

1 **Assessing the effects of seasonal grazing on holm oak regeneration: implications**
2 **for the conservation of Mediterranean dehesas**

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4 Carlos P. Carmona^{1*}, Francisco M. Azcárate¹, Elisa Oteros-Rozas², José A. González²,
5 Begoña Peco¹

6 ¹ *Terrestrial Ecology Group (TEG). Department of Ecology. Universidad Autónoma*
7 *de Madrid. Madrid, Spain.*

8 ² *Social-Ecological Systems Laboratory. Department of Ecology. Universidad*
9 *Autónoma de Madrid. Madrid, Spain*

10

11 *Corresponding author:

12 Terrestrial Ecology Group (TEG). Department of Ecology. Universidad Autónoma de
13 Madrid. C/ Darwin, 2. E-28049. Madrid. Spain. Tel.: (+34) 914972780; Fax: (+34) 497
14 8001; E-mail: carlos.perez@uam.es

15 **ABSTRACT**

16 Scattered trees in agricultural landscapes are globally declining due to the
17 intensification of agricultural practices. Dehesas, highly species-diverse Mediterranean
18 open woodlands, are seriously affected by this decline, because of a generalized
19 regeneration failure of oaks, which compromise their long-term stability. Traditionally,
20 *dehesas* were the wintering areas for transhumant herds, but transhumance is
21 disappearing in the Mediterranean, due to multiple causes. Reductions in grazing
22 intensity or grazing abandonment have been proposed to improve oaks regeneration in
23 dehesas, but the effect of the recovery of non-continuous grazing practices such as
24 transhumance has not been tested to date. We measured different indicators of holm
25 oaks regeneration and condition in dehesas under transhumant grazing and in dehesas
26 under permanent grazing in southern Spain. Oak juveniles were remarkably less
27 browsed and their canopies covered a much higher surface in transhumant estates. As a
28 consequence, the median density of saplings was more than four times higher in
29 transhumant than in permanently-grazed estates. Although transhumant grazing is
30 necessarily associated with a reduction in the stock capacity, the timing of grazing was
31 always included as a predictor in the best models to explain the condition and density of
32 the holm oaks. Our results suggest that the lack of oak regeneration in dehesas can be
33 caused not only by the increases in stocking rates, but also by the recent abandonment
34 of traditional grazing practices like transhumance. We propose the recovery of seasonal
35 grazing regimes based on transhumant pastoralism as a measure to improve the
36 conservation status of dehesas.

37 **Key-words:** Agricultural intensification; Agroforestry; Browsing; *Quercus ilex*;
38 Transhumance

39 **1. INTRODUCTION**

40 Scattered trees in agricultural landscapes are widely recognized as keystone structures
41 because of the large number of ecological functions that depend upon their presence
42 (Fischer et al., 2010; Manning et al., 2006), but they are globally declining due to the
43 intensification of agricultural practices (Gibbons et al., 2008). Among these landscapes,
44 *dehesas*, Mediterranean open woodlands resulting from the clearing of original
45 evergreen oak woodland and shrubland areas (Plieninger, 2007), also known as
46 *montados* in Portugal, constitute an example of agrosilvopastoral ecosystems with a
47 high biodiversity. *Dehesas*, when adequately managed, are considered as the paradigm
48 of a sustainable land-use (eg. Pinto-Correia et al., 2011). These systems occupy a large
49 surface in the Iberian Peninsula and its conservation is considered very important for
50 both environmental and socio-economic reasons (Moreno and Pulido, 2008). Many
51 production activities take place in *dehesas*, being livestock production the most
52 important in those dominated by holm oaks (*Quercus ilex* subsp. *ballota*; Pinto-Correia
53 and Mascarenhas, 1999; Pinto-Correia et al., 2011). Traditionally, *dehesas* have been
54 grazed by sheep, the most suited species for most *dehesas*, at low stocking rates, with
55 cattle restricted to the most humid ones (Peco et al., 2006; Moreno and Pulido, 2009).
56 Besides, pigs are introduced to many *dehesas* between October and January to take
57 advantage of the abundant acorns production that takes place in autumn. Livestock feed
58 on the acorns and grass under the tree canopy, which also provides firewood. Trees are
59 therefore viewed as an integrated part of the system, and as a result are managed and
60 regularly pruned (Blondel, 2006).
61 Mediterranean climate is characterized by marked differences between wet winters and
62 dry summers and great inter-annual variability in rainfall. These temporal changes in

