



7

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

Rafael da Silveira Bueno · Daniel García · Mauro Galetti · Tommaso La Mantia

Received: 29 September 2019 / Accepted: 22 January 2020
© Springer Nature B.V. 2020

Abstract Vegetation natural regeneration after agricultural abandonment is changing the landscape patterns in many areas worldwide. However, the expansion rate, spatio-temporal dynamics, and the role of past vegetation cover in shaping such patterns are still barely quantified in fine and meso scales. Here, we aim to quantify the expansion rate and assess the spatio-temporal patterns and the effects of past cover on natural woody vegetation cover increase. We sampled woodland and shrubland cover from 1992 to 2016 in 30 ha in a formerly managed pastureland in Sicily, Italy. We combined field sampling, GIS tools, and spatial analysis to assess the spatial structure

dynamics and test the effects of past cover amount and type and distance from forest or nearest woody patch on the proportional expansion of natural regeneration. After 24 years, woody cover increased 68%, despite the aggregated spatial structure in 1992 remaining almost unchanged in 2016. The past vegetation cover was the best predictor of woody vegetation expansion in two out of three plots. Distance to continuous forest and to the nearest woody patch, as well as cover type, was not relevant. Our study highlights the importance of fine- and meso-scale studies to reveal both the deterministic and stochastic facet of woody vegetation dynamics. Natural regeneration may strongly change landscape patterns even under constant herbivory pressure and long-term deforestation. The detection of cold and hotspots of regeneration provide an important prompt for the design of restoration programs and landscape management.

Keywords Landscape pattern · Natural regeneration · Scale · Spatial regression · Vegetation dynamics

Introduction

In the Mediterranean region, human land use has altered the cover, composition and spatial patterns of natural vegetation over millennia, in many cases

Communicated by James D. A. Millington.

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s11258-020-01006-3>) contains supplementary material, which is available to authorized users.

R. da Silveira Bueno (✉) · T. La Mantia
Dipartimento di Scienze Agrarie, Alimentari e Forestali,
Università degli Studi di Palermo (UNIPA), Palermo,
Italy
e-mail: rafael.dasilveirabueno@unipa.it

R. da Silveira Bueno · M. Galetti
Departamento de Ecologia, Universidade Estadual
Paulista (UNESP), São Paulo, Brazil

D. García
Departamento de Biología de Organismos y Sistemas –
UMIB, University of Oviedo, Oviedo, Spain

Author Proof

46 favoring annual and perennial herbaceous vegetation
 47 over woody vegetation (Pausas and Millán 2019;
 48 Plieninger et al. 2014). However, due to the current
 49 trend of land abandonment in rural areas, the natural
 50 recovery of woody vegetation on deforested land
 51 through secondary succession is highly expected,
 52 although frequently influenced by concomitant
 53 changes in major disturbance regimes, such as fire
 54 and herbivore pressure (Amici et al. 2013; Falcucci
 55 et al. 2007; Massa and La Mantia 2007). A process of
 56 succession such as this has long been described in
 57 floristic and phytosociological terms (e.g., Debussche
 58 et al. 1982; Ne'eman and Izhaki 1996), but the
 59 intrinsic spatial dynamics of woody vegetation over
 60 time and the mechanisms underpinning those dynam-
 61 ics are still poorly understood (Allen et al. 2016;
 62 Méndez et al. 2008; Quero et al. 2011). Even basic
 63 questions, such as how intense in magnitude and how
 64 fast woody vegetation recovery can be, still remain
 65 unsatisfactorily answered for mesic woodlands (but
 66 see Abadie et al. 2018; Álvarez-Martínez et al. 2014).
 67 Studies have focused mainly on analysis in extreme
 68 environments, such as semi-arid or mountain areas
 69 (Alodos et al. 2004; Bonet and Pausas 2004; Martínez-
 70 Duro et al. 2010; Pueyo and Begueria 2007) or on
 71 herbaceous or shrub communities (Bashan and Bar-
 72 Massada 2017; Carmel and Kadmon 1999; La Mantia
 73 et al. 2008; Ne'eman and Izhaki 1996). Similarly, little
 74 attention has been devoted to the spatial structure
 75 acquired by woody vegetation during succession,
 76 whether aggregated or random (Carmel et al. 2001).
 77 This is a relevant gap in knowledge given that spatial
 78 patterns result from, and, therefore, may be informa-
 79 tive of, cumulative ecological processes involving
 80 both responses to abiotic conditions and, especially,
 81 interspecific interactions (Carmel and Flather 2004;
 82 García et al. 2011; Keitt 2003). This spatio-temporal
 83 pattern analysis has a number of applications in
 84 landscape management. For example, the identifica-
 85 tion of those areas with greater potential for passive
 86 restoration (i.e., vegetation expansion through natural
 87 regeneration) may optimize resource use for active
 88 restoration (e.g., seedling plantation), directing efforts
 89 towards areas with lower recovery potential or regen-
 90 eration cold spots (Berdugo et al. 2017; Carmel et al.
 91 ^{AQ1}2001; Holl et al. 2018).

92 Abiotic factors such as climate, topography and soil
 93 may influence vegetation expansion and induce non-
 94 random spatial structures even on a small scale

(Gallego Fernández et al. 2004; García et al. 2014; 95
 Pueyo and Begueria 2007), although abiotic influence 96
 on some tolerant species may be less significant 97
 (Bacaro et al. 2008; Getzin et al. 2008; Quero et al. 98
 2011). In such cases, intensity and type of past land 99
 use, the amount and distribution of past vegetation 100
 cover, and biotic mechanisms become the main 101
 interrelated drivers of vegetation expansion, defining 102
 spatial resilience in a determined site (Allen et al. 103
 2016; Carmel and Flather 2004; Holl et al. 2018). 104
 Vegetative growth (e.g., canopy expansion and clonal 105
 reproduction), and facilitation (e.g., when a small 106
 plant enables the recruitment of a larger one) are 107
 inherently dependent upon past cover (Bakker et al. 108
 2004; Garcia and Obeso 2003). In turn, the process of 109
 seed dispersal in woody plants, which in many 110
 ecosystems such as tropical forests or in the Mediter- 111
 ranean is highly dependent upon animals (i.e., zoo- 112
 chory), may shape the spatial structure of woody 113
 recovery in different ways. On the one hand, most 114
 seeds are deposited at short distances from their 115
 source, thus, most recruitment and vegetation expan- 116
 sion is expected near source (González-Varo et al. 117
 2017; Martínez and García 2015). On the other hand, 118
 depending on the degree of redundancy or comple- 119
 mentarity of the dispersal vectors, dispersed seeds may 120
 eventually reach greater distances but might be 121
 conditioned by the existing woody cover in different 122
 levels (Bueno et al. 2013; Garcia et al. 2011; Jordano 123
 2017). Notwithstanding the above, the spatial template 124
 generated by seed dispersal is often subject to 125
 subsequent modification by recruitment losses due to 126
 small-scale disturbances, such as seed predation and 127
 herbivory, or large-scale disturbances, such as fire 128
 (Baeza et al. 2007; Carmel and Kadmon 1999; 129
 Gómez-Aparicio 2008). Cover type (i.e., shrubland 130
 or woodland), therefore, may affect seed dispersal and 131
 recruitment. Shrubs may attract seed dispersers and 132
 seed predators, and may compete with or facilitate 133
 other plants differently than higher trees, the same 134
 being true for patches or isolated individuals (Andivia 135
 et al. 2017; Lasky and Keitt 2012; Olff et al. 1999). 136
 Consequently, studies that quantify expansion rates 137
 and spatial patterns of woody vegetation over time and 138
 relate them to pre-existing vegetation cover are 139
 necessary in order to reveal the footprints that the 140
 ecological processes driving secondary succession 141
 leave behind (Chuang et al. 2018; García et al. 2014; 142
 Holl et al. 2018). Furthermore, these studies may 143

144 contribute to disentangle the role of spatial effects
145 (e.g., spatial autocorrelation and random dispersal)
146 affecting vegetation expansion and dynamics, and can
147 enhance the effectiveness of management plans of
148 protected areas and the recovery of degraded sites (Hu
149 et al. 2012; Méndez et al. 2008; Quero et al. 2011).

