

# Establishment limitation of holm oak (*Quercus ilex* subsp. *ballota* (Desf.) Samp.) in a Mediterranean savanna – forest ecosystem

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## Abstract

• Tree recruitment in Mediterranean savannas is generally hampered, in contrast with the original oak forests where these savannas are derived from. We asked whether this difference in recruitment success can be explained by differential post-dispersal survival. For one year we monitored experimentally cached holm oak acorns in a savanna – forest ecosystem in Central Spain, and recorded cache pilferage, type of pilferer, boar rooting, seedling emergence, seedling survival and the cause of mortality.

• Cache pilferage was significantly lower in savanna (8%) than in forest (21%). However, the higher cache survival was more than offset by lower seedling emergence and, particularly, by nine times higher seedling mortality in savanna, mainly due to desiccation. Wild boar rooting did not differ between experimental caches and controls without acorns, indicating that individual cached acorns do not trigger rooting activity.

• Our results indicate that the difference in post-dispersal survival between savanna and forest is due to lower emergence and, primarily, higher seedling mortality in savanna, not to higher cache pilferage. Absence of safe sites such as shrubs, abundantly present in the forest, may well explain the lack of recruitment in the savanna. Management measures appear necessary for long-term persistence of Mediterranean savannas in general.

## Résumé – Limitation de l'installation du chêne vert (*Quercus ilex* subsp. *ballota* (Desf.) Samp.) dans un écosystème de savane forestière méditerranéenne.

• Le recrutement des arbres dans les savanes méditerranéennes est généralement entravé, ce qui contraste avec les forêts de chênes originelles dont ces savanes sont issues. Nous nous sommes demandé si cette différence dans le succès du recrutement pouvait être expliqué par une différence de survie post-dissémination. Pendant une année, nous avons suivi expérimentalement des glands de chêne vert cachés dans un écosystème de savane forestière en Espagne centrale, et nous avons enregistré les chapardages des caches, les types de chapardage, la fouille des sangliers, l'émergence des semis, la survie des semis et les causes de la mortalité

• Le chapardage dans les caches a été significativement plus faible dans la savane (8 %) que dans la forêt (21 %). Toutefois, la survie plus élevée dans les caches été plus que compensée par une baisse de l'émergence des semis et, en particulier, par une mortalité des semis neuf fois plus élevée dans la savane, principalement due à la dessiccation. La fouille des racines par les sangliers n'est pas différente entre les caches expérimentales et les témoins sans glands, indiquant que les mises en cache des glands ne déclenchent pas activité de fouille des racines.

• Nos résultats indiquent que la différence de survie post-dissémination entre la savane et la forêt est due à la baisse d'émergence et en premier lieu, à une mortalité plus élevée des semis dans la savane, et non pas à des chapardages des caches plus élevés. L'absence de sites abris tels que les arbustes, très présents dans la forêt, peut expliquer l'absence de recrutement dans la savane. Des mesures de gestion apparaissent nécessaires pour une persistance à long terme des savanes méditerranéennes.

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## 1. INTRODUCTION

Approximately 31 000 km<sup>2</sup> of Spain and Portugal are covered with intensively manipulated savanna-like ecosystems, locally called dehesa or montado. The predominant trees in these ecosystems are scattered holm oak (*Quercus ilex*) and cork oak (*Quercus suber*) that grow over a grassland matrix that is commonly used for extensive livestock grazing. These savannas were derived from the original Mediterranean forests by shrub clearing, ploughing and tree thinning since the late Middle Ages, but mostly between 1850 and 1950 (Díaz et al., 1997). Besides high economic and social values these savannas harbour a high and unique biological diversity and have therefore qualified to be preserved within the EU Habitats Directive. However, the long-term persistence of the savannas is threatened by a chronic lack of natural recruitment of oaks, in contrast with the original forests where natural tree recruitment is occurring frequently (Gómez, 2004; Leiva and Fernández-Alés, 2003; Pulido et al., 2001). This means that when adult trees in savanna are lost, they are rarely replaced by recruits, causing the now typical landscape to convert to treeless pastures.