63 water availability generate remarkable variations in the productivity of Mediterranean
64 grasslands. This, along with the high variability in topographic conditions, makes
65 transhumance a successful grazing management practice in these environments
66 (Manzano and Casas, 2010; Niamir-Fuller and Turner, 1999; Weber and Horst, 2011).
67 Transhumance practices consist in a regular and periodic movement of livestock from
68 winter pastures (valley bottoms and/or southern latitudes) to summer pastures
69 (mountains and/or northern latitudes; Weber and Horst, 2011). These practices optimize
70 the use of the existing resources by matching the presence of animals in a given zone
71 with the annual peak in productivity (Ruiz and Ruiz, 1986). Because of its size, climate,
72 topography and anthropological characteristics, transhumance systems have historically
73 had a great importance in the Iberian Peninsula. In Spain, transhumance reached its
74 peak in the Middle Ages, when up to four million sheep were involved in transhumant
75 practices and an extensive network of protected drove roads was created (Manzano and
76 Casas, 2010; Oteros-Rozas et al., 2012a; Ruiz and Ruiz, 1986). However, the
77 breakdown of the Merino breed monopoly during the 19th century originated a
78 continuous decline of transhumance in Spain, aggravated in the 20th century by the use
79 of rail and truck transport as alternatives to the movement of herds along drove roads
80 (Oteros-Rozas et al., 2012a). As a consequence, the number of transhumant sheep has
81 been reduced to ca. 250,000, of which only a 10% are moved by foot (MARM, 2011;
82 Oteros-Rozas et al. 2012a). Simultaneously, the intensification of agricultural practices
83 that European agricultural systems have been facing for more than a century
84 (Ostermann, 1998, Stoate et al., 2009), have caused a drastic decline of traditional
85 extensive grazing management practices. Extensive practices, which are characterized
86 by low grazing intensities with traditional livestock races like the merino sheep, are

87 being substituted by more intensive regimes that include the preference for large-scale
88 free range grazing over traditional shepherding, increases in stocking rates and the use
89 of heavier breeds of cattle (Pinto-Correia and Mascarenhas, 1999; Peco et al., 2001).
90 Dehesas, that have traditionally been the wintering areas for transhumant herds, are
91 currently facing deterioration partly because of the overgrazing of estates, which is
92 somewhat related with the sedentarization of previously transhumant herds. Similarly to
93 other landscapes composed by scattered trees, the last decades have seen a remarkable
94 decrease in the total area covered by dehesas as well as in the tree densities of the
95 remaining ones (Moreno and Pulido, 2008). Studies on the tree size structure of dehesas
96 have shown that these systems are characterized by over-aged oak stands, because of a
97 disruption in the forest cycle characterized by an extensive lack of regeneration
98 (Montoya, 1998; Plieninger et al., 2003; Plieninger, 2007). Whether the lack of
99 regeneration of trees in dehesas is caused by the aforementioned shifts towards more
100 intensive regimes or is an inherent feature of grazed dehesas independent of grazing
101 intensity is a question that has not been definitely answered to date (Moreno and Pulido,
102 2008; Plieninger et al., 2011). Regardless of its causes, lack of regeneration of the tree
103 layer is threatening the long-term stability of dehesas, because of the capital importance
104 that oaks have on these systems (Joffre et al., 1999; Plieninger et al., 2003).
105 Consequently, there is an urgent need to develop measures that would improve the
106 regeneration of oaks in dehesas (Gibbons et al., 2008; Pinto-Correia et al., 2011).
107 Several options have been proposed to achieve this objective, such as reductions in
108 grazing intensity, afforestation or temporary grazing abandonment (e.g. Plieninger et al.,
109 2003; Ramírez and Díaz, 2008). However, the implementation of these options is not
110 possible without severe ecological and socio-economic costs. For example, the drastic

111 reductions in the stock capacity that would be necessary to achieve a carrying capacity
112 compatible with the regeneration of holm oak would be associated with very high socio-
113 economic costs for farmers (Plieninger, 2007). Furthermore, a total abandonment of
114 grazing would reduce the soils nutrient availability, and, more importantly, lead to shrub
115 encroachment, with the subsequent accumulation of vegetation fuel on the ground that
116 would increase the risk of severe wildfires compromising the sustainability of these
117 systems (Joffre et al., 1999; Peco et al. 2006).

118 Among the proposed management options for the tree regeneration of dehesas, a
119 spatially and temporally limited set-aside of grazing and cultivation by means of
120 rotating fences is the one that has more often been preferred in both management and
121 scientific literature (Gibbons et al., 2008; Montoya, 1998; Plieninger et al., 2003). In
122 Mediterranean systems there is a very marked drought during summer, which results in
123 reduction in the availability and quality of herbaceous vegetation. This is associated
124 with a great increase in both the amount of supplementary feed needed by livestock
125 during the summer (Gutman et al., 2000) and in the intensity of browsing in this season
126 compared to spring, when there is a much higher availability of fodder (de Miguel et al.,
127 1997). This fact has led to the proposal of the recovery of transhumance practices as a
128 measure to solve the problem of the lack of regeneration of the tree layer in dehesas
129 (Garzón-Heydt, 2004). In fact, the adoption of non-continuous grazing management
130 schemes has been recently proposed as a measure to ensure the regeneration of scattered
131 trees in Australian landscapes (Dorrrough, 2005; Fischer et al., 2010). Nevertheless, to
132 date no study has tested the effects of seasonal grazing regimes on tree regeneration in
133 dehesas.