150 Here we combined current field sampling, GIS-
151 based interpretation of sequential, high-resolution
152 images (satellite and aerial photographs) and spatially
153 explicit analysis to evaluate magnitude, spatial pat-
154 terns and potential drivers of expansion (i.e., increase)
155 relating to woody vegetation cover over 24 years in a
156 Mediterranean woodland pasture. We sought to
157 answer the following questions: How fast, in terms
158 of the magnitude of expansion over time, does woody
159 vegetation recover in pastureland? How dynamic is
160 the spatial structure along such expansion? Are current
161 cover and expansion spatially correlated with the
162 amount of past woody vegetation cover? And to what
163 extent might distance to the continuous forest and to
164 the nearest woody patch affect cover expansion? Our
165 study presents an appropriate system in order to seek
166 answers to those questions as it combines relatively
167 homogeneous abiotic conditions with an absence of
168 fire, providing a clearer quantification of woody
169 vegetation recovery potential and interpretation of
170 vegetation dynamics due to major biotic processes,
171 such as zoochory and herbivory.

172 Methods

173 Study site

174 The study was conducted at Alpe Cucco (37° 52' and
175 13° 24'), a site located in the center of the “Bosco della
176 Ficuzza, Rocca Busambra, Bosco del Cappelliere e
177 Gorgo del Drago” nature reserve (hereafter FBCD),
178 which is a 7397 ha protected area composing the last,
179 large remnant of forest in western Sicily (Badalamenti
180 et al. 2017; Gianguzzi and La Mantia 2004). The site is
181 a 160 ha woodland pasture comprising seasonal
182 pastures intermingled with woody vegetation, sur-
183 rounded by forest patches (Fig. 1). The local climate is
184 mesic Mediterranean, with an average rainfall of
185 850 mm concentrated mostly in autumn and winter,
186 and mean annual temperatures of 14.3 °C, with
187 average temperatures of 9.4 °C in the coldest months

(January and February) increasing to an average of 188
23.5 °C in the hottest months (July and August). 189

190 Vegetation in Alpe Cucco corresponds to the Meso-
191 Mediterranean type, based on a classification of
192 altitudinal belts (Rivas-Martínez 2008). Surrounding
193 forest patches are mostly composed of holm oak
194 (*Quercus ilex*), downy oak (*Quercus pubescens*) and,
195 to a lesser extent, maple (*Acer campestre*) and manna
196 ash (*Fraxinus ornus*) (Badalamenti et al. 2017;
197 Gianguzzi and La Mantia 2004). The woodland
198 pasture is dominated by seasonal grasses and forbs
199 (see Bianchetto et al. 2015 for a species list) with
200 isolated shrubs and trees, and varied-sized patches of
201 woody vegetation comprising mostly six fleshy-
202 fruited species (*Pyrus amygdaliformis*, *Crataegus*
203 *monogyna*, *Crataegus laciniata*, *Rubus ulmifolius*,
204 *Rosa canina* and *Prunus spinosa*) and, to a lesser
205 degree, one dry-fruited shrub (*Calicotome infesta*), the
206 two oaks and maple (Gianguzzi and La Mantia 2004).
207 The site was subject to a reforestation program during
208 the decade 1970–1980; individuals of *Fraxinus*
209 *angustifolia* and *Pinus halepensis*, two species previ-
210 ously absent in the pasture, were planted in scattered
211 patches and isolated individuals in a part of the Alpe
212 Cucco area (Gianguzzi and La Mantia 2004). Exten-
213 sive cattle (cow) raising has a long history in Alpe
214 Cucco, and is still present nowadays, whereas an
215 active pastureland management program including
216 irrigation, plowing, and seeding was developed during
217 the period 1960–1990. (A.S.F.D 1959; Bianchetto
218 et al. 2015).

219 Sampling design

220 In September 2016, we established three
221 500 × 200 m plots, each divided into 160 subplots
222 of 25 × 25 m (sampling unit) covering a gradient
223 from continuous forest to woodland pasture (Fig. 1).
224 The minimum and maximum distances between plot
225 edges were 300 m and 510 m (700 m from the
226 centroid). All plots extended over relatively homoge-
227 neous flat areas (average slope 15%) with northern
228 exposure. Plot 1 has an average altitude of 975 m
229 (± 17 SD), plot 2—1004 m (± 36) and plot 3—
230 901 m (± 9), with maximum altitudinal difference
231 between subplots of 190 m (880 to 1070 m a.s.l.) All
232 plots are classified as having deep soils (> 100 cm),
233 sub-alkaline, clay-dominated vertic haploxeralfs (Rai-
234 mondi 1983) and share mostly the same plant species.

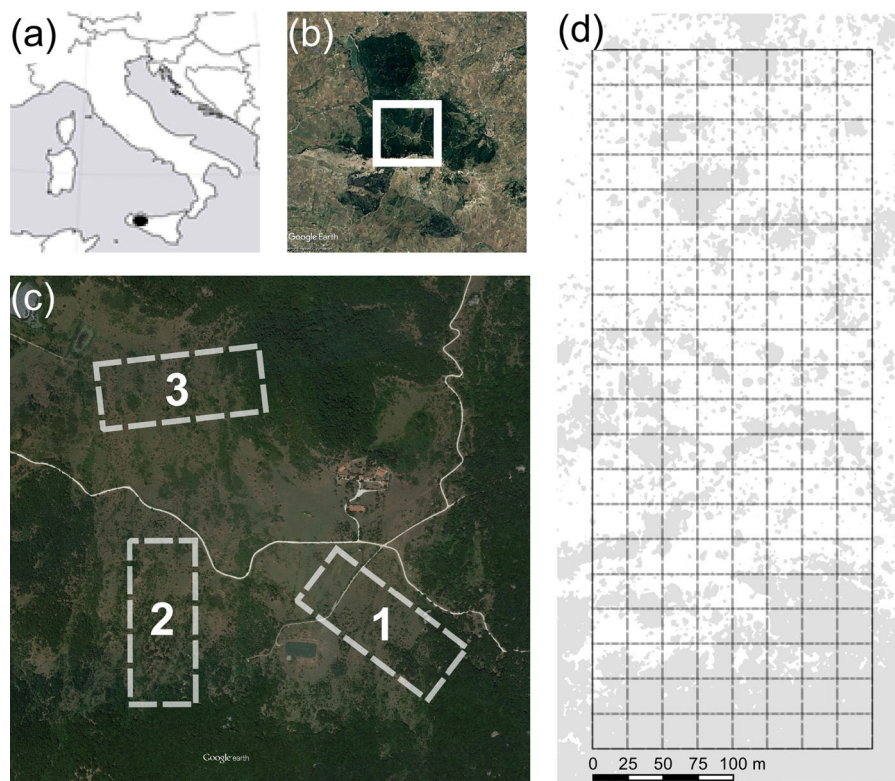


Fig. 1 **a** Location of the Ficuzza Reserve in Sicily (black spot). **b** Google Earth 2016 image showing the Ficuzza forest remnant and location of Alpe Cucco inside the reserve (white square). **c** Google Earth 2016 image with the three 500 × 200 m study

plots established in the Alpe Cucco woodland pasture, covering the gradient from continuous forest to pastureland. **d** Example of the 160 (625 m²) subplot grids that was delimited inside each plot over the 2016 vegetation cover (light gray area)

235 For example, the two most abundant tree species,
 236 *P. amygdaliformis* and *C. monogyna* have established
 237 individuals scattered across 76% and 55% of the
 238 subplots (Bianchetto et al. 2015; Bueno unpub. data).
 239 Consequently, we assume that our plots are rather
 240 uniform regarding key environmental features such as
 241 precipitation, exposition, soil and temperature.

