  
25 418RT0555)

26 **Abstract**

27 Vegetation natural regeneration after agricultural abandonment is changing the landscape patterns in  
28 many areas worldwide. However, the expansion rate, spatio-temporal dynamics and the role of past  
29 vegetation cover in shaping such patterns still barely quantified in fine and meso scales.

30 Here we aim to quantify the expansion rate, assess the spatio-temporal patterns and the effects of past  
31 cover on natural woody vegetation cover increase. We sampled woodland and shrubland cover from  
32 1992 to 2016 in 30 ha in a formerly managed pastureland in Sicily, Italy. We combined field sampling,  
33 GIS tools, and spatial analysis to assess the spatial structure dynamics and test the effects of past cover  
34 amount and type, distance from forest or nearest woody patch on the proportional expansion of natural  
35 regeneration. After 24 years, woody cover increased 68%, despite the aggregated spatial structure in  
36 1992 remained almost unchanged in 2016. The past vegetation cover was the best predictor of woody  
37 vegetation expansion in two out of three plots. Distance to continuous forest and to the nearest woody  
38 patch, as well as cover type, were not relevant. Our study highlight the importance of fine and meso-  
39 scale studies to reveal both the deterministic and stochastic facet of woody vegetation dynamics. Natural  
40 regeneration may strongly change landscape patterns even under constant herbivory pressure and long-  
41 term deforestation. The detection of cold and hotspots of regeneration provide an important prompt for  
42 the design of restoration programs and landscape management.

43

44 Keywords: landscape pattern; natural regeneration; scale; spatial regression; vegetation dynamics

45

46

47

48

49

50

## 51 **Introduction**

52           In the Mediterranean region, human land use has altered the cover, composition and spatial  
53 patterns of natural vegetation over millennia, in many cases favoring annual and perennial herbaceous  
54 vegetation over woody vegetation (Pausas & Millán 2019; Plieninger et al. 2014). However, due to the  
55 current trend of land abandonment in rural areas, the natural recovery of woody vegetation on  
56 deforested land through secondary succession is highly expected, although frequently influenced by  
57 concomitant changes in major disturbance regimes, such as fire and herbivore pressure (Amici et al.  
58 2013; Falcucci et al. 2007; Massa & La Mantia 2007). A process of succession such as this has long  
59 been described in floristic and phytosociological terms (e.g. Debussche et al. 1982; Ne'eman & Izhaki  
60 1996), but the intrinsic spatial dynamics of woody vegetation over time and the mechanisms  
61 underpinning those dynamics are still poorly understood (Allen et al. 2016; Méndez et al. 2008; Quero  
62 et al. 2011). Even basic questions, such as how intense in magnitude and how fast woody vegetation  
63 recovery can be, still remain unsatisfactorily answered for mesic woodlands (but see Abadie et al. 2018;  
64 Álvarez-Martínez et al. 2014). Studies have focused mainly on analysis in extreme environments, such  
65 as semi-arid or mountain areas (Alodos et al. 2004; Bonet & Pausas 2004; Martínez-Duro et al. 2010;  
66 Pueyo & Begueria 2007) or on herbaceous or shrub communities (Bashan & Bar-Massada 2017; Carmel  
67 & Kadmon 1999; La Mantia et al. 2008; Ne'eman & Izhaki 1996). Similarly, little attention has been  
68 devoted to the spatial structure acquired by woody vegetation during succession, whether aggregated or  
69 random (Carmel et al. 2001). This is a relevant gap in knowledge given that spatial patterns result from,  
70 and, therefore, may be informative of, cumulative ecological processes involving both responses to  
71 abiotic conditions and, especially, interspecific interactions (Carmel & Flather 2004; Garcia et al. 2011;  
72 Keitt 2003). This spatio-temporal pattern analysis has a number of applications in landscape  
73 management. For example, the identification of those areas with greater potential for passive restoration  
74 (i.e. vegetation expansion through natural regeneration) may optimize resource use for active restoration  
75 (e.g. seedling plantation), directing efforts towards areas with lower recovery potential or regeneration  
76 cold spots (Berdugo et al. 2017; Carmel et al. 2001; Holl et al. 2018).

77           Abiotic factors such as climate, topography and soil may influence vegetation expansion and  
78 induce non-random spatial structures even on a small scale (Gallego Fernández et al. 2004; García et al.

79 2014; Pueyo & Begueria 2007), although abiotic influence on some tolerant species may be less  
80 significant (Bacaro et al. 2008; Getzin et al. 2008; Quero et al. 2011). In such cases, intensity and type  
81 of past land use, the amount and distribution of past vegetation cover, and biotic mechanisms become  
82 the main interrelated drivers of vegetation expansion, defining spatial resilience in a determined site  
83 (Allen et al. 2016; Carmel & Flather 2004; Holl et al. 2018). Vegetative growth (e.g. canopy expansion  
84 and clonal reproduction), and facilitation (e.g. when a small plant enables the recruitment of a larger  
85 one) are inherently dependent upon past cover (Bakker et al. 2004; Garcia & Obeso 2003). In turn, the  
86 process of seed dispersal in woody plants, which in many ecosystems such as tropical forests or in the  
87 Mediterranean is highly dependent upon animals (i.e. zoochory), may shape the spatial structure of  
88 woody recovery in different ways. On the one hand, most seeds are deposited at short distances from  
89 their source, thus, most recruitment and vegetation expansion is expected near source (González-Varo et  
90 al. 2017; Martínez & García 2015). On the other hand, depending on the degree of redundancy or  
91 complementarity of the dispersal vectors, dispersed seeds may eventually reach greater distances but  
92 might be conditioned by the existing woody cover in different levels (Bueno et al. 2013; Garcia et al.  
93 2011; Jordano 2017). Notwithstanding the above, the spatial template generated by seed dispersal is  
94 often subject to subsequent modification by recruitment losses due to small-scale disturbances, such as  
95 seed predation and herbivory, or large-scale disturbances, such as fire (Baeza et al. 2007; Carmel &  
96 Kadmon 1999; Gómez-Aparicio 2008). Cover type (i.e. shrubland or woodland), therefore, may affect  
97 seed dispersal and recruitment. Shrubs may attract seed dispersers and seed predators, and may  
98 compete with or facilitate other plants differently than higher trees, the same being true for patches or  
99 isolated individuals (Andivia et al. 2017; Lasky & Keitt 2012; Olff et al. 1999). Consequently, studies  
100 that quantify expansion rates and spatial patterns of woody vegetation over time and relate them to pre-  
101 existing vegetation cover are necessary in order to reveal the footprints that the ecological processes  
102 driving secondary succession leave behind (Chuang et al. 2018; García et al. 2014; Holl et al. 2018).  
103 Furthermore, these studies may contribute to disentangle the role of spatial effects (e.g. spatial  
104 autocorrelation and random dispersal) affecting vegetation expansion and dynamics, and can enhance  
105 the effectiveness of management plans of protected areas and the recovery of degraded sites (Hu et al.  
106 2012; Méndez et al. 2008; Quero et al. 2011).

107 Here we combined current field sampling, GIS-based interpretation of sequential, high-resolution  
108 images (satellite and aerial photographs) and spatially-explicit analysis to evaluate magnitude, spatial  
109 patterns and potential drivers of expansion (i.e. increase) relating to woody vegetation cover over 24  
110 years in a Mediterranean woodland pasture. We sought to answer the following questions: How fast, in  
111 terms of the magnitude of expansion over time, does woody vegetation recover in pastureland? How  
112 dynamic is the spatial structure along such expansion? Are current cover and expansion spatially  
113 correlated with the amount of past woody vegetation cover? And to what extent might distance to the  
114 continuous forest and to the nearest woody patch affect cover expansion? Our study presents an  
115 appropriate system in order to seek answers to those questions as it combines relatively homogeneous  
116 abiotic conditions with an absence of fire, providing a clearer quantification of woody vegetation  
117 recovery potential and interpretation of vegetation dynamics due to major biotic processes, such as  
118 zoochory and herbivory.