134 In the present paper we analyze the effects of transhumant pastoralism on the
135 regeneration of holm oaks, by comparing several indicators of tree regeneration and
136 condition in different dehesas with contrasting management regimes (transhumant
137 seasonal grazing vs. permanent grazing). We hypothesize that the conservation and
138 regeneration status of holm oak saplings and trees will be better in estates managed
139 under transhumance regimes than in estates with permanent grazing regimes.

140 2. MATERIAL & METHODS

141 2.1. Study area and sampling design

142 The study area is located in the municipalities of La Carolina, Vilches and Santa Elena
143 (38°20' N, 3°30' W; 400-600 m.a.s.l.) in South-Central Spain (Fig. 1). The climate is
144 typical Mediterranean, with very dry summers and annual rainfalls concentrated in
145 spring and autumn. Annual rainfall is ca. 600 mm, and mean annual temperature ca. 17
146 °C. These dehesas are located in one of the wintering areas for transhumant livestock of
147 the Conquense Drove Road, one of the major drove roads still in use on foot
148 transhumance by sheep and cattle in Spain.

149 We selected 18 estates of two different types according to grazing seasonality: nine of
150 them were grazed throughout the year (“Permanent”), while the other nine were
151 managed by transhumant livestock raisers and grazed only for six months each year
152 (between December and May; “Transhumant”). The estates were holm oak-dominated
153 *dehesas*, which were selected in order to cover a large range of adult trees densities (20
154 to ca. 400 adult holm oaks·ha⁻¹), always ensuring that this density was similar in
155 Transhumant (99.43 trees·ha⁻¹ ±23.44) and Permanent (98.64 ±22.28) estates. We also
156 made sure that we sampled a diversity of grazing alternatives: among the studied
157 estates, some were grazed by sheep (9 estates), some by cattle (6) and some by both (3),
158 with a balanced distribution of these alternatives between Transhumant and Permanent
159 estates. Interviews with landowners and shepherds revealed that all the selected estates
160 have maintained their current grazing seasonality and grazing pressure for at least the
161 last 10 years and that, besides grazing, small game hunting is the only noteworthy
162 practice that takes place both in Transhumant and Permanent estates. Interviews also
163 showed that the estates, including the transhumant ones, are leased by herders

164 throughout the year, independently of the time of permanence of livestock on the
165 estates. The area of the states ranged between 20 and 480 ha, with no significant
166 differences between Transhumant (210.15 ha \pm 25.82; mean \pm SE) and Permanent
167 (193.91 \pm 19.56) states.

168 In each estate we randomly selected between 2 and 6 points, always in North-facing
169 slopes, the most common orientation in the study area, in order to reduce as much as
170 possible the ecological variability among observations. Minimal distance between
171 points belonging to the same estate was set to 100 m. After interviewing shepherds and
172 landowners about the number of grazers, we calculated for each estate the grazing
173 pressure expressed in Livestock Units (LU) * day * ha⁻¹ (1 cattle=1 LU, 1 sheep=0.15
174 LU), in order to have a comparable measure between estates. Grazing pressure can also
175 vary within farms according to different factors such as topography, livestock
176 preferences or the location of grazing management infrastructures (Carmona et al.,
177 unpublished). To have an estimation of the local grazing pressure, we performed
178 livestock excrements counts in four 10x1 m transects (starting in the selected point
179 towards the N, S, E and W directions). On each meter along the axis of each transect we
180 registered the presence or absence of excrements bigger than 3 cm and recorded the
181 number of presences, finally obtaining a value between 0 and 10 for this parameter.

182 In the surroundings of each point (referred to as "site" from here onwards), we
183 measured three groups of variables (browsing indicators, regeneration indicators and
184 woodland structure indicators) to characterize the condition of the holm oaks. The
185 *browsing indicators* included two variables: the intricacy index and the percentage of
186 eaten shoots. These variables were measured in the four holm oaks nearest to the
187 selected point that presented branches accessible to livestock at a height less than 1 m.

188 In each of these oaks we randomly selected a branch with no visible damage and with a
189 basal diameter of 0.5 to 1 cm and a length greater than 10 cm. The intricacy index was
190 calculated as the ratio between the number of times that the selected branch ramifies and
191 its total length, and it is expected to increase with the intensity of browsing (Orueta et
192 al., 1998). In the same oaks, we determined the percentage of eaten shoots. For this
193 purpose, we randomly selected 10 branches of the outer part of the tree to a height of
194 less than 1 m and counted how many of them were eaten (absent terminal bud).