242 Vegetation mapping and classification

243 To measure the spatial pattern of woody vegetation
 244 cover over the years, we contrasted aerial photogra-
 245 phies from the year 1992 (scale 1:29,000, 1 pixel =
 246 1 m) and satellite images from 2016 (Google Earth,
 247 RGB bands, 1 pixel = 0.13 m, rescaled to 1 m), in a
 248 time lapse of 24 years, incorporated into a Geographi-
 249 cal Information System (GIS) platform belonging to
 250 our study system (see Online Appendix S1 for details
 251 of woody cover extraction procedure). Although older
 252 images were available, the 1992 images were the

oldest following cessation of pasture management,
 representing a conservative date to address vegetation
 recovery through secondary succession without fur-
 further large-scale, human-provoked disturbance.

We sought to differentiate three types of woody
 cover in aerial views: woodland patches, shrubland
 patches, and isolated trees, shrubs and small nuclea-
 tion patches of trees or shrubs (hereafter ITSN). In
 the 2016 extracted cover, woodland patches
 (> 50 m²) were classified by contrasting with the
 original high-resolution image as well as by the
 heterogeneous dark gray texture which produced
 conspicuous black shadows (field checked as > 2 m
 in height) (see Online Appendix S1 and S2 for
 details). The species composing this vegetation type
 were *Quercus pubescens*, *Quercus ilex*, *Acer cam-
 pestris*, *Pyrus amygdaliformis*, *Crataegus monogyna*,
Crataegus laciniata, together with *Fraxinus angus-
 tifolia* and *Pinus halepensis*, two species naturally
 absent from the study area and that dominate the

253
 254
 255
 256
 257
 258
 259
 260
 261
 262
 263
 264
 265
 266
 267
 268
 269
 270
 271
 272

273 canopy cover wherever planted. Shrubland patches
 274 were defined as with an area of $> 50 \text{ m}^2$, homoge-
 275 neous texture with a lighter-gray pattern compared to
 276 woodlands and which produced no conspicuous
 277 shadow ($< 2 \text{ m}$ tall), with or without trees. The
 278 species composing this cover type were *Rubus*
 279 *ulmifolius*, *Prunus spinosa*, *Rosa canina* and *Cali-*
 280 *cotome infesta* together with juveniles of *P. amyg-*
 281 *daliformis* and *C. monogyna*. The remaining woody
 282 cover with a surface of $< 50 \text{ m}^2$ was classified as
 283 ITSN. All the woody vegetation cover extracted
 284 from the images was added as a new layer
 285 (polygons) to the GIS platform (Online Appendix
 286 S2). As the digital pixel value did not enable us to
 287 differentiate clearly between woodland and shrub-
 288 land boundaries which occurred within the same
 289 polygon, we divided the 2016 and 1992 woody cover
 290 using photointerpretation, separating the different
 291 cover types into distinct polygons (Online Appendix
 292 S2). We had no reasons to correct the woody cover
 293 extraction output (i.e., no woody cover signed over
 294 the grassland or vice versa), but in order to validate
 295 cover-type classification and its boundaries, all
 296 polygons were numbered and checked in the field,
 297 where minor differences were corrected (accu-
 298 racy $> 98\%$); the subplot woody cover surface (m^2)
 299 of the different vegetation types was subsequently
 300 obtained (Online Appendix S2). Continuous forest,
 301 mainly comprising *Quercus ilex* and *Quercus pub-*
 302 *escens*, was defined as a single woodland patch
 303 which contained the dense continuous woodland
 304 remnant surrounding Alpe Cucco. Distance predic-
 305 tors were calculated from the centroid of each
 306 subplot up to the nearest border of the continuous
 307 forest and to the nearest woodland patch (Online
 308 Appendix S2). According to the oldest aerial image
 309 available (1955), most plot surface was already
 310 deforested at that time (Online Appendix S3). As we
 311 were particularly interested in the expansion of
 312 woody cover due to natural regeneration, we differ-
 313 entiated the cover attributable to natural processes
 314 from that attributable to human-made plantation (see
 315 Pueyo and Begueria 2007 for a similar procedure;
 316 Appendix S2). Woody cover extraction, classifica-
 317 tion and figures were done using software QGIS
 318 (QGIS Development Team 2016).

Spatial structure of the woody vegetation cover 319
 over time 320

We were interested in characterize the degree of 321
 stability of the spatial structure of woody vegetation 322
 cover from 1992 to 2016. For this purpose we used the 323
 Spatial Analysis by Distance Index—SADIE (see 324
 Perry et al. 1999). SADIE uses a transportation 325
 algorithm to estimate the distance to regularity (D), 326
 that represents the minimum distances that the values 327
 of each spatially located variable (in our case woody 328
 cover in each subplot) need to move to reach a regular 329
 spatial distribution across all subplots, based on the 330
 concept of donors and receivers (Perry et al. 1999). 331
 The ratio between D and its average values, estimated 332
 through randomization, generate the global aggrega- 333
 tion index (I_a) as well as its significance values at 95% 334
 confidence intervals (p). An index around 1 indicate a 335
 randomly distributed woody cover, lower than 1 336
 indicate regular distribution and higher than 1 repre- 337
 sent an aggregated or patchy pattern. The I_a is 338
 composed by specific subplot clustering values (v), 339
 showing the magnitude of the contribution of each 340
 sampling unit to the overall cluster values and 341
 indicating if the cover value of a subplot is member 342
 of an above average patch (v_i) or if a member of below 343
 average gap (v_j) (Perry and Dixon 2002; Perry et al. 344
 1999). We calculated the SADIE aggregation indexes 345
 of the 1992 and 2016 woody vegetation cover 346
 separately (considering only the natural vegetation in 347
 2016). 348

SADIE methodology also enabled us to quantify 349
 the spatial association index (X_p) of woody cover, 350
 derived from the mean values of 1992 and 2016 woody 351
 cover in the same subplot (i.e., correlation between the 352
 v_i and v_j indexes of both periods) (Perry and Dixon 353
 2002). The index range from -1 to 1 and is significant 354
 if $p < 0.05$, where a positive association means that 355
 the vegetation cover spatial distribution remained 356
 stable from 1992 to 2016 (both if a woody patch or a 357
 grassland gap), while a negative value means a 358
 mismatch of cover values along the 24 years (e.g., a 359
 grassland occupied by woody vegetation). 360

The next step was to exclude the planted cover to 361
 obtain values for proportional expansion of the natural 362
 regeneration cover from 1992 to 2016 (hereafter PE), 363
 calculated with the formula ($2016 \text{ natural regeneration}$ 364
 $\text{cover} - 1992 \text{ cover}) / (625 - 1992 \text{ cover})$. We 365
 selected such relative variable instead of the amount 366

of increase to avoid the geometrical constriction of the quadratic relationship between available space and maximum cover increase. Thus, our PE represents the magnitude of cover expansion within each subplot in each 1 m² unit, enabling the comparison of plots with different past covers independently from the absolute quantity of past cover within the subplot. We then performed another SADIE analysis to obtain the spatial structure (*Ia*, *vi* and *vj*) of PE. For this SADIE analysis, we excluded those subplots with full woody vegetation cover in 1992 and, consequently, zero expansion due to lack of space; there then remained 155 subplots in plot 1, 160 in plot 2, and 152 in plot 3. SADIE indexes are continuous variables (Perry and Dixon 2002), thus we incorporated the *vi* and *vj* indexes of 1992 and 2016 cover, and those of PE into bi-dimensional contour maps to obtain a more comprehensive view of the spatial pattern structure and to visualize coldspots (i.e., areas with zero or low cover increase) and hotspots (i.e., areas with high cover increase). Sadie aggregation indexes were obtained with SadieShell 2.0 and the spatial association was calculated with N_AShell 1.0 (Perry et al. 1999). Contour maps were prepared using the plugin contour of the software QGIS (QGIS Development Team 2016).