Ecologists have identified various possible causes for the oak recruitment failure. In general, tree recruitment may be hampered by limitations at the source (source limitation), at dispersal (dispersal limitation), or at establishment (establishment limitation), being neither mutually exclusive nor independent (Nathan and Muller-Landau, 2000; Schupp et al., 2002). In holm oak savannas, source limitation, occurring when the number of available seeds (at parent tree) limits recruitment, does not appear to play an important role. The yearly acorn crops in both savanna and forest, although irregular, are massive (up to 38 000 acorns/tree (Díaz et al., 2007)) and the effects of insect damage to flower and fruit production are negligible (Díaz et al., 2004). However, high damage rates of acorns by weevils (*Curculio elephas*) can locally occur (Bonal et al., 2007). Dispersal limitation, on the other hand, occurring when recruitment is limited by the dispersal of the available seeds, has been suggested as an important cause of the lack of oak recruitment in the Mediterranean savanna (Pulido and Díaz, 2005). Oaks largely depend on scatter-hoarding animals to disperse seeds. These animals cache acorns in the soil away from the parent tree, retrieving them later when food is less available (Den Ouden et al., 2005; Gómez, 2003). Non-retrieved cached acorns have a higher chance to become seedlings than non-cached acorns as caching reduces seed predation and desiccation (Herrera, 1995; Leiva and Fernández-Alés, 2003) and facilitates seed germination, seedling emergence and seedling establishment (Gómez, 2004); hence, scatter hoarders effectively act as seed dispersers. However, the number of acorns successfully dispersed and cached are reported to be lower in savanna than in forest, possibly due to lower rodent and jay densities, fewer suitable cache sites and higher rates of seed predation by large ungulates (Muñoz and Bonal, 2007; Pulido and Díaz, 2005). While dispersal limitation is now recognized as important factor affecting tree recruitment in the savanna, relatively little is known about the importance of establishment limitation –

the survival of seeds and seedlings *after* successful dispersal and caching by scatter hoarders. Hence, there is a great need of studies that include tracking of dispersed acorns to identify limiting factors for oak recruitment (Pulido and Díaz, 2005).

We suggest three main processes that may cause establishment limitation of oaks. Firstly, cached acorns may be recovered and consumed by the individual that cached them or by pilfering con-specifics. Cache pilferage by con-specifics is likely as rodents generally detect caches by olfaction (Leaver and Daly, 2001; Vander Wall and Jenkins, 2003). Furthermore, cached acorns may be excavated and consumed by other granivorous animals: wild boar (*Sus scrofa*) appears to trace and pilfer cached acorns (Focardi et al., 2000; Pulido and Díaz, 2005). Secondly, cached acorns may fail to germinate and emerge due to rotting or desiccation when cached in unsuitable habitat. Thirdly, the emerged seedling may die due to summer drought, the main mortality cause for one-year old seedlings in Mediterranean systems (Gómez, 2004; Gómez-Aparicio et al., 2006), or by herbivory from insects, rodents or ungulates (Gómez et al., 2003). We expect that the magnitude of these various forms of establishment limitation (cache survival, seedling emergence and seedling survival) differs largely between savanna and forest and contributes to the observed difference in final recruitment success between these habitats.

The main aim of this study was to investigate whether differential establishment limitation contributes to the difference in oak recruitment success between the Mediterranean savanna and forest. Our approach was to mimic successfully dispersed seeds by experimentally caching individual acorns in both habitats. The additional value to prior studies is that we monitored cache survival, emergence and seedling survival of the same cohort during one year, at increasing distance from seed bearing trees, and that we quantified wild boar activity which we related to cache survival. We hypothesized that establishment limitation of holm oak was greater in savanna than in forest due to (1) higher pilferage in savanna than in forest from rodents and rooting wild boar, (2) lower seedling emergence in savanna than forest due to desiccation of the cached acorns, and (3) higher seedling mortality in savanna than in forest due to desiccation as well as herbivory.

## 2. MATERIALS AND METHODS

### 2.1. Study area

Fieldwork was carried out at the Cabañeros national park, Ciudad Real province in central Spain (39° 24 N, 3° 35 W) from early November 2005 to mid October 2006. The park represents a Mediterranean savanna – forest ecosystem of ca 38 000 ha that is characteristic for the Iberian Peninsula considering climate, species composition, land-use, history and presently raised limited tree regeneration. The climate is continental Mediterranean with a mean annual precipitation of 522.9 mm and a mean annual temperature ranging from 9–14 °C, with minima and maxima of –11.3 °C and 43 °C in winter and summer, respectively (personal communication parque nacional de Cabañeros). The park consists of two contrasting habitat types: (1) a large continuous Mediterranean montane forest (hereafter forest)

with a tree density of ca 30 trees ha<sup>-1</sup> dominated by holm oak (*Quercus ilex* subsp. *ballota* (Desf.) Samp.) and cork oak (*Quercus suber* L.) and a dense shrub layer dominated by the tall sclerophyllous evergreens *Cistus ladanifer* L. and *Phyllirea angustifolia* L., and; (2) a large continuous Mediterranean oak savanna (hereafter savanna), i.e. a plane grassland with scattered oaks (ca 14 trees ha<sup>-1</sup>, predominantly holm oak) and a nearly absent shrub layer. This savanna was primarily created in the 1950's and 60's through shrub clearing and tree thinning to promote grassland for extensive livestock grazing. All farming activities ceased in the 1970's after which the area was mainly used for big game hunting until 1995, when the National Park was founded. Similar transitions from livestock grazing towards natural grazing with wild ungulates have occurred in both Spain and Portugal.