195 We selected four 3x3 m plots associated to each site (distant 7 m from the selected point
196 in the N, S, E and W directions) in which we measured the *regeneration indicators*. In
197 each plot we counted the number of isolated juvenile holm oaks (<1 cm DBH or less
198 than 1.3 m height) and recorded their base diameter and height. Whenever we found a
199 group of very aggregated stems with a similar height and leaf morphology, we classified
200 that aggregation as a group of juveniles, and assigned for the whole group the height
201 and diameter of the highest juvenile in the group (Pulido et al., 2001; Plieninger et al.,
202 2004). We considered two groups as different when their external borders were more
203 than 25 cm apart (Plieninger et al., 2004). To estimate the cover of each juvenile or
204 group of juveniles, we measured the longest length of the crown and the length of the
205 perpendicular axis. For each plot we calculated the average base diameter and height of
206 juveniles and the proportion of the surface covered by them.

207 Since livestock (especially cattle) can break and consequently kill holm oaks of up to 7-
208 9 cm of DBH (Pérez-Fernández and Gómez-Gutiérrez, 1995), the *woodland structure*
209 *indicators* were chosen in order to detect the effects of grazing on the density of three
210 different size classes: young saplings (DBH between 1 and 5 cm), old saplings (DBH
211 between 5 and 10 cm) and adult holm oaks (DBH > 10 cm). We first measured the

212 distance from the selected point to the closest holm oak of each of the three size classes.
213 After that, from each of those trees we measured the distance to its restricted second
214 neighbor and applied a T-square sampling to determine the density (trees*ha⁻¹) of each
215 size class (Besag and Gleaves, 1973). We calculated a site-averaged value for all the
216 indicators that were measured more than once in each site and used that average in the
217 subsequent analyses.

218 **2.2.Statistical analysis**

219 We analyzed the relationships between grazing variables or factors and each of the
220 browsing, regeneration and tree size structure indicators with mixed linear models.
221 Grazing regime (GR; categorical with 2 levels: Permanent and Transhumant grazing),
222 number of excrements (E; continuous), grazing pressure at the farm level (GP;
223 continuous) and the type of grazer (TG; categorical with 3 levels: Sheep, Cattle and
224 Both), were included in the models as fixed effects and farm was included as a random
225 factor in order to account for variability among the farms due to other non-measured
226 variables. The relationship between the grazing variables and factors was previously
227 analyzed with t-test and chi-square in order to discard multicollinearity in the models.
228 These tests revealed that the only variables that were significantly correlated were
229 grazing regime and grazing pressure ($t_{16}=5.60$, $p<0.001$), with higher values of grazing
230 pressure in permanently grazed than in transhumant estates (185.98 ± 14.99 and $94.20 \pm$
231 7.58 LU*day*ha⁻¹, respectively).

232 The response variables used (Intricacy index, percentage of eaten shoots, % of surface
233 covered by young oaks, diameter and height of young oaks, and density of young
234 saplings, old saplings and mature oaks) were log-transformed in order to attain
235 normality and homoscedasticity of residuals. Since GR and GP were correlated, we

236 never used them simultaneously in the same model; thus, for each response variable we
237 fitted two sets of linear mixed models. One set included GR, E, TG and all the first
238 order interactions as fixed effects and the other set included GP, E, TG and all the first
239 order interactions as fixed effects. These saturated models were simplified via
240 backwards stepwise selection in order to attain two final candidate models. Among
241 these final models, we selected the one with the lowest AIC value (Burnham and
242 Anderson, 2002) as the one that better explained the observed data. All the analyses
243 were performed using the program R version 2.14.1 (R Development Core Team,
244 2011).

245

246 **3. RESULTS**

247 **3.1. Browsing indicators.**

248 Differences between estates accounted for more than 40% of the variability in browsing
249 indicators. GR was found to be a much better predictor of these variables than GP, as
250 indicated by the great differences in the AIC values between the models including each
251 predictor (Table 1). The selected model for the intricacy index of oak saplings contained
252 only grazing regime as a statistically significant predictor, accounting for a 15.11% of
253 the total variability and revealed that this index was much higher in sites under
254 permanent grazing regimes than in those used by transhumant livestock (Fig. 2A). As
255 expected, the direction and magnitude of the effect of grazing regime on the percentage
256 of eaten shoots were similar than the effect on the Intricacy index. Nevertheless, the
257 selected model for the percentage of eaten shoots revealed a positive correlation
258 between this variable and the amount of excrements in the site, indicating the significant
259 effect of within-estate variability in grazing pressure.

260 **3.2. Stand regeneration indicators.**

261 Again, grazing regime, instead of grazing pressure, was generally included in the most
262 parsimonious models for these variables (Table 1). The estate factor accounted for a
263 40% of the variability in the proportion of surface covered by oak juveniles, but it was
264 less important for the diameter and height of the juveniles (Fig. 2B). The selected model
265 for the proportion of the surface covered by oaks in the regeneration stage included only
266 grazing regime as a predictor. As expected, this proportion of surface was higher in
267 transhumant than in permanent grazing sites. None of the studied predictors showed any
268 effect on the diameter of the juveniles, but we observed an important effect of grazing

269 regime on the height of these juveniles ($80.79 \text{ cm} \pm 7.22$ in transhumant estates vs.
270 43.86 ± 4.19 in permanently grazed estates; Fig. 2B).