393 Factors affecting the expansion of woody 394 vegetation cover

We sought to assess whether the quantity, identity and spatial configuration of past woody vegetation cover affected its further expansion over the 24 years period of study. Thus, we used multiple regression models, including the values of PE at the subplot level as a response variable and the amount of woody vegetation cover, distance to the continuous forest and distance to the nearest woodland in 1992 as continuous predictor variables. We also incorporated, as a qualitative predictor, the cover type in the 1992 subplot, classified as 0 if there was no cover, 1 for ITSN, 2 for shrubland, 3 for mixed cover (2 or more types) and 4 for woodlands). Cover type 1, 2 and 4 were defined if reaching > 70%, otherwise was mixed. We excluded the subplots with full cover in 1992 and those with negative PE values (i.e., entreatment of woody vegetation cover) from the analysis, resulting in 145 subplots in plot 1, 152 in plot 2 and 152 in plot 3. PE was square-root transformed to achieve normality and

reduce heteroscedasticity. Before running regressions we tested for multicollinearity among predictors using the variance inflation factor (mean = 2.73, highest = 4.11) and the three continuous predictors (amount of woody vegetation cover, distance to the continuous forest and distance to the nearest woodland in 1992) were standardized prior to the analysis. The model was calibrated and validated by correlating the measured and predicted PE values across all plots, with $p < 0.001$ in all cases (Online Appendix S5).

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

459 **Results**

460 From 1992 to 2016, the overall woody vegetation
 461 cover in the three plots increased by 6822 ha (90.1%),
 462 rising from 7568 to 14,390 ha. Most of the increase
 463 was due to natural regeneration (5159 ha), including
 464 2849 ha of woodland, 2164 ha of shrubland and
 465 0146 ha of ITSN (Fig. 2, Online Appendix S4).
 466 However, proportionally (i.e., increase relative to
 467 initial cover), shrubland almost doubled in surface
 468 (94.9%), followed by woodland (67.1%) and ITSN
 469 (14.1%). Planted cover accounted for the remaining
 470 24.4% (1663 ha). We found no correlation between
 471 2016 planted cover and woody vegetation cover in
 472 1992 (Pearson $r = -0.01$, $p = 0.69$), suggesting that
 473 the development of planted cover occurred almost
 474 exclusively throughout the 24-year period. The three
 475 plots differed in the average proportional expansion of
 476 natural regeneration woody cover (ANOVA
 477 $F = 45.94$, $p < 0.001$) with contrasting variations in
 478 each cover-type contribution to expansion (Fig. 2).

479 Spatial structure of the woody vegetation cover
 480 over years

481 The SADIE I_a index indicated that global spatial
 482 structure of woody vegetation cover was significantly
 483 aggregated and remained stable over time (from 1992
 484 to 2016) (Table 1). Furthermore, the significant X_p
 485 index indicated a strong spatial correlation between v_i
 486 and v_j values in the same subplot over time, denoting a
 487 conservative, small-scale spatial trend in vegetation
 488 dynamics (i.e., few subplots members of a gap became

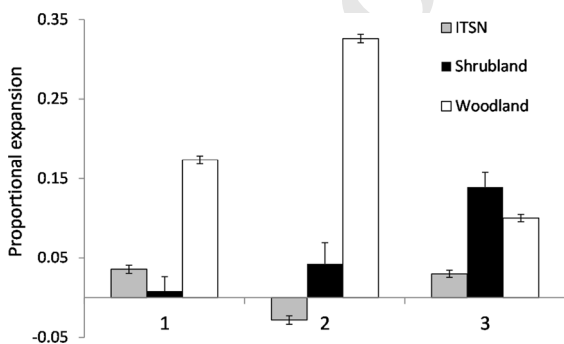


Fig. 2 Average (\pm SE) subplot values of proportional expansion (PE) of isolated trees, shrubs, and small nucleation (ITSN), shrubland, and woodland patches in plots 1, 2 and 3 from 1992 to 2016

Table 1 Summary of SADIE analysis

Plot	I_a		X_p	I_a PE
	1992	2016	1992 \times 2016	
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**

Index of aggregation (I_a) and spatial association index (X_p) of the 1992 woody cover and 2016 natural regeneration woody cover, and the index of aggregation of the proportional expansion (PE) of natural regeneration woody cover in the three study plots (*** $p < 0.001$, ** $p = 0.003$)

members of a patch or vice versa) (Table 1). The PE aggregation index also showed positive and significant values across plots, suggesting marked patchiness in the distribution of woody vegetation cover expansion within each plot, with no clear sign of broad, gradient-like spatial structure from the continuous forest towards open areas (Table 1; Fig. 3).

Factors affecting the expansion of woody vegetation cover

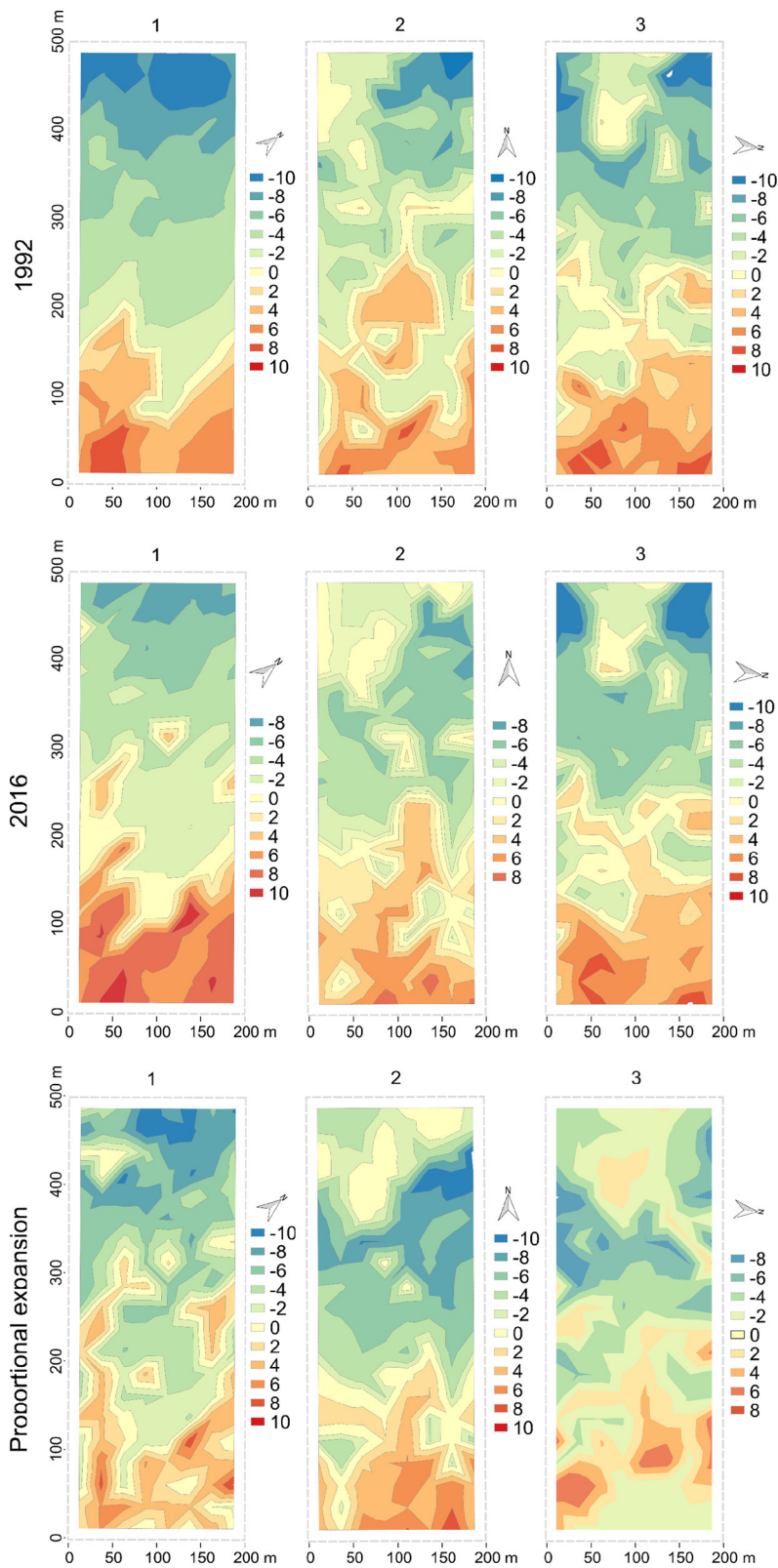
The SARerr model showed the best fit in comparison with SARlag models in all plots when assessing the effects of past cover, distance to continuous forest, distance to nearest woody patch and cover type on the proportional expansion of the natural regeneration of woody vegetation (Online Appendix S5)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