Current densities of red deer *Cervus elaphus* are relatively high (0.13 ha<sup>-1</sup>, Parque Nacional de Cabañeros, personal communications) and are, together with wild boar (*Sus scrofa*), the main acorn predators at the study site (Bonal and Muñoz, 2007). Other mammalian consumers of acorns and seedlings in the study site are wood mouse (*Apodemus sylvaticus*), Algerian mouse (*Mus spretus*) and, to a lesser extent, roe deer (*Capreolus capreolus*), Iberian hare (*Lepus granatensis*) and rabbit (*Oryctolagus cuniculus*). Avian acorn consumers in the park are wood pigeon (*Columba palumbus*) and European jay (*Garrulus glandarius*), the latter being rare in the savanna. Scatter hoarding Wood mouse and Algerian mouse are the main dispersers of acorns at the study site (Díaz et al., 2007; Muñoz and Bonal, 2007).

## 2.2. Experimental design

Early November 2005 we picked approximately 2000 acorns directly from the canopy of 20 randomly selected trees that were widely distributed over the study area. We discarded all unsound acorns and acorns with weevil oviposition marks, as well as the largest and the smallest acorns, to homogenize the size of experimental seeds. Mean fresh weight of the remaining acorns was 6.04 g (SD: 1.37;  $n = 200$ ; measured without cap). All acorns were stored at 4 °C until further handling.

On 15 November 2005, around the peak of seed fall, we selected 20 large seed-bearing holm oaks in each of the two habitat types (forest and savanna). To warrant independence between trees within each habitat type we selected isolated trees with no other seed bearing individuals present within 50 m radius. We considered this distance large enough to avoid interference of other seed bearing holm oaks considering additional seed input and attractiveness to seed predators. Nearest distance between selected trees for both habitat types was on average  $167 \pm 75$  m and ranged between 60 and 298 m. The selected 40 holm oaks were widely scattered over both habitat types, hence are replicated units within habitat type at our study site.

We mimicked a rodent-made cache by burying a single acorn horizontally at approximately 2 cm depth (Den Ouden et al., 2005). To test for possible effects of distance to the tree on cache survival we made four caches per tree; one under the tree canopy (0 m) and one at 5, 15 and 30 m distance from the tree base along a transect radiating in a random direction. These four caches per transect were marked with small 1 × 12 cm wooden sticks placed in the soil (with maximal 2 cm visible) at the selected four distances. Acorns were buried 50 cm from these sticks, alternating north and south, while minimizing soil disturbance to avoid attracting seed pilferers. Prior

studies showed that the applied marking technique did not significantly attract seed pilferers, such as wild boar or rodents (Smit et al, unpublished data). All acorn handling was done wearing gloves to minimize human scent on acorns (Duncan et al., 2002). The savanna plots were situated in grassland, with an average vegetation height of ca 40 cm (measured in June 2006), and the forest plots were all situated under shrub canopy. In order to test for random or directed wild boar rooting (attracted by the presence of a cached acorn), we placed and marked a second paired transect of four plots, without placing acorns, in opposite direction from the first transects.