271 **3.3. Tree size structure indicators.**

272 Inter-estate variability was not important for explaining the density of young saplings,
273 but in contrast it accounted for higher proportions of the variability of the density of old
274 saplings and especially of mature oak trees (Fig. 2C). Once more, the AIC values
275 indicated that the models that included GR were more parsimonious than those
276 including GP. Despite the fact that the average values of the density of the three size
277 classes was higher in transhumant than in permanent grazed sites, grazing regime did
278 not present a significant effect on the density of mature trees. We found a weak effect of
279 grazing regime on the density of young saplings, while this variable had a more
280 important effect in the model for the density of old saplings (DBH between 5 and 10
281 cm; Fig. 2C).

282 **4. DISCUSSION**

283 The present study provides evidence for the important effect that the early cessation of
284 grazing and the reduction in grazing pressure associated with transhumance practices
285 have on the regeneration of the tree layer in dehesas. There is an obvious association
286 between grazing regime and grazing pressure, caused by the increased amount of time
287 that animals spend in the permanently grazed estates rather than by differences in the
288 number of animals per surface unit. Nevertheless, the most parsimonious models to
289 predict the different indicators of the tree layer status generally included grazing regime
290 rather than just grazing pressure. This result indicates that, not only the number of
291 animals that graze in an estate, but also the timing of grazing determines the condition
292 and density of the holm oaks.

293 **4.1. EFFECTS OF GRAZING REGIME ON TREE REGENERATION**

294 In Mediterranean dehesas, herbaceous vegetation gets completely consumed or dried
295 during the summer. This reduction in the availability and quality of the herbaceous
296 vegetation (Papachristou, 2005) increases the use of browse as a food resource for
297 ungulates during summer, with the subsequent effects on saplings and juveniles
298 (Bugalho and Milne, 2003; Zamora et al., 2001). As shown by the browsing indicators,
299 juvenile oaks in sites under transhumant practices clearly suffered much smaller levels
300 of herbivory than those situated in permanently grazed sites. This reduction in browsing
301 by herbivores was probably caused by the earlier cessation of grazing in transhumant
302 estates in which herds are moved to summer pasturelands as soon as primary
303 productivity, and hence pasture availability, declines.

304 The differences in the rate of consumption of woody vegetation by livestock between
305 estates with different grazing regimes resulted in significant differences between their
306 populations of holm oak juveniles. First, the smaller height of the juveniles in
307 permanently grazed estates compared to those in transhumant sites, along with the lack
308 of any significant effect on the diameter of juveniles (Fig 2B), suggest a reduction in the
309 net growth rate of oak juveniles. Slower growth in juveniles suffering high levels of
310 herbivory can have important consequences at the stand level because it can greatly
311 increase the age required to reach the height threshold that allows the young trees to
312 avoid being browsed (Pérez-Fernández and Gómez-Gutiérrez, 1995; Zamora et al.,
313 2001). However, specific studies comparing the growth rates of trees in permanent and
314 transhumant estates should be made to further clarify this point. Second, permanent
315 grazing also reduced the proportion of the total surface covered by juveniles. We did not
316 find significant differences between estates with different grazing regimes in their
317 number of groups of juveniles, which indicates that the reduced cover in permanent
318 grazing sites is more likely to be related with a significant reduction in the
319 photosynthetic tissue of the juveniles, rather than with an increase in their mortality rate.
320 These observations suggest that the development of oak juveniles is seriously reduced
321 under continuous grazing conditions, probably because of a great reduction in their leaf
322 area (Putman, 1996).

323 It has to be noted that the reduced browsing indicators and the higher cover of juveniles
324 in transhumant estates does not necessarily secure long-term regeneration in those
325 estates because grazers can significantly damage or even remove saplings before they
326 reach maturity, as found in previous studies (Pérez-Fernández and Gómez-Gutiérrez,
327 1995; Tiver and Andrew, 1997). In relation with this, although we only found a weak

328 effect of grazing regime on the density of young saplings, transhumant sites presented
329 on average a much higher density of old saplings (DBH between 5 and 10 cm) than
330 permanently grazed sites. Important reductions in the density of saplings have
331 previously been observed in grazed areas compared to abandoned ones (Dufour-Dror,
332 2007). Our findings suggest that the likelihood of young holm oak individuals to reach
333 the next class size is significantly reduced in estates in which grazers spend the summer
334 and confirm that oaks of more than 5 cm DBH are sensible to livestock action. Thus,
335 our results suggest that not only the seedling stage (Plieninger et al., 2004), but also the
336 transition from the sapling to the adult phase can be considered as a critical stage
337 determining the lack of success of holm oak recruitment in *dehesas*.