Discussion

In our study, we quantified the intensity of woody cover expansion and revealed, on the one hand, overall maintenance of the aggregated spatial pattern of

Author Proof

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



Author Proof

Table 2 Summary of the results of the SARerr model in the three study plots with the pseudo- R^2 showing model variance explanation of the proportional expansion of natural regeneration woody cover

	Predictor	Coefficient	Standard error	z	p
Plot 1 $R^2 = 0.61$	Constant	0.337	0.031	10.898	< 0.001
	Past woody cover	0.124	0.028	4.479	< 0.001
	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 $R^2 = 0.63$	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 $R^2 = 0.24$	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

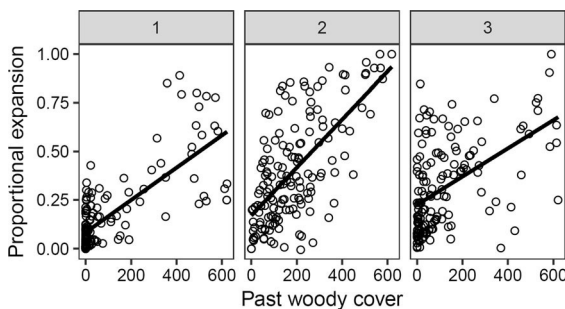


Fig. 4 The relationship between 1992 past woody cover (m^2) and proportional expansion of natural regeneration woody cover in plots 1, 2, and 3 expressed in a simple linear regression. Each dot represents a different subplot within the plot

519 woody vegetation cover over 24 years, even under
 520 strong expansion. On the other hand, we detected
 521 quantitative (i.e., cover expansion) and qualitative
 522 (i.e., cover type composing the expansion) differences
 523 even in closely located plots. The increase in natural
 524 woody vegetation found in our study would seem to be
 525 relatively high, considering the current structural
 526 complexity of varied-size woodland and shrubland
 527 patches, and the deforestation, anthropic use and
 528 herbivory pressure, at least over the last 80 years
 529 inside the plots (Bianchetto et al. 2015).

Woody vegetation natural regeneration

530

531 It has been demonstrated that livestock herbivory can
 532 slow down or even hamper woody vegetation recovery
 533 (Carmel and Kadmon 1999; La Mantia et al. 2013;
 534 Laskurain et al. 2013). No precise information on
 535 cattle density was available for our site, nor regarding
 536 the increasing population of fallow deer (*Dama dama*)
 537 (Bianchetto et al. 2015), thus limiting our interpreta-
 538 tions. However, judging by the observed recovery rate,
 539 no significant negative influence of herbivory in cover
 540 expansion seems to be occurring, at least over the past
 541 24 years. A similar outcome was also observed in
 542 other Mediterranean areas (e.g., Bashan and Bar-
 543 Massada 2017). Besides the magnitude of expansion,
 544 the quality of vegetation recovery in our study system
 545 also differed from other studies in the Mediterranean
 546 region. Bonet and Pausas (2004), for example, found
 547 an average woody vegetation cover increase of 26%
 548 after 60 years; however, less than 20% of that cover
 549 was composed of endozoochoric species, while La
 550 Mantia et al. (2008) found an increase of 57%,
 551 comprising mostly one dry-fruited species. On our
 552 site, the 68% natural regeneration woody cover
 553 increase was composed mainly of a mix of six
 554 zoochoric species (*Pyrus amygdaliformis*, *Crataegus*
 555 *laciniata* *Crataegus monogyna*, *Rubus ulmifolius*,

- 556 *Prunus spinosa*, *Rosa canina*) (R.S.Bueno unpub.
557 data).
- 558 Spatial structure of the woody vegetation cover
559 over years
- 560 Our SADIE analysis demonstrated that the woody
561 vegetation cover kept its highly spatially aggregated
562 pattern on both a landscape (plot) and a local (subplot)
563 scale throughout the 24 years, even when faced with
564 considerable expansion (Table 1). The maintenance of
565 aggregated patterns is the expected result of expansion
566 from previous cover (Bakker et al. 2004). In fact, past
567 woody cover positively influenced vegetation expansion
568 in plot 1 and 2 (Table 2; Fig. 4). In addition to the
569 effects of past cover, herbivory intensity may be one of
570 the factors not measured here that can influence
571 vegetation spatial configuration, although a range of
572 responses has been found so far (Adler et al. 2001;
573 Bashan and Bar-Massada 2017). Seifan and Kadmon
574 (2006), for example, found that cattle herbivory
575 changed the spatial pattern of a scrub community by
576 reducing the aggregation level (clumpiness), although
577 the cover increase was not affected by different levels
578 of herbivory intensity. In our study, we found that the
579 aggregated pattern remained unchanged, while cover
580 expansion varied among plots sharing the same
581 herbivory pressure (Fig. 2).
- 582 Influence of past cover, cover type and distance
583 to remnant vegetation
- 584 Grass cover and canopy closure (i.e., a proxy of woody
585 cover) were deemed to be the most relevant predictors
586 in tropical forest recovery (Holl et al. 2018), although
587 differential influences of past cover have been found
588 across Mediterranean-type ecosystems (Carmel and
589 Flather 2004). On our site, we found a differential
590 contribution of past cover at plot scale, once this
591 predictor was found to be non-significant in explaining
592 expansion in plot 3 (Table 2). This plot showed some
593 large patches resulting from the direct colonization of
594 open ground, far from any previous woody vegetation
595 cover, and this would explain the lack of effect of past
596 cover in the regression model, as well as the lowest
597 SADIE aggregation index. Another fact potentially
598 affecting the lack of effect of past cover on expansion
599 is that some types of early woody cover can them-
600 selves impede further development of ecological
601 succession (i.e., arrested succession) (Acácio et al.
602 2007). On our site, for example, a number of *R.*
603 *ulmifolius* patches remained almost unchanged over
604 the 24 years, and a few large, old trees had virtually no
605 vegetation increase in their surroundings. In the first
606 case, the absence of cover increase in bramble patches
607 may derive from a strong competitive effect (Fotelli
608 et al. 2001). In the case of isolated large trees, the lack
609 of structure for facilitating protection against her-
610 bivory, such as basal branching and protective spiny
611 leaves at the ground level (Garcia and Obeso 2003)
612 could explain the above pattern.
- 613 Contrary to our expectations, distance from the
614 continuous forest proved non-significant in predicting
615 vegetation expansion. Remnant forests usually act as a
616 source of propagules for the colonization of open
617 areas. Therefore, given the overall distance constraints
618 of seed dispersal, a decreasing rate of vegetation
619 expansion when moving away from the forest is
620 expected (García et al. 2014). Our sampling design,
621 with plots sharing similar configuration of continuous
622 forest (one side forest), should be effective to check
623 for distance effects by forcing a very large distance
624 gradient in sampling points without lateral influence.
625 However, on our study site, the continuous forest
626 comprised mostly oaks (*Q. pubescens* and *Q. ilex*),
627 while the majority of the mid-successional woody
628 plants species composing the bulk of cover increase
629 were located mostly in pastureland. For example, one
630 of the most important species in terms of cover
631 expansion (*P. amygdaliformis*) occurs at very low
632 density inside the forest and is dispersed almost
633 exclusively by mammals (Fedriani et al. 2010);
634 therefore, even the longest distances within plots (ca.
635 1400 m) can fall within the mammals seed dispersal
636 potential (González-Varo et al. 2017). Complementarily,
637 a recent study in Mediterranean has verified no
638 differences in seed arrival in old fields of species
639 dispersed by both birds and mammals up to 90 m from
640 the seed source (La Mantia et al. 2019). In addition,
641 higher fruit availability in woodland pasture compared
642 to continuous forest coupled with vegetation structural
643 complexity (i.e., presence of different perches and
644 woody patches) may influence the behavior of those
645 birds acting as seed dispersers, fostering movement
646 away from the forest and towards fruit-rich environ-
647 ments (La Mantia and Bueno 2016; Lasky and Keitt
648 2012). However, later in the process of secondary
649 succession, an increase in the influence of distance to

650 continuous forest in cover species composition is
651 expected, when the mid-successional species compos-
652 ing current expansion facilitate oak establishment in
653 woodland pasture (Alias et al. 2010; Amici et al.
654 2013).

655 Distance to woody patch, in turn, was found to
656 negatively affect the expansion of woody vegetation;
657 however, this pattern was only significant in plot 2. A
658 negative influence was expected established that
659 proximity to even small patches of woody vegetation
660 is a proxy for higher seed rain and consequent
661 recruitment (Martínez and García 2015; Navarro-
662 González et al. 2013). The initial configuration of
663 woody vegetation in plot 2, with many scattered, small
664 patches, would have strengthened this negative rela-
665 tionship. The lack of relationship in the other two plots
666 may derive, firstly, from a random distribution of
667 mammal dispersed species (e.g., *P. amygdaliformis*) at
668 this spatial scale. Secondly, the average distance range
669 between patches may be easily covered by birds,
670 resulting in a cover-cover directed seed dispersal (i.e.,
671 from a perch to another perch), with a consequent gap
672 in recruitment between close patches (García et al.
673 2011; Pausas et al. 2006). Refining the scale of the
674 study using smaller subplots should provide additional
675 information, although a species-specific differential
676 response of each plant is also expected.

677 Woody cover expansion was independent of the
678 type of patch composing the past cover, suggesting
679 that, in our system, small patches of isolated trees and
680 shrubs have the same potential to promote or prevent
681 expansion as larger patches of shrubland and wood-
682 land. Moreover, we also observed subplots free of
683 woody vegetation in 1992 occupied by woodland
684 patches in 2016. For example, most oak-dominated
685 woodland patches showed smaller expansion than
686 mixed shrubland patches, probably an outcome of
687 selective grazing and browsing (Carmel and Kadmon
688 1999; García and Obeso 2003). On our site, palatable,
689 late successional species (e.g., *Quercus sp.*) were
690 almost absent from the woody cover under expansion,
691 and mid-successional and herbivore-defended species
692 are actually those developing woodland. Autoregres-
693 sive parameters (λ) obtained in our models,
694 however, indicate that other factors not measured in
695 our analysis are influencing cover expansion, a similar
696 outcome was found also for species distribution (Hu
697 et al. 2012). This strong neutral effect corroborates the

importance of taking autocorrelation into considera- 698
tion in spatial analysis (Ver Hoef et al. 2018). 699

Large-scale approaches are necessary in order to 700
detect landscape and global patterns (Sluiter and de 701
Jong 2007). However, considering the similarities 702
(e.g., the aggregated spatial structure) and the differ- 703
ences (e.g., variation in the dominant cover type 704
composing expansion) in closely located plots which 705
share the same historical contingency, pool of species, 706
grazing pressure and environmental conditions, the 707
patterns found in our study highlight the complemen- 708
tarity of smaller scale investigations when interpreting 709
vegetation dynamics and recovery (Hu et al. 2012; 710
Quero et al. 2011). As an example, in an applied 711
perspective, this complementarity may refine the 712
calculation of ecosystem services, such as carbon 713
stock, it may improve the evaluation of scale-depen- 714
dent species richness patterns and, consequently, help 715
design more effective restoration programs (Chuang 716
et al. 2018; Méndez et al. 2008; Novara et al. 2017). 717
Finally, we demonstrate that in favorable conditions, 718
especially in the presence of remnant woody cover and 719
in the absence of fire, even a long history of 720
deforestation, land use and the presence of livestock 721
do not crush the potential for intense woody vegetation 722
expansion, even though previous cover tends to 723
“sequester” this potential for recovery. 724

Acknowledgements We thanks Giovanni Giardina for 725
sharing helpful information regarding the history of Ficuzza 726
and the Sicilian Dipartimento Regionale dello Sviluppo Rurale e 727
Territoriale for the logistical support. Funding: RSB received a 728
Ph.D. fellowship from the University of Palermo. Fieldwork and 729
TL were funded by Italian “Ministero dell’Istruzione 730
dell’Università e della Ricerca” (CARBOTREES— 731
201049EXTW). DG was supported by Spanish “Ministerio de 732
Economía y Empresa” (FEDER CGL2015-68963- C2-2-R) and 733
DG & MG were supported by CYTED program (Red Temática 734
418RT0555). 735

Author contributions RDSB, TLM and MG conceived the 736
study. RDSB and DG developed the sampling design, 737
methodology and the analytical framework, and interpreted 738
results. RDSB collected and analyzed the data and wrote the first 739
manuscript. DG revised the first manuscript and all authors 740
revised and improved the final version. 741

Compliance with ethical standards 743

Conflict of interest The authors declare that they have no 744
conflict of interest. 745