## 119 **Methods**

### 120 **Study site**

121 The study was conducted at Alpe Cucco (37°52' and 13°24'), a site located in the center of the  
122 “Bosco della Ficuzza, Rocca Busambra, Bosco del Cappelliere e Gorgo del Drago” nature reserve  
123 (hereafter FBCD), which is a 7,397 ha protected area composing the last, large remnant of forest in  
124 western Sicily (Badalamenti et al. 2017; Gianguzzi & La Mantia 2004). The site is a 160 ha woodland  
125 pasture comprising seasonal pastures intermingled with woody vegetation, surrounded by forest patches  
126 (Fig. 1). The local climate is mesic Mediterranean, with an average rainfall of 850 mm concentrated  
127 mostly in autumn and winter, and mean annual temperatures of 14.3 °C, with average temperatures of  
128 9.4°C in the coldest months (January and February) increasing to an average of 23.5 °C in the hottest  
129 months (July and August).

130 Vegetation in Alpe Cucco corresponds to the Meso-Mediterranean type, based on a classification  
131 of altitudinal belts (Rivas-Martínez 2008). Surrounding forest patches are mostly composed of holm oak  
132 (*Quercus ilex*), downy oak (*Quercus pubescens*) and, to a lesser extent, maple (*Acer campestre*) and  
133 manna ash (*Fraxinus ornus*) (Badalamenti et al. 2017; Gianguzzi & La Mantia 2004). The woodland  
134 pasture is dominated by seasonal grasses and forbs (see Bianchetto et al. 2015 for a species list) with

135 isolated shrubs and trees, and varied-sized patches of woody vegetation comprising mostly six fleshy-  
136 fruited species (*Pyrus amygdaliformis*, *Crataegus monogyna*, *Crataegus laciniata*, *Rubus ulmifolius*,  
137 *Rosa canina* and *Prunus spinosa*) and, to a lesser degree, one dry-fruited shrub (*Calicotome infesta*),  
138 the two oaks and maple (Gianguzzi & La Mantia 2004). The site was subject to a reforestation program  
139 during the decade 1970-1980; individuals of *Fraxinus angustifolia* and *Pinus halepensis*, two species  
140 previously absent in the pasture, were planted in scattered patches and isolated individuals in a part of  
141 the Alpe Cucco area (Gianguzzi & La Mantia 2004). Extensive cattle (cow) raising has a long history in  
142 Alpe Cucco, and is still present nowadays, whereas an active pastureland management program  
143 including irrigation, ploughing and seeding was developed during the period 1960-1990. (A.S.F.D 1959;  
144 Bianchetto et al. 2015).

#### 145 **Sampling design**

146 In September 2016, we established three 500 x 200 m plots, each divided into 160 subplots of 25 x 25 m  
147 (sampling unit) covering a gradient from continuous forest to woodland pasture (Fig. 1). The minimum  
148 and maximum distances between plot edges were 300 m and 510 m. All plots extended over relatively  
149 homogeneous flat areas (average slope 15%) and northern exposure. The maximum altitudinal  
150 difference between points located in different plots was 190 m (880 to 1070 m a.s.l.), and the average  
151 altitude per plot was 960 m. Soils are deep (> 100 cm), sub-alkaline, clay-dominated vertic haploxeralfs  
152 (Raimondi 1983).

#### 153 **Vegetation mapping and classification**

154 To measure the spatial pattern of woody vegetation cover over the years, we contrasted aerial  
155 photographs from the year 1992 (scale 1:29000, 1 pixel = 1m) and satellite images from 2016 (Google  
156 Earth, RGB bands, 1 pixel = 0.13m, rescaled to 1m), in a time lapse of 24 years, incorporated into a  
157 Geographical Information System (GIS) platform belonging to our study system (see Online appendix  
158 S1 for details of woody cover extraction procedure). Although older images were available, the 1992  
159 images were the oldest following cessation of pasture management, representing a conservative date to  
160 address vegetation recovery through secondary succession without further large-scale, human-provoked  
161 disturbance.

162 We sought to differentiate three types of woody cover in aerial views: woodland patches, shrubland  
163 patches, and isolated trees, shrubs and small nucleation patches of trees or shrubs (hereafter ITSN).

164 First, in the 2016 images, woodland patches ( $> 50 \text{ m}^2$ ) were mapped following the heterogeneous dark-  
165 gray texture which produced conspicuous black shadows ( $> 2 \text{ m}$  in height) (see Online appendix S1 and  
166 S2 for details). The species composing this vegetation type were *Quercus pubescens*, *Quercus ilex*, *Acer*  
167 *campestris*, *Pyrus amygdaliformis*, *Crataegus monogyna*, *Crataegus laciniata*, together with *Fraxinus*  
168 *angustifolia* and *Pinus halepensis*, two species naturally absent from the study area and that dominate  
169 the canopy cover wherever planted. Shrubland patches were defined as with an area of  $> 50 \text{ m}^2$ ,  
170 homogeneous texture with a lighter-gray pattern compared to woodlands and which produced no  
171 conspicuous shadow ( $< 2 \text{ m}$  tall), with or without trees. The species composing this cover type were  
172 *Rubus ulmifolius*, *Prunus spinosa*, *Rosa canina* and *Calicotome infesta* together with juveniles of *P.*  
173 *amygdaliformis* and *C. monogyna*. The remaining woody cover with a surface of  $< 50 \text{ m}^2$  was classified  
174 as ITSN. All the woody vegetation cover extracted from the images was added as a new layer  
175 (polygons) to the GIS platform (Online appendix S2). As the digital pixel value did not enable us to  
176 differentiate clearly between woodland and shrubland boundaries which occurred within the same  
177 polygon, we divided the 2016 and 1992 woody cover using photointerpretation, separating the different  
178 cover types into distinct polygons (Online appendix S2). We had no reasons to correct the woody cover  
179 extraction output (i.e. no woody cover signed over the grassland or vice versa), but in order to validate  
180 cover-type classification and its boundaries, all polygons were numbered and checked in the field,  
181 where minor differences were corrected (accuracy  $> 98\%$ ); the subplot woody cover surface ( $\text{m}^2$ ) of the  
182 different vegetation types was subsequently obtained (Online appendix S2). Continuous forest, mainly  
183 comprising *Quercus ilex* and *Quercus pubescens*, was defined as a single woodland patch which  
184 contained the dense continuous woodland remnant surrounding Alpe Cucco. Distance predictors were  
185 calculated from the centroid of each subplot up to the nearest border of the continuous forest and to the  
186 nearest woodland patch (Online appendix S2). According to the oldest aerial image available (1955),  
187 most plot surface was already deforested at that time (Online appendix S3). As we were particularly  
188 interested in the expansion of woody cover due to natural regeneration, we differentiated the cover  
189 attributable to natural processes from that attributable to human-made plantation (see Pueyo & Begueria  
190 2007 for a similar procedure; Appendix S2). Woody cover extraction, classification and figures were  
191 done using software QGIS (QGIS Development Team 2016).

192

### 193 **Spatial structure of the woody vegetation cover over time**

194 We were interested in characterize the degree of stability of the spatial structure of woody  
195 vegetation cover from 1992 to 2016. For this purpose we used the Spatial Analysis by Distance Index -  
196 SADIE (see Perry et al. 1999). SADIE uses a transportation algorithm to estimate the distance to  
197 regularity (D), that represents the minimum distances that the values of each spatially located variable  
198 (in our case woody cover in each sub-plot) need to move to reach a regular spatial distribution across all  
199 sub-plots, based on the concept of donors and receivers (REF). The ratio between D and its average  
200 values, estimated through randomization, generate the global aggregation index ( $Ia$ ) as well as its  
201 significance values at 95% confidence intervals ( $p$ ). An index around 1 indicate a randomly distributed  
202 woody cover, lower than 1 indicate regular distribution and higher than 1 represent an aggregated or  
203 patchy pattern. The  $Ia$  is composed by specific sub-plot clustering values ( $v$ ), showing the magnitude of  
204 the contribution of each sampling unit to the overall cluster values and indicating if the cover value of a  
205 sub-plot is member of an above average patch ( $v_i$ ) or if a member of below average gap ( $v_j$ ) (Perry &  
206 Dixon 2002; Perry et al. 1999). We calculated the SADIE aggregation indexes of the 1992 and 2016  
207 woody vegetation cover separately (considering only the natural vegetation in 2016).

208 SADIE methodology also enabled us to quantify the spatial association index ( $Xp$ ) of woody  
209 cover, derived from the mean values of 1992 and 2016 woody cover in the same sub-plot (i.e.  
210 correlation between the  $v_i$  and  $v_j$  indexes of both periods) (Perry & Dixon 2002). The index range from -  
211 1 to 1 and is significant if  $p < 0.05$ , where a positive association means that the vegetation cover spatial  
212 distribution remained stable from 1992 to 2016 (both if a woody patch or a grassland gap), while a  
213 negative value means a mismatch of cover values along the 24 years (e.g a grassland occupied by  
214 woody vegetation).

215 The next step was to exclude the planted cover to obtain values for proportional expansion of the  
216 natural regeneration cover from 1992 to 2016 (hereafter PE), calculated with the formula (*2016 natural  
217 regeneration cover – 1992 cover*)/(625 – 1992 cover). We selected such relative variable instead of the  
218 amount of increase to avoid the geometrical constriction of the quadratic relationship between available  
219 space and maximum cover increase. Thus, our PE represents the magnitude of cover expansion within



220 each subplot in each 1m<sup>2</sup> unit, enabling the comparison of plots with different past covers independently  
221 from the absolute quantity of past cover within the sub-plot,. We then performed another SADIE  
222 analysis to obtain the spatial structure (*Ia, vi and vj*) of PE. For this SADIE analysis, we excluded those  
223 subplots with full woody vegetation cover in 1992 and, consequently, zero expansion due to lack of  
224 space; there then remained 155 subplots in plot 1, 160 in plot 2 and 152 in plot 3. SADIE indexes are  
225 continuous variables (Perry & Dixon 2002), thus we incorporated the *vi and vj* indexes of 1992 and  
226 2016 cover, and those of PE into bi-dimensional contour maps to obtain a more comprehensive view of  
227 the spatial pattern structure and to visualize coldspots (i.e. areas with zero or low cover increase) and  
228 hotspots (i.e. areas with high cover increase). Sadie aggregation indexes were obtained with SadieShell  
229 2.0 and the spatial association was calculated with N\_AShell 1.0 (Perry et al. 1999). Contour maps were  
230 prepared using the plugin contour of the software QGIS (QGIS Development Team 2016).

231

### 232 **Factors affecting the expansion of woody vegetation cover**

233 We sought to assess whether the quantity, identity and spatial configuration of past woody  
234 vegetation cover affected its further expansion over the 24 y period of study. Thus, we used multiple  
235 regression models, including the values of PE at the subplot level as a response variable and the amount  
236 of woody vegetation cover, distance to the continuous forest and distance to the nearest woodland in  
237 1992 as continuous predictor variables. We also incorporated, as a qualitative predictor, the dominant  
238 cover type (> 70%) in the 1992 subplot, classified as 0 if there was no cover, 1 for ITSN, 2 for  
239 shrubland, 3 for mixed cover (2 or more types in the same subplot) and 4 for woodlands). We excluded  
240 the subplots with full cover in 1992 and those with negative PE values (i.e. retreatment of woody  
241 vegetation cover) from the analysis, resulting in 145 subplots in plot 1, 152 in plot 2 and 152 in plot 3.  
242 PE was square-root transformed to achieve normality and reduce heteroscedasticity. Before running  
243 regressions we tested for multicollinearity among predictors using the variance inflation factor (mean =  
244 2.73, highest = 4.11) and the three continuous predictors (amount of woody vegetation cover, distance  
245 to the continuous forest and distance to the nearest woodland in 1992) were standardized prior to the  
246 analysis. The model was calibrated by correlating the measured and predicted PE values in plot 1, and  
247 validated correlating the measured and predicted values using plot 2 and 3 predictor values (Appendix S5).

248 As sampling included the use of spatially contiguous subplots, and vegetation expansion may  
249 present a contagious pattern (e.g. Bakker et al. 2004), we tested for the presence of spatial  
250 autocorrelation (Dormann et al. 2007; Keitt et al. 2002). Initially, we performed a global (all plots) and  
251 independent (each plot) non-spatial ordinary least squares (OLS) multiple regressions. Once all OLS  
252 models presented strong spatial autocorrelation (Moran's  $I p < 0.001$ ; Online appendix S5), and this  
253 issue can cause strong bias in the results (Dormann et al. 2007; Kissling & Carl 2008) we discarded  
254 OLS results and tested both Spatial AutoRegressive Lag and Error Models (SARlag or SARerror).  
255 These regression analysis takes into account spatial autocorrelation in data through a weight matrix that  
256 incorporates the neighborhood values of that location (SARlag) or of the errors (SARerr) (Kissling &  
257 Carl 2008; Ver Hoef et al. 2018). In our case, the weight matrix was row-standardized and based on  
258 different distance classes of neighbor points (subplot centroids), starting at 36 m, which included all the  
259 immediate surrounding neighbors (borders and vertex first order) and the consequent orders of  
260 neighbors at each 36 m-distance class. Due to our sampling design (spatially discontinuous sets of  
261 equally spaced grids), the differences in the weight matrix among plots (Online appendix S5) and the  
262 objective to test for meso-scale differences in vegetation expansion, we ran independent SAR models  
263 for the different plots. The best model from SARlag and SARerr was selected based on lowest AICc,  
264 highest log-likelihood values, minimum residual spatial autocorrelation and model fit (pseudo-R<sup>2</sup>). All  
265 the spatial tests and regressions were performed with GEODA 1.8 (Anselin et al. 2006).

266

## 267 **Results**

268 From 1992 to 2016, the overall woody vegetation cover in the three plots increased by 6,822 ha  
269 (90.1%), rising from 7,568 ha to 14,390 ha. Most of the increase was due to natural regeneration (5,159  
270 ha), including 2,849 ha of woodland, 2,164 ha of shrubland and 0,146 ha of ITSN (Fig. 2, Online  
271 appendix S4). However, proportionally (i.e. increase relative to initial cover), shrubland almost doubled  
272 in surface (94.9%), followed by woodland (67.1%) and ITSN (14.1%). Planted cover accounted for the  
273 remaining 24.4% (1,663 ha). We found no correlation between 2016 planted cover and woody

274 vegetation cover in 1992 (Pearson  $r = -0.01$ ,  $p = 0.69$ ), suggesting that the development of planted  
275 cover occurred almost exclusively throughout the 24-year period. The three plots differed in the average  
276 proportional expansion of natural regeneration woody cover (ANOVA  $F = 45.94$ ,  $p < 0.001$ ) with  
277 contrasting variations in each cover-type contribution to expansion (Fig. 2).

278

### 279 **Spatial structure of the woody vegetation cover over years**

280 The SADIE  $Ia$  index indicated that global spatial structure of woody vegetation cover was  
281 significantly aggregated and remained stable over time (from 1992 to 2016) (Table 1). Furthermore, the  
282 significant  $Xp$  index indicated a strong spatial correlation between  $v_i$  and  $v_j$  values in the same subplot  
283 over time, denoting a conservative, small-scale spatial trend in vegetation dynamics (i.e few sub-plots  
284 members of a gap became members of a patch or vice-versa) (Table 1). The PE aggregation index also  
285 showed positive and significant values across plots, suggesting marked patchiness in the distribution of  
286 woody vegetation cover expansion within each plot, with no clear sign of broad, gradient-like spatial  
287 structure from the continuous forest towards open areas (Table 1, Fig. 3).

288

### 289 **Factors affecting the expansion of woody vegetation cover**

290 The SARerr model showed the best fit in comparison with SARlag models in all plots when  
291 assessing the effects of past cover, distance to continuous forest, distance to nearest woody patch and  
292 cover type on the proportional expansion of the natural regeneration of woody vegetation (Online  
293 appendix S5) and subsequent results refers to this model. Woody cover in 1992 was the strongest  
294 predictor of proportional expansion (PE) across all plots, with a positive and significant effect in plots 1  
295 and 2 (Table 2, Fig 4). Distance to the continuous forest showed no significant effect on PE in any plot  
296 (Table 2). However, PE tended to increase at shorter distances from the nearest woody patch, as  
297 illustrated by the negative coefficient values of this predictor across plots ( $p = 0.07$  in plot 1;  $p < 0.001$   
298 in plot 2). PE was also independent of the type of woody vegetation cover in all plots (Table 2).

299

## 300 **Discussion**

301 In our study, we quantified the intensity of woody cover expansion and revealed, on the one hand,  
302 overall maintenance of the aggregated spatial pattern of woody vegetation cover over 24 years, even  
303 under strong expansion. On the other hand, we detected quantitative (i.e. cover expansion) and  
304 qualitative (i.e. cover type composing the expansion) differences even in closely located plots. The  
305 increase in natural woody vegetation found in our study would seem to be relatively high, considering  
306 the current structural complexity of varied-size woodland and shrubland patches, and the deforestation,  
307 anthropic use and herbivory pressure, at least over the last 80 years inside the plots (Bianchetto et al.  
308 2015).

### 309 **Woody vegetation natural regeneration**

310 It has been demonstrated that livestock herbivory can slow down or even hamper woody  
311 vegetation recovery (Carmel & Kadmon 1999; La Mantia et al. 2013; Laskurain et al. 2013). No precise  
312 information on cattle density was available for our site, nor regarding the increasing population of  
313 fallow deer (*Dama dama*) (Bianchetto et al. 2015), thus limiting our interpretations. However, judging  
314 by the observed recovery rate, no significant negative influence of herbivory in cover expansion seems  
315 to be occurring, at least over the past 24 years. A similar outcome was also observed in other  
316 Mediterranean areas (e.g. Bashan & Bar-Massada 2017). Besides the magnitude of expansion, the  
317 quality of vegetation recovery in our study system also differed from other studies in the Mediterranean  
318 region. Bonet and Pausas (2004), for example, found an average woody vegetation cover increase of  
319 26% after 60 years; however, less than 20% of that cover was composed of endozoochoric species,  
320 while La Mantia et al. (2008), studying ungrazed terraces on a Sicilian smaller island, found an increase  
321 of 57%, comprising mostly one dry-fruited species. On our site, the 68% natural regeneration woody  
322 cover increase was composed mainly of a mix of six zoochoric species (*Pyrus amygdaliformis*,  
323 *Crataegus laciniata* *Crataegus monogyna*, *Rubus ulmifolius*, *Prunus spinosa*, *Rosa canina*) (R.S.Bueno  
324 *unpub. data*).

325

### 326 **Spatial structure of the woody vegetation cover over years**

327 Our SADIE analysis demonstrated that the woody vegetation cover kept its highly spatially  
328 aggregated pattern on both a landscape (plot) and a local (subplot) scale throughout the 24 years, even

329 when faced with considerable expansion (Table 1). The maintenance of aggregated patterns is the  
330 expected result of expansion from previous cover (Bakker et al. 2004). In fact, past woody cover  
331 positively influenced vegetation expansion in plot 1 and 2 (Table 2, Fig. 4). In addition to the effects of  
332 past cover, herbivory intensity may be one of the factors not measured here that can influence  
333 vegetation spatial configuration, although a range of responses has been found so far (Adler et al. 2001;  
334 Bashan & Bar-Massada 2017). Seifan and Kadmon (2006), for example, found that cattle herbivory  
335 changed the spatial pattern of a scrub community by reducing the aggregation level (clumpiness),  
336 although the cover increase was not affected by different levels of herbivory intensity. In our study, we  
337 found that the aggregated pattern remained unchanged, while cover expansion varied among plots  
338 sharing the same herbivory pressure (Fig. 2). These contrasting findings indicate that more studies  
339 comprising species-specific and community-wide responses are needed for a more comprehensive  
340 interpretation of vegetation spatial-pattern dynamics.

341

#### 342 **Influence of past cover, cover type and distance to remnant vegetation**

343 Grass cover and canopy closure (i.e. a proxy of woody cover) were deemed to be the most  
344 relevant predictors in tropical forest recovery (Holl et al. 2018), although differential influences of past  
345 cover have been found across Mediterranean-type ecosystems (Carmel & Flather 2004). On our site, we  
346 found a differential contribution of past cover at plot scale, once this predictor was found to be non-  
347 significant in explaining expansion in plot 3 (Table 2). This plot showed some large patches resulting  
348 from the direct colonization of open ground, far from any previous woody vegetation cover, and this  
349 would explain the lack of effect of past cover in the regression model, as well as the lowest SADIE  
350 aggregation index. Another fact potentially affecting the lack of effect of past cover on expansion is that  
351 some types of early woody cover can themselves impede further development of ecological succession  
352 (i.e. arrested succession) (Acácio et al. 2007). On our site, for example, a number of *R. ulmifolius*  
353 patches remained almost unchanged over the 24 years, and a few large, old trees had virtually no  
354 vegetation increase in their surroundings. In the first case, the absence of cover increase in bramble  
355 patches may derive from a strong competitive effect (Fotelli et al. 2001). In the case of isolated large

356 trees, the lack of structure for facilitating protection against herbivory, such as basal branching and  
357 protective spiny leaves at the ground level (Garcia & Obeso 2003) could explain the above pattern.

358         Contrary to our expectations, distance from the continuous forest proved non-significant in  
359 predicting vegetation expansion. Remnant forests usually act as a source of propagules for the  
360 colonization of open areas. Therefore, given the overall distance constraints of seed dispersal, a  
361 decreasing rate of vegetation expansion when moving away from the forest is expected (García et al.  
362 2014). Our sampling design, with plots sharing similar configuration of continuous forest (one side  
363 forest), should be effective to check for distance effects by forcing a very large distance gradient in  
364 sampling points without lateral influence. However, on our study site, the continuous forest comprised  
365 mostly oaks (*Q. pubescens* and *Q. ilex*), while the majority of the mid-successional woody plants  
366 species composing the bulk of cover increase were located mostly in pastureland. For example, one of  
367 the most important species in terms of cover expansion (*P. amygdaliformis*) occurs at very low density  
368 inside the forest and is dispersed almost exclusively by mammals (Fedriani et al. 2010); therefore, even  
369 the longest distances within plots (ca. 1,400 m) can fall within the mammals seed dispersal potential  
370 (González-Varo et al. 2017). Complementarily, a recent study in Mediterranean has verified no  
371 differences in seed arrival in old fields of species dispersed by both birds and mammals up to 90 m from  
372 the seed source (La Mantia et al. 2019). In addition, higher fruit-availability in woodland pasture  
373 compared to continuous forest, coupled with vegetation structural complexity (i.e. presence of different  
374 perches and woody patches) may influence the behavior of those birds acting as seed dispersers;  
375 fostering movement away from the forest and towards fruit-rich environments (La Mantia & Bueno  
376 2016; Lasky & Keitt 2012). However, later in the process of secondary succession, an increase in the  
377 influence of distance to continuous forest in cover-species composition is expected, when the mid-  
378 successional species composing current expansion facilitate oak establishment in woodland pasture  
379 (Alias et al. 2010; Amici et al. 2013).

380         Distance to woody patch, in turn, was found to negatively affect the expansion of woody  
381 vegetation; however, this pattern was only significant in plot 2. A negative influence was expected  
382 established that proximity to even small patches of woody vegetation is a proxy for higher seed rain and  
383 consequent recruitment (Martínez & García 2015; Navarro-González et al. 2013). The initial

384 configuration of woody vegetation in plot 2, with many scattered, small patches, would have  
385 strengthened this negative relationship. The lack of relationship in the other two plots may derive,  
386 firstly, from a random distribution of mammal dispersed species (e.g. *P. amygdaliformis*) at this spatial  
387 scale. Secondly, the average distance range between patches may be easily covered by birds, resulting in  
388 a cover-cover directed seed dispersal (i.e. from a perch to another perch), with a consequent gap in  
389 recruitment between close patches (Garcia et al. 2011; Pausas et al. 2006). Refining the scale of the  
390 study using smaller subplots should provide additional information, although a species-specific  
391 differential response of each plant is also expected.

392 Woody cover expansion was independent of the type of patch composing the past cover,  
393 suggesting that, in our system, small patches of isolated trees and shrubs have the same potential to  
394 promote or prevent expansion as larger patches of shrubland and woodland. Moreover, we also  
395 observed the direct evolution from pastureland to woodlands given that various subplots free of woody  
396 vegetation in 1992 contained woodland patches in 2016. For example, most oak-dominated woodland  
397 patches showed smaller expansion than mixed shrubland patches. Furthermore, selective grazing and  
398 browsing were also seen to influence the outcome of vegetation development, often hampering  
399 woodlands development (Carmel & Kadmon 1999; Garcia & Obeso 2003). On our site, palatable, late-  
400 successional species (e.g. *Quercus sp.*) were almost absent from the woody cover under expansion, and  
401 mid-successional and herbivory-defended species are actually those developing woodland.  
402 Autoregressive parameters ( $\lambda$ ) obtained in our models, however, indicate that other factors not  
403 measured in our analysis are influencing cover expansion, a similar outcome was found also for species  
404 distribution (Hu et al. 2012). This strong neutral effect corroborates the importance of taking  
405 autocorrelation into consideration in spatial analysis (Dormann et al. 2007; Ver Hoef et al. 2018).

406 Large-scale approaches are necessary in order to detect landscape and global patterns (Sluiter &  
407 de Jong 2007). However, considering the similarities (e.g. the aggregated spatial structure) and the  
408 differences (e.g. variation in the dominant cover type composing expansion) in closely located plots  
409 which share the same historical contingency, pool of species, grazing pressure and environmental  
410 conditions, the patterns found in our study highlight the complementarity of smaller scale investigations  
411 when interpreting vegetation dynamics and recovery (Hu et al. 2012; Quero et al. 2011). As an example,

412 in an applied perspective, this complementarity may refine the calculation of ecosystem services, such  
413 as carbon stock, it may improve the evaluation of scale-dependent species richness patterns and,  
414 consequently, help design more effective restoration programs (Chuang et al. 2018; Méndez et al. 2008;  
415 Novara et al. 2017). Finally, we demonstrate that in favorable conditions, especially in the presence of  
416 remnant woody cover and in the absence of fire, even a long history of deforestation, land use and the  
417 presence of livestock do not crush the potential for intense woody vegetation expansion, even though  
418 previous cover tends to “sequester” this potential for recovery.

419

420

421 Conflict of Interest: The authors declare that they have no conflict of interest.

422

## 423 **References**

- 424 A.S.F.D. 1959. L’Azienda di Stato per le Foreste Demaniali. . Edizione A.B.E.T.E., Roma.
- 425 Abadie J., Dupouey J.-L., Avon C., Rochel X., Tatoni T. and Bergès L. 2018. Forest recovery since 1860 in  
426 a Mediterranean region: drivers and implications for land use and land cover spatial distribution.  
427 *Landscape Ecology* 33: 289-305.
- 428 Acácio V., Holmgren M., Jansen P.A. and Schrotter O. 2007. Multiple Recruitment Limitation Causes  
429 Arrested Succession in Mediterranean Cork Oak Systems. *Ecosystems* 10: 1220-1230.
- 430 Adler P., Raff D. and Lauenroth W. 2001. The effect of grazing on the spatial heterogeneity of  
431 vegetation. *Oecologia* 128: 465-479.
- 432 Alias S., Bianchi L., Calamini G., Gregori E. and Sioni S. 2010. Shrub facilitation of *Quercus ilex* and  
433 *Quercus pubescens* regeneration in a wooded pasture in central Sardinia (Italy). *iForest -*  
434 *Biogeosciences and Forestry* 3: 16-22.
- 435 Allen C.R., Angeler D.G., Cumming G.S., Folke C., Twidwell D. and Uden D.R. 2016. Quantifying spatial  
436 resilience. *Journal of Applied Ecology* 53: 625-635.
- 437 Alodos C.L., Pueyo Y., Barrantes O., Escós J., Giner L. and Robles A.B. 2004. Variations in landscape  
438 patterns and vegetation cover between 1957 and 1994 in a semiarid Mediterranean ecosystem.  
439 *Landscape Ecology* 19: 543-559.
- 440 Álvarez-Martínez J.M., Suárez-Seoane S., Stoorvogel J.J., de Luis Calabuig E. and Gilliam F. 2014.  
441 Influence of land use and climate on recent forest expansion: a case study in the Eurosiberian-  
442 Mediterranean limit of north-west Spain. *Journal of Ecology* 102: 905-919.
- 443 Amici V., Santi E., Filibeck G., Diekmann M., Geri F., Landi S., Scoppola A., Chiarucci A. and Vetaas O.  
444 2013. Influence of secondary forest succession on plant diversity patterns in a Mediterranean  
445 landscape. *Journal of Biogeography* 40: 2335-2347.
- 446 Andivia E., Villar-Salvador P., Tovar L., Rabasa S. and Rey Benayas J.M. 2017. Multiscale assessment of  
447 woody species recruitment in Mediterranean shrublands: facilitation and beyond. *Journal of*  
448 *Vegetation Science* 28: 639-648.
- 449 Anselin L., Syabri I. and Kho Y. 2006. GeoDa: An Introduction to Spatial Data Analysis. *Geographical*  
450 *Analysis* 38: 5-22.



451 Bacaro G., Rocchini D., Bonini I., Marignani M., Maccherini S. and Chiarucci A. 2008. The role of  
452 regional and local scale predictors for plant species richness in Mediterranean forests. *Plant*  
453 *Biosystems - An International Journal Dealing with all Aspects of Plant Biology* 142: 630-642.

454 Badalamenti E., La Mantia T., La Mantia G., Cairone A. and La Mela Veca D. 2017. Living and Dead  
455 Aboveground Biomass in Mediterranean Forests: Evidence of Old-Growth Traits in a *Quercus*  
456 *pubescens* Willd. s.l. *Stand. Forests* 8: 187.

457 Baeza M.J., Valdecantos A., Alloza J.A. and Vallejo V.R. 2007. Human disturbance and environmental  
458 factors as drivers of long-term post-fire regeneration patterns in Mediterranean forests. *Journal of*  
459 *Vegetation Science* 18: 243-252.

460 Bakker E.S., Olff H., Vandenbergh C., De Maeyer K., Smit R., Gleichman J.M. and Vera F.W.M. 2004.  
461 Ecological anachronisms in the recruitment of temperate light-demanding tree species in wooded  
462 pastures. *Journal of Applied Ecology* 41: 571-582.

463 Bashan D. and Bar-Massada A. 2017. Regeneration dynamics of woody vegetation in a Mediterranean  
464 landscape under different disturbance-based management treatments. *Applied Vegetation Science* 20:  
465 106-114.

466 Berdugo M., Kéfi S., Soliveres S. and Maestre F.T. 2017. Plant spatial patterns identify alternative  
467 ecosystem multifunctionality states in global drylands. *Nature Ecology & Evolution* 1: 0003.

468 Bianchetto E., Buscemi I., Corona P., Giardina G., La Mantia T. and Pasta S. 2015. Fitting the Stocking  
469 Rate with Pastoral Resources to Manage and Preserve Mediterranean Forestlands: A Case Study.  
470 *Sustainability* 7: 7232-7244.

471 Bonet A. and Pausas J.G. 2004. Species richness and cover along a 60-year chronosequence in old-  
472 fields of southeastern Spain. *Plant Ecology* 174: 257-270.

473 Bueno R.S., Guevara R., Ribeiro M.C., Culot L., Bufalo F.S. and Galetti M. 2013. Functional Redundancy  
474 and Complementarities of Seed Dispersal by the Last Neotropical Megafrugivores. *PLOS ONE* 8:  
475 e56252.

476 Carmel Y. and Flather C.H. 2004. Comparing landscape scale vegetation dynamics following recent  
477 disturbance in climatically similar sites in California and the Mediterranean basin. *Landscape Ecology*  
478 19: 573-590.

479 Carmel Y. and Kadmon R. 1999. Effects of grazing and topography on long-term vegetation changes in  
480 a Mediterranean ecosystem in Israel. *Plant Ecology* 145: 243-254.

481 Carmel Y., Kadmon R. and Nirel R. 2001. Spatiotemporal predictive models of mediterranean  
482 vegetation dynamics. *Ecological Applications* 11: 268-280.

483 Chuang W.C., Garmestani A., Eason T.N., Spanbauer T.L., Fried-Petersen H.B., Roberts C.P., Sundstrom  
484 S.M., Burnett J.L., Angeler D.G., Chaffin B.C., Gunderson L., Twidwell D. and Allen C.R. 2018. Enhancing  
485 quantitative approaches for assessing community resilience. *Journal of Environmental Management*  
486 213: 353-362.

487 Debussche M., Escarré J. and Lepart J. 1982. Ornithochory and plant succession in mediterranean  
488 abandoned orchards. *Vegetatio* 48: 255-266.

489 Dormann F.C., M. McPherson J., B. Araújo M., Bivand R., Bolliger J., Carl G., G. Davies R., Hirzel A., Jetz  
490 W., Daniel Kissling W., Kühn I., Ohlemüller R., R. Peres-Neto P., Reineking B., Schröder B., M. Schurr F.  
491 and Wilson R. 2007. Methods to account for spatial autocorrelation in the analysis of species  
492 distributional data: a review. *Ecography* 30: 609-628.

493 Falcucci A., Maiorano L. and Boitani L. 2007. Changes in land-use/land-cover patterns in Italy and their  
494 implications for biodiversity conservation. *Landscape Ecology* 22: 617-631.

495 Fedriani J.M., Wiegand T. and Delibes M. 2010. Spatial pattern of adult trees and the mammal-  
496 generated seed rain in the Iberian pear. *Ecography*.

497 Fotelli M.N., Geßler A., Peuke A.D. and Rennenberg H. 2001. Drought affects the competitive  
498 interactions between *Fagus sylvatica* seedlings and an early successional species, *Rubus fruticosus*:  
499 responses of growth, water status and  $\delta^{13}\text{C}$  composition. *New Phytologist* 151: 427-435.

500 Gallego Fernández J.B., Rosario García Mora M. and García Novo F. 2004. Vegetation dynamics of  
501 Mediterranean shrublands in former cultural landscape at Grazalema Mountains, South Spain. *Plant*  
502 *Ecology* 172: 83-94.

503 García C., Moracho E., Díaz-Delgado R., Jordano P. and Matlack G. 2014. Long-term expansion of  
504 juniper populations in managed landscapes: patterns in space and time. *Journal of Ecology* 102: 1562-  
505 1571.

506 Garcia D. and Obeso J.R. 2003. Facilitation by herbivore-mediated nurse plants in a threatened tree,  
507 *Taxus baccata*: local effects and landscape level consistency. *Ecography* 26: 739-750.

508 Garcia D., Zamora R. and Amico G.C. 2011. The spatial scale of plant-animal interactions: effects of  
509 resource availability and habitat structure. *Ecological Monographs* 81: 103-121.

510 Getzin S., Wiegand T., Wiegand K. and He F. 2008. Heterogeneity influences spatial patterns and  
511 demographics in forest stands. *Journal of Ecology* 96: 807-820.

512 Gianguzzi L. and La Mantia A. 2004. Le serie di vegetazione della riserva "Bosco Ficuzza, Rocca  
513 Busambra, Bosco del Cappeliere e Gorgo del Drago" (Provincia di Palermo Naturalista Siciliano XXVIII).

514 Gómez-Aparicio L. 2008. Spatial patterns of recruitment in Mediterranean plant species: linking the  
515 fate of seeds, seedlings and saplings in heterogeneous landscapes at different scales. *Journal of*  
516 *Ecology* 96: 1128-1140.

517 González-Varo J.P., Carvalho C.S., Arroyo J.M. and Jordano P. 2017. Unravelling seed dispersal through  
518 fragmented landscapes: Frugivore species operate unevenly as mobile links. *Molecular Ecology* 26:  
519 4309-4321.

520 Holl K.D., Reid J.L., Oviedo-Brenes F., Kulikowski A.J. and Zahawi R.A. 2018. Rules of thumb for  
521 predicting tropical forest recovery. *Applied Vegetation Science* 21: 669-677.

522 Hu Y.-H., Lan G.-Y., Sha L.-Q., Cao M., Tang Y., Li Y.-D. and Xu D.-P. 2012. Strong Neutral Spatial Effects  
523 Shape Tree Species Distributions across Life Stages at Multiple Scales. *PLOS ONE* 7: e38247.

524 Jordano P. 2017. What is long-distance dispersal? And a taxonomy of dispersal events. *Journal of*  
525 *Ecology* 105: 75-84.

526 Keitt T.H. 2003. Spatial Autocorrelation, Dispersal and the Maintenance of Source-Sink Populations. In:  
527 Bradshaw G. A. and Marquet P. A. (eds), *How Landscapes Change: Human Disturbance and Ecosystem*  
528 *Fragmentation in the Americas*. Springer Berlin Heidelberg, Berlin, Heidelberg, pp. 225-238.

529 Keitt T.H., Bjørnstad O.N., Dixon P.M. and Citron-Pousty S. 2002. Accounting for spatial pattern when  
530 modeling organism-environment interactions. *Ecography* 25: 616-625.

531 Kissling W.D. and Carl G. 2008. Spatial autocorrelation and the selection of simultaneous  
532 autoregressive models. *Global Ecology and Biogeography* 0: 070618060123007-???

533 La Mantia T. and Bueno R.S. 2016. Colonization of eurasian jay *Garrulus glandarius* and holm oaks  
534 *Quercus ilex*: the establishment of ecological interactions in urban areas. *Avocetta* 40: 85-87.

535 La Mantia T., Gristina L., Rivaldo E., Pasta S., Novara A. and Rühl J. 2013. The effects of post-pasture  
536 woody plant colonization on soil and aboveground litter carbon and nitrogen along a bioclimatic  
537 transect. *iForest - Biogeosciences and Forestry* 6: 238-246.

538 La Mantia T., Rühl J., Massa B., Pipitone S., Lo Verde G. and Bueno R.S. 2019. Vertebrate-mediated  
539 seed rain and artificial perches contribute to overcome seed dispersal limitation in a Mediterranean  
540 old field. *Restoration Ecology* in press.

541 La Mantia T., Rühl J., Pasta S., Campisi D.G. and Terrazzino G. 2008. Structural analysis of woody  
542 species in Mediterranean old fields. *Plant Biosystems - An International Journal Dealing with all*  
543 *Aspects of Plant Biology* 142: 462-471.

544 Laskurain N.A., Aldezabal A., Olano J.M., Loidi J. and Escudero A. 2013. Intensification of domestic  
545 ungulate grazing delays secondary forest succession: evidence from enclosure plots. *Journal of*  
546 *Vegetation Science* 24: 320-331.

547 Lasky J.R. and Keitt T.H. 2012. The Effect of Spatial Structure of Pasture Tree Cover on Avian Frugivores  
548 in Eastern Amazonia. *Biotropica* 44: 489-497.

549 Martínez-Duro E., Ferrandis P., Escudero A., Luzuriaga A.L. and Herranz J.M. 2010. Secondary old-field  
550 succession in an ecosystem with restrictive soils: does time from abandonment matter? *Applied*  
551 *Vegetation Science* 13: 234-248.

552 Martínez D. and García D. 2015. Changes in the fruiting landscape relax restrictions on  
553 endozoochorous tree dispersal into deforested lands. *Applied Vegetation Science* 18: 197-208.

554 Massa B. and La Mantia T. 2007. Forestry, pasture, agriculture and fauna correlated to recent changes  
555 in Sicily. *Forest@ - Rivista di Selvicoltura ed Ecologia Forestale*: 418-438.

556 Méndez M., García D., Maestre F.T. and Escudero A. 2008. More Ecology is Needed to Restore  
557 Mediterranean Ecosystems: A Reply to Valladares and Gianoli. *Restoration Ecology* 16: 210-216.

558 Navarro-González I., Pérez-Luque A.J., Bonet F.J. and Zamora R. 2013. The weight of the past: land-use  
559 legacies and recolonization of pine plantations by oak trees. *Ecological Applications* 23: 1267-1276.

560 Ne'eman G. and Izhaki I. 1996. Colonization in an abandoned East-Mediterranean vineyard. *Journal of*  
561 *Vegetation Science* 7: 465-472.

562 Novara A., Gristina L., Sala G., Galati A., Crescimanno M., Cerdà A., Badalamenti E. and La Mantia T.  
563 2017. Agricultural land abandonment in Mediterranean environment provides ecosystem services via  
564 soil carbon sequestration. *Science of the Total Environment* 576: 420-429.

565 Olff H., Vera F.W.M., Bokdam J., Bakker E.S., Gleichman J.M., de Maeyer K. and Smit R. 1999. Shifting  
566 Mosaics in Grazed Woodlands Driven by the Alternation of Plant Facilitation and Competition. *Plant*  
567 *Biology* 1: 127-137.

568 Pausas J.G., Bonet A., Maestre F.T. and Climent A. 2006. The role of the perch effect on the nucleation  
569 process in Mediterranean semi-arid oldfields. *Acta Oecologica* 29: 346-352.

570 Pausas J.G. and Millán M.M. 2019. Greening and Browning in a Climate Change Hotspot: The  
571 Mediterranean Basin. *Bioscience*: *biy157-biy157*.

572 Perry J.N. and Dixon P.M. 2002. A new method to measure spatial association for ecological count  
573 data. *Ecoscience* 9: 133-141.

574 Perry J.N., Winder L., Holland J.M. and Alston R.D. 1999. Red–blue plots for detecting clusters in count  
575 data. *Ecology Letters* 2: 106-113.

576 Plieninger T., Hui C., Gaertner M. and Huntsinger L. 2014. The Impact of Land Abandonment on Species  
577 Richness and Abundance in the Mediterranean Basin: A Meta-Analysis. *PLOS ONE* 9: e98355.

578 Pueyo Y. and Begueria S. 2007. Modelling the rate of secondary succession after farmland  
579 abandonment in a Mediterranean mountain area. *Landscape and Urban Planning* 83: 245-254.

580 QGIS Development Team. 2016. QGIS Geographic Information System. Open Source Geospatial  
581 Foundation Project. <http://qgis.osgeo.org>

582 Quero J.L., Herrero A. and Zamora R. 2011. Linking stochasticity to determinism of woody plant  
583 recruitment in a mosaic landscape: A spatially explicit approach. *Basic and Applied Ecology* 12: 161-  
584 171.

585 Raimondi S., Dazzi, C., Cirrito, V. 1983. Modello di studio integrato del territorio (Ficuzza-Palermo),  
586 nota n.5. I suoli. *Quaderni di Agronomia* 10: 89-131.

587 Rivas-Martínez S. 2008. Global bioclimatics (Clasificación bioclimática de la Tierra) (versión 01-12-2008).  
588 [www.globalbioclimatics.org](http://www.globalbioclimatics.org), [www.globalbioclimatics.org](http://www.globalbioclimatics.org).

589 Seifan M. and Kadmon R. 2006. Indirect effects of cattle grazing on shrub spatial pattern in a  
590 mediterranean scrub community. *Basic and Applied Ecology* 7: 496-506.

591 Sluiter R. and de Jong S.M. 2007. Spatial patterns of Mediterranean land abandonment and related  
592 land cover transitions. *Landscape Ecology* 22: 559-576.

593 Ver Hoef J.M., Peterson E.E., Hooten M.B., Hanks E.M. and Fortin M.-J. 2018. Spatial autoregressive  
594 models for statistical inference from ecological data. *Ecological Monographs* 88: 36-59.

595

596

597

598

599

600

601 Additional information can be found in the online version of this article:

602 Online appendix S1 - Details of the procedure for images overlay and vegetation mapping

603 Online appendix S2 - Example of the main steps to classify the vegetation cover

604 Online appendix S3 - Aerial image of 1955 showing the high level of deforestation in the three plots.

605 Online appendix S4 – Woodlands, shrublands and isolated trees, shrubs and small nucleation (ITSN)  
606 natural regeneration woody cover (hectares) at each plot in 1992 and 2016.

607 Online appendix S5 – Comparison between non spatial OLS, SARlag and SARerr regressions.

608

609

610

611 **Table 1.** Summary of SADIE analysis. Index of aggregation (*Ia*) and spatial association index (*Xp*) of  
 612 the 1992 woody cover and 2016 natural regeneration woody cover, and the index of aggregation of the  
 613 proportional expansion (PE) of natural regeneration woody cover in the three study plots (\*\**p* <  
 614 0.001, \*\* *p* = 0.003).

PLOT	<i>Ia</i>		<i>Xp</i>	<i>Ia</i>
	1992	2016	1992x2016	PE
1	5.69***	5.89***	0.89***	4.25***
2	4.42***	4.38***	0.65***	3.91***
3	5.72***	5.19***	0.79***	2.76**

615

616 **Table 2.** Summary of the results of the SARerr model in the three study plots with the pseudo-R<sup>2</sup>  
 617 showing model variance explanation of the proportional expansion of natural regeneration woody cover.

Predictor	Coefficient	Std. error	<i>z</i>	<i>p</i>	
					Constant
Past woody cover	0.124	0.028	4.479	< 0.001	
PLOT 1 R <sup>2</sup> = 0.61	Distance continuous	-0.004	0.030	-0.139	0.889
	Distance woody patch	-0.051	0.028	-1.825	0.068
	Cover type	0.019	0.016	1.142	0.254
	Lambda	0.345	0.117	2.947	0.003
PLOT 2 R <sup>2</sup> = 0.63	Constant	0.612	0.067	9.132	< 0.001
	Past woody cover	0.077	0.019	4.138	< 0.001
	Distance continuous	-0.037	0.048	-0.780	0.436
	Distance woody patch	-0.068	0.020	-3.376	0.001
	Cover type	-0.008	0.016	-0.516	0.606
	Lambda	0.800	0.082	9.708	< 0.001
PLOT 3 R <sup>2</sup> = 0.24	Constant	0.485	0.053	9.080	< 0.001
	Past woody cover	0.054	0.039	1.376	0.169
	Distance continuous	-0.008	0.037	-0.209	0.835
	Distance woody patch	-0.010	0.032	-0.314	0.753
	Cover type	0.018	0.023	0.761	0.447
	Lambda	0.445	0.109	4.101	< 0.001

618

619

620

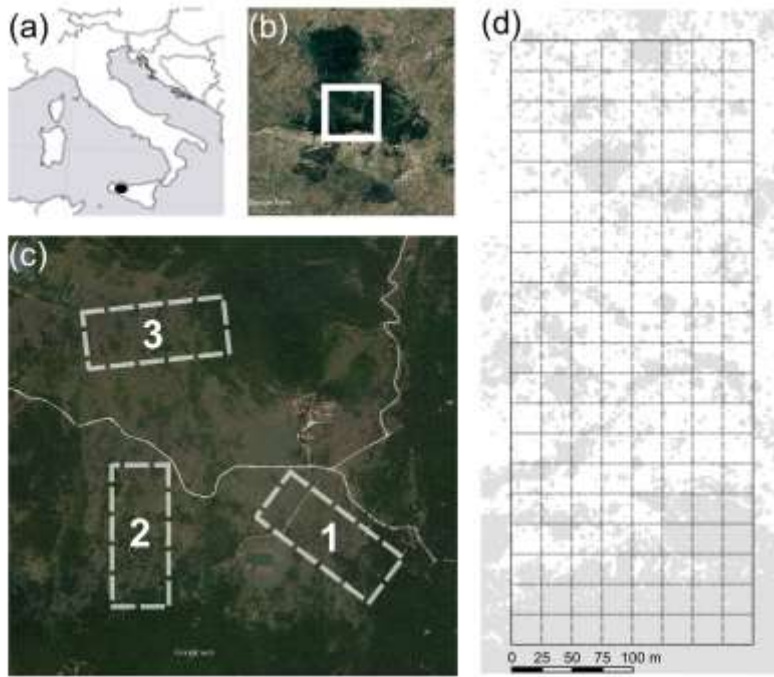
621 **Fig. 1** (a) Location of the Ficuzza Nature Reserve in Sicily (black spot). (b) Google Earth 2016 image  
622 showing the Ficuzza forest remnant and location of Alpe Cucco inside the reserve (white square). (c)  
623 Google Earth 2016 image with the three 500 x 200 m study plots established in the Alpe Cucco  
624 woodland pasture, covering the gradient from continuous forest to pastureland. (d) Example of the 160  
625 (625m<sup>2</sup>) subplot grids that was delimited inside each plot over the 2016 vegetation cover (light gray  
626 area)