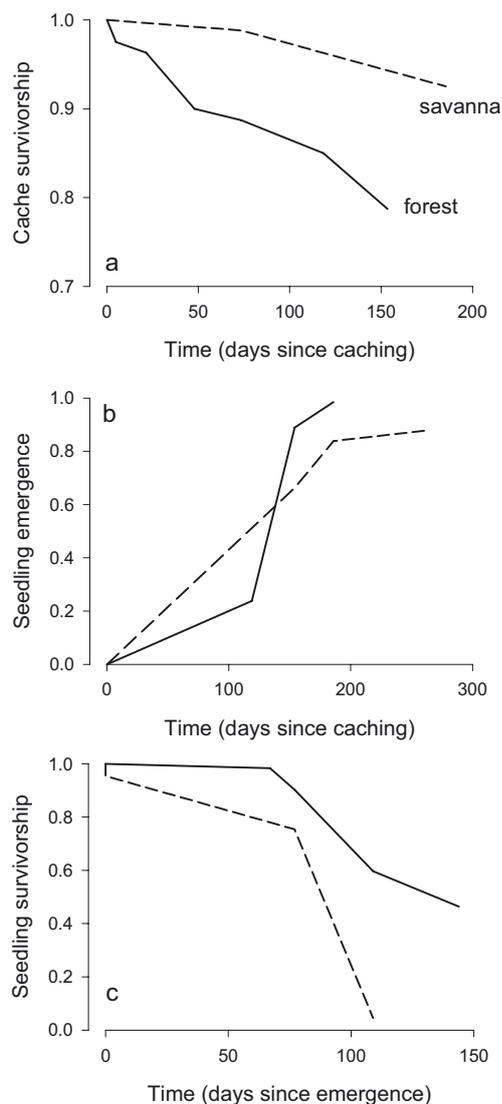
We monitored the plots for nearly one full year, 9 times in total, at 11, 34, 64, 85, 106, 133, 176, 207 and 340 days after caching. For each cached acorn ( $n = 160$ ) we recorded: cache fate (acorn present or removed by careful touching), acorn emergence (above-ground seedling parts visible), and seedling survival. If an acorn was removed we recorded type of cache predator (wild boar: soil uprooted but cotyledons present; rodent: acorn removed, shallow digging marks). We did not consider re-caching of removed acorns by rodents, assuming that the vast majority of excavated seeds were killed. When a seedling had died we tried to assess the mortality cause (drought, herbivory, pilfering). We assumed that seedlings died of desiccation when stems were completely dried out and when no more chlorophyll was visible. We recorded rooting rates of wild boars by estimating the proportion of freshly uprooted soil in a 4 m<sup>2</sup> quadrat around the plots with and without acorns ( $n = 320$ ) using the 7-level Braun-Blanquet scale (Braun-Blanquet, 1964). Fresh and old rooting activities were easily distinguished in the field; hence, overestimation of rooting activities by double counting of the same event was unlikely. Rooting rates were recorded 6 times in total; at 11, 34, 64, 85, 106, 133 days after caching.

## 2.3. Analyses

We used time-to-event analysis (a.k.a. survival analysis, duration analysis or reliability analysis) to examine and compare the effects of habitat and distance to trees on cache pilferage, seedling emergence, seedling mortality and rooting activity by wild boar. Rooting of plots with acorns was analyzed as binomial variable ( $> 5\%$  plot rooted or  $< 5\%$  rooted). Waiting times (e.g., time-to-removal and time-to-emergence for seeds, time-to-death for seedlings) were analyzed with Cox Proportional Hazard modelling. Cox models were fitted with the survival library in R 2.4.0 (R Development Core Team, 2006). We used the cluster option and robust log-rank statistics, based on grouped jackknife estimates of the variance, to account for dependence of observations on seeds and seedlings located around the same experimental tree. To test whether presence of cached acorns affected wild boar rooting we used paired  $t$ -tests (two-tailed). We converted the Braun-Blanquet rooting values into percentage median values and calculated the mean rooting and cumulative rooting over the measured period for each quadrat. To avoid pseudo-replication, we took the average of these values across the four distances per tree (0, 5, 15, 30 m) and then compared pairwise between quadrats with and without cached acorns of the same experimental tree ( $n = 40$ ).

## 3. RESULTS

*Cache survival* – In total, 14% of the cached acorns were removed before they emerged. Rates of pre-emergence seed



**Figure 1.** Post-dispersal fate of *Quercus ilex* seeds and seedlings compared between Mediterranean oak forest and savanna, since caching at 15 November 2005. Proportions shown are Kaplan-Meier survival estimates. (a) removal of seeds from artificial caches prior to seedling emergence; (b) emergence of seedlings from non-pilfered caches; (c) mortality of seedlings after emergence; note that here  $t = 0$  reflects time since emergence, which differs between savanna and forest.

survival were significantly higher in savanna than in forest (Cox regression, robust log-rank test:  $e^{\beta} = 0.4$ ,  $\chi_1^2 = 6.33$ ,  $P = 0.012$ ; Fig. 1a). Ultimately, the proportion of caches pilfered was more than twice as high in forest (21%) as in savanna (8%). This result is not in agreement with our first prediction. Also, most cache pilferage (78%) was due to rodents rather than wild boar, especially in the forest (88%).

The overall rooting by wild boars was  $1.3\% \pm 1.6$  in the savanna quadrats and  $1.6\% \pm 1.6$  in forest quadrats (means  $\pm$  sd). Rooting rates were not significantly different between savanna and forest (Cox regression, robust log-rank test:  $\chi_1^2 =$

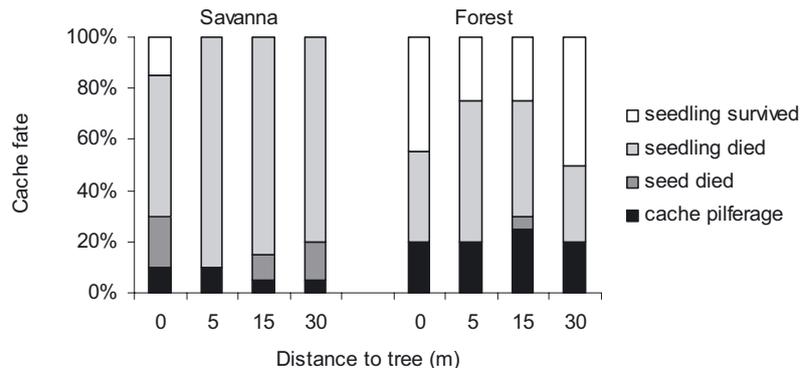
0.06,  $P = 0.81$ ). Also, paired t-tests showed that quadrats with and without acorns did not differ significantly in mean rooting ( $1.4\% \pm 1.5$  versus  $1.4\% \pm 1.6$ ,  $t$ -value =  $-0.056$ ,  $P = 0.955$ ) or cumulative rooting ( $7.9\% \pm 8.7$  versus  $8.5\% \pm 9.8$ ,  $t$ -value =  $-0.366$ ,  $P = 0.716$ ). Hence, the presence of individual cached acorns did not affect wild boar rooting behaviour.

**Seedling emergence** – The overall emergence of non-removed acorns was relatively high (94%). However, the rates of seedling emergence were significantly lower in savanna than in forest (Cox regression with pilfered caches as censored observations:  $e^{\beta} = 2.0$ ,  $\chi_1^2 = 12.2$ ,  $P < 0.001$ ; Fig. 1b). For non-pilfered caches, the proportion of seeds failing to emerge was six times greater in savanna (9 out of 74 non-pilfered caches = 12%) than in forest (1 out of 63 non-pilfered caches = 2%) (Chi-squared test:  $\chi_1^2 = 4.2$ ,  $P < 0.05$ ). This result is in agreement with our second hypothesis.

**Seedling survival** – Among emerged seedlings ( $n = 127$ ), survival rates were significantly lower in savanna than in forest ( $e^{\beta} = 4.0$ ,  $\chi_1^2 = 25.7$ ,  $P < 0.001$ ; Fig. 1c). At the end of the study, the proportion of seedlings surviving was nine times higher in forest (47%,  $n = 62$ ) than in savanna (5%,  $n = 65$ ). This result is in agreement with our third hypothesis. Desiccation during summer drought was identified as the main cause of seedling death in savanna and forest (84 out of 95 seedlings = 88%). The other 12% of the emerged seedlings (11 out of 95) died after removal of the still attached acorn by rodents, but as some undamaged seedlings did not die immediately after this separation it is possible that they also died of desiccation rather than of acorn removal. At the end of the experiment one seedling had survived after removal of the acorn by rodents. There was no seedling mortality due to herbivory by insects, rodents or ungulates. The high seedling mortality in savanna was associated with lack of tree canopy cover: three of 14 seedlings located below trees (distance = 0 m) survived, while none of 51 seedlings located away from tree cover (5, 15, 30 m distance) survived (Chi-squared test:  $\chi_1^2 = 44.7$ ,  $P < 0.001$ ). This contrasts with the forest where 9 of 16 seedlings located below trees survived, against 20 of 50 seedlings away from trees (Chi-squared test:  $\chi_1^2 = 1.0$ ,  $P < 0.317$ ). Overall, cached seeds were more likely to escape pilferage by rodents in savanna than in forest, but this advantage was more than offset by lower rates of seedling emergence and particularly by higher seedling mortality due to desiccation (Fig. 2). Distance to tree did not contribute significantly to any of the Cox models above.

#### 4. DISCUSSION

**Cache survival** – Cache pilferage did not play an important role in limiting oak recruitment in the savanna (8%). We acknowledge that we may have underestimated cache pilferage as natural caches (e.g. by scatter hoarding rodents) are probably retrieved faster, particularly by the original scatter-hoarding rodents (Vander Wall et al., 2006), than the artificial caches used in our experiment. Yet, we consider it unlikely that this affected the observed difference in establishment success between savanna and forest. In fact, in contrast to our



**Figure 2.** Final cache fate (cache pilferage, death of seed and seedling and seedling survival) in savanna and forest at 0, 5, 15 and 30 m from tree, 340 days after caching.

hypothesis, cache pilferage was significantly higher in the forest than in the savanna. This difference in cache pilferage by rodents and wild boar between the two habitats probably reflects differences in animal densities. Rodent densities are generally higher in areas with higher shrub cover (Pons and Pausas, 2007), offering more food and protection against predators. In the savanna, where such a protective shrub layer is generally lacking, rodent densities are commonly relatively low (Díaz et al., 1993). This lower rodent abundance in savannas may also be an effect of higher ungulate densities, not so much by alteration of vegetation cover or by food competition, but by direct disturbance of rodent habitat via soil compaction, trampling and rooting (Muñoz et al., 2008).

Cache pilferage by wild boars was very low in our study, even in the forest plots, despite frequent and numerous rooting traces and visual observations suggesting high densities. These results are in contrast with studies of others who claim that wild boars are important predators of (buried) acorns in Mediterranean forests (Focardi et al., 2000; Gómez et al., 2003; Pulido and Díaz, 2005). There are several explanations for this observed difference. Firstly, we think that the individually-cached acorns were not easily detected by the boars because of the low acorn density. Others used higher acorn densities in their experiments and higher densities may increase the chance of being detected by wild boar (Winterink, 2006). Secondly, it is possible that boars did detect the cached acorns but didn't find them rewarding enough to start rooting. However, our data does not support this idea because squares with and without cached acorns were equally rooted. Thirdly, it is possible that wild boar do not actively look for cached acorns per se (as suggested by Focardi et al., 2000), but more generally search for available food by smell in random search patterns. This may explain why in some plots with cached acorns rooting was observed, while the cached acorn itself was not taken away.

*Seedling emergence and survival* – Although the rate of emergence was relatively high and similar to that found by others (Pulido and Díaz, 2005), it was lower in savanna than in forest, mostly due to desiccation. This suggests that protection against summer drought is important already during seedling emergence. Desiccation during summer drought was also the

main mortality cause for establishing oak seedlings, while no seedlings died from insect or ungulate herbivory. Previous studies have shown that shrubs, absent in savannas but omnipresent in forests, facilitate oak seedling survival particularly by shading (Smit et al., 2008). Protection of first year's tree seedlings against summer drought is of crucial importance for survival in harsh Mediterranean environments (Castro et al., 2004; Gómez-Aparicio et al., 2006). Because of the lower emergence and seedling survival we suggest that the recruitment limitation in the Mediterranean savanna is, at least partly, caused by the absence of a protective shrub layer.

Twelve percent of the seedlings had their acorns removed by rodents after emergence, although this did not immediately lead to seedling death. In fact, one of these seedlings with a removed acorn managed to survive until the end of this experiment. Similar results have been found by others (García-Cebrian et al., 2003) who showed that seedling survival of *Quercus robur* was not affected by the removal of cotyledons, although it did have negative consequences for seedling growth (notably stem length and biomass). It appears that cotyledon removal only has dramatic effects when it happens in the first week after emergence. These studies again show the advantages to the players of the 'symbiosis' between oaks and animals: the tree profits from dispersers as its seeds reach safe sites and establish as seedlings, while the disperser is rewarded by the nutritious seeds when it comes back to the caches during food scarcity.

*Distance dependence and discordance* – Distance to trees did not affect cache pilferage, seedling emergence, seedling survival or rooting by wild boar in our study. This is in contrast with the classical distance-dependant recruitment hypothesis of Janzen and Connell and findings of others (Janzen, 1970; Nathan and Muller-Landau, 2000) stating that the survival of seeds and seedlings increases as distance from the parent tree increases. In fact, we found that the only three surviving seedlings in the savanna were situated under trees. While in most of these studies the increased seed and seedling mortality near parent trees is attributed to higher risk of predation, herbivory or fungal attack, we found that desiccation was the most important cause of mortality. Mortality was not affected by distance to trees but was, in contrast, strongly dependent on

habitat. This indicates that the availability of suitable habitat, e.g. shrubs providing shade, is a better explanatory variable for post-dispersal seedling survival than just the distance to trees.

The final recruitment pattern, as found in our study, deviates considerably from the original caching pattern. Similar discordance among seed rain and recruitment has been found for a wide range of woody species, predominantly for animal dispersed fruits (e.g. Jordano and Herrera, 1995), but also for wind dispersed seeds (Smit et al., 2006). In our study, discordance was not caused by cache pilferage, but appeared due to the distribution of suitable habitat and its effect on desiccation. The distribution of suitable habitat appears the main driver behind our observed final recruitment pattern. This and the absence of any distance-dependent effects are consistent with the recent findings of Hyatt et al. (2003) who could not discover any general support for the distance-dependant recruitment hypothesis in a meta-analysis of temperate and tropical forests.

*Oak recruitment failure in Mediterranean savannas* – Although we acknowledge the limited scope of our study, with focus on Cabañeros National Park, we consider our results relevant to other Mediterranean savanna ecosystems given the representative conditions of our site concerning climate, species composition, land-use, history and limited oak recruitment. When we extrapolate our results to recruitment failure in Mediterranean oak savannas in general it appears that, besides the already suggested role of dispersal limitation (Pulido and Díaz, 2005), establishment limitation plays an important role in hampering recruitment. This implies that tree recruitment failure in oak savannas is multiple-staged: to begin with, seed dispersal is insufficient due to low rodent and jay densities, despite large amounts of acorns available in autumn. As a consequence, few acorns arrive safely cached in the soil. Second, chances of any cached seeds establishing into seedlings and surviving the first summer drought are very small. This seems largely due to the lack of safe sites, such as near shrubs, which help protect emerging and establishing seedlings from desiccation. So, both dispersal and establishment limitation simultaneously hinder holm oak recruitment in the Mediterranean savanna, resulting in an ecosystem with arrested succession, a phenomenon described for various ecosystems, particularly after large-scale disturbances (Scheffer et al., 2001). In order to restart and maintain oak recruitment in the Mediterranean savanna management measures are needed that act at multiple stages. One possibility is to focus on maintaining and increasing a protective shrub layer, for example, by temporary set-aside management (Ramírez and Díaz, 2008). This would probably lead to increased rodent densities, needed for dispersal, and at the same time improved survival chances for tree seedlings by providing shade. Facilitation by shrubs may become increasingly important in the Mediterranean savanna given the expected prolonged droughts due to climate change. Management measures appear indispensable to overcome the multiple-staged recruitment limitations and to promote long-term persistence of the Mediterranean savanna.

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## REFERENCES

- Bonal R., Muñoz A., and Díaz M., 2007. Satiation of predispersal seed predators: the importance of considering both plant and seed levels. *Evol. Ecol.* 21: 367–380.
- Bonal R. and Muñoz A., 2007. Multi-trophic effects of ungulate intraguild predation on acorn weevils. *Oecologia* 152: 533–540.
- Braun-Blanquet J., 1964. *Pflanzensoziologie. Grundzüge der Vegetationskunde.* Springer, Wien, New York.
- Castro J., Zamora R., Hódar J.A., Gómez J.M., and Gómez-Aparicio L., 2004. Benefits of using shrubs as nurse plants for reforestation in Mediterranean mountains: A 4-year study. *Restor. Ecol.* 12: 352–358.
- Den Ouden J., Jansen P.A., and Smit R., 2005. Jays, Mice and Oaks: predation and dispersal of *Quercus robur* and *Q. petraea* in North-western Europe. In: Forget J.E., Lambert P.E., Vander Wall S.B. (Eds.), *Seed Fate*, CAB International, pp. 223–239.
- Díaz M., Alonso C.L., Arroyo L., Bonal R., Muñoz A., and Smit C., 2007. Desarrollo de un protocolo de seguimiento a largo plazo de los organismos clave para el funcionamiento de los bosques mediterráneos. In: Ramírez L. (Ed.), *Investigación en la red organismo autónomo parques nacionales*, Madrid.
- Díaz M., Campos P., and Pulido F.J., 1997. The Spanish dehesas: a diversity of land use and wildlife. In: D. Pain and M. Pienkowski (Ed.), *Farming and birds in Europe*, Academic Press, London, pp. 178–209.
- Díaz M., Gonzalez E., Munozpulido R., and Naveso M.A., 1993. Effects of food abundance and habitat structure on seed-eating rodents in Spain wintering in Man-Made habitats. *Mamm. Biol.* 58: 302–311.
- Díaz M., Pulido F.J., and Moller A.P., 2004. Herbivore effects on developmental instability and fecundity of holm oaks. *Oecologia* 139: 224–234.
- Duncan R.S., Wenny D.G., Spritzer M.D., and Whelan C.J., 2002. Does human scent bias seed removal studies? *Ecology* 83: 2630–2636.
- Focardi S., Capizzi D., and Monetti D., 2000. Competition for acorns among wild boar (*Sus scrofa*) and small mammals in a Mediterranean woodland. *J. Zool.* 250: 329–334.
- García-Cebrian F., Esteso-Martínez J., and Gil-Pelegrin E., 2003. Influence of cotyledon removal on early seedling growth in *Quercus robur* L. *Ann. For. Sci.* 60: 69–73.
- Gómez-Aparicio L., Valladares F., and Zamora R., 2006. Differential light responses of Mediterranean tree saplings: linking ecophysiology with regeneration niche in four co-occurring species. *Tree Physiol.* 26: 947–958.
- Gómez J.M., 2003. Spatial patterns in long-distance dispersal of *Quercus ilex* acorns by jays in a heterogeneous landscape. *Ecography* 26: 573–584.
- Gómez J.M., 2004. Importance of microhabitat and acorn burial on *Quercus ilex* early recruitment: non-additive effects on multiple demographic processes. *Plant Ecol.* 172: 287–297.
- Gómez J.M., Garcia D., and Zamora R., 2003. Impact of vertebrate acorn- and seedling-predators on a Mediterranean *Quercus pyrenaica* forest. *For. Ecol. Manage.* 180: 125–134.
- Herrera J., 1995. Acorn predation and seedling production in a low-density population of cork oak (*Quercus suber* L.). *For. Ecol. Manage.* 76: 197–201.

- Hyatt L.A., Rosenberg M.S., Howard T.G., Bole G., Fang W., Anastasia J., Brown K., Grella R., Hinman K., Kurdziel J.P., and Gurevitch J., 2003. The distance dependence prediction of the Janzen-Connell hypothesis: a meta-analysis. *Oikos* 103: 590–602.
- Janzen D.H., 1970. Herbivores and number of tree species in tropical forests. *Am. Nat.* 104: 501–528.
- Jordano P. and Herrera C.M., 1995. Shuffling the offspring: uncoupling and spatial discordance of multiple stages in vertebrate seed dispersal. *Ecoscience* 2: 230–237.
- Leaver L.A. and Daly M., 2001. Food caching and differential cache pilferage: a field study of coexistence of sympatric kangaroo rats and pocket mice. *Oecologia* 128: 577–584.
- Leiva M.J. and Fernández-Alés R., 2003. Post-dispersive losses of acorns from Mediterranean savannah-like forests and shrublands. *For. Ecol. Manage.* 176: 265–271.
- Muñoz A. and Bonal R., 2007. Rodents change acorn dispersal behaviour in response to ungulate presence. *Oikos* 116: 1631–1638.
- Muñoz A., Bonal R., and Díaz M., 2009. Ungulates, rodents, shrubs: interactions in a diverse Mediterranean ecosystem. *Basic Appl. Ecol.* 10: 151–160.
- Nathan R. and Muller-Landau H.C., 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends Ecol. Evol.* 15: 278–285.
- Pons J. and Pausas J.G., 2007. Rodent acorn selection in a Mediterranean oak landscape. *Ecol. Res.*, 22: 535–541.
- Pulido F.J. and Díaz M., 2005. Regeneration of a Mediterranean oak: a whole-cycle approach. *Ecoscience* 12: 92–102.
- Pulido F.J., Díaz M., and de Trucios S.J.H., 2001. Size structure and regeneration of Spanish holm oak *Quercus ilex* forests and dehesas: effects of agroforestry use on their long-term sustainability. *For. Ecol. Manage.* 146: 1–13.
- R Development Core Team, 2006. R: A language and environment for statistical computing. R foundation for statistical Computing, Vienna, Austria.
- Ramírez J.A. and Díaz M., 2008. The role of temporal shrub encroachment for the maintenance of Spanish holm oak *Quercus ilex* dehesas. *For. Ecol. Manage.* 255: 1976–1983.
- Scheffer M., Carpenter S., Foley J.A., Folke C., and Walker B., 2001. Catastrophic shifts in ecosystems. *Nature* 413: 591–596.
- Schupp E.W., Milleron T., and Russo S.E., 2002. Dissemination limitation and the origin and maintenance of species-rich tropical forests. In: Levey D.J., Sivila W.R., Galetti M. (Eds.), *Seed dispersal and frugivory: ecology, evolution and conservation*, CAB International, Wallingford, pp. 19–33.
- Smit C., Den Ouden J., and Díaz M., 2008. Facilitation of holm oak recruitment by shrubs in Mediterranean open woodlands. *J. Veg. Sci.* 19: 193–200.
- Smit C., Gusberti M., and Müller-Schärer H., 2006. Safe for saplings; safe for seeds? *For. Ecol. Manage.* 237: 471–477.
- Vander Wall S.B., Briggs J.S., Jenkins S.H., Kuhn K.M., Thayer T.C., and Beck M.J., 2006. Do food-hoarding animals have a cache recovery advantage? Determining recovery of stored food. *Anim. Behav.* 72: 189–197.
- Vander Wall S.B. and Jenkins S.H., 2003. Reciprocal pilferage and the evolution of food-hoarding behavior. *Behav. Ecol.* 14: 656–667.
- Winterink A., 2006. Does miss Piggy rob Micky Mouse? Research on seed dispersal by wood mice (*Apodemus sylvaticus*) and seed predation by wild boar (*Sus scrofa*). MSc thesis, Wageningen University, Wageningen.