References

- 748 A.S.F.D, (1959) L'Azienda di Stato per le Foreste Demaniali.
749 Edizione A.B.E.T.E, Roma
- 750 Abadie J, Dupouey J-L, Avon C, Rochel X, Taton T, Bergès L
751 (2018) Forest recovery since 1860 in a Mediterranean
752 region: drivers and implications for land use and land cover
753 spatial distribution. *Landsc Ecol* 33:289–305
- 754 Acácio V, Holmgren M, Jansen PA, Schrotter O (2007) Multiple
755 recruitment limitation causes arrested succession in
756 Mediterranean Cork oak Systems. *Ecosystems*
757 10:1220–1230
- 758 Adler P, Raff D, Lauenroth W (2001) The effect of grazing on
759 the spatial heterogeneity of vegetation. *Oecologia*
760 128:465–479
- 761 Alias S, Bianchi L, Calamini G, Gregori E, Sioni S (2010) Shrub
762 facilitation of *Quercus ilex* and *Quercus pubescens*
763 regeneration in a wooded pasture in central Sardinia (Italy).
764 *iForest* 3(1):16–22
- 765 Allen CR, Angeler DG, Cumming GS, Folke C, Twidwell D,
766 Uden DR (2016) Quantifying spatial resilience. *J Appl*
767 *Ecol* 53:625–635
- 768 Alodos CL, Pueyo Y, Barrantes O, Escós J, Giner L, Robles AB
769 (2004) Variations in landscape patterns and vegetation
770 cover between 1957 and 1994 in a semiarid Mediterranean
771 ecosystem. *Landsc Ecol* 19:543–559
- 772 Álvarez-Martínez JM, Suárez-Seoane S, Stoorvogel JJ, de Luis
773 CE, Gilliam F (2014) Influence of land use and climate on
774 recent forest expansion: a case study in the Eurosiberian-
775 Mediterranean limit of north-west Spain. *J Ecol*
776 102:905–919
- 777 Amici V, Santi E, Filibeck G, Diekmann M, Geri F, Landi S,
778 Scoppola A, Chiarucci A, Vetaas O (2013) Influence of
779 secondary forest succession on plant diversity patterns in a
780 Mediterranean landscape. *J Biogeogr* 40:2335–2347
- 781 Andivia E, Villar-Salvador P, Tovar L, Rabasa S, Rey Benayas
782 JM (2017) Multiscale assessment of woody species
783 recruitment in Mediterranean shrublands: facilitation and
784 beyond. *J Veg Sci* 28:639–648
- 785 Anselin L, Syabri I, Kho Y (2006) GeoDa: an introduction to
786 spatial data analysis. *Geogr Anal* 38:5–22
- 787 Bacaro G, Rocchini D, Bonini I, Marignani M, Maccherini S,
788 Chiarucci A (2008) The role of regional and local scale
789 predictors for plant species richness in Mediterranean
790 forests. *Plant Biosyst* 142:630–642
- 791 Badalamenti E, La Mantia T, La Mantia G, Cairone A, La Mela
792 Veca D (2017) Living and dead aboveground biomass in
793 Mediterranean forests: evidence of old-growth traits in a
794 *Quercus pubescens* willd. s.l. stand. *Forests* 8(6):187
- 795 Baeza MJ, Valdecantos A, Alloza JA, Vallejo VR (2007)
796 Human disturbance and environmental factors as drivers of
797 long-term post-fire regeneration patterns in Mediterranean
798 forests. *J Veg Sci* 18:243–252
- 799 Bakker ES, Olff H, Vandenberghe C, De Maeyer K, Smit R,
800 Gleichman JM, Vera FWM (2004) Ecological anachro-
801 nisms in the recruitment of temperate light-demanding tree
802 species in wooded pastures. *J Appl Ecol* 41:571–582
- 803 Bashan D, Bar-Massada A (2017) Regeneration dynamics of
804 woody vegetation in a Mediterranean landscape under
different disturbance-based management treatments. *Appl*
805 *Veg Sci* 20:106–114
- Berdugo M, Kéfi S, Soliveres S, Maestre FT (2017) Plant spatial
806 patterns identify alternative ecosystem multifunctionality
807 states in global drylands. *Nat Ecol Evolut* 1(2):0003
808
- Bianchetto E, Buscemi I, Corona P, Giardina G, La Mantia T,
809 Pasta S (2015) Fitting the stocking rate with pastoral
810 resources to manage and preserve Mediterranean forest-
811 lands: a case study. *Sustainability* 7:7232–7244
812
- Bonet A, Pausas JG (2004) Species richness and cover along a
813 60-year chronosequence in old-fields of southeastern
814 Spain. *Plant Ecol* 174:257–270
815
- Bueno RS, Guevara R, Ribeiro MC, Culot L, Bufalo FS, Galetti
816 M (2013) Functional redundancy and complementarities of
817 seed dispersal by the last neotropical Megafrugivores.
818 *PLoS ONE* 8:e56252
819
- Carmel Y, Flather CH (2004) Comparing landscape scale veg-
820 etation dynamics following recent disturbance in climati-
821 cally similar sites in California and the Mediterranean
822 basin. *Landsc Ecol* 19:573–590
823
- Carmel Y, Kadmon R (1999) Effects of grazing and topography
824 on long-term vegetation changes in a Mediterranean
825 ecosystem in Israel. *Plant Ecol* 145:243–254
826
- Carmel Y, Kadmon R, Nirel R (2001) Spatiotemporal predictive
827 models of mediterranean vegetation dynamics. *Ecol Appl*
828 11:268–280
829
- Chuang WC, Garmestani A, Eason TN, Spanbauer TL, Fried-
830 Petersen HB, Roberts CP, Sundstrom SM, Burnett JL,
831 Angeler DG, Chaffin BC, Gunderson L, Twidwell D, Allen
832 CR (2018) Enhancing quantitative approaches for assess-
833 ing community resilience. *J Environ Manage* 213:353–362
834
- Debussche M, Escarré J, Lepart J (1982) Ornithochory and plant
835 succession in mediterranean abandoned orchards. *Vegetatio*
836 48:255–266
837
- Dormann FC, McPherson MJ, Araújo BM, Bivand R, Bolliger J,
838 Carl G, Davies GR, Hirzel A, Jetz W, Daniel Kissling W,
839 Kühn I, Ohlemüller R, Peres-Neto RP, Reineking B,
840 Schröder B, Schurr MF, Wilson R (2007) Methods to
841 account for spatial autocorrelation in the analysis of species
842 distributional data: a review. *Ecography* 30(5):609–628
843
- Falcucci A, Maiorano L, Boitani L (2007) Changes in land-
844 use/land-cover patterns in Italy and their implications for
845 biodiversity conservation. *Landsc Ecol* 22:617–631
846
- Fedriani JM, Wiegand T, Delibes M (2010) Spatial pattern of
847 adult trees and the mammal-generated seed rain in the
848 Iberian pear. *Ecography* 33(3):545–555
849
- Fotelli MN, Geßler A, Peuke AD, Rennenberg H (2001)
850 Drought affects the competitive interactions between
851 *Fagus sylvatica* seedlings and an early successional species,
852 *Rubus fruticosus*: responses of growth, water status
853 and $\delta^{13}\text{C}$ composition. *New Phytol* 151:427–435
854
- Gallego Fernández JB, Mora RG, M., and García Novo F.
855 (2004) Vegetation dynamics of Mediterranean shrublands
856 in former cultural landscape at Grazalema Mountains,
857 South Spain. *Plant Ecol* 172:83–94
858
- García D, Obeso JR (2003) Facilitation by herbivore-mediated
859 nurse plants in a threatened tree, *Taxus baccata*: local
860 effects and landscape level consistency. *Ecography*
861 26:739–750
862