338 Holm oak juveniles in grazed *dehesas* are generally assumed to come from asexual
339 reproduction, because true seedlings do not persist even under low grazing pressures
340 (Plieninger et al., 2004). Complementary, seedling recruitment have been observed in
341 grazing abandoned *dehesas*, an observation that have led some authors to propose a
342 temporal cessation of grazing in *dehesas* in order to promote the maintenance of the tree
343 layer (e.g. Ramírez and Díaz, 2008). Although we did not recorded the sexual or asexual
344 origin of the sampled juveniles, we observed the existence of isolated juveniles in some
345 of the sites in transhumant estates. These juveniles grew away from any other holm oak,
346 either sapling or adult, a fact that suggests that they came from true seedlings. These
347 observations indicate that transhumance practices could favor seedling recruitment in
348 holm oak *dehesas*, but this aspect requires specific research.

349 The great importance of the difference among estates suggests that environmental
350 attributes such as rock cover, slope or shrub cover, that we have not included in our
351 analyses, are important determinants of the regeneration stage of holm oaks (Plieninger

352 et al., 2004). At the same time, among the grazing variables, only grazing regime
353 presented a consistent effect on the studied holm oak status indicators. In general,
354 grazing regime was a much better predictor than only grazing pressure at the estate level
355 (Table 1). Similarly, grazing pressure at the site level (indicated by the number of
356 excrements) usually presented a non-significant effect, in accordance with the lack of
357 effects of grazing impact indicators on holm oak regeneration indicators observed in
358 other studies in dehesas (Plieninger et al., 2003, 2004; Plieninger, 2007). To explain
359 these observations, Plieninger (2007) proposed a model assuming that current stocking
360 rates in dehesas are above the threshold for safe regeneration of holm oaks. We propose
361 the timing of grazing and whether it is or not coupled with seasonal changes in the
362 availability of herbaceous vegetation as a factor that should be taken into account, along
363 with stocking rates, in order to study the failure of the tree layer regeneration in dehesas.
364 Our results suggest that the lack of regeneration of the tree layer in dehesas can be
365 caused not only by the increases in stocking rates experienced by these systems, but also
366 by the recent abandonment of traditional grazing practices like transhumance, and
367 probably by a combination of both processes. Complementary to this observation,
368 previous studies in Mediterranean grasslands have described that seasonal grazing
369 allows for higher stocking rates than continuous grazing with supplementary feed
370 (Gutman et al., 1999). However, further research on the conditions that would ensure
371 tree regeneration in dehesas is needed in order to determine realistic thresholds of
372 grazing density both for continuous and non-continuous grazing regimes. Although we
373 expected cattle to have a bigger impact than sheep on the studied parameters, among the
374 most parsimonious models, only the one for the intricacy index retained this predictor.
375 Nevertheless, we want to stress that this aspect was secondary in our design, and that

376 more specific research should be carried on before any conclusion can be reached
377 regarding this issue.

378 4.2.IMPLICATIONS FOR THE CONSERVATION OF MEDITERRANEAN 379 DEHESAS

380 Scattered trees are a keystone feature of agricultural landscapes, which makes
381 the problem of its lack of regeneration an issue that has to be faced urgently (Fischer
382 et al., 2009; Manning et al., 2006). Our study shows that grazing cessation during
383 summer and autumn can be applied to improve the regeneration of scattered trees,
384 while substantially reducing the high opportunity costs of permanent livestock
385 exclusion (Dufour-Dror, 2007; Fischer et al., 2009, 2010; Gutman et al., 1999).
386 However, this result could probably be achieved through some management options
387 other than traditional transhumance. For example, at the whole-state level,
388 summertime indoor breeding or motorized transhumance could be feasible options in
389 the current socio-economical context. An alternative option is the designation of farm
390 sectors in which tree regeneration is promoted by the prevention of summer grazing,
391 until oak saplings reach a DBH threshold of 10 cm. Nevertheless, we clearly advocate
392 for the recovery of seasonal grazing regimes based on transhumant pastoralism.
393 Besides the improvement in the regeneration of the tree layer of dehesas, there is a
394 great number of ecosystem services linked to transhumance practices, not only in the
395 winter and summer pastures, but also in the drove roads where flocks spend about two
396 months per year. These include regulating services such as fire prevention, soil
397 fertility, seed dispersal or biodiversity conservation as well as provisioning and
398 cultural services, such as provision of high quality meat, cultural identity related with

399 the nomadic way of life and traditional ecological knowledge associated to
400 transhumance (Bunce et al., 2004; Oteros-Rozas et al., 2012b).

401 Multifunctional systems in the Mediterranean, and more precisely *dehesas* and
402 their typical scattered tree structures, are considered an example of resilient social-
403 ecological systems (Blondel, 2006; Manning et al., 2006). Transhumance is a
404 millenary practice that has proved to combine the provision of a wide range of
405 ecosystem services with the conservation of dehesa cultural landscapes, by allowing a
406 sustainable regeneration of the tree structure. Several social and economic factors (e.g.
407 lack of economic profitability due to competition with industrialised production,
408 social difficulties of the transhumant way of life, scarce generational turnover,
409 competition with other land uses such as hunting or the development of infrastructures
410 that interfere with drove roads) lie behind the negative trend experienced by
411 transhumance practices (González et al. 2012). How to realise new functions of
412 ecosystems and still guarantee the sustainability of qualities of the past is a major
413 concern in nearly all the old cultural landscapes in Europe (Vos and Meekes, 1999). In
414 this context, it is essential to develop adequate policies, such as the implementation of
415 certain schemes of payments for ecosystem services, the facilitation of cooperation
416 among pastoralists, the improvement of products marketing in order to visualize their
417 values, the conservation of drove roads' networks, the empowerment and training of
418 new generations of shepherds and the improvement of institutional coordination
419 (Oteros-Rozas et al., 2012b) that would help in the process of recovery of customary
420 management practices like transhumance.

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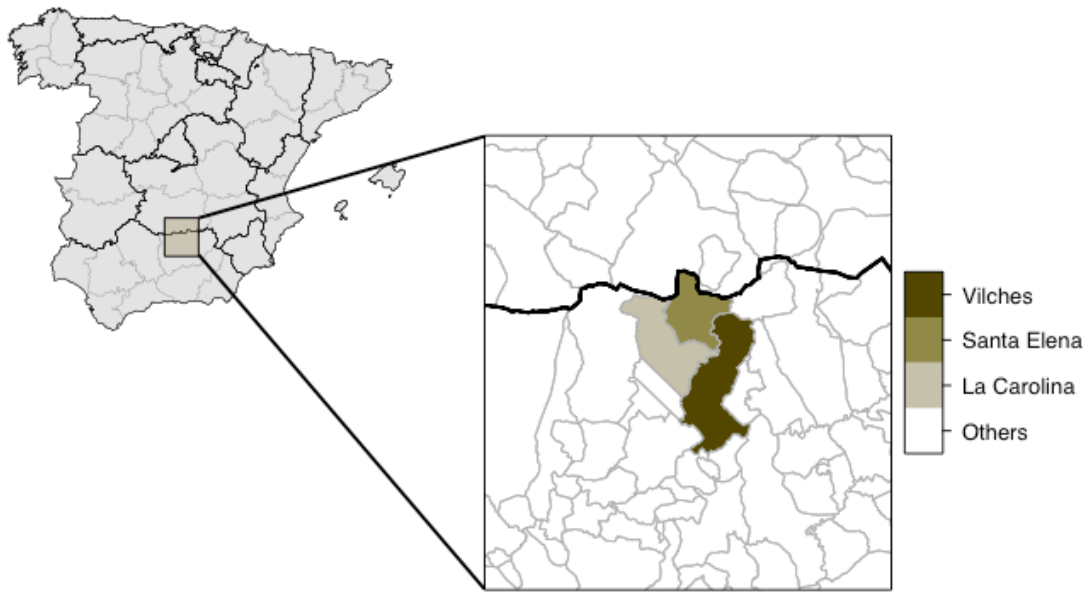
571 **Table 1.** Predictors included in the most parsimonious linear mixed-effects models for
 572 the set of models that included grazing regime (GR) and the set of models that
 573 included grazing pressure (GP). The other predictors were the proportion of
 574 excrements (E) and the type of grazer (TG). For each model, we show its AIC value as
 575 well as the proportion of the total variance explained by the fixed effects (%VE). In
 576 bold, the lowest AIC value for each response variable is shown.

Response Variable	Set of models	Most parsimonious model	AIC	%VE
<i>Intricacy</i>				
	Grazing regime	~ GR + E + TG + S:E	-4.48	17.54
	Grazing pressure	~ GP + E + GP:E	3.22	8.59
<i>Eaten shoots</i>				
	Grazing regime	~ GR + E	172.24	19.32
	Grazing pressure	~ GP + E + GP:E	180.66	12.41
<i>Regeneration surface</i>				
	Grazing regime	~ GR	175.06	7.86
	Grazing pressure	~ GP	177.00	5.73
<i>Regeneration diameter</i>				
	Grazing regime	~	67.67	~
	Grazing pressure	~	67.67	~
<i>Regeneration height</i>				
	Grazing regime	~ GR	85.48	13.99
	Grazing pressure	~ GP	90.36	5.86
<i>Density young saplings</i>				
	Grazing regime	~ GR	240.54	8.25
	Grazing pressure	~ GP + TG	244.86	7.65
<i>Density old saplings</i>				
	Grazing regime	~ GR	218.23	8.64
	Grazing pressure	~ E + TG	220.52	7.59
<i>Density mature trees</i>				
	Grazing regime	~	170.56	~
	Grazing pressure	~	170.56	~

578 **FIGURE CAPTIONS**

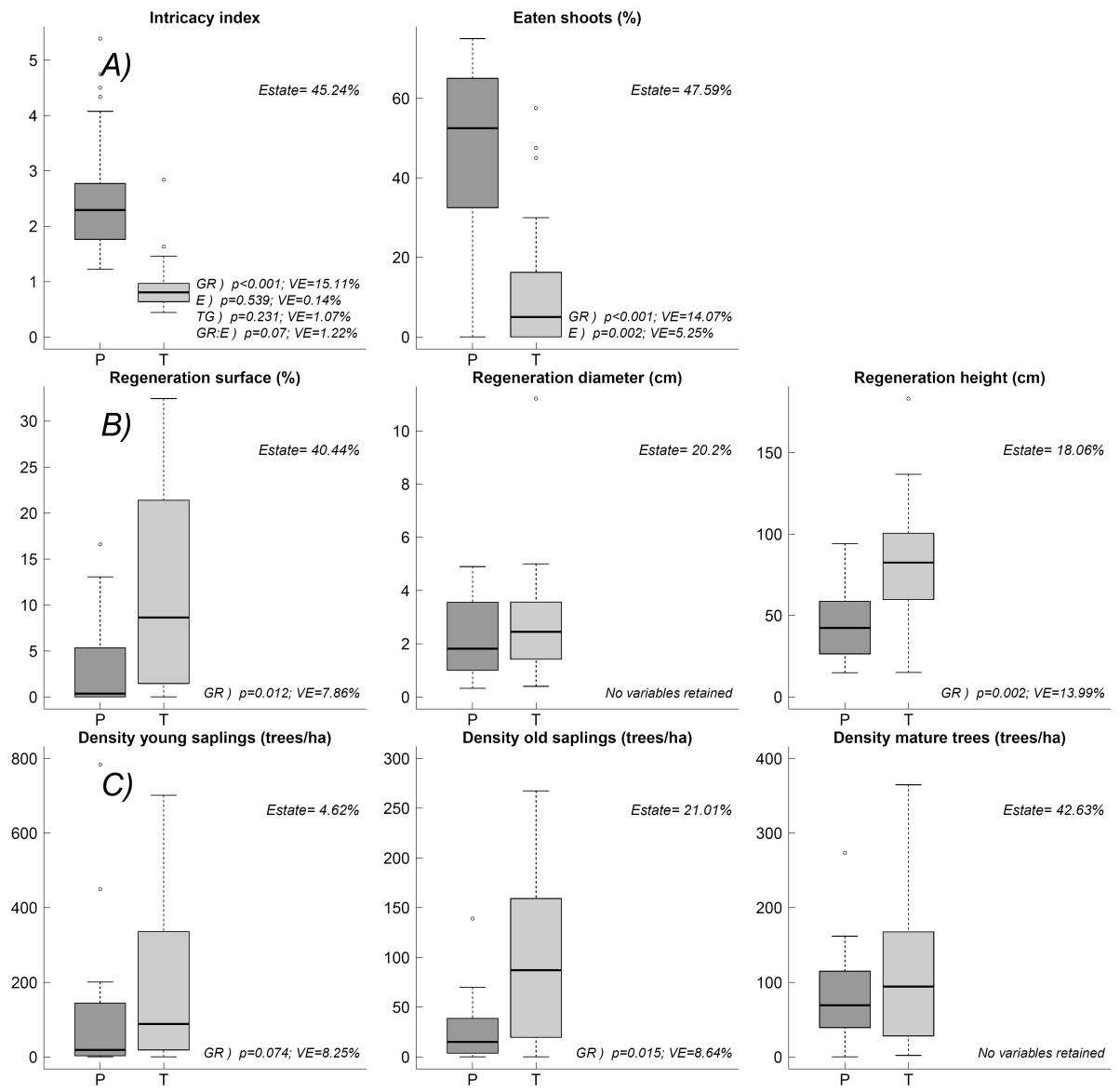
579 Fig. 1. Overview of Spain and the location of the three municipalities in which the
580 study area was situated, in northern Jaén province.

581 Fig. 2. Boxplots showing the effect of grazing regime (P: Permanent grazing; T:
582 Transhumant grazing) on the different indicators of holm oak browsing (A),
583 regeneration (B) and forest size structure (C). For each predictor we show the p-values
584 and the proportion of variance explained (VE) by each of the independent variables
585 retained in the most parsimonious model (see text; GR: Grazing regime; E: Proportion
586 of excrements; TG: Type of grazer). The proportion of the total variance due to
587 differences among different estates is shown in the upper-right side of each plot.



588
589

Figure 1



590
591 Figure 2