627  
628 **Fig. 2** Average ( $\pm$ SE) subplot values of proportional expansion (PE) of isolated trees, shrubs and small  
629 nucleation (ITSN), shrubland and woodland patches in plots 1, 2 and 3 from 1992 to 2016

630  
631 **Fig. 3** Contour maps showing the SADIE aggregation indexes of the 1992 woody cover, 2016 natural  
632 regeneration woody cover and the natural regeneration proportional expansion (PE) for the three study  
633 plots. The legend shows the specific subplot aggregation index  $v_i$  and  $v_j$  value ranges

634  
635 **Fig. 4** The relationship between 1992 past woody cover (m<sup>2</sup>) and proportional expansion of natural  
636 regeneration woody cover in plots 1, 2 and 3 expressed in a simple linear regression. Each dot  
637 represents a different subplot within the plot

638  
639  
640  
641  
642  
643  
644  
645  
646  
647  
648



649

650 Figure 1.

651

652

653

654

655

656

657

658

659

660

661

662

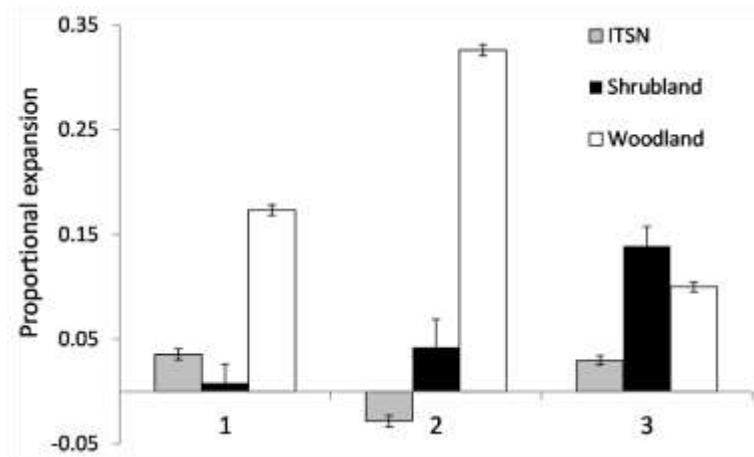
663

664

665

666

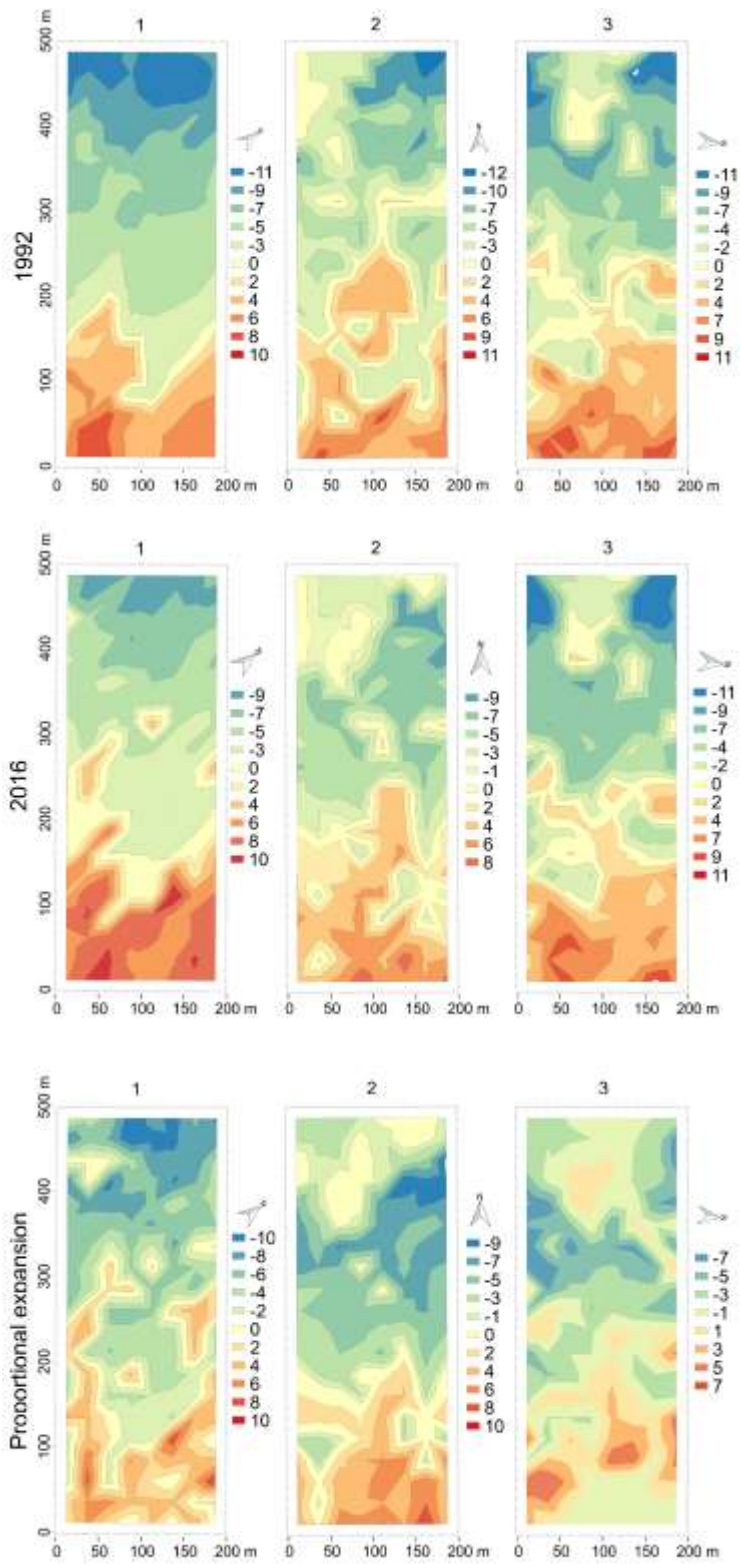
667



668

669 Figure 2.





670

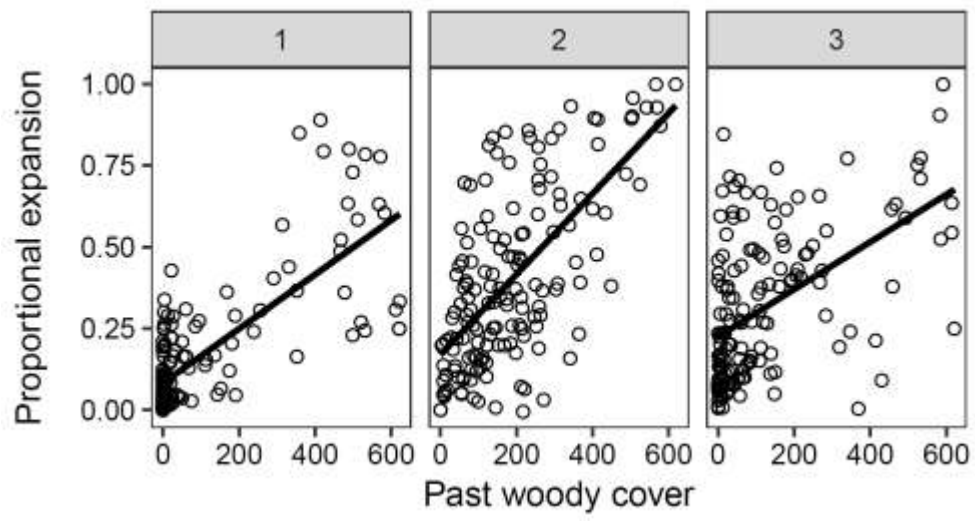
671 Figure 3.

672

673

674

675



676

677 Figure 4.