- 864 Garcia D, Zamora R, Amico GC (2011) The spatial scale of
865 plant-animal interactions: effects of resource availability
866 and habitat structure. *Ecol Monogr* 81:103–121
- 867 García C, Moracho E, Díaz-Delgado R, Jordano P, Matlack G
868 (2014) Long-term expansion of juniper populations in
869 managed landscapes: patterns in space and time. *J Ecol*
870 102:1562–1571
- 871 Getzin S, Wiegand T, Wiegand K, He F (2008) Heterogeneity
872 influences spatial patterns and demographics in forest
873 stands. *J Ecol* 96:807–820
- 874 Gianguzzi L, La Mantia A (2004) Le serie di vegetazione della
875 riserva Bosco Ficuzza, Rocca Busambra, Bosco del Cap-
876 peliere e Gorgo del Drago Provincia di Palermo. *Nat Sicil*
877 28(1):265–326
- 878 Gómez-Aparicio L (2008) Spatial patterns of recruitment in
879 Mediterranean plant species: linking the fate of seeds,
880 seedlings and saplings in heterogeneous landscapes at
881 different scales. *J Ecol* 96:1128–1140
- 882 González-Varo JP, Carvalho CS, Arroyo JM, Jordano P (2017)
883 Unravelling seed dispersal through fragmented landscapes:
884 Frugivore species operate unevenly as mobile links. *Mol*
885 *Ecol* 26:4309–4321
- 886 Holl KD, Reid JL, Oviedo-Brenes F, Kulikowski AJ, Zahawi
887 RA (2018) Rules of thumb for predicting tropical forest
888 recovery. *Appl Veg Sci* 21:669–677
- 889 Hu Y-H, Lan G-Y, Sha L-Q, Cao M, Tang Y, Li Y-D, Xu D-P
890 (2012) Strong neutral spatial effects shape tree species
891 distributions across life stages at multiple scales. *PLoS*
892 *ONE* 7:e38247
- 893 Jordano P (2017) What is long-distance dispersal? And a tax-
894 onomy of dispersal events. *J Ecol* 105:75–84
- 895 Keitt TH (2003) Spatial autocorrelation, dispersal and the
896 maintenance of source-sink populations. In: Bradshaw GA,
897 Marquet PA (eds) *How landscapes change: human distur-*
898 *bance and ecosystem fragmentation in the Americas.*
899 Springer, Berlin Heidelberg, Berlin, Heidelberg,
900 pp 225–238
- 901 Keitt TH, Bjørnstad ON, Dixon PM, Citron-Pousty S (2002)
902 Accounting for spatial pattern when modeling organism-
903 environment interactions. *Ecography* 25:616–625
- 904 Kissling WD, Carl G (2008) Spatial autocorrelation and the
905 selection of simultaneous autoregressive models. *Glob*
906 *Ecol Biogeogr* 17(1):59–71
- 907 La Mantia T, Bueno RS (2016) Colonization of eurasian jay
908 *Garrulus glandarius* and holm oaks *Quercus ilex*: the
909 establishment of ecological interactions in urban areas.
910 *Avocetta* 40:85–87
- 911 La Mantia T, Rühl J, Pasta S, Campisi DG, Terrazzino G (2008)
912 Structural analysis of woody species in Mediterranean old
913 fields. *Plant Biosyst* 142:462–471
- 914 La Mantia T, Gristina L, Rivaldo E, Pasta S, Novara A, Rühl J
915 (2013) The effects of post-pasture woody plant coloniza-
916 tion on soil and aboveground litter carbon and nitrogen
917 along a bioclimatic transect. *iForest* 6(5):238–246
- 918 La Mantia T, Rühl J, Massa B, Pipitone S, Lo Verde G, Bueno
919 RS (2019) Vertebrate-mediated seed rain and artificial
920 perches contribute to overcome seed dispersal limitation in
921 a Mediterranean old field. *Restor Ecol* 27(6):1393–1400
- 922 Laskurain NA, Aldezabal A, Olano JM, Loidi J, Escudero A
923 (2013) Intensification of domestic ungulate grazing delays
secondary forest succession: evidence from enclosure
plots. *J Veg Sci* 24:320–331
- Lasky JR, Keitt TH (2012) The effect of spatial structure of
pasture tree cover on Avian frugivores in eastern Amazonia. *Biotropica* 44:489–497
- Martínez D, García D (2015) Changes in the fruiting landscape
relax restrictions on endozoochorous tree dispersal into
deforested lands. *Appl Veg Sci* 18:197–208
- Martínez-Duro E, Ferrandis P, Escudero A, Luzuriaga AL,
Herranz JM (2010) Secondary old-field succession in an
ecosystem with restrictive soils: does time from abandon-
ment matter? *Appl Veg Sci* 13:234–248
- Massa B, La Mantia T (2007) Forestry, pasture, agriculture and
fauna correlated to recent changes in Sicily. *Forest*
4(4):418–438
- Méndez M, García D, Maestre FT, Escudero A (2008) More
ecology is needed to restore Mediterranean ecosystems: a
reply to valladares and gianoli. *Restor Ecol* 16:210–216
- Navarro-González I, Pérez-Luque AJ, Bonet FJ, Zamora R
(2013) The weight of the past: land-use legacies and
recolonization of pine plantations by oak trees. *Ecol Appl*
23:1267–1276
- Ne'eman G, Izhaki I (1996) Colonization in an abandoned East-
Mediterranean vineyard. *J Veg Sci* 7:465–472
- Novara A, Gristina L, Sala G, Galati A, Crescimanno M, Cerdà
A, Badalamenti E, La Mantia T (2017) Agricultural land
abandonment in Mediterranean environment provides
ecosystem services via soil carbon sequestration. *Sci Total*
Environ 576:420–429
- Olf H, Vera FWM, Bokdam J, Bakker ES, Gleichman JM, de
Maeyer K, Smit R (1999) Shifting mosaics in grazed
woodlands driven by the alternation of plant facilitation
and competition. *Plant Biol* 1:127–137
- Pausas JG, Millán MM (2019) Greening and browning in a
climate change hotspot: the Mediterranean basin. *Bio-*
science 69(2):143–151
- Pausas JG, Bonet A, Maestre FT, Climent A (2006) The role of
the perch effect on the nucleation process in Mediterranean
semi-arid oldfields. *Acta Oecol* 29:346–352
- Perry JN, Dixon PM (2002) A new method to measure spatial
association for ecological count data. *EcoScience*
9:133–141
- Perry JN, Winder L, Holland JM, Alston RD (1999) Red-blue
plots for detecting clusters in count data. *Ecol Lett*
2:106–113
- Plieninger T, Hui C, Gaertner M, Huntsinger L (2014) The
impact of land abandonment on species richness and
abundance in the Mediterranean basin: a meta-analysis.
PLoS ONE 9:e98355
- Pueyo Y, Begueria S (2007) Modelling the rate of secondary
succession after farmland abandonment in a Mediterranean
mountain area. *Landsc Urban Plan* 83:245–254
- QGIS Development Team (2016) QGIS geographic information
system. Open Source Geospatial Foundation Project.
<https://qgis.osgeo.org>
- Quero JL, Herrero A, Zamora R (2011) Linking stochasticity to
determinism of woody plant recruitment in a mosaic
landscape: a spatially explicit approach. *Basic Appl Ecol*
12:161–171

- 983 Raimondi S, Dazzi C, Cirrito V (1983) Modello di studio inte- 992
 984 grato del territorio (Ficuzza-Palermo), nota n.5. I suoli. 993
 985 Quaderni di Agronomia 10:89–131 994
 986 Rivas-Martínez S (2008) Global bioclimatics (Clasificación 995
 987 bioclimática de la Tierra) (versión 01–12–2008). [www.](http://www.globalbioclimatics.org) 996
 988 [globalbioclimatics.org](http://www.globalbioclimatics.org), www.globalbioclimatics.org. 997
 989 Seifan M, Kadmon R (2006) Indirect effects of cattle grazing on
 990 shrub spatial pattern in a mediterranean scrub community.
 991 Basic Appl Ecol 7:496–506
- Sluiter R, de Jong SM (2007) Spatial patterns of Mediterranean
 land abandonment and related land cover transitions.
 Landsc Ecol 22:559–576
- Ver Hoef JM, Peterson EE, Hooten MB, Hanks EM, Fortin M-J
 (2018) Spatial autoregressive models for statistical infer-
 ence from ecological data. Ecol Monogr 88:36–59

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

UNCORRECTED PROOF