Factores determinantes del reclutamiento de encinas (*Quercus ilex*) en mosaicos agroforestales.

Dispersión de bellotas por urracas (*Pica pica*) y establecimiento de plántulas.

Tesis Doctoral

Loreto Martínez de Baroja Villalón
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A mi familia

Índice

Abstract

Forest restoration is a major ecological challenge in many regions of the world. In Mediterranean environments, aridity, lack of propagules and their dispersers, seed predation, herbivory, and some plant-plant interactions such as competition, are major limitations for the restoration of forests in old fields. The main objective of this PhD Thesis was to assess the effect of different ecological factors on the recruitment of holm oak (*Quercus ilex*) in old fields. The Thesis focuses on the dispersal of acorns by magpie (*Pica pica*) and the emergence, the survival, and the establishment of holm oak seedlings.

The Thesis contains seven chapters. **Chapter 1** is a general introduction in which the main factors that determine oak recruitment are presented. There are four research chapters. **Chapters 2** and **3** quantify and assess acorn dispersal by magpie. **Chapters 4** and **5** study the post-dispersal processes driving emergence, early survival and establishment of holm oak juveniles. **Chapter 6** integrates and discusses the results of the research chapters in the framework of oak colonization and proposes applications for old field restoration and future research lines. Finally, **Chapter 7** summarizes the main conclusions of this Thesis.

In **Chapter 2** we quantified the acorn dispersal capacity by magpie, according to their breeding status (breeding individuals vs. juveniles) and sex. The magpies removed more than half of the annual production of acorns from the trees. Breeding magpies were the main acorn scatter-hoarders, especially breeding males, which dispersed around twice as many acorns as breeding females. Magpies cache 86% of the acorns they remove, and one magpie can store more than 1,300 acorns for 6 weeks at an average distance of 32.5 m (1.4-210 m) from the holm oak. Up to 2.4% of the acorns dispersed by magpies were not recovered or predated, resulting in a high density of emerged oak seedlings (56–439 seedlings/ha). These results indicate that the magpie is a massive and effective acorn disperser and may play a key role in recruitment of oaks in open agroforestry systems.

In **Chapter 3** we studied the role of caching territories and spatial preferences at different scales by magpies to cache acorns. The selection of sites to cache acorns followed a hierarchical decision-making process in which the caching territories constrained both the dispersal distance and the availability at different spatial scales of sites to cache the acorns. At the coarsest spatial scale (habitat), magpies selected the tilled areas over the oak plantation and this woodland over the old fields. At the sub-habitat scale, magpies selected the areas with high plant-productivity within the plantation. At the microsite and type of material scale (the finest scale), they selected the structures built by animals and the least abundant material in each site to cache the acorns. Habitat-scale preferences matched the density of emerged seedlings in different habitat types. Therefore, magpie caching territoriality indirectly drives the emergence of oak seedlings, and thereby potential oak recruitment and forest regeneration.

In **Chapter 4** we analyse how post-dispersive acorn and seedling predation and the orientation and distance to planted woodland islets affect the emergence and early survival of seedlings. The 96.9% of the unprotected acorns were predated. The least harsh microclimate in the least sun exposed orientation (north) promoted the emergence of twice as many seedlings (42.9%) than in the south orientation (13.2%). Survival of the spontaneously established seedlings was 28.6% after the first summer. Drought (45%) and seedling herbivory (35%) were the main causes of mortality.

In **Chapter 5** we evaluate the effect of woodland islets, which were planted 25 years ago to assist natural holm oak regeneration in old fields, on oak seedling emergence and short-term survival for four consecutive years and the long-term establishment of juveniles. Wet springs and summers increased both seedling emergence and survival. Seedlings emerged in wet springs had higher survival after summer drought. Emergence and survival were highest in the less sun-exposed orientations. Microsites close to the islets in less sun-exposed orientations and far from the islets in the most sun-exposed orientation enhanced oak seedling emergence and early survival but did not affected annual growth rate. Herb biomass was lower near the islets due to the competition of the planted oaks. Twenty-five years after the plantation of the holm oak forest islets, 92 new individuals have been established spontaneously, resulting in a recruitment rate of 5.7 individuals ha^{-1} year^{-1}. Planted islets were effective for the passive restoration of Mediterranean woodland on old fields.

In conclusion, this Thesis shows that magpies are massive and effective acorn scatter-hoarders, which are keys for oak recruitment in old fields. Magpie territories constrain dispersal distance and the availability of places to cache acorns. Habitat types preference for acorn caching matched the density of emerged seedlings in the different habitats. The distance and orientation to the seed source determines the fate of acorns as they drive the emergence, early survival, and establishment of new individuals. Holm oak woodland islets provide the necessary acorns for the restoration of old fields where the remnants of this type of vegetation are scarce. Conservation and promotion of magpie populations, woodland islets plantation, ploughing old fields after abandonment and controlling acorn predators and herbivores could speed oak forest restoration in old fields.

Keywords: abandoned fields, acorn predation, acorn caching preferences, applied nucleation, *Corvidae*, forest recovery, forest natural regeneration, herbivory, Mediterranean forest, oak forest regeneration, plant-animal interaction, plant-plant interaction, seed-dispersal effectiveness, seed scatter-hoarding, seedling survival, summer drought, synzoochory, tree islets, zoochory.

Resumen

La restauración forestal es uno de los grandes retos ecológicos en muchas regiones del mundo. En ambientes mediterráneos existen factores como la aridez, la falta de propágulos y sus dispersores, la depredación de semillas, la herbivoría y algunas interacciones planta-planta como la competencia, que limitan la restauración forestal en los campos agrícolas abandonados. El objetivo general de esta Tesis Doctoral fue evaluar el efecto de diferentes factores en el reclutamiento de encinas (*Quercus ilex*) en campos agrícolas abandonados, centrándose en la dispersión de bellotas por urracas (*Pica pica*) y en la emergencia, la supervivencia y el establecimiento de plántulas de encina.

La Tesis consta de siete Capítulos. El **Capítulo 1** es una Introducción general que presenta los principales factores que determinan el reclutamiento de encinas. Hay cuatro capítulos de investigación (**Capítulos 2-5**). En los dos primeros se cuantifica y evalúa el papel de la urraca como dispersora de bellotas. En los dos siguientes se estudian los procesos post-dispersivos que afectan a la emergencia, la supervivencia temprana y el establecimiento de individuos de encina. El **Capítulo 6** integra y discute los resultados obtenidos en los capítulos de investigación en el marco de la colonización de encinas y propone aplicaciones de lo aprendido en esta Tesis a la restauración de campos abandonados y futuras líneas de investigación. Por último, el **Capítulo 7** sintetiza las principales conclusiones de la Tesis.

En el **Capítulo 2** cuantificamos la capacidad de las urracas para dispersar bellotas, teniendo en cuenta el estatus reproductor (reproductores vs. juveniles) y el sexo de los individuos. Las urracas retiraron más de la mitad de la producción anual de bellotas de los árboles. Los adultos reproductores fueron los que más bellotas dispersaron, en especial los machos, que dispersaron casi el doble de bellotas que las hembras. Las urracas almacenan un 86% de las bellotas que remueven, por lo que una urraca puede llegar a almacenar más de 1.300 bellotas durante seis semanas a una distancia media de 32,5 m (1,4-210 m) de la encina madre. Hasta el 2,4% de las bellotas dispersadas por las urracas no fueron recuperadas ni depredadas por estas u otros animales, lo que produjo una alta densidad de

plántulas de quercíneas (56–439 plántulas/ha). Estos resultados indican que la urraca es una dispersora masiva y efectiva de bellotas pudiendo tener un papel clave en el reclutamiento de quercíneas en sistemas agroforestales abiertos.

En el **Capítulo 3** estudiamos el papel de los territorios de almacenamiento y las preferencias de las urracas a distintas escalas espaciales para almacenar las bellotas. La selección de los lugares para el almacenamiento siguió un proceso jerárquico de toma de decisiones en el que los territorios de almacenamiento restringieron tanto la distancia de dispersión como la disponibilidad espacial a distintas escalas de los sitios para esconder las bellotas. A la escala más amplia (hábitat), las urracas seleccionaron las zonas aradas antes que el bosquete y este antes que el herbazal. A escala de sub-hábitat, dentro del bosquete seleccionaron las zonas con alta productividad vegetal. A nivel de micrositio y tipo de materiales (la escala más pequeña), seleccionaron las estructuras creadas por animales y los materiales menos comunes en cada lugar para esconder las bellotas. La preferencia a escala de hábitat coincidió con la densidad de plántulas emergidas en los diferentes hábitats. Por tanto, la territorialidad de la urraca dirige indirectamente la emergencia de plántulas de quercíneas pudiendo determinar su reclutamiento y la regeneración del bosque.

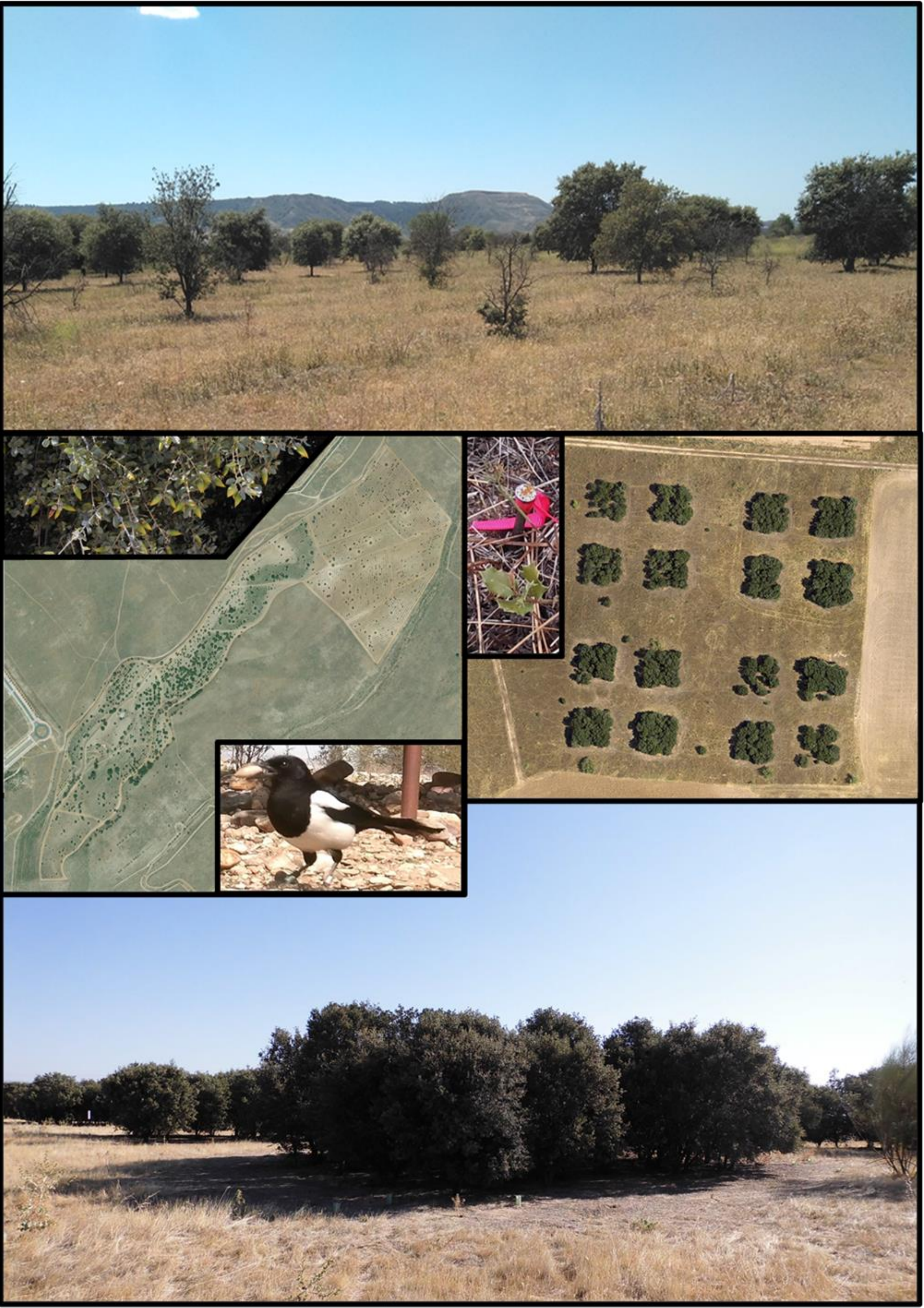
En el **Capítulo 4** analizamos cómo la depredación post-dispersiva de las bellotas, la herbivoría, la orientación y la distancia a los islotes forestales plantados afecta a la emergencia y la supervivencia temprana de las plántulas. El 96,9% de las bellotas sin proteger fueron depredadas. El microclima menos limitante de la orientación norte, la menos expuesta a la insolación, propició que emergieran el doble de plántulas (42,9%) que en la orientación sur (13,2%). La supervivencia de las plántulas establecidas espontáneamente fue del 28,6% tras el primer verano debido principalmente a la mortalidad por sequía (45%) y herbivoría (35%).

En el **Capítulo 5** evaluamos la emergencia y la supervivencia de las plántulas durante cuatro años a partir de islotes forestales plantados hace 25 años, así como el establecimiento a largo plazo de los juveniles. Las primaveras y los veranos húmedos favorecieron tanto la emergencia como la supervivencia de las plántulas. Las plántulas emergidas en primaveras húmedas fueron más tolerantes a la sequía estival. La emergencia y la supervivencia fueron mayores cerca de los islotes en las orientaciones menos expuestas al sol y lejos de los islotes en las más

expuestas, pero la tasa de crecimiento no fue afectada por estos factores. La biomasa de las herbáceas fue menor cerca de los islotes por la competencia de las encinas plantadas. Transcurridos 25 años desde la plantación de los islotes forestales de encina se han establecido de manera espontánea 92 nuevos individuos, con una tasa de reclutamiento de 5,7 individuos ha^{-1} año^{-1}. Los islotes forestales plantados resultaron efectivos para la restauración pasiva de los bosques mediterráneos en campos agrícolas abandonados.

En conclusión, esta Tesis Doctoral demuestra que las urracas son dispersoras masivas y efectivas de bellotas, claves en el reclutamiento de encinas en campos agrícolas abandonados. Los territorios de urraca limitan la distancia de dispersión y la disponibilidad de los lugares para almacenar las bellotas. La preferencia de almacenamiento de bellotas a escala de hábitat coincide con la densidad de las plántulas recién emergidas de quercíneas. La distancia y la orientación a la fuente de semillas determinan el destino de las bellotas, porque afecta a la emergencia, la supervivencia temprana y al establecimiento de nuevos individuos. Los islotes forestales de encinas proveen las bellotas necesarias para la restauración de campos agrícolas abandonados donde los remanentes de este tipo de vegetación son escasos. Algunas medidas como fomentar las poblaciones de urracas, la plantación de islotes forestales inmersos en zonas agrícolas, la roturación de los campos agrícolas tras el abandono y el control de las densidades de depredadores de bellotas y plántulas de encinas pueden acelerar la restauración forestal de campos agrícolas abandonados.

Palabras clave: almacenes dispersos de semillas, bosque mediterráneo, campos abandonados, *Corvidae*, depredación de bellotas, efectividad de dispersión de semillas, herbivoría, interacción animal-planta, interacción planta-planta, islotes forestales, nucleación aplicada, preferencias de almacenamiento de bellotas, recuperación forestal, regeneración forestal de quercíneas, regeneración natural forestal, sequía estival, supervivencia de plántulas, sinzoocoria, zoocoria.



Imágenes de arriba a abajo y de izquierda a derecha:

Vista de la finca El Carmen (campus de la Universidad de Alcalá, Alcalá de Henares, Madrid)
Bellotas en encina y urraca con bellota en el pico sobre ortofoto de la finca El Carmen
Plántula de encina reclutada y marcada para el seguimiento sobre ortofoto de la finca La Higueruela del CSIC (Santa Olalla, Toledo)
Vista de un islote forestal de encinas en la finca La Higueruela
Fuente de las imágenes: L. Martínez-Baroja, vuelo dron y Plan Nacional de Ortofotografía Aérea (PNOA)

Capítulo 1

Introducción general

Comprender los factores que determinan el reclutamiento de especies leñosas es esencial para la restauración de tierras agrícolas abandonadas. Se conocen algunos de los factores y procesos determinantes del reclutamiento de las plantas en general (Jordano et al., 2008), pero se desconoce o es poco conocida la actividad de algunos animales que intervienen en dichos procesos de reclutamiento. Esta Tesis Doctoral se ha centrado en algunas interacciones animal-planta y planta-planta implicadas en procesos claves de la regeneración forestal en tierras agrícolas abandonadas en ambientes mediterráneos. Para ello se han identificado, descrito y cuantificado dichos procesos. El conocimiento, las ideas y las herramientas de gestión que se aportan tienen un valor aplicado para la restauración forestal.

1.1. Abandono de tierras agrícolas y restauración forestal

Los cambios de usos del suelo son uno de los componentes del cambio global. Una consecuencia de estos cambios de uso es el abandono de tierras agrícolas (*old fields* en inglés), producido principalmente por cambios ambientales y socio-económicos (Cramer et al., 2008). El abandono de tierras agrícolas es un fenómeno extendido en muchos lugares de la Tierra, pero en Europa ha sido más intenso que en otras partes, aumentando la superficie forestal en 300.000 ha/año por la reforestación y la regeneración natural tras el abandono de tierras agrícolas en el periodo 2010-2020 (FAO, 2020). Además, se estima que se abandonarán entre 10 y 29 millones de hectáreas de tierras agrícolas desde el 2000 hasta el 2030 (Navarro and Pereira, 2012, **Figura 1.1**), según el escenario intermedio de abandono descrito por Verburg y Overmars (2009). En España, se ha abandonado el 24,6% de las tierras agrícolas en los últimos 60 años (Garrote et al., 2019). Por lo tanto, el abandono de tierras agrícolas es un fenómeno con efectos relevantes en el pasado, presente y futuro.

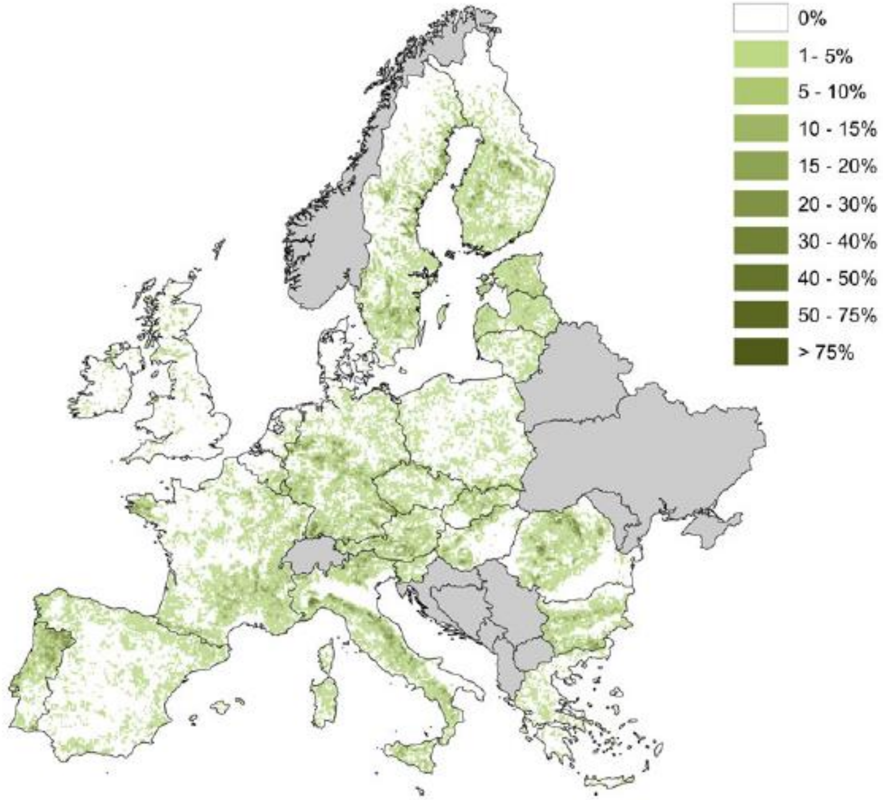


Figura 1.1. Localización de las zonas con mayor potencial para la regeneración forestal natural como consecuencia del abandono agrícola en Europa. Estas zonas son áreas clasificadas como terreno agrícola en el año 2000 que pueden ser restauradas en el año 2030 y que son comunes a los cuatro escenarios del modelo CLUE descrito por Verburg y Overmars (2009). El gradiente de color indica el porcentaje posible de superficie a restaurar en celdas de 10 km^2. Para la elaboración de este mapa se consideran zonas agrícolas las zonas aradas (no regadas), los pastos, las zonas aradas regadas y los cultivos permanentes. Las áreas restauradas y reforestadas corresponden a vegetación semi-natural, bosque, tierras cultivables recientemente abandonadas y tierras de pastoreo recientemente abandonadas. Fuente: Navarro y Pereira, 2012.

Hay dos modos de percibir los cambios que se producen en las tierras agrícolas abandonadas. Uno de ellos es como una pérdida del hábitat agrícola y cultural (Izquierdo, 2012); el otro es una oportunidad para recuperar ecosistemas anteriores a la explotación agrícola o para algún tipo de restauración (Cramer y Hobbs, 2007). Así, se estima que en el planeta hay espacio para 900 millones de hectáreas adicionales de bosques que podrían almacenar 205 gigatoneladas de carbono, contribuyendo de manera relevante a mitigar el cambio climático (Bastin et al., 2019). Del mismo modo, Strassburg et al. (2020) estimaron que la restauración del 15% de las tierras degradadas localizadas en áreas prioritarias podría evitar el 60% de las extinciones esperadas de especies y secuestrar 299 gigatoneldas de carbono, es decir, el 30% del incremento total de CO_2 atmosférico desde la Revolución Industrial.

Teniendo en cuenta las cifras de abandono de tierras agrícolas y los efectos que podrían tener los bosques en estas áreas, la restauración forestal de las tierras agrícolas abandonadas es uno de los grandes retos ecológicos a los que nos enfrentamos. La restauración forestal puede facilitar la recuperación de algunos de los cuatro grandes tipos de servicios ecosistémicos producidos por los bosques: soporte (hábitat, ciclo de nutrientes, etc.), provisión (bienes consumidos), regulación (de la escorrentía, las plagas, etc.) y cultural (ocio, usos tradicionales, etc.) (Millennium Ecosystem Assessment, 2005). Por ejemplo, la restauración puede aumentar o modificar la biodiversidad y los bienes y los servicios asociados a esa biodiversidad. Para la restauración de bosques en tierras agrícolas abandonadas se pueden seguir dos vías de forma simultánea, promoviendo 1) la reintroducción de especies clave que han desaparecido debido a los usos de la tierra en el pasado y 2) las interacciones entre animales y plantas (Bonet y Pausas, 2007), especialmente las relaciones mutualistas como la polinización y la dispersión de semillas. Se han propuesto distintas estrategias de restauración para llevar a cabo estas acciones.

1.2. Estrategias de restauración en campos agrícolas abandonados

Los procesos ecológicos más importantes para la recolonización de los campos de cultivo abandonados por parte de las plantas son: 1) la dispersión, 2) la germinación de las semillas y 3) el establecimiento de las nuevas plántulas (Kollmann y Schill 1996). Para esto debe haber disponibilidad de semillas y de sus dispersores en caso de plantas zoócoras y unas condiciones ambientales favorables para la germinación y el establecimiento de las nuevas plantas (Standish et al., 2007). Sin embargo, es frecuente que en los campos de cultivo abandonados no haya remanentes de vegetación del ecosistema de referencia que se pretende alcanzar con la restauración, en particular de las especies leñosas. Esto genera un primer cuello de botella para la restauración por la falta de árboles o arbustos “madre” productores de semillas que, además, puede afectar de manera negativa a la riqueza y la abundancia de dispersores. Como consecuencia, la regeneración de los bosques y matorrales se ve bloqueada o limitada (Rey-Benayas et al., 2008; Rey-Benayas y Bullock, 2012, 2015; Andivia et al., 2017).

La recuperación de la vegetación del ecosistema de referencia se puede llevar a cabo de diferentes maneras. En algunos casos puede ocurrir sin intervención humana, pero en otros muchos casos es necesario algún tipo de actuación que desencadene o acelere la recuperación (Cramer et al., 2008). Esto es especialmente importante cuando la transformación previa y la intensificación de la explotación agraria eliminaron los remanentes de vegetación natural, como los parches forestales, setos y árboles aislados, que aportan los propágulos que inician el proceso de la restauración forestal (Manning et al., 2006; Gibbons et al., 2008). Existen distintas estrategias para aportar propágulos para la restauración forestal de campos agrícolas abandonados, que se clasifican en función de la intervención humana. Estas estrategias van desde una mayor intervención, lo que se denomina restauración activa, a una menor o nula intervención, denominada restauración pasiva (Corbin y Holl, 2012; Meli et al., 2017). Recientemente se ha propuesto una clasificación complementaria que diferencia dos estrategias dentro de la restauración pasiva teniendo en cuenta el nivel de intervención y otros factores como el grado de degradación, que puede determinar el nivel de intervención para la restauración. Esta clasificación distingue, de menor a mayor grado de intervención: 1) restauración natural o espontánea, 2) restauración asistida y 3) restauración reconstructiva (Gann et al., 2019; Atkinson y Bonser, 2020). Las tres estrategias presentan diferencias en la velocidad de expansión de la cobertura de la vegetación y en la recuperación de la biodiversidad (**Figura 1.2).**

Un ejemplo de restauración asistida es la nucleación aplicada (Bechara et al., 2016) como los islotes forestales plantados o núcleos de dispersión y reclamo (Rey Benayas et al., 2008; Corbin and Holl, 2012; García-Martí and Ferrer, 2013; Rey-Benayas and Bullock, 2015; Holl et al., 2020). La técnica de los islotes forestales consiste en introducir pequeños núcleos de vegetación en la matriz que se desea restaurar. Al disminuir la superficie en la que se actúa, se reducen los costes de la actuación (Rey Benayas et al., 2008; Holl et al., 2020). Además, los resultados que se obtienen en cuanto a la cobertura del dosel arbóreo y la biodiversidad pueden tener valores intermedios respecto a las otras dos estrategias (Corbin y Holl, 2012; Holl et al., 2020).

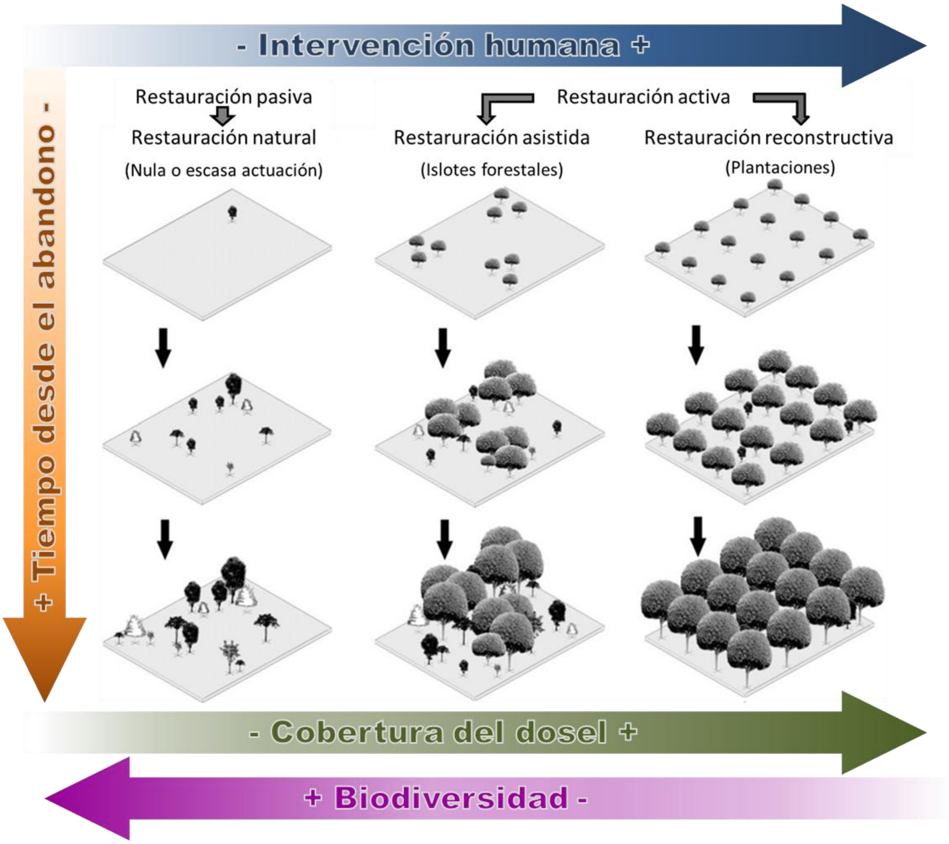


Figura 1.2. Secuencia temporal de la restauración forestal en campos agrícolas abandonados poniendo como ejemplo tres estrategias empleadas comúnmente. Por un lado, la restauración pasiva, también denominada restauración espontánea o restauración natural y, por otro, la restauración activa. Esta última puede ser de dos tipos en función del grado de intervención humana (flecha azul): restauración asistida, por ejemplo mediante islotes forestales plantados; y la restauración reconstructiva, por ejemplo mediante plantaciones forestales. A medida que avanza el tiempo desde el abandono de los campos agrícolas (de arriba hacia abajo en el esquema, flecha naranja), la cubierta arbórea se expande debido al crecimiento de los árboles y la colonización. La restauración pasiva produce una comunidad forestal más diversa (flecha morada), aunque alcanza la menor cubierta forestal de las tres estrategias (flecha verde). Sin embargo, la restauración asistida produce una mayor cubierta forestal en comparación con la restauración natural pero menor que en la restauración reconstructiva, aunque la comunidad es más diversa que en esta última. Se trata de un esquema en el que se presenta sólo un tipo de árbol plantado mientras que las otras especies se han establecido naturalmente. No obstante, tanto los islotes forestales como las plantaciones pueden variar en la composición de especies y en el número y densidad de árboles plantados. Modificado de Corbin y Holl, (2012) y añadiendo los términos de las distintas estrategias de Gann et al. (2019) y Atkinson y Bonser (2020).

Los islotes forestales deberían expandirse desde su perímetro y aportar propágulos a las zonas colindantes según el esquema del modelo de islotes forestales en mares agrícolas propuesto por Rey-Benayas et al., (2008). Sin embargo, se ha observado que el reclutamiento de leñosas es lento en campos agrícolas abandonados en ambientes mediterráneos debido a diversos factores que limitan la regeneración forestal (Cruz-Alonso et al., 2019; Martínez-Muñoz et al., 2019).

1.3. Factores limitantes de la regeneración forestal en los campos agrícolas abandonados en ambientes mediterráneos

La regeneración de las poblaciones de plantas incluye principalmente cinco etapas (Wang y Smith, 2002; Jordano et al., 2008; Gelmi-Candusso et al., 2019): 1) la remoción de semillas; 2) la dispersión de semillas; 3) la germinación de las semillas y posterior emergencia de las plántulas; 4) el establecimiento de las plántulas para proporcionar juveniles reclutados; y 5) el paso de juvenil establecido a una planta adulta (etapa reproductiva). Varios factores limitan la transición de una etapa a otra, haciendo que cada etapa pueda ser un cuello de botella para el reclutamiento (Jordano et al., 2008; Pérez-Ramos y Marañón, 2008; Andivia et al., 2018; Bastias et al., 2019). Jordano et al. (2008) identificaron tres grupos de factores limitantes de la restauración natural: 1) Limitaciones de la producción de propágulos (*source limitation*), son limitaciones pre-dispersivas, es decir, que afectan a las semillas antes de la dispersión, como la falta de fuentes de semillas o las plagas que afectan a la cantidad de semillas disponibles. 2) Limitación de la dispersión o diseminación (*dispersal limitation*), como la falta de dispersores o la cantidad de semillas consumidas frente a las dispersadas. Y 3) limitación del establecimiento y madurez sexual (*recruitment limitation*), como la herbivoría o la severidad ambiental, la facilitación y la competencia.

Los factores limitantes determinan el éxito de las distintas estrategias empleadas para la restauración de los campos agrícolas abandonados, especialmente en el caso de los ambientes mediterráneos debido a la severidad ambiental (Cuesta et al., 2010; Andivia et al., 2017; Martínez-Muñoz et al., 2019). De este modo, el clima continental mediterráneo, caracterizado por veranos secos y calurosos e inviernos fríos (Puerta-Piñero et al., 2007), dificulta la regeneración natural de los bosques. Otra característica singular de este clima es su alta variabilidad interanual, sobre todo de la precipitación, que puede afectar entre otros al crecimiento de las plantas y a la producción de semillas (Bogdziewicz et al., 2017; Forner et al., 2018). Por ello, los estudios durante varios años para recoger esta variación, como se hace en esta Tesis, son particularmente interesantes. Además, en los campos agrícolas abandonados mediterráneos concurren otros factores limitantes como la falta de propágulos (Rey Benayas et al., 2008), la ausencia o bajas densidades de dispersores a larga distancia de bellotas de quercíneas, como el arrendajo (Pons y Pausas, 2007a; Gianpasquale y Alberto, 2019) y las altas densidades de herbívoros silvestres y domésticos (Gómez y Hódar, 2008; López-Sánchez et al., 2018).

Esta Tesis Doctoral aborda los factores que determinan las etapas dispersivas y post-dispersivas de la regeneración de la encina (*Quercus ilex* L.) en agroecosistemas, es decir, la dispersión y germinación de las bellotas, la emergencia de las plántulas y el establecimiento de las plántulas a juveniles. Los factores estudiados afectan desde la remoción de la bellota hasta el reclutamiento de juveniles (**Figura 1.3**). La limitación de la disponibilidad de semillas, el primero de los grupos de factores limitantes, se solucionó introduciendo las fuentes de semillas que faltaban tras el abandono de los campos agrícolas. Así, en una de las zonas de estudio donde se realizó esta Tesis se utilizó una plantación forestal de encina y quejigo, es decir, una restauración reconstructiva *sensu* Gann et al. (2019) y Atkinson y Bonser (2020) (**Figura 1.2**); en otra de las zonas de estudio se utilizaron islotes forestales plantados o núcleos de dispersión, un ejemplo de regeneración asistida. Para evaluar la dispersión se llevaron a cabo experimentos de dispersión de bellotas, por ejemplo mediante comederos diseñados para aves, por los beneficios que presentan los córvidos en el proceso de la dispersión. Finalmente, para evaluar las limitaciones en el reclutamiento se estudió si la heterogeneidad espacial generada por las distintas orientaciones y distancias desde los islotes (Corbin et al., 2016; Benítez-Malvido et al., 2018; Holl et al., 2020), que determinan el microclima del sitio al que llegan las bellotas, influye en la emergencia y la supervivencia de plántulas y en la supervivencia y el crecimiento de los juveniles.

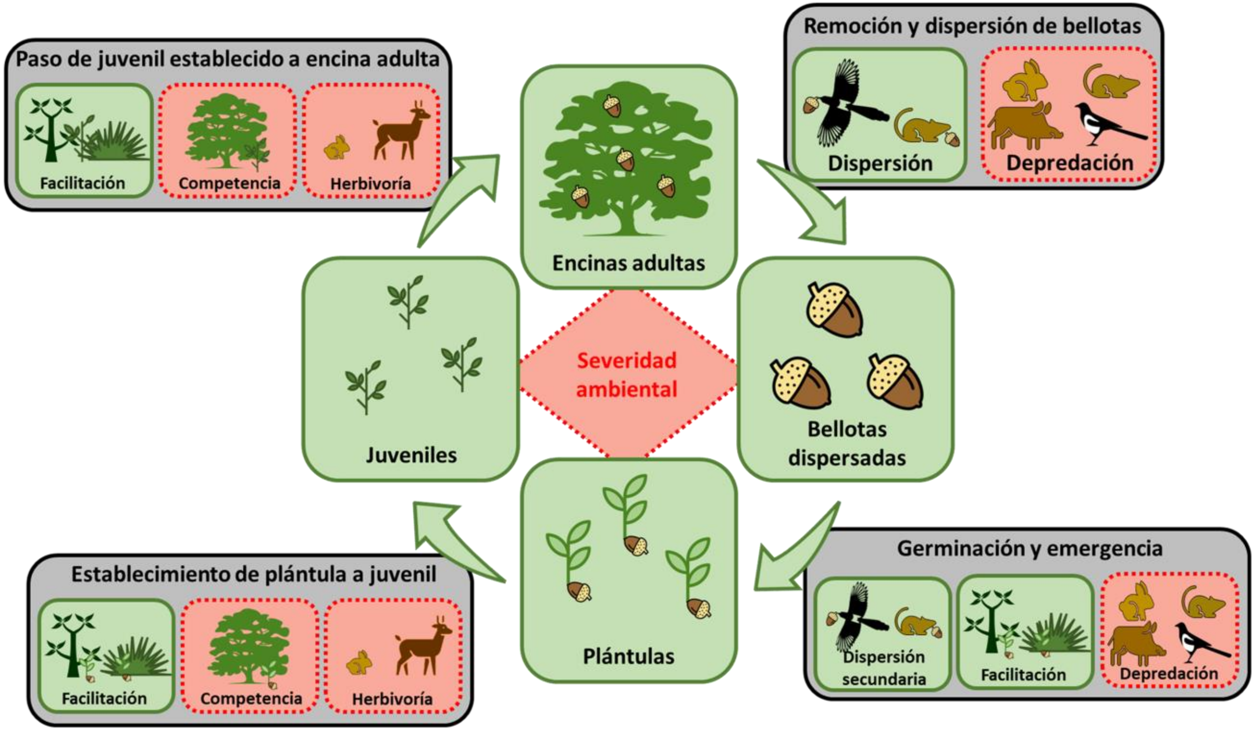


Figura 1.3. Ciclo de la regeneración de encinas en campos agrícolas abandonados mediterráneos donde la severidad ambiental limita todas las etapas del proceso. Las flechas representan el paso entre los diferentes eventos, desde las bellotas hasta el reclutamiento de las encinas adultas, que a su vez producirán más bellotas. Los cuadros grises representan las principales etapas que determinan la transición de una etapa a la siguiente; dentro de ellos se representan los factores bióticos, en verde y línea continua los que tienen efectos positivos y en rojo y línea discontinua los que tienen efectos negativos. Fuente: elaboración propia con información extraída de los esquemas de Schupp y Fuentes (1995), Wang y Smith (2002), Jordano et al. (2008) y Gelmi-Candusso et al. (2019). Iconos: Humberto Cesar Pomaro, VM, Cedric Villain, Ray Design, Philipp Lehmann, Mahabbah, DigitalShards de Noun Project y freepik.

1.4. La dispersión de bellotas

La dispersión de semillas grandes la realizan principalmente los animales, lo que se conoce como dispersión zoócora. En el caso de los árboles de biomas templados, más del 60% de las especies se dispersan de esta manera (Howe y Smallwood, 1982). La sinzoocoria (*synzoochory* en inglés) es un tipo de zoocoria que se caracteriza porque los animales almacenan las semillas después de transportarlas (Gómez et al., 2019); es el caso de las semillas de las quercíneas, las bellotas.

La dispersión de bellotas por parte de aves y mamíferos presenta ventajas para las quercíneas (Steele y Smallwood, 2002). 1) Aleja las semillas de los árboles fuente, lo que reduce la competencia local entre los juveniles y sus madres y la depredación denso-dependiente cerca de los árboles parentales. 2) Generalmente las bellotas son escondidas en lugares que reducen la depredación post-dispersiva de bellotas y mejoran la germinación y la supervivencia de las plántulas recién emergidas. Y 3) incrementa la posibilidad de cruzamiento entre distintos individuos de la población (Vander Wall, 1990). Los principales dispersores de bellotas de encina conocidos hasta esta Tesis son algunos córvidos, principalmente el arrendajo euroasiático (*Garrulus glandarius* L.), y en menor medida algunas especies de ratones (Gómez et al., 2019). La dispersión de bellotas por córvidos presenta otras ventajas adicionales: 4) generalmente seleccionan bellotas sanas (Bossema, 1979; Pons y Pausas, 2008; Pesendorfer et al., 2016); 5) transportan las bellotas a distintos ambientes y sobre todo a distancias mayores que los mamíferos (Bossema, 1979; Kurek et al., 2018); y 6) almacenan las bellotas dispersadas de una en una a pocos centímetros de la superficie del suelo (*scatter-hoarding* en inglés), reduciendo la depredación post-dispersiva, la desecación de la bellota y la competencia con otros congéneres, incrementando la emergencia y la supervivencia de las plántulas (Kurek et al., 2018; Pesendorfer et al., 2016; Vander Wall, 1990; **Figura 1.4**).

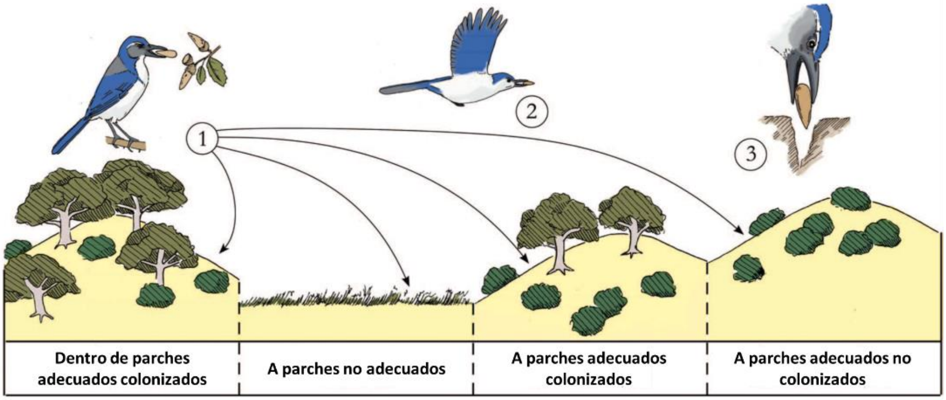


Figura 1.4. Pasos clave en la dispersión de semillas por animales que crean almacenes dispersos de semillas (*scatter-hoarders*). 1) Selección de la/s semilla/s. 2) Transporte de la/s semillas/s. 3) Almacenamiento de la/s semilla/s de manera individual. Las semillas pueden ser escondidas dentro del mismo parche y entre parches de hábitats adecuados ya colonizados por la especie dispersada, parches de hábitats inadecuados o parches de hábitats adecuados para la especie dispersada que aún no han sido colonizados por esa especie dispersada. Fuente: dibujo extraído y traducido de la ilustración realizada por Emily Underwood para el artículo de Pesendorfer et al. (2016).

Las principales aves dispersoras de las bellotas de encina en los bosques son los arrendajos, pero estos se encuentran ausentes en zonas deforestadas, como ocurre en muchos paisajes agrícolas con campos abandonados (Bossema, 1979; Pons y Pausas, 2008; Gianpasquale y Alberto, 2019). Sin embargo, en los campos abandonados y eriales en ocasiones se observan encinas reclutadas a distancias relativamente largas, hasta centenares de metros, de las encinas reproductoras más cercanas que han sobrevivido a la deforestación. Estas distancias son muy grandes para ser atribuidas a dispersiones por los ratones, incluso por dispersión secundaria, puesto que las distancias medias de dispersión de los ratones varían habitualmente entre 4 y 5 m (Pons y Pausas, 2007b; Morán-López et al., 2018). Ello hace pensar en que algún ave disperse las bellotas en estos sistemas. Uno de los objetivos de esta Tesis Doctoral es identificar esas especies de aves y estudiar el proceso de la dispersión de bellotas que realizan en los campos agrícolas abandonados. La urraca (*Pica pica* L.), que como el arrendajo pertenece a la familia de los córvidos, es abundante en zonas deforestadas y presenta características apropiadas para ser una buena dispersora de bellotas. Además, si la urraca se comporta como otros córvidos dispersores de bellotas, las distancias relativamente largas y la selección de sitios en la dispersión podrían ser beneficiosas para el reclutamiento de encinas en campos agrícolas abandonados.

1.5. Qué se estudia y cómo en esta Tesis Doctoral

Especies y zonas de estudio

La Tesis Doctoral se ha centrado en **dos especies**, la encina (**Figura 1.5**) como especie dispersada y la urraca como especie dispersora. La encina es una quercínea dominante en muchos bosques y agroecosistemas, principalmente en la cuenca mediterránea occidental (Pulido y Díaz, 2005). En muchas zonas constituía la especie leñosa predominante previa a la explotación agrícola. Sus bellotas (**Figura 1.5 B y C**) son transportadas a distintas distancias del árbol fuente por distintos animales. En el caso de las quercíneas, su dispersión es sinzoócora, puesto que las bellotas son transportadas sin ingerirlas, generalmente en la boca o en el pico, para ser almacenadas posteriormente (Gómez et al., 2019). La producción de bellotas se encuentra disponible durante un corto periodo de tiempo, por lo que algunos animales las almacenan para disponer de este recurso durante más tiempo (Bossema, 1979; Clarkson et al., 1986; Vander Wall, 1990). Además, la encina es una especie vecera (Bogdziewicz et al., 2017), lo que significa que se alternan años de producción relativamente elevada de bellotas a nivel poblacional con años de escasa producción, lo que también puede afectar el comportamiento de almacenamiento de los animales (Schubert et al., 2018). Los almacenes que realizan los animales con las bellotas pueden ser de dos tipos: pocos almacenes con numerosas semillas, generalmente en galerías profundas en el suelo, troncos, etc. (*larder-hoarding* en inglés), o muchos almacenes dispersos con una o pocas semillas (*scatter-hoarding*) (Vander Wall, 2001). Estos últimos resultan fundamentales para la regeneración de las plantas porque se suelen realizar a poca profundidad de la superficie, permiten alejar a los nuevos individuos en el espacio con consecuencias positivas para la estructura genética de la población y pueden presentar un elevado éxito de reclutamiento dependiendo del lugar en el que se almacenen (Jordano, 2017; García-Cervigón et al., 2018). Además, habitualmente los animales no recuperan todas las semillas que esconden (Vander Wall, 1990; Whelan et al., 2008; Pesendorfer et al., 2016). Estudiar la emergencia y la supervivencia de las plántulas en función de la heterogeneidad espacial, determinada por factores como la distancia y la orientación a la fuente de bellotas y las características del micrositio donde son depositadas las bellotas, resulta crucial para comprender los patrones de regeneración de la encina en campos agrícolas abandonados.

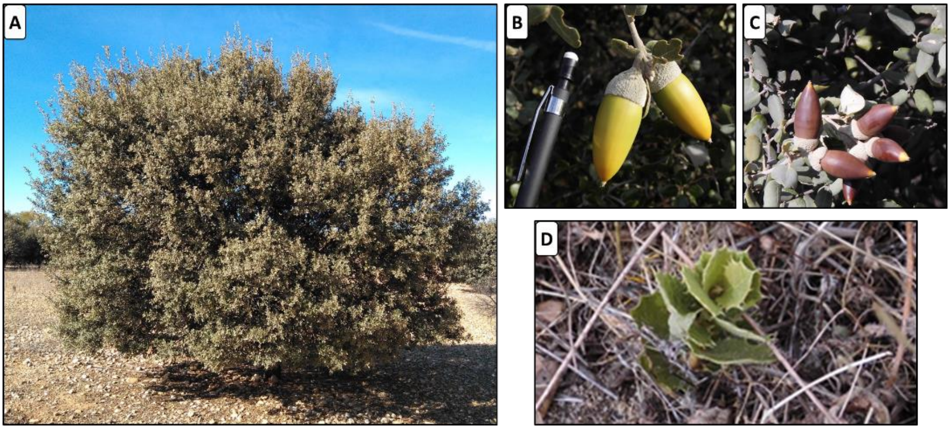


Figura 1.5. Distintas etapas del proceso de regeneración de las encinas. A) Encina adulta. Frutos de la encina, bellotas B) verdes y C) marrones (nótese que las bellotas pueden estar verdes y ser maduras a la vez). D) Plántula de encina menor de un año. Fuente de las imágenes: L. Martínez-Baroja.

La urraca (**Figura 1.6**) es bien conocida por su comportamiento de almacenamiento de comida (Waite, 1985; Vander Wall, 1990; Birkhead, 1991) y de semillas (Homet-Gutiérrez et al., 2015; Castro et al., 2017; Gómez et al., 2019) y las distribuciones espaciales de las quercíneas y las urracas solapan en buena parte de su rango mundial (hemisferio norte, principalmente Eurasia), incluidos los ambientes mediterráneos (Birkhead, 1991; Pesendorfer et al., 2016; Denk et al., 2017). Sin embargo, hasta la realización de esta Tesis, se desconocía el papel que las urracas podrían jugar en la dispersión de las bellotas y, por lo tanto, en la restauración de los campos agrícolas abandonados. Además, se ha sugerido que las urracas, que son animales territoriales para la nidificación, pueden emplear sus territorios también para almacenar comida (Clarkson et al., 1986; Birkhead, 1991). Sin embargo, no se ha estudiado si este comportamiento territorial puede tener consecuencias en el almacenamiento de bellotas, en la selección espacial de almacenes y en el establecimiento de plántulas y, por ende, en la regeneración forestal.

Se han seleccionado estas dos especies (la encina y la urraca) porque la encina es muy frecuente en paisajes mediterráneos, incluido el agroforestal, y se observan plántulas de encinas alejadas cientos de metros de los posibles árboles madre en paisajes deforestados. Además, el solapamiento en las distribuciones, el que distintas especies de córvidos sean los principales dispersores efectivos de bellotas (Gómez et al., 2019), junto con la presencia de las urracas en sistemas agroforestales abiertos, nos hicieron pensar que las urracas podrían ser clave para la regeneración y expansión a larga distancia de las encinas en estas zonas abiertas mediterráneas.

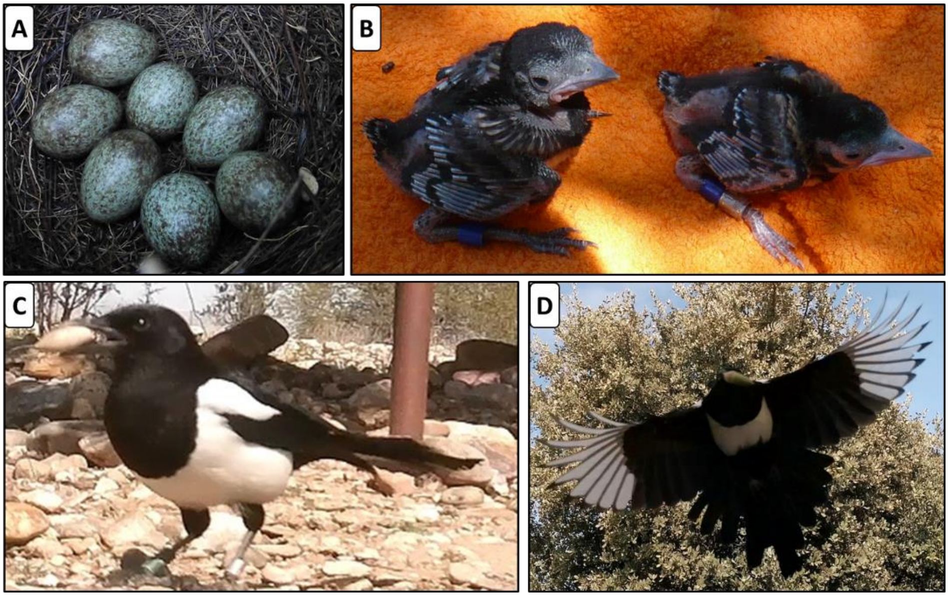


Figura 1.6. Distintas etapas del ciclo vital de las urracas. A) Puesta de huevos en el nido. B) Pollos de unos 15 días desde la eclosión del huevo. C) Urraca adulta transportando una bellota en el pico. D) Urraca adulta en vuelo transportando una bellota en el pico cogida por el pedúnculo de la cúpula de la bellota. Fuente de las imágenes: L. Martínez-Baroja y grupo de investigación SERAVI.

La investigación de esta Tesis se ha abordado mediante experimentos realizados en dos **áreas de estudio** atendiendo a las ventajas que presentaban para la realización de cada uno de ellos (**Figura 1.7 A**). Por un lado, se investigó en la finca El Carmen, situada en el campus externo de la Universidad de Alcalá (Alcalá de Henares, Madrid, 40°31’0” N, 3°19’55” O; **Figura 1.7 C**). En esta área de estudio se llevó a cabo una plantación de encinas y algunos quejigos siguiendo una estructura regular (restauración reconstructiva) en 1995, sobre una extensión de 28,4 ha. La plantación se encuentra rodeada de campos abandonados en 1990, previamente dedicados al cultivo de cereal. En esta finca se desarrollaron los experimentos relativos a la dispersión de bellotas, por su alta densidad de urracas (175 nidos activos por km^2) y su mayor superficie (la plantación más el herbazal colindante). Sin embargo, la alta densidad de conejos (23 individuos por ha en primavera), que depredan tanto las bellotas como las plántulas de encina (Zamora et al., 1985; Herrera, 1995; Mancilla-Leytón et al., 2012), no favorecía el seguimiento de la emergencia y la supervivencia de las plántulas. Por ello, también se investigó en la Finca Experimental La Higueruela del CSIC (Santa Olalla, Toledo, 40°3’ N, 4°24’ O; **Figura 1.7 B**) en una parcela de 1 ha inmersa en un campo de cultivo de cereal abandonado. En esta parcela se llevó a cabo una plantación de encinas en 16 islotes forestales (regeneración asistida) de 10 x 10 m en el año 1993. En ella se realizaron los experimentos relacionados con los procesos post-dispersivos, que se basaron en el seguimiento de la emergencia y la supervivencia de las plántulas de encinas y la sucesión desde el abandono del campo agrícola. La densidad de conejos en esta finca era menor y, además, la plantación de los islotes forestales permitió el estudio del efecto del microambiente generado en las distintas orientaciones y distancias en el reclutamiento de las nuevas encinas.

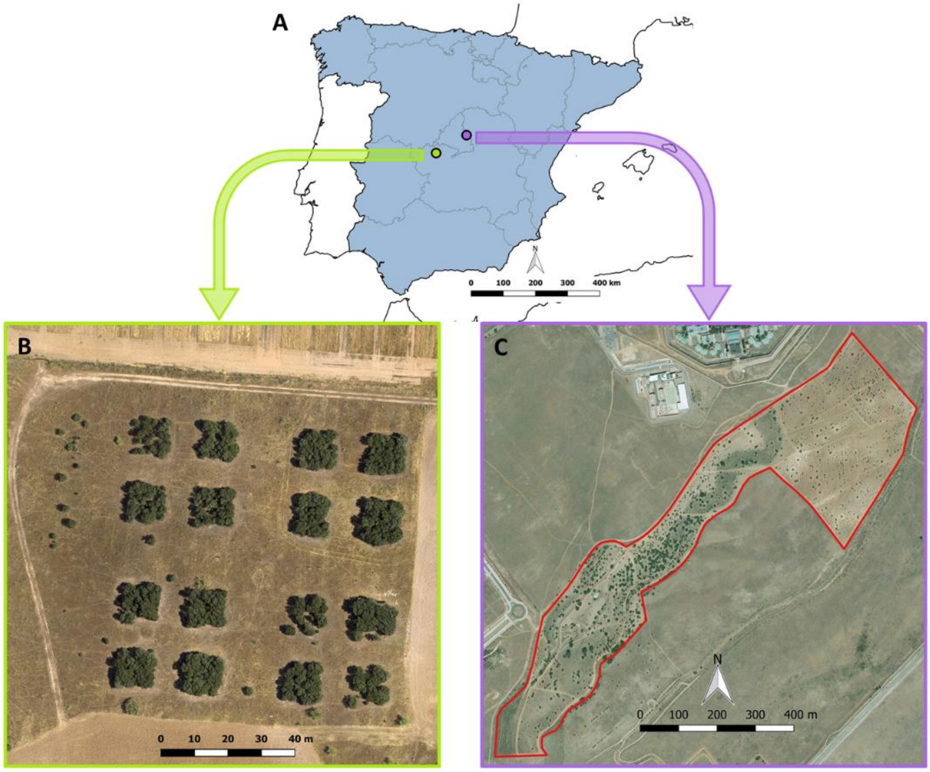


Figura 1.7. A) Localización de las dos parcelas de estudio. B) Detalle del experimento en la finca La Higueruela (Santa Olalla, Toledo; punto verde del mapa). C) Detalle de la finca El Carmen (Alcalá de Henares, Madrid; punto morado del mapa). Fuente: elaboración propia con ortofoto realizada con dron de la finca La Higueruela y del Plan Nacional de Ortofotografía aérea de la finca El Carmen.

Estructura y objetivos de la Tesis Doctoral

Esta memoria de Tesis Doctoral está compuesta por siete capítulos y un resumen general. El **Capítulo 1** es esta **Introducción general**. Los **Capítulos 2-5** son los **de Investigación** de la Tesis; se han escrito en inglés por estar publicados o en revisión en revistas científicas internacionales, aunque se ha añadido un resumen en español en cada uno. El **Capítulo 6** es una **Discusión general** de la Tesis. Por último, el **Capítulo 7** presenta las **Conclusiones** principales de esta Tesis Doctoral.

El **objetivo general** de la Tesis es evaluar el efecto de distintos factores que determinan el reclutamiento natural de las encinas en campos agrícolas abandonados mediterráneos. Concretamente, esta Tesis se ha centrado en la fase de la dispersión de bellotas (**capítulos 2 y 3**) y de los procesos post-dispersivos (**capítulos 4 y 5**). La **hipótesis general** es que la urraca es un dispersor masivo, efectivo y clave para la expansión de la encina en los agroecosistemas localizados en paisajes deforestados. Se predice que (1) el comportamiento como *scatter-hoarder* de la urraca con la comida, su preferencia por determinados sitios para enterrarla y su carácter territorial determinarán el patrón espacial de dispersión de las bellotas. Y (2) la variabilidad interanual de la aridez del clima, la herbivoría, la distancia de las fuentes de propágulos y el microambiente en el que se dispersan las bellotas determinan la emergencia, supervivencia y crecimiento de los juveniles y, por tanto, la tasa y el patrón espacial de reclutamiento de la encina.

Esta Tesis ha formado parte del proyecto "Servicios de la avifauna (*high mobile link species*) en mosaicos agroforestales: regeneración forestal y regulación de plagas" (SERAVI) del Ministerio de Economía y Competitividad. El objetivo principal del proyecto fue analizar los servicios ecosistémicos relevantes regulados por interacciones biológicas mediadas por la avifauna en paisajes heterogéneos, en particular su papel en la regeneración forestal y el control de plagas, que tienen un impacto elevado en el bienestar humano. La hipótesis general del proyecto fue que las actividades de ciertos componentes de la avifauna resultan en servicios ecosistémicos clave en mosaicos agrícolas y forestales.

Los **objetivos específicos** abordados en los distintos capítulos (**Tabla 1.1**) y las **hipótesis específicas** relacionadas con los mismos son los siguientes:

El **Capítulo 2** "Massive and effective acorn dispersal into agroforestry systems by an overlooked vector, the Eurasian magpie (*Pica pica*)" (Martínez-Baroja et al., 2019) cuantifica la capacidad de dispersión de las urracas, contabilizando el número de bellotas que se llevaron desde los comederos por individuo, diferenciando según el estado reproductor (reproductores *vs*. juveniles) y sexo de los individuos dispersores. A nivel poblacional, se cuantificó la fracción de bellotas producidas por las encinas que fue dispersada por las urracas, frente a la fracción consumida por esta y otras especies animales, así como su evolución hasta plántulas emergidas. La hipótesis de este capítulo fue que las urracas, un córvido abundante en sistemas agroforestales, realizan una función de dispersión similar a la realizada por los arrendajos en sistemas forestales, es decir, de dispersión masiva y efectiva de bellotas.

El **Capítulo 3** "Caching territoriality and site preferences by a scatter-hoarder drive the spatial pattern of seed dispersal and affect seedling emergence" (Martínez-Baroja et al., en segunda revisión en *Journal of Ecology*) analiza el patrón espacial de la dispersión de bellotas por las urracas en un mosaico agroforestal y su implicación para la regeneración forestal, con énfasis en el papel de la territorialidad y la selección de hábitats y micrositios para almacenarlas. Además, analiza si la densidad de plántulas emergidas de quercíneas coincide con las preferencias de almacenamiento de bellotas de la urraca. Nuestra hipótesis principal fue que las urracas tienen territorios de almacenamiento en los que esconden las bellotas siguiendo un patrón espacial de selección de lugares a distintas escalas y que este patrón se mantiene en la emergencia de plántulas de las bellotas dispersadas.

El **Capítulo 4** "Predation and aridity slow down the spread of 21-year-old planted woodland islets in restored Mediterranean farmland" (Rey-Benayas et al., 2015) analiza la depredación post-dispersiva de las bellotas, la herbivoría de las plántulas, la importancia de la orientación y la distancia a los islotes forestales plantados en la emergencia y la supervivencia de nuevas plántulas de encinas durante un año de estudio. La hipótesis inicial es que la alta depredación de bellotas y plántulas no protegidas y la exposición a orientaciones y distancias con mayor insolación resultan en una menor emergencia y supervivencia de plántulas, limitando la regeneración de las encinas.

El **Capítulo 5** **“**Drivers of oak establishment in Mediterranean old fields from 25-year-old woodland islets planted to assist natural regeneration**”** (Martínez-Baroja et al., en revisión en *Forest Ecology and Management*) analiza el efecto de la variabilidad interanual del clima mediterráneo y del microclima generado por los islotes forestales plantados (extinción de luz, cantidad de biomasa herbácea y humedad del suelo) según su orientación y distancia en la emergencia y la supervivencia de las plántulas de encina. Además, se estudia el establecimiento de encinas en campos agrícolas abandonados transcurridos 25 años desde la plantación de los islotes forestales como técnica de restauración asistida impulsora de la restauración forestal. Nuestras hipótesis principales son que las primaveras y los veranos lluviosos y las orientaciones y las distancias con menor insolación producen mayores tasas de emergencia y supervivencia de plántulas y que la competencia de los islotes y la herbivoría ralentiza intensamente la colonización de encinas y el crecimiento de herbáceas alrededor de los islotes forestales.

Tabla 1.1. Reseña de los capítulos de investigación y las publicaciones que se presentan en esta Tesis Doctoral.

Capítulo	Título	Objetivos	Finca de estudio	Publicación
Capítulo 2	Massive and effective acorn dispersal into agroforestry systems by an overlooked vector, the Eurasian magpie (*Pica pica*)	Cuantificar la dispersión de bellotas por urraca a escala de individuo, según las características de los individuos dispersores, y a escala poblacional, evaluando su efecto en la emergencia de plántulas	El Carmen	Martínez-Baroja et al. (2019). *Ecosphere*
Capítulo 3	Caching territoriality and site preferences by a scatter-hoarder drive the spatial pattern of seed dispersal and affect seedling emergence	Determinar la importancia del territorio de almacenamiento y la preferencia espacial a distintas escalas en el almacenamiento de bellotas de encina por urracas y en la emergencia de las plántulas	El Carmen	Martínez-Baroja et al. (en segunda revisión). *Journal of Ecology*
Capítulo 4	Predation and aridity slow down the spread of 21-year-old planted woodland islets in restored Mediterranean farmland	Analizar la depredación de bellotas de encina y el efecto de la distancia y la orientación a los islotes forestales y la herbivoría en la emergencia y la supervivencia de las plántulas de encina	La Higueruela	Rey Benayas et al. (2015). *New Forests**
Capítulo 5	Drivers of oak establishment in Mediterranean old fields from 25-year-old woodland islets planted to assist natural regeneration	Analizar el efecto de la variación climática interanual, la distancia y la orientación a los islotes forestales y las características del micrositio en la emergencia y la supervivencia de las plántulas y el establecimiento de encinas pasados 25 años desde la plantación de los islotes	La Higueruela	Martínez-Baroja et al. (en primera revisión). *Forest Ecology and Management*

* El **Capítulo 4** reproduce parte del Trabajo Fin de Máster titulado: "*Reclutamiento de encinas a partir de islotes forestales plantados en campos agrícolas mediterráneos*" (Martínez-Baroja, 2014). Dirigido por José María Rey Benayas para el Máster U. en Restauración de Ecosistemas.

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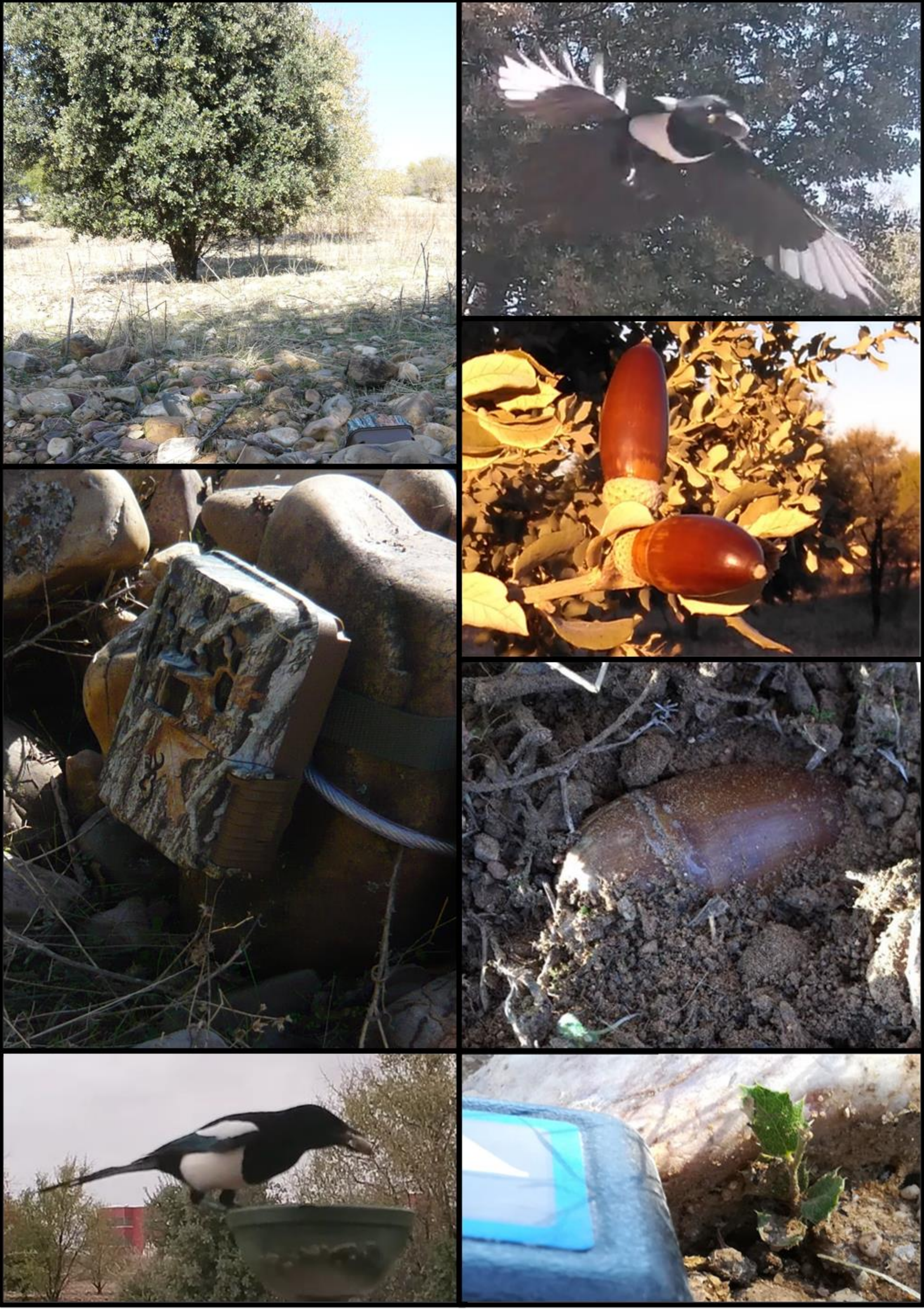

Imágenes de arriba a abajo y de izquierda a derecha:

Cámara de fototrampeo enfocando a encina con bellotas
Una urraca se lleva una bellota desde una encina
Dos bellotas en una rama, en la de abajo se observa el corte para introducir el radiotransmisor
Cámara de fototrampeo colocada en el campo
Bellota con radiotransmisor enterrada por una urraca
Urraca posada en uno de los comederos con dos bellotas en el pico
Plántula emergida de una bellota dispersada por una urraca junto a detector de metales
Fuente de las imágenes: L. Martínez-Baroja y grupo de investigación SERAVI

Capítulo 2

Massive and effective acorn dispersal into agroforestry systems by an overlooked vector, the Eurasian magpie (*Pica pica*)[1]

Abstract

Oak regeneration and the expansion of forested sites in Eurasia rely on acorn dispersal by animals, especially the Eurasian jay (*Garrulus glandarius*). However, in open agroforestry systems where jays are absent, such as old fields far from acorn sources, oak recruitment still occurs. We hypothesize that the Eurasian magpie (*Pica pica*), an abundant corvid in this system, substitutes the jay in its seed dispersal function. By ringing 169 magpies, video recording >7500 acorn removal events with trail cameras, and radio-tagging 337 acorns, we quantified that (1) magpies cached 41–56% of the annual acorn production of *Quercus ilex* trees in single caches on the ground; (2) breeding pairs, and especially males, were the main acorn dispersers; (3) each breeding magpie cached 169–1372 acorns in 6 weeks; and (4) the effectiveness of dispersal (percentage of cached acorns resulting in seedlings) was 0.6–2.4%, which (5) yielded a high density of emerged seedlings (56–439 seedlings/ha). We evidence that magpie could be a key species in the regeneration of oak agroforestry mosaics because they massively and effectively dispersed acorns. However, in our particular study site, effectiveness was low probably due to herbivory and summer drought stress (i.e., a context limitation rather than an intrinsic limitation of the disperser). As the distributions of magpies and oaks overlap widely in Eurasia, effective acorn dispersal by magpies could have a significant role in large-scale oak forest recovery in strongly fragmented landscapes.

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[1] This chapter fully reproduces the article:

Martínez-Baroja, L., Pérez-Camacho, L., Villar-Salvador, P., Rebollo, S., Quiles, P., Gómez-Sánchez, D., Molina-Morales, M., Leverkus, A.B., Castro, J., Rey-Benayas, J.M., 2019. Massive and effective acorn dispersal into agroforestry systems by an overlooked vector, the Eurasian magpie (*Pica pica*). Ecosphere 10, . https://doi.org/10.1002/ecs2.2989

Resumen

La regeneración y expansión de los bosques de quercíneas en Eurasia depende de la dispersión de bellotas por animales, especialmente el arrendajo euroasiático (*Garrulus glandarius*). Sin embargo, en los sistemas agroforestales donde el arrendajo está ausente, como son los campos de cultivo abandonados y alejados de las fuentes de bellotas, también se produce el reclutamiento de quercíneas. Hipotetizamos que la urraca (*Pica pica*), un córvido abundante en este tipo de sistemas, sustituye al arrendajo en su función de dispersor de bellotas. Mediante el anillamiento de 169 urracas, la grabación de más de 7.500 eventos de remoción de bellotas con cámaras de fototrampeo y el radio-seguimiento de 337 bellotas se cuantificó (1) que las urracas escondieron el 41-56% de la producción anual de bellotas de encina (*Quercus ilex*) en almacenes individuales en el suelo; (2) las parejas reproductoras, especialmente los machos, fueron los principales dispersores; (3) cada urraca reproductora escondió entre 169-1.372 bellotas en 6 semanas; y (4) la efectividad de la dispersión (el porcentaje de bellotas escondidas que dieron lugar a una plántula) fue del 0,6-2,4%, lo que (5) resultó en una alta densidad de plántulas emergidas (56-439 plántulas ha^{-1}). En este estudio demostramos que las urracas podrían ser una especie clave en la regeneración de las quercíneas en mosaicos agroforestales porque son capaces de dispersar bellotas de manera masiva y efectiva. Sin embargo, en nuestra área de estudio, la efectividad fue baja probablemente debido a la herbivoría y a la sequía estival (es decir, una limitación dependiente del contexto más que una limitación intrínseca del dispersor). Dado que las distribuciones de las urracas y las quercíneas se solapan en gran parte en Eurasia, la dispersión efectiva de bellotas por urracas podría tener un papel importante a gran escala en la regeneración de los bosques de quercíneas en paisajes fuertemente fragmentados.

2.1. Introduction

Forest regeneration is paramount to counteract centuries of land degradation (Chazdon, 2017), combat climate change (Nabuurs et al., 2007), and attain the Sustainable Development Goals (U.N., 2017). However, natural forest regeneration is limited by the ability of tree species to spread naturally (Rey Benayas et al., 2008, 2015). Animal-mediated seed dispersal of large-seeded trees, like acorns, constitutes a major ecosystem service that allows the regeneration, densification, and expansion of forests (Whelan et al., 2008). More than 60% of tree species in communities of temperate biomes are zoochorous (Howe and Smallwood, 1982). Synzoochory, seed dispersal by seed-caching seed predators (Gómez et al., 2019), is especially relevant in Quercus species (henceforth “oaks”) and other large-seeded trees (Pesendorfer et al., 2016a). Oaks include more than 400 species widely distributed in the Northern Hemisphere (Denk et al., 2017). The strong fragmentation and degradation of oak forests, coupled with the usually slow recruitment of oaks, have transformed many of those landscapes into cropland and agroforestry mosaic systems with few scattered oak remnants (Rey Benayas et al., 2015). The holm oak (*Quercus ilex*) is an abundant oak in the Mediterranean Basin. It dominates many forests and agroforestry mosaics such as the *dehesas*, which are savannah-like ecosystems of great ecological, economic, and historical importance (Pulido and Díaz, 2005).

Corvids are the main dispersers of acorns (Vander Wall, 1990; Whelan et al., 2008; Gómez et al., 2019). Several corvid species are key for medium and long-distance oak dispersal (Pesendorfer et al., 2016a). In Eurasia, only two corvids are known as major acorn dispersers, namely the Eurasian jay (*Garrulus glandarius*) and, to a lesser degree, the rook (*Corvus frugilegus*) (Källander, 2007; Pesendorfer et al., 2016a). These corvids usually make scattered caches of food, which allows them to store resources that are abundant for short periods, like acorns in autumn, for later consumption (Bossema, 1979; Clarkson et al., 1986; Vander Wall, 1990). However, many acorns remain unrecovered and can develop into seedlings (Vander Wall, 1990; Whelan et al., 2008; Pesendorfer et al., 2016a). This behavior has additional benefits for oaks. First, corvids usually select sound acorns, that is, the biggest and healthiest (Bossema, 1979; Pons and Pausas, 2008; Pesendorfer et al., 2016a). Second, they carry acorns away from mother trees, reducing kin competition. Third, they make single-acorn caches, which reduces post-dispersal predation, desiccation, and competition and increases seedling emergence and survival (Vander Wall, 1990; Pesendorfer et al., 2016a; Kurek et al., 2018).

The Eurasian jay plays a central role in acorn dispersal dynamics of oak forests (Bossema, 1979; Gómez, 2003; Pons and Pausas, 2007a, 2008; Morán-López et al., 2015; Leverkus et al., 2016). However, in strongly deforested farmland of the Mediterranean landscapes where jays are very scarce or absent (Bossema, 1979;

Pons and Pausas, 2008; Gianpasquale and Alberto, 2019), recruitment of oak juveniles has often been observed at long distances (above several tens of meters) from remnant oak trees and small forest patches (Andivia et al., 2017 and authors' observations). Such recruitment cannot be attributed to dispersal by rodents as these disperse acorns at small distances (Pons and Pausas, 2007b; Morán-López et al., 2018). The long-distance disperser(s) of acorns in open systems thus remains to be unveiled.

The Eurasian magpie (Pica pica; henceforth "magpie") abounds in open landscapes (Kryukov et al., 2017). Several lines of evidence suggest that magpies might act as the unknown acorn dispersers in these open landscapes: (1) They cache a wide variety of food types (Waite, 1985; Vander Wall, 1990; Birkhead, 1991); (2) they disperse and promote the recruitment of the common walnut (*Juglans regia*) (Castro et al., 2017), and some authors suggested that they disperse other large-seeded trees such as the almond tree (*Prunus dulcis*) (Homet-Gutiérrez et al., 2015) and the chestnut tree (*Castanea sativa*) (Gómez et al., 2019); and (3) several authors have pointed out that magpies occasionally cache acorns of some oaks (Waite, 1985; Clarkson et al., 1986; Birkhead, 1991; den Ouden et al., 2005). However, despite magpies being among the most common corvids in Eurasia (Birkhead, 1991; Kryukov et al., 2017) and their distribution largely overlapping with that of the Quercus genus (Kappelle, 2006; Pesendorfer et al., 2016; Denk et al., 2017; **Figure 2.1**), neither the potential of magpies as acorn dispersers nor the effectiveness of such dispersal for oak seedling recruitment has been quantified yet. We hypothesized that magpies are effective and long-distance dispersers of acorns in open agroforestry systems and thus contribute to the natural regeneration of Mediterranean oak forests. Moreover, differences between individuals, that is, sex and reproductive status, could affect acorn dispersal, due to the different role in food provision among sex and territoriality (Birkhead, 1991). For example, if mortality differs between sexes or reproductive status (Birkhead, 1991), the amount of abandoned cached acorns could be different. These aspects have been little studied in scatter-hoarding corvids (DeGange et al., 1989), and they may affect oak regeneration.

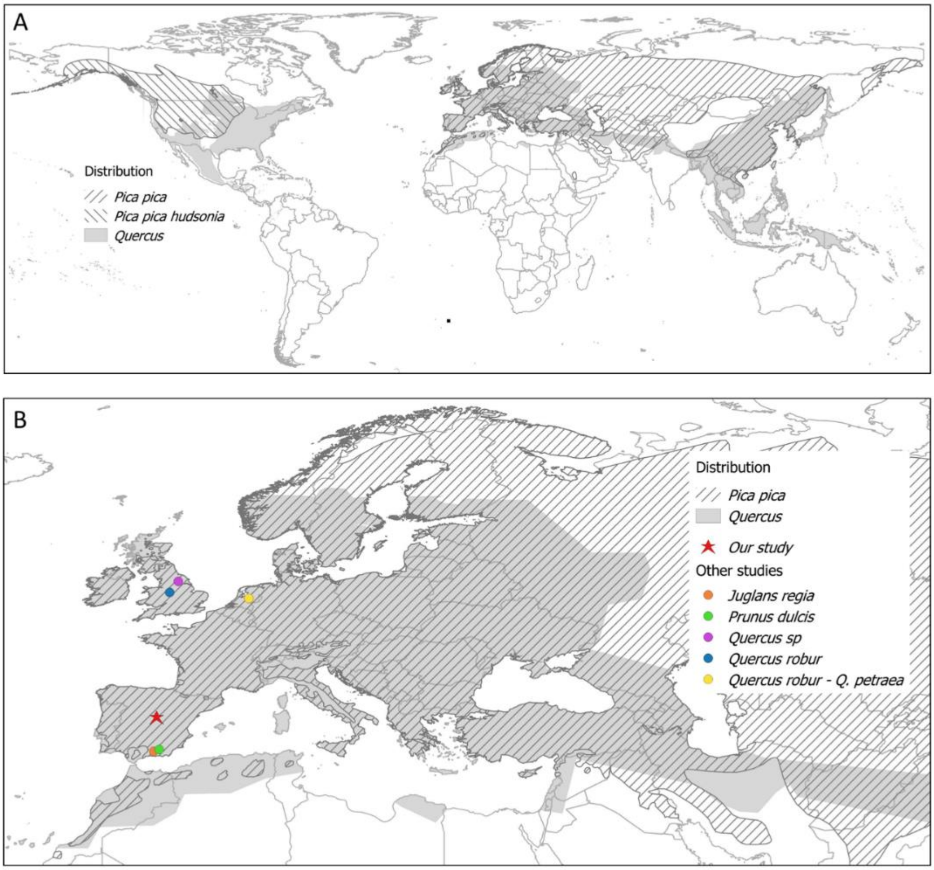

Figure 2. 1. Distribution of magpies (*Pica pica*) and oaks (*Quercus* spp.) in the world (A) and in Europe (B). The red star shows the location of our study site. The color dots show the location of studies on dispersal of acorns and other nuts by magpies (Waite, 1985; Clarkson et al., 1986; Birkhead, 1991; den Ouden et al., 2005; Homet-Gutiérrez et al., 2015; Castro et al., 2017). Source of bird distribution: Handbook of the Birds of the World and BirdLife International, 2017. Sources of oak distribution: Kappelle, 2006; Pesendorfer et al., 2016; Denk et al., 2017.

In this study, we analyzed the role of magpies as dispersers of oaks by assessing several quantitative and qualitative aspects of holm oak acorn dispersal in a Mediterranean agroecosystem in central Spain. We quantified acorn dispersal of the holm oak and the effectiveness of dispersal (measured as seedling emergence, *sensu* Schupp et al., 2010) of oaks. Our specific aims were to (1) quantify acorn dispersal (removal and caching) by magpies directly from the oak trees; (2) quantify the proportion of removed acorns that are cached and assess whether magpies are acorn scatter hoarders; (3) quantify the amount of cached acorns per individual throughout the dispersal season; (4) assess acorn dispersal effectiveness; and (5) determine whether sex and reproductive status (i.e., breeders vs. juveniles) determine acorn dispersal. Bearing in mind the wide distribution of magpies and oaks, demonstrating that magpies are effective acorn dispersers can open a new perspective in the ecology, regeneration, and restoration of Eurasian oaks in sparsely forested agroforestry mosaics, which may change our vision of the ecological role of magpies in agroforestry systems.

2.2. Materials and methods

Study site

To test our hypotheses, we selected a study site located in an open agroforestry system in an alluvial terrace of the Henares River (central Spain 40°31′0″ N, 3°19′55″ W, elevation 605 m) where jays are absent. The climate is continental Mediterranean, with dry and hot summers and cold winters. The mean annual temperature is 13.8°C, and the annual rainfall is 425 mm. The study site comprised a 28.4-ha plantation of holm oaks and some Portuguese oaks (*Quercus faginea*) established in 1995, surrounded by abandoned cereal fields. Cereal cultivation in the old fields ceased in 1990, and the fields are currently dominated by annual herbaceous vegetation. The oak plantation also included dispersed almond trees and a few Siberian elms (*Ulmus pumila*), olive trees (*Olea europea*), common figs (*Ficus carica*), common walnuts, white mulberries (*Morus alba*), and black locusts (*Robinia pseudoacacia*). A diverse community of vertebrates thrives in the area. Noteworthy is the high density of magpies and rabbits (Oryctolagus cuniculus), which are potential acorn predators. Other present acorn consumers were common wood pigeons (*Columba palumbus*), jackdaws (*Corvus monedula*), wood mice (*Apodemus sylvaticus*), and European roe deer (*Capreolus capreolus*). Potential magpie predators included several raptors (e.g., booted eagles (*Aquila pennata*) and Eurasian eagle–owls (*Bubo bubo*), red foxes (*Vulpes vulpes*), European polecats (*Mustela putorius*), and domestic cats (*Felis silvestris catus*)).

Magpies are relatively short-lived (mean life expectancy of 1.2–3.5 yr in the wild for adults) and medium-sized (170–270 g; various races) corvids (Birkhead, 1991). They display territorial behavior in the breeding season, and breeding pairs remain together during the autumn and winter (Birkhead, 1991). The holm oak is an evergreen tree up to 25 m high, very long-lived (up to hundreds of years), and mainly distributed around the central-western Mediterranean basin. The fresh weight of holm oak acorns varies between 2 and 10 g (Villar-Salvador et al., 2013); they mature in autumn, and the seedlings emerge in late spring.

Identification of acorn dispersers from the trees and acorn caching

To investigate whether acorn removal from oak tree canopies is a common behavior of magpies and the species that remove or predate acorns, we installed motion-sensor trail cameras (Browning Dark Ops HD Elite, Browning Trail Cameras, USA). Five holm oaks were recorded in 2016 and a different set of nine trees were recorded in 2017. In both years, we installed the trail cameras on the ground at 5.5 m from the target tree, pointing up towards the crown, in mid-October, when the acorns were almost ripe but still green (emergence rate was >80%, see Results). Our trail-cameras were not capable of capturing small animals such as mice at the distance they were placed. Cameras recorded videos for 30 seconds whenever they detected animal motion until removal of all acorns of the tree crowns (by early November). We viewed the recorded videos to estimate the percentage of removed or predated acorns by each animal species.

We assessed whether magpies cached acorns from holm oaks by means of radio-tracked acorns. The size and shape of the radio-tracked acorns were similar to those of the unmanipulated acorns because the both groups of acorns were a random sample from the same acorn crop. We inserted a radio transmitter (PIP2 Tag Ag392; Biotrack, Wareham, Dorset, UK; weight: 2,2 g) inside acorns following the methodology of Pons and Pausas (2007). We transversally cut the acorns and emptied a part of the cotyledons to fit the radio transmitter with the antenna rolled up (the weight of the acorn with the transmitter was similar to that of the non-manipulated acorn, data not shown). Finally, we closed the acorns with instantaneous cyanoacrylate adhesive (**Figure S2.1**). To assess acorn removal from the oak trees, we glued 1-3 radio-tracked acorns per tree with cyanoacrylate adhesive onto acorn caps of the current year still attached to the branches of five trees. This manipulation was done during 10 days in November 2017 when there were few acorns left in the crowns. Once magpies removed radio-tagged acorns, they were re-located on the same day to avoid predation by rodents and rabbits or possible secondary dispersal by magpies. We located the radio-tagged acorns using a unidirectional Yagi antenna connected to a radio receiver (Biotrack SIKA Radio Tracking Receiver, Wareham, Dorset, UK). Once the general caching vicinity was detected, the precise location of the acorns was found using a hand-held metal detector (White's Auto-Scan Personal Search Detector, Tulsa, Oklahoma, USA). Then, we assessed whether the acorns were predated or cached intact. We considered an acorn to be predated when we found the radio-transmitter on the ground or hanging from branches, without the acorn or with the acorn partially consumed.

To identify the species that consumed or removed acorns from the ground below trees, we positioned 100 acorns inside a camouflaged shallow plate on the ground below six holm oaks in December 2018 (600 acorns in total). We installed trail cameras at 1 m from the plate that recorded videos for 1 minute whenever they detected animal motion. We viewed the recorded videos to estimate the percentage of consumed or removed acorns by each animal species. Complementarily, we assessed detectability of the consumed or removed acorns by the different species in the videos. In both cases, either the oak canopy or the ground, trees were the sample unit, because acorns between different trees were more independent than acorns within the same tree.

Proportion of active feeders by magpies

To experimentally quantify acorn removal and dispersal by magpies, in November 2015 we installed 14 feeders with 10 acorns each, which were monitored until December 2015 - April 2016 (**Figure 2.2 A**). We worked on this relatively “late” period to encourage magpies to remove acorns from the feeders and then tracked the radio-tagged acorns. The feeders consisted of a domestic colander attached to a metallic rod (60-70 cm high) to avoid acorn predation by rabbits and mice and were placed below the crown edge of holm oak trees (**Figure S2.2**). We then installed trail cameras (Moultrie MCG-12634; Moultrie Products, Alabama, USA) on the ground, pointed at the feeders, to record videos for 1 minute whenever motion was detected. We viewed the recorded videos to know the bird species that removed each acorn and to estimate the percentage of feeders used by magpies (active feeders).

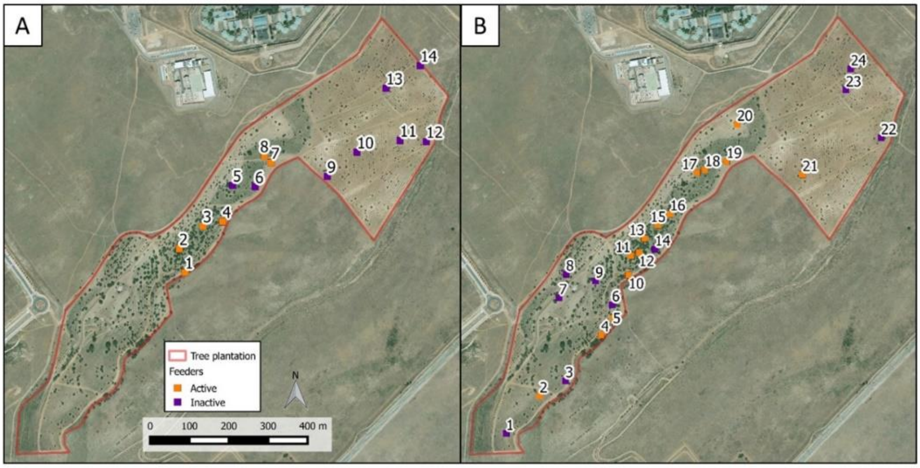

Figure 2.2. Location of active and inactive feeders in the study site in 2015–2016 (A) and 2016–2017 (B). Trees on the image are mostly holm oaks and almond trees.

The type of feeders, their position and materials, and the surveillance method were key aspects for magpies to use them. Preliminary observations revealed that magpies avoided auto pet feeders (n = 24) or colanders with large mesh size (≥ 0.6 cm) (n = 2), and hardly used feeders placed in the oak crowns (n = 6) (**Figure S2.3**). Moreover, watching from hides or cars (n = 9) interrupted dispersal from previously active feeders surveyed by trail cameras. For this reason, we only used trail cameras to quantify acorn removal. Other authors have made direct observations to quantify the dispersed acorns by less skittish corvids (Darley-Hill and Johnson, 1981; Pesendorfer et al., 2016c).

Quantification of acorn dispersal

We assessed the proportion of cached acorns with respect to the removed acorns from the feeders, and the characteristics of caches, through radio-tracked acorns (method described above; (Pons and Pausas 2007b)) in the 2015-16 period. When the feeders were visited by magpies in 2015-16, we placed 15 acorns per trial (three to 10 trials per feeder), five to 10 of which had a radio transmitter (260 radio-tagged acorns in total); the remaining were non-manipulated acorns with a scratch imitating the scar produced after inserting the radio transmitters. Previous trials showed the importance of scratching non-manipulated acorns to minimize the rejection of acorns containing transmitters (L. Martínez-Baroja et al., unpublished data).

To quantify the acorn removal rates per individual magpie, we color-banded 33 breeders of 24 active nests out of 53 active nests and 136 nestlings in 51 active nests in the spring of 2016. We ringed nestlings when they were at least 15 days old and thus could thermoregulate (Molina-Morales et al. 2012). Birds were tarsus-ringed with a standard ornithological ring of stainless steel with a unique identifier number and two or three colored aluminum rings; thus, each magpie had a different color combination for later identification. To capture breeding magpies, we placed a Sherman trap with a caged magpie as decoy under all trees with active nests. In December 2016, we placed a feeder under the crown of each tree with active nest where at least one adult of the breeding pair was ringed (**Figure 2.2B**). To minimize the territorial disputes between neighboring magpies for the use of the feeders, we placed them under the tree with active nest or under a nearby tree that were in a central point of the magpies' territories. For 6 weeks, we continuously refilled the feeders, which held up to 300 acorns, mimicking their availability in oak ecosystems (Pulido and Díaz 2005). We placed motion-sensor trail cameras to record the feeders and later identify the individuals that removed and dispersed acorns. We analyzed the data of the feeders where ringed magpies removed acorns for more than 20 days to calculate daily acorn removal rates (males n = 7 and females n = 4).

Similarly, in one magpie territory, we monitored one Portuguese oak tree and one feeder with its acorns for 10 days to assess whether the magpies removed and cached acorns of this oak species. In this study and only for illustrative purposes, we just show that magpies did remove and cache Portuguese oak acorns from feeders and trees and almonds from the ground (**Videos S1 – S5**)[2].

To check whether the acorns removed by magpies were cached in the 2016-2017 sampling period, we radio-tracked one to nine acorns from each feeder following the previously described methodology (77 radio-tagged acorns in total). However, this small sample did not allow to accurately calculate the proportion of removed acorns that were cached and predated.

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[2] Videos available in: S1: ecs22989-sup-0001-VideoS1.mp4; S2: ecs22989-sup-0002-VideoS2.mp4; S3: ecs22989-sup-0003-VideoS3.mp4; S4: ecs22989-sup-0004-VideoS4.mp4; S5: ecs22989-sup-0005-VideoS5.mp4

Effectiveness of acorn dispersal

In both feeder experiments (i.e., 2015-16 and 2016-17), the cached radio-tracked acorns found intact were replaced with unmanipulated acorns, trying not to disturb the micro-site and using latex gloves to avoid impregnating the acorns with human smell. We tested emergence rate of brown fully ripened acorns in the lab, resulting in an average of 95.0% and 83.3%, respectively, for years 2015-16 and 2016-17. The acorns were harvested from the holm oak canopy as most of the acorns dispersed by magpies. We monitored the replaced acorns to know if they remained *in situ* and eventually produced a seedling or they were removed and consequently subjected to post-dispersal predation or secondary dispersal. As we did not follow the fate of the acorns removed from caches, we assumed that all disappeared acorns were predated. Cached acorns were geopositioned and we buried a 2-cm long nail under them to facilitate their relocation with a hand-held metal detector. We checked the acorns every week during the first month after acorn dispersion and every other week until the end of the experiment in mid-June.

To complement the results of seedling emergence from the monitored acorns, we sampled the abundance of holm oak and Portuguese oak emerged seedling in 200-m^2 transects in July 2016 and July 2017. Each year we surveyed the same 18 transects, nine of them next to three feeders (three transects per feeder 1, 4 and 7 **Figure 2.2A**) and nine of them farther away from these feeders (mean = 39.3 m, range = 26.8-48.6 m). If there were trees in the set transects, we circumvented the area below tree crowns to avoid the dispersion by gravity. We attributed most of the emerged oak seedlings to acorn dispersal by magpies as seedling emergence due to acorn dispersal by wood mice in Mediterranean environments is very low (Gómez, 2003; Gómez et al., 2019).

Characteristics of the magpie individuals that dispersed acorns

To identify breeding magpie adults and juveniles that removed acorns, we watched all the videos taken in the feeders in 2016-17; juveniles were the ringed nestlings in the previous breeding season. We sexed breeding magpies by drawing a drop of blood from each trapped individual with standard molecular procedures (Fridolfsson and Ellegren, 1999). Of the ringed breeding magpies, 19 were females and 14 were males. We captured both individuals of the breeding pairs for nine out of the 24 territorial breeding pairs. We never captured two individuals of the same sex in these territories. Later, to verify whether the ringed individuals were the breeding magpies of the territories, we installed trail cameras below the nest trees. We frequently observed ringed individuals in the breeding territories where they had been trapped. Additionally to the ringed breeding magpies, we were able to identify some un-ringed individuals as breeding magpies due to their cooperative behavior with the ringed breeding individual of the territory (for instance, an un-ringed magpie often offered acorns to a ringed female and, often, both individuals of the territorial breeding pairs defended together the feeder against other magpies). Moreover, some of these un-ringed individuals had a body mark or distinctive behavior (e.g., a small crest or stain, turning around itself before getting on the feeder, etc.).

Statistical analyses

We used generalized linear mixed-effects model with a Poisson error distribution and a log link function to analyze differences in the number of acorns removed by magpies depending on sex, feeder and time (days) (fixed effects) (package lme4; (Bates et al., 2015)). Individuals were the random effect. We performed two analyses using the data from feeders where magpies removed acorns for 42 days. In the first analysis, we only used the feeders where both sexes from the same breeding territory removed acorns (both males and females n = 3). In the second analysis, data from all feeders where at least one of the sexes removed acorns were analyzed (males n = 6, females n = 3). The variable “time” was standardized by rescaling to a mean of 0 and standard deviation of 1. Akaike’s information criterion (AIC) was calculated for each model; a smaller AIC indicates a better-fitting model as determined from the parsimony in the number of parameters. We used the cut-off of ΔAIC < 2 units to differentiate models with better explanatory power (package MuMin; Barton 2019). The analyses were performed in R (R Core Team, 2018).

2.3. Results

Identification of acorn dispersers from the trees and acorn caching

Trail cameras detected three bird species, namely magpie, wood pigeon, and jackdaw, removing or consuming acorns from the crown of the holm oaks. The magpie was the species that removed most acorns from the 14 studied holm oaks

(65%; **Table S2.1**). We recorded 93 removal events by magpies from all the five studied holm oaks, in 2016 and 174 removal events from the nine studied holm oaks in 2017. The acorns that were consumed or removed from the crown (**Video S6**)[3] before falling to the ground were mostly green but already ripe and sound (emergence rate > 80% according to our lab tests). Therefore, we observed that most of the acorn production was removed from the tree crowns while only a small proportion of acorns ended on the ground. The magpie was the only detected species that cached acorns after taking them from the oaks. Jackdaws removed acorns but we did not observe any single caching event, which is in accordance with Waite's (1985) study. We found seven radio-tagged cached acorns that were directly removed by magpies from five trees. We recorded five species consuming or removing acorns placed on the ground, in the following order of frequency: magpie (48%) > rabbit > wood mouse > wood pigeon > red-legged partridge (*Alectoris rufa*) (**Table S2.2**).

Proportion of active feeders by magpies and quantification of acorn dispersal

We recorded acorn removal by magpies in six out of 14 (43%) feeders in 2015-2016 and 14 out of 24 (58%) feeders in 2016-2017 (**Figure 2.2**). Magpies also removed most acorns from the feeders (84% of 694 acorns recorded in 2015–2016). The majority (> 90%) of acorns removed by magpies was taken one by one, carrying the acorns in their bills. Occasionally, they carried two or three acorns at the same time, one of them in the enlarged buccal cavity, partially swallowed, and the rest in the bill (**Videos S7-S9**)[4].

Magpies were also the only species that cached acorns once taken from feeders. They cached 178 radio-tagged acorns in 2015-16 (**Table 2.1**) and 42 in 2016-17; the dispersal distance ranged between 1.4 and 210 m (mean 32.5 ± 23.5 m; n = 220; **Figure 2.3**). Each cache always contained a single acorn. Videos showed that magpies usually flew and walked testing different sites before selecting the final caching site; then, the acorn was inserted into the ground and hammered with

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[3] Video S6 available in: ecs22989-sup-0006-VideoS6.mp4

[4] Videos available in: S7: ecs22989-sup-0007-VideoS7.mp4; S8: ecs22989-sup-0008-VideoS8.mp4: S9: ecs22989-sup-0009-VideoS9.mp4

the bill until it was totally or partially cached into the ground. The cached acorn was often covered with small stones (43.7%), litter or leaves (36.1%), or buried (20.2%) at a depth of 1-2 cm (**Videos S10-S11**)[5]. We also watched magpies recovering acorns from the caches in some videos (**Video S12**)[6]; however, we do not know if the recovered acorns were consumed or recached. To produce conservative estimates, we considered that acorns that disappeared had been predated.

Table 2.1. Number of acorns with radio-transmitter that were cached by magpies, consumed by magpies or jackdaws, or lost, and the species that removed acorns from each feeder in 2015-2016.

Number of active feeder (2015-2016)	Number of removed acorns with transmitter							Species that removed acorns
	Total	Cached acorns		Consumed acorns		Lost acorns		
	Number	Number	%	Number	%	Number	%	
1	46	21	45.7	22	47.8	3	6.5	Magpie and perhaps jackdaw
2	55	23	41.8	31	56.4	1	1.8	Magpie and perhaps jackdaw
3	29	29	100	0	0	0	0	Magpie
4	52	41	78.9	11	21.1	0	0	Magpie
7	38	32	84.2	6	15.8	0	0	Magpie
8	40	32	80.0	8	20.0	0	0	Magpie
Summary of all feeders	260	178	71.7	78	30.0	4	1.5	
Summary of feeders from which only magpies removed acorns	159	134	85.8	25	14.2	0	0	

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[5] Videos available in: S10: ecs22989-sup-0010-VideoS10.mp4; S11: ecs22989-sup-0011-VideoS11.mp4

[6] Video S12 available in: ecs22989-sup-0012-VideoS12.mp4

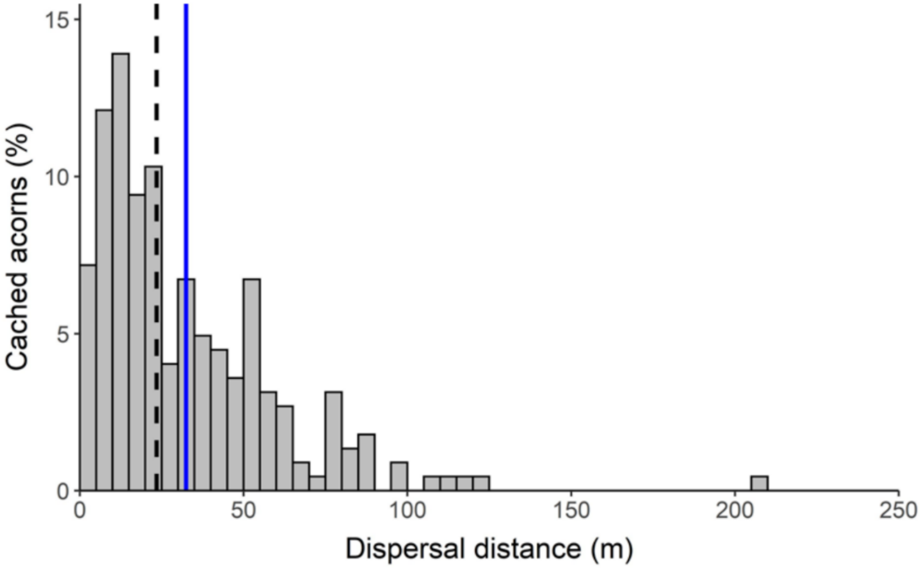

Figure 2.3. Frequency of dispersal distances of cached radio-tagged acorns in 2015-2016 (n = 178) and 2016–2017 (n = 45). The blue line represents the mean (32.4 m), and the dashed black line is the median (23.5 m).

During 2016-2017, 1214 ± 280 (mean ± SE) acorns per feeder (n = 6; range 409-2165) were removed over 6 weeks by one or the two individuals of the breeding pairs. Of the four feeders from where only magpies removed acorns in 2015-2016, 86% (134 of 159) of the removed acorns were cached and the remaining were consumed immediately after removal (**Table 2.1**). Therefore, we estimate that one or two magpies could cache a mean of 1044 ± 240 (86% of 1214) acorns per feeder (range 352-1862 acorns) in 6 weeks.

Effectiveness of acorn dispersal

Just one seedling emerged each year out of all cached acorns that were located using radio-tracking in the two studied years (emergence was 0.6% and 2.4% in 2015-16 and 2016-17, respectively). The remaining acorns were either removed or consumed (99.4% and 85.7% in 2015-16 and 2016-17, respectively) or dried out (0% and 11.9% in 2015-16 and 2016-17, respectively).

Our surveys in the transects revealed that, in 2016, 439 ± 234 and 289 ± 141 (mean ± S.E.) oak seedlings ha^{-1} emerged in sites near and far away from the feeders, respectively; while in 2017, the density was 56 ± 23 and 56 ± 21 seedlings ha^{-1}, respectively. No trace of the seedlings located in 2016 was found in 2017, suggesting strong predation by rabbits.

Characteristics of the magpie individuals that dispersed acorns

Acorns were removed from the feeders mainly by breeding magpies. We detected 14 out of the 33 ringed breeding magpies but only one out of the 136 ringed nestlings removing acorns from the feeders. Breeding magpies removed acorns regularly and mainly from the feeder located in their territory (6515 or 89.4% of the removed acorns); they seldom removed acorns from feeders located in other territories (4 acorns or 0.1%). Occasionally, juveniles and unidentified magpies removed acorns from the feeders (213 acorns or 2.9% and 551 acorns or 7.6%, respectively). Magpie behavior was different when they removed acorns from the feeders in their own territory (“normal” behavior) than when they did it in other territories ("skittish" behavior). When both sexes of the same breeding territory removed acorns from the feeders, males removed significantly more acorns (61.6%) than females (38.4%). The number of removed acorns decreased slightly with time and differed among feeders (**Table 2.2** and **Figure 2.4**). Similar results were observed in the feeders where at least one of the sexes removed acorns (**Figure S2.4** and **Table S2.3**).

Table 2.2. Model selection for generalized linear mixed-effects model of acorns removed by magpies in the feeders where both sexes removed acorns (both males and females n = 3)

Model parameters	df	AICc	ΔAIC	Weight
sex + feeder + time	6	3944.3	0	0.997
feeder + time	5	3956.6	12.31	0.002
time	3	3960.6	16.37	0
sex + time	4	3961.1	16.86	0
feeder + sex	5	4085.8	141.49	0
feeder	4	4098.1	153.82	0
null model	2	4102.2	157.91	0
sex	3	4102.6	158.38	0

Notes: Global model, number of acorns removed ~ sex + feeder + time + (1|individual), was the best model (marginal pseudo-R2 = 0.818). Degrees of freedom, AICc, ΔAIC, and model weight are shown.

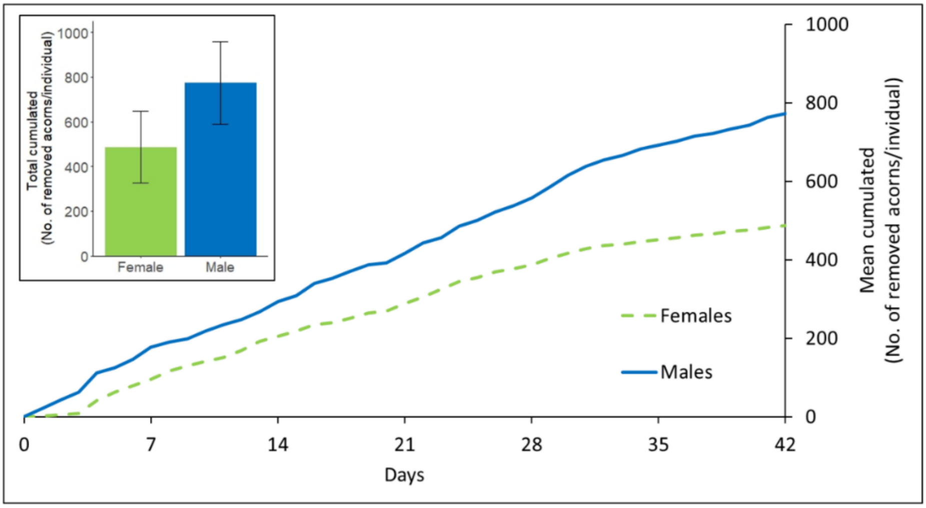

Figure 2.4. Mean number of daily-cumulated acorns removed by females (n = 3) and males (n = 3). Data from feeders where both sexes from the same breeding territory removed acorns for at least 42 d during 2016–2017. Inset figure shows the mean total cumulated number of removed acorns per individual at the end of the studied period, and error bars represent one standard error of the mean.

Considering the data of all feeders, breeding males (n = 7) removed 17.5 ± 4.3 (mean ± S.E.) acorns per day (range 5.2 - 38.0 acorns) and 805 ± 199 acorns (n = 6) in 6 weeks (range 219-1595 acorns). Breeding females (n = 4) removed 13.3 ± 3.2 acorns per day (range 4.7 - 18.6 acorns) and 487 ± 159 acorns (n = 3) in 6 weeks (range 197-747 acorns) (**Figure S2.5** and **Table S2.4**). Daily removal rates were calculated based on eight feeders, six with at least 42 days of acorn removal activity plus two feeders with at least 20 days of activity.

Since 86% of the acorns removed by magpies were cached, we estimate that a breeding male cached 15 acorns per day and 692 acorns during the 6 weeks period of dispersal on average. Similarly, a breeding female cached 11.4 acorns per day and 419 acorns in 6 weeks on average.

2.4. Discussion

This study confirms our hypothesis that magpies, one of the most common corvids in Eurasia, are effective and long-distance dispersers of acorns in open agroforestry systems. Acorn dispersal by magpies was massive and not just an occasional activity as previously considered (Clarkson et al., 1986; Waite, 1985;

Birkhead, 1991; den Ouden et al., 2005). Magpies produced hundreds to thousands of scattered caches of one single acorn. This resembles the strategy shown by Eurasian jay, which maximizes the potential for seedling emergence (Kurek et al., 2018), among other reasons. Our data revealed that a yearly average of 1.5% of the cached acorns resulted in emerged seedlings. The breeding status and gender of the magpies determined acorn dispersal propensity, and adult magpies were the dominant hoarders. Thus, acorn dispersal by magpies may have important implications for the recovery of oak forests in open agroforestry systems and abandoned croplands, where these birds are very abundant. Considering that magpies disperse other large seeds in Europe (Waite, 1985; Clarkson et al., 1986; den Ouden et al., 2005; Castro et al., 2017; Gómez et al., 2019), we suggest that this process could occur in large areas of Eurasia. Besides its ecological and practical ramifications, the results from this study should improve the tarnished reputation of magpies, which persists due to misconceptions about their adverse effects on crops, small game animals, and songbirds (Madden et al., 2015).

Magnitude of acorn dispersal by magpies

The magpie was the bird species that removed the greatest number of acorns from experimental feeders and tree crowns, and the only bird species that cached acorns (169-1,372 acorns per individual in 6 weeks). Our estimates of the amount of acorns removed and cached from the feeders are highly conservative because: 1) we observed that many magpies noticeably suspected the feeders; 2) magpies only used the feeders when acorns in trees disappeared, i.e., the amount of removed acorns from the feeders was only a fraction of the total removed acorns; 3) some acorn removal events were not recorded by trail-cameras, particularly when magpies removed acorns very quickly; and 4) acorn handling to insert the radio transmitter may have increased acorn predation rate by magpies suspecting the cutting marks. All these pieces of evidence suggest that the number of dispersed acorns per individual could be higher with a more protracted acorn supply. For instance, Pulido and Díaz (2005) determined that holm oak acorn supply lasted for 13-20 weeks in oak agroforestry systems (*dehesas*) in central-western Spain. Previous studies suggest magpie-mediated dispersal of almonds and chestnuts (Homet-Gutiérrez et al., 2015; Gómez et al., 2019) or study acorns and walnuts dispersal from feeders by magpies (Waite, 1985; Castro et al., 2017).

However, no study had previously quantified the magnitude of acorn dispersal by magpies.

A better understanding of the ecological relevance of the interaction between magpies and oaks requires estimating the intensity of such interaction (see Wootton and Emmerson (2005) for other animal-plant interactions). Gómez *et al.* (2019) suggested that the most reliable estimate of the quantity component of synzoochory effectiveness is the proportion of the seed crop that is dispersed by the hoarding animal, irrespective of the final fate of the seed after dispersal. In our study, as magpies removed 65% of acorns from the holm oak crowns and cached 86% of the removed acorns, we estimated that they cached 56% of all acorns from the oak crowns (**Figure 2.5 A**). Other studies have reported cached proportions of removed walnuts by magpies of 89.4% (Castro et al., 2017) and 64% of removed acorns by Eurasian jays (Pons and Pausas, 2007a). The fate of crown acorns was likely representative of what happened to most of the acorn production of trees in our study area because acorns were mostly removed or consumed before falling to the ground. Moreover, we estimated that magpies cached 41% of all acorns from the ground (**Figure 2.5 B**). These values from oak crowns and ground of our study coincide with the value found, pooling many studies of synzoochory, by Gómez *et al.* (2019), who reported that 48% of the seed crop was harvested and dispersed by corvids.

In short, our data suggest that the interaction between magpies and holm oaks is likely a major mean by which this tree species disperses in open landscapes. Magpies are thus likely to have a strong ecological and evolutionary impact on their interacting tree partners, and vice versa. However, this massive acorn dispersal behavior by magpies has remained undetected, likely due to the birds' mistrust of humans. Only the combination of trail cameras and radio tracking allowed us to discover this behavior in our study site (see Material and methods section for effective and ineffective methodology).

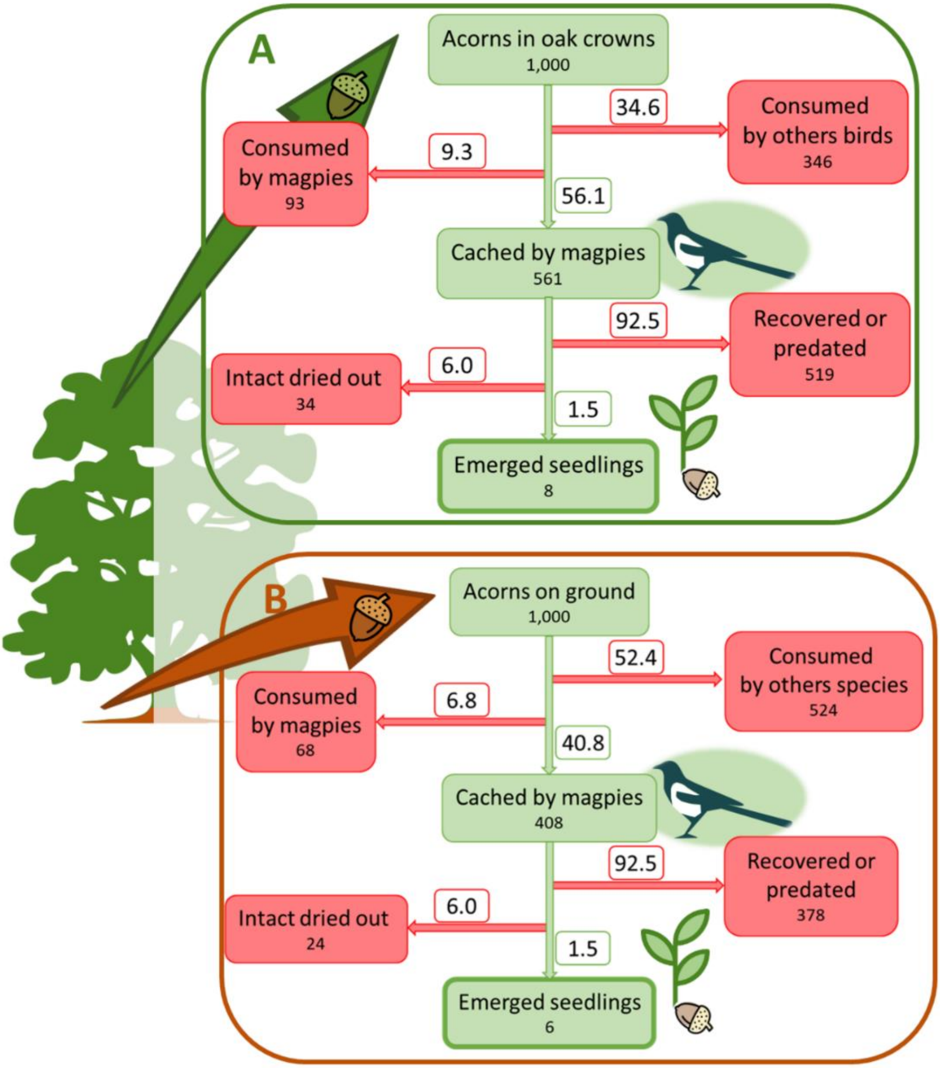

Figure 2.5. Path diagrams of acorn fate after acorn removal. Numbers inside the boxes indicate the standardized number of acorns in every stage with a starting amount of 1000 acorns. A) Removal from the holm oak crowns by birds and B) from the ground by all species until seedling emergence. The numbers associated to the arrows indicate the percentage of available acorns for the next stage (arrows pointing to the green boxes) or lost acorns (arrows pointing to the red boxes). Cached acorns by magpies that were "recovered or predated" could be also secondary dispersal.

Magpies can be considered effective acorn dispersers (*sensu* Schupp *et al.* (2010)) because a fraction of cached acorns became seedlings. We estimated that 0.8% of all acorns from the holm oak crowns and 0.6% of all acorns from the ground below oaks resulted in emerged seedlings in early summer (**Figure 2.5**). Despite these relative low proportions of emerged oak, we observed a high seedling density in the study site because of the high absolute magnitude of the acorn crops. We attribute most of these emerged oak seedlings to acorns that were dispersed by magpies, since the other potential acorn disperser in the study site –the wood mice– consumes nearly all the acorns they disperse (Gómez, 2003; Gómez et al., 2019). In an experiment that we conducted in a site close to our study area, none of the 809 acorns of holm and Portuguese oaks removed by wood mice became a seedling because all were consumed (unpublished data).

Seedling emergence was possibly favored by several reasons, namely 1) a portion of the acorns was not recovered because magpies forgot them after being cached; 2) magpies did not need to recover all cached acorns due to excess of acorns or other food types; and 3) dispersers died or lost their territory (Bossema, 1979; Darley-Hill and Johnson, 1981; Schupp et al., 2010). Some facts support these reasons, including that our study area had plenty of food for magpies (acorns, almonds, walnuts, rabbit carrion, etc.) and a great diversity of magpie predators. However, the presence of rodents, high density of rabbits that consumed both acorns and seedlings, and strong drought stress were important bottlenecks for oak recruitment in our study area. These context-dependent factors might also explain the lower dispersal effectiveness compared to a previous study of walnut dispersal by magpies (Castro et al., 2017). Consistently with this pattern, Pesendorfer *et al.* (2016b) reported a significant recovery of oak species with the presence of an acorn disperser corvid when herbivores were removed in a Californian island.

Comparison with the dispersal capacity of other corvid species

The number of acorns removed and cached by magpies was lower than the values reported for other corvids. Pesendorfer *et al.* (2016c) estimated that Island scrub-jays (*Aphelocoma insularis*) cached between 3,500 and 5,000 acorns per individual in a dispersal period of 110 days, with a rate of 7.2 acorns per hour. DeGange *et al.* (1989) estimated that Florida scrub-jays (*Aphelocoma coerulescens*) cached about 5,000 acorns per dispersal season of four months. Bossema (1979) reported that Eurasian jays could cache about 4,600 acorns per dispersal season. Four reasons could explain the lower estimated dispersal by magpie individuals compared to other corvids, including the 1) different quantification methodology; 2) different length of the dispersal period; 3) fear of removing acorns from the feeders by some magpies; and 4) more generalist diet of magpies than of the other corvids (Birkhead, 1991).

Differences in dispersal behavior between individual magpies

Non-breeding individuals removed few acorns from the feeders with respect to the breeding pairs, probably due to the magpie territorial behavior, who forced their offspring to leave. However, this scarce acorn dispersal by non-breeding individuals could be qualitatively relevant for oak regeneration because they could be dispersed over longer distances than the ones dispersed by breeding individuals (Birkhead, 1991). Despite low replication, breeding male magpies dispersed around twice as many acorns as breeding females. Future studies should confirm this result and elucidate the ecological implications of differences in dispersal behavior among sex or reproductive status on oak regeneration. It is possible that if mortality differs between sexes or reproductive status (Birkhead, 1991), this could affect also the amount of abandoned cached acorns, leading to different amount of seedling emergence.

We detected acorn removal by magpies only in half of the feeders we installed. Some explanations for this are: 1) the above-mentioned fear of some magpies to the feeders; 2) the death or loss of territories by some individuals [territory tenure by magpies was 1.7 years at our study site (n = 33), calculated following (Birkhead, 1991)]; and 3) territories with low primary productivity in autumn-winter may have been abandoned during this period.

Ecological implications of acorn dispersal by magpies

Our study shows for the first time a strong interaction between oaks and magpies. As a result, we hypothesize that the massive behavior of acorn dispersal by magpies could be a common behavior where its distribution overlaps with that of oak species (**Figure 2.1**). Several lines of evidence support this hypothesis: 1) magpies are known to cache food (Birkhead, 1991); 2) acorn dispersal in our study was massive despite the existence of other food sources; 3) we recorded magpies caching acorns of two oak species and almonds; 4) magpies have been found to cache other large seeds too (Homet-Gutiérrez et al., 2015; Castro et al., 2017; Gómez et al., 2019); and 5) other authors occasionally detected magpies caching acorns of oak species other than holm oak and Portuguese oak such as pedunculate oak (*Q. robur*) and sessile oak (*Q. petraea*) (Waite, 1985; Clarkson et al., 1986; Birkhead, 1991; den Ouden et al., 2005). This hypothesis should be tested in other areas with different landscape structure and where other oak species and magpie species coexist, opening a research field that could have deep implications for forest restoration in strongly deforested landscapes (Andivia et al., 2017). Moreover, the habitat complementarity between the Eurasian jay and the magpie suggests broad biogeographical implications throughout Eurasia mediated by extensive acorn dispersal.

Magpies have traditionally been considered a pest by farmers and hunters (Madden et al., 2015). It is our hope that this view progressively changes as we increase our understanding of the ecological role of magpies in the provision of ecosystem services such as acorn dispersal. This ecosystem service could have strong implications in the current context of farmland abandonment across Eurasia (Verburg and Overmars, 2009). Analyzing the spatial pattern of acorn dispersal by magpies and oak recruitment would help further understand how magpies may transform open habitats into woodlands, as has previously been assessed for other corvids (Waite, 1985; Gómez, 2003; Pesendorfer et al., 2016b). Taking all these ideas together, our study suggests that magpies could be a key species, as major acorn dispersers in open agroforestry systems and in landscapes with remnants of small oak patches or scattered oaks.

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Authors' contribution: LMB, LPC, PVS, SR, MMM, ABL, JC, and JMRB conceived and designed the experiments. LMB, LPC, PVS, SR, PQ, and DGS performed the experiments and collected the data. LMB, LPC, PQ, and DGS reviewed the videos and processed the data. LMB and LPC wrote the draft of the manuscript. All authors discussed the results and reviewed the manuscript.

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2.7. Supporting information

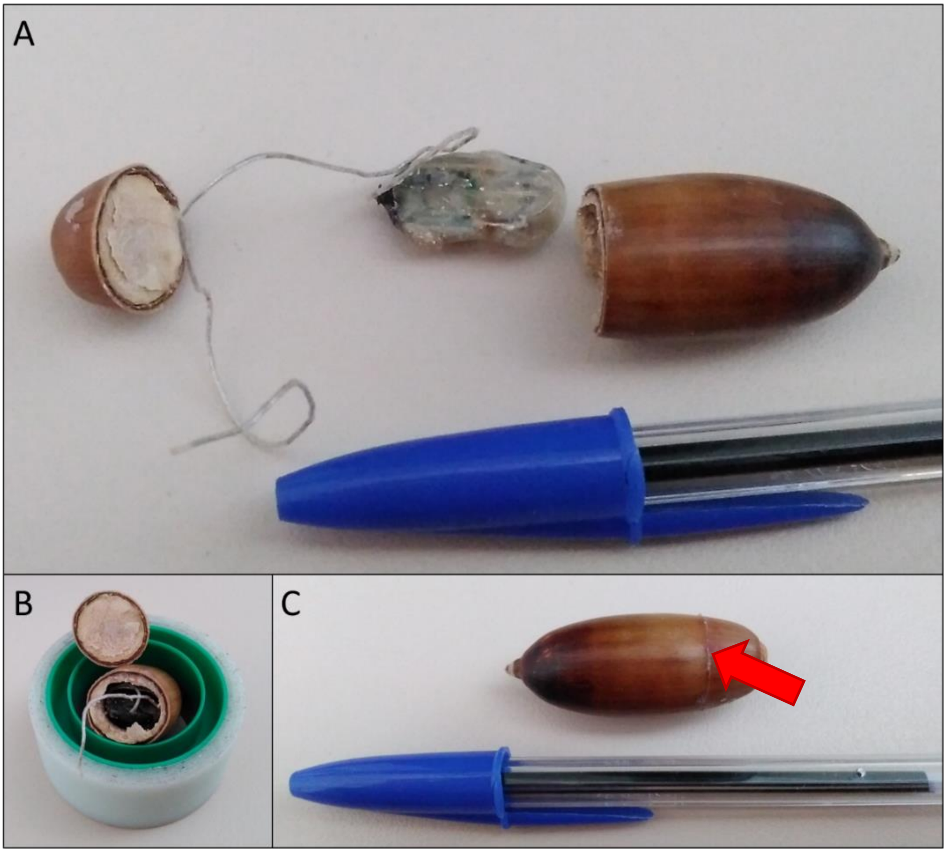

Figure S2.1. Steps for inserting a radio transmitter inside an acorn. A) Cut acorn and radio transmitter. B) Acorn with radio transmitter inserted. C) Closed acorn with radio transmitter inserted, red arrow signs the excision scar.

Figure S2.2. Ground feeder used in the experiment with acorns.

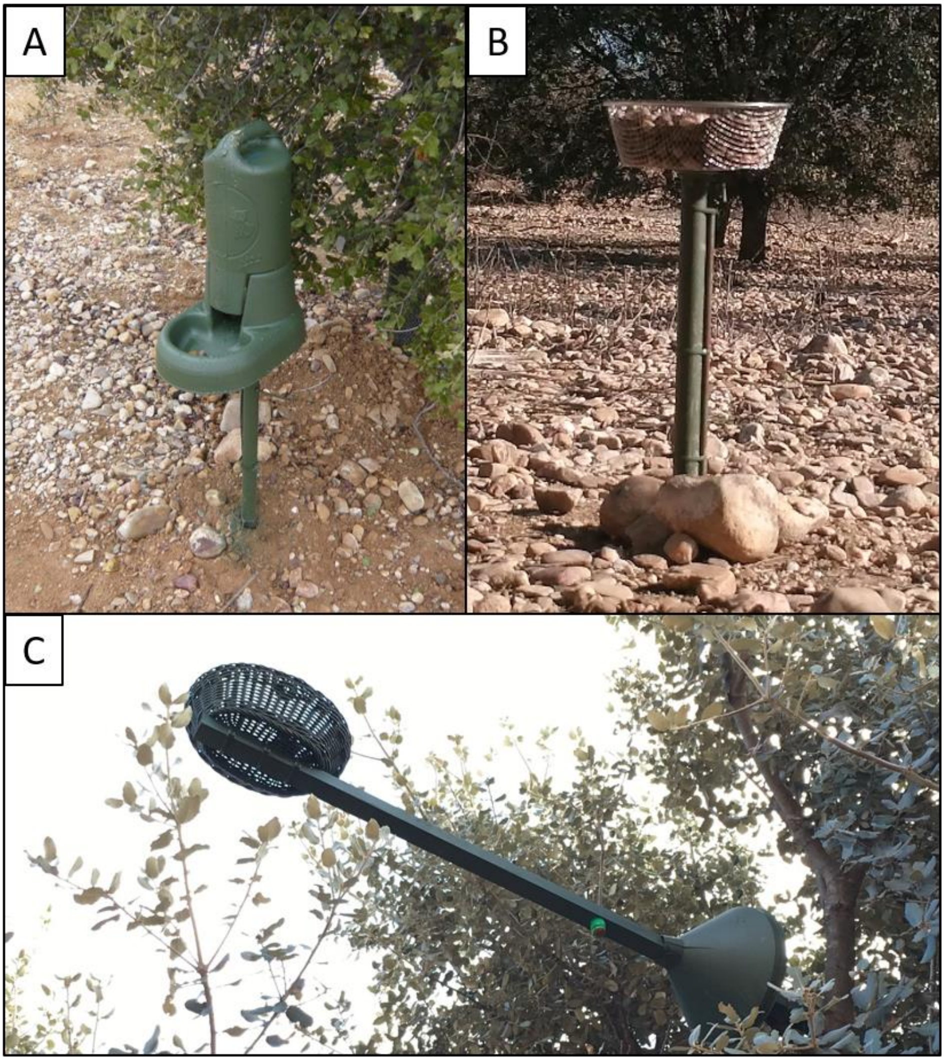

Figure S2.3. Types of feeders tested that magpies refused: A) Auto pet feeder. B) Feeder with large mesh size. C) Feeder in the tree canopy.

Table S2.1. Number and proportion of consumed or removed acorns from the crown of holm oak trees by different bird species in 2016 (n=5) and 2017 (n=9). Reported percentages refer to each tree and year and to all trees after two years.

		Magpie		Wood pigeon		Jackdaw	
Year	Holm oak	Number of acorns	%	Number of acorns	%	Number of acorns	%
2016	1	4	66.7	2	33.3	0	0
	2	19	100	0	0	0	0
	3	29	82.9	0	0	6	17.1
	4	1	0.9	102	92.7	7	6.4
	5	40	37.0	10	9.3	58	53.7
2016	**Total**		**57.5**		**27.1**		**15.4**
2017	6	18	81.8	0	0	4	18.2
	7	11	52.4	10	47.6	0	0
	8	26	100	0	0	0	0
	9	44	86.3	5	9.8	2	3.9
	10	18	81.8	2	9.1	2	9.1
	11	17	94.4	1	5.6	0	0
	12	3	20.0	12	80.0	0	0
	13	25	43.9	3	5.3	29	50.9
	14	12	100	0	0	0	0
2017	**Total**		**73.4**		**17.5**		**9.1**
Two years	**Total**		**65.4**		**22.3**		**12.3**

Table S1.1. Number and proportion of consumed or removed acorns on the ground below six holm oak trees in 2018 by different animals. Percentages refer to each ground feeder or all feeders. The other bird species are wood pigeon and red-legged partridge. Detectability of the consumed or removed acorns were 98% for wood mouse, 80% for rabbit and 32% for magpie.

Ground feeders (2018)	No. of removed acorns	Number of removed acorns that were video recorded									Unrecorded removed acorns
		Magpie		Rabbit		Wood mouse		Other bird species		Total	
		Number	%	Number	%	Number	%	Number	%	Number	
1	47	21	96	0	0	0	0	1	5	22	25
2	54	0	0	0	0	51	100	0	0	51	3
3	100	0	0	77	99	0	0	1	1	78	22
4	100	36	90	0	0	0	0	4	10	40	60
5	50	0	0	34	100	0	0	0	0	34	16
6	100	14	100	0	0	0	0	0	0	14	86
Total			**48**		**33**		**17**		**3**		

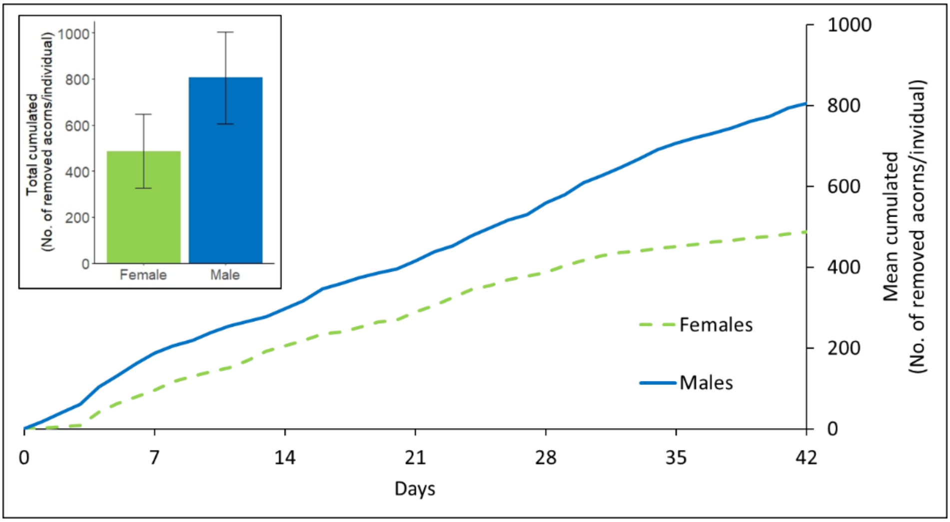

Figure S2.4. Mean number of daily-cumulated acorns removed by females (n=3) and males (n=6) from feeders where at least one of the sexes removed acorns for 42 days during 2016-2017. In the square inside the graphic we show the mean total number of acorns at the end of these days, error bars represent standard error.

Table S1.2. Model selection for generalized linear mixed-effects model of acorns removed by magpies in the feeders where at least one of the sexes removed acorns were analyzed (males n = 6, females = 3). Global model: number of acorns removed ~ sex + feeder + time + (1|individual); was the best model (marginal pseudo-R^2 = 0.873). Degrees of freedom, AICc, ΔAIC and model weight.

Model parameters	df	AICc	ΔAIC	Weight
sex + feeder + time	9	5651.8	0	1
feeder + time	8	5671.7	19.8	0
time	3	5680.4	28.6	0
sex + time	4	5681.4	29.6	0
feeder + sex	8	5778.8	127.0	0
feeder	7	5798.7	146.9	0
null model	2	5807.5	155.6	0
sex	3	5808.5	156.6	0

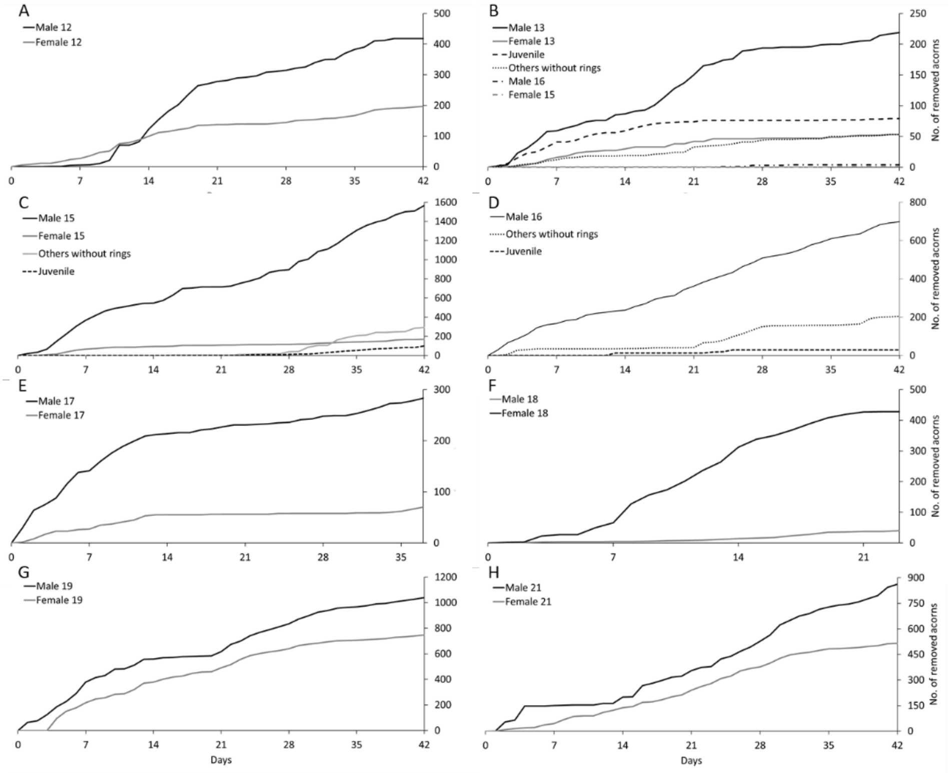

Figure S2. 5. Cumulated acorn removal from each feeder for males and females of breeding magpie pairs: feeders' number 12 (A), 13 (B), 15 (C), 16 (D), 17 (E), 18 (F), 19 (G), and 21 (H). Other magpies that occasionally removed acorns from these feeders are also shown: one juvenile, males and females of other feeders and other magpies without rings. Male 18, female 13, 15 and 17 only removed acorns from the ground. Ground acorns are the acorns that fell out of the feeder, so their number was very limited and subjected to predation by rabbits and mice.

Table S1.3. Data summary of the feeders where at least one individual of the breeding magpie pair removed acorns during more than 20 days in the dispersal period of 2016-2017 (see **Figure 2.2**).

Number of active feeders (2016-2017)	Days of recording	Male visited the feeder	Daily removal rate of males (acorns day^{-1})	Female visited the feeder	Daily removal rate of females (acorns day^{-1})
12	42	Yes	10.0	Yes	4.7
13	42	Yes	5.2	No	1.3*
15	42	Yes	38.0	No	4.1*
16	42	Yes	16.6	-	-
17	37	Yes	7.6	No	1.9*
18	23	No	1.7*	Yes	18.6
19	42	Yes	24.7	Yes	17.8
21	42	Yes	20.5	Yes	12.3
Total			15.6 (n=8)		8.7 (n=7)
Total (calculated only with the magpies that visited the feeder)			17.5 (n=7)		13.3 (n=4)

(-) The ringed individual was not watched in any video.

(*) From acorns that fell from the feeders and were removed from the ground.

Imágenes de arriba a abajo y de izquierda a derecha:

Finca El Carmen: Zona arada
Finca El Carmen: Bosquete
Alrededores de la finca El Carmen: herbazal
Urraca posada en uno de los comederos con bellota en el pico
Bellota con radiotransmisor escondida por una urraca entre hojarasca
A la izquierda bellota con radiotransmisor enterrada, a la derecha misma bellota con transmisor ya desenterrada
Fuente de las imágenes: L. Martínez-Baroja y grupo de investigación SERAVI

Capítulo 3

Caching territoriality and site preferences by a scatter-hoarder drive the spatial pattern of seed dispersal and affect seedling emergence[7]

Abstract

1. For plants with seeds dispersed by scatter-hoarders, decision-making by animals when caching determines the spatial pattern of seed dispersal and lays the initial template for recruitment, driving the regeneration of many species. However, the mechanism by which animal behaviour shapes seed distributions in spatially complex landscapes is not well understood. We investigated caching territoriality and site preferences to determine the spatial pattern of seed caching at different scales and whether scatter-hoarding behaviour drives the spatial distribution of seedling emergence.
2. We used radio-tracking and automatic wildlife cameras to monitor holm oak (*Quercus ilex*) acorn caching by Eurasian magpies (*Pica pica*), who are effective scatter-hoarders in agroforestry systems. We assessed the effect of caching territories, distance to seed source, habitat, sub-habitat, microsites, and caching material in the spatial pattern of acorn dispersal by magpies. In addition, we analysed the relationship between the density of cached acorns and of emerged seedlings in different habitats.
3. Breeding magpies cached the acorns inside their caching territories, where they preferred tilled areas over oak plantations and mostly avoided old fields. These differences in habitat preference were maximized at relatively short to medium dispersal distances, where most acorns were cached, and decreased or disappeared at long-distances. Within tree plantations,

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[7] This chapter fully reproduces the manuscript sent for publication:

Martínez-Baroja, L., Pérez-Camacho, L., Villar-Salvador, P., Rebollo, S, Leverkus, A.B., Pesendorfer, M.B., Molina-Morales, M, Castro, J. In second review. Caching territoriality and site preferences by a scatter-hoarder drive the spatial pattern of seed dispersal and affect seedling emergence. Journal of Ecology.

magpies preferred high plant-productivity sites over low productivity ones. At the finest spatial scale, magpies preferred structures built by animals, such as rabbit grit mounds and latrines and ant litter mounds, to cache the acorns. In many sites, magpies selected uncommon materials such as stones and litter to cover caches. In the subsequent spring, seedling emergence was positively correlated with acorn cache density.

4. *Synthesis*. Scatter-hoarding is a hierarchical process in which caching sites are selected using different criteria at different spatial scales driven by territoriality and site preferences. Territoriality constrained dispersal distance and the habitats available for acorn caching. Magpie territoriality therefore indirectly drives oak seedling emergence and can determine oak recruitment and forest regeneration.

Resumen

1. Para las plantas con semillas dispersadas por animales que hacen almacenes dispersos (*scatter-hoarders*), la toma de decisiones de los animales cuando almacenan las semillas determina el patrón espacial de dispersión y la plantilla inicial del reclutamiento, lo que dirige la regeneración de muchas especies. Sin embargo, no se comprende bien el mecanismo por el cual el comportamiento animal da forma a la distribución de semillas en paisajes espacialmente complejos. En este estudio investigamos cómo la territorialidad para el almacenamiento de semillas y las preferencias espaciales del animal determinan el patrón espacial del almacenamiento de semillas a distintas escalas espaciales y si el comportamiento de realizar almacenes dispersos afecta a la densidad de plántulas emergidas.

2. Monitoreamos el almacenamiento de bellotas de encina (*Quercus ilex*) por la urraca (*Pica pica*), un dispersor efectivo en sistemas agroforestales, mediante radio-seguimiento y cámaras de fototrampeo. Evaluamos el efecto de los territorios de almacenamiento, la distancia a la fuente de semillas, el hábitat, el sub-hábitat, el micrositio y el material de almacenamiento en el patrón espacial de la dispersión de bellotas. Además, se analizó la relación entre la densidad de bellotas almacenadas y la de las plántulas emergidas en los distintos hábitats.

3. Las urracas reproductoras almacenaron las bellotas dentro de sus territorios de almacenamiento y prefirieron zonas abiertas aradas a plantaciones forestales de quercíneas, evitando generalmente el herbazal que rodea las plantaciones forestales. Estas diferencias en la preferencia por los distintos hábitats fueron máximas a distancias de dispersión relativamente cortas o medias, donde se almacenaron la mayor parte de las bellotas, y decrecieron o desaparecieron a distancias largas. Dentro de la plantación forestal, las urracas prefirieron los sub-hábitats de mayor productividad vegetal para almacenar bellotas. A escala de micrositio, prefirieron las estructuras hechas por animales, como escarbaduras y letrinas de conejos y hormigueros. En muchos lugares las urracas seleccionaron los materiales menos abundantes como piedras y hojarasca para ocultar las bellotas. En la primavera siguiente la densidad de plántulas recién emergidas en los hábitats se correlacionó con la densidad de bellotas almacenadas.

4. *Síntesis*. El proceso de toma de decisiones en el almacenamiento disperso de semillas es jerárquico dado que los lugares de almacenamiento se seleccionan a distintas escalas espaciales determinados por la territorialidad y las preferencias espaciales de almacenamiento. La territorialidad restringió la distancia de dispersión y la disponibilidad de hábitats para el almacenamiento de bellotas. En consecuencia, la territorialidad de las urracas determina indirectamente la emergencia de plántulas y puede determinar el reclutamiento de quercíneas y la regeneración del bosque.

3.1. Introduction

Seed dispersal is a central process in the plant life cycle that provides connectivity among populations, colonization of empty habitats, and range mobility in response to climate change (González-Varo et al., 2017). For zoochorous plants, animal behaviour drives seed fate because animals do not disperse seeds randomly in the landscape (Alcántara et al., 2000; Rodríguez-Pérez et al., 2012). Therefore, understanding the seed dispersal behaviour of animals is fundamental to unravel how seeds are distributed in space, the process which forms the initial template for plant recruitment (Nathan & Muller-Landau, 2000; Schupp & Fuentes, 1995) and forest regeneration (Leverkus & Castro, 2017).

Synzoochory is a special case of zoochory in which animals deliberately cache the seeds for later consumption (Gómez et al., 2019; Lichti et al., 2017). In scatter-hoarding animals, which superficially bury individual seeds in caches, the spatial pattern of seed dispersal results from a complex decision-making process (Lichti et al., 2017) aimed at maximizing retrieval of cached seeds (Pesendorfer et al., 2016; Waite & Reeve, 1992). Seed caching decisions involve trade-offs between seed caching effort and seed retrieval, risk of disperser predation, and avoidance of seed pilfering and damage (Clarkson et al., 1986; Lichti et al., 2017). From the plant perspective, the spatial distribution of individuals, reproductive success, and population genetic structure depend on the characteristics of seed caching sites, from the habitat to the microsite scale (García-Cervigón et al., 2018; Jordano, 2017; Scofield et al., 2010; Stiles, 2000).

Although synzoochory is context-specific and depends on animal and plant species’ idiosyncrasies, several general features of the seed scatter-hoarding process may determine seed spatial pattern and, consequently, plant recruitment (Cousens et al., 2010; Scofield et al., 2010). For instance, several scatter-hoarding birds tend to cache food in the vicinity of their nests or inside their home ranges (Birkhead, 1991; DeGange et al., 1989; Jokinen & Suhonen, 1995; Tomback, 2016). However, little is known about the existence of “caching territories”, i.e. areas where individuals cache seeds in exclusivity and that are defended to avoid seed pilfering (Lorenz et al., 2011). The existence of "caching territories" and their characteristics could determine the spatial pattern of seed dispersal, plant regeneration, and gene flow.

In spatially heterogeneous environments, scatter-hoarders often show strong preferences for sites with specific soil or vegetation characteristics to cache seeds (Gómez, 2003; Morán-López et al., 2015; Pons & Pausas, 2007; Vander Wall, 1990). In this context, distance from seed sources to caching sites can affect the density and site preference of caches (Clarkson et al., 1986; Waite & Reeve, 1992). However, distance has been little considered in modelling site selection for food caching by scatter-hoarders. We also do not know whether caching territoriality constrains site preferences for seed caching. Similarly, little is known about the variation of caching preferences at different spatial scales (Gómez, 2003) and whether these preferences drive the spatial pattern of seedling emergence (Lenda et al., 2012).

Here, we study the importance of caching territoriality, site preferences, and caching distance as drivers of 1) seed caching at different spatial scales and 2) subsequent seedling emergence at a coarse spatial scale. To address this goal, we used the interaction among Eurasian magpies (*Pica pica* L.) and holm oaks (*Quercus ilex* L.) as our study system. Magpies are massive acorn scatter-hoarders, i.e. that disperse large numbers of acorns (Martínez-Baroja et al., 2019), and territorial breeders (Baeyens, 1981; Birkhead, 1991; Szala et al., 2020) that inhabit open landscapes. The holm oak is the most important tree in agroforestry systems in the western Mediterranean Basin (Pulido & Díaz, 2005). Acorn dispersal was monitored with radiotracking and cameras to address three objectives. First, we aimed to ascertain whether acorn caching in space is constrained by territorial behaviour of the scatter-hoarder. If magpies monopolised some areas for acorn caching, this would support our hypothesis of the existence of seed caching territories (H1). Our second objective was to investigate whether acorn-caching preferences occur at different spatial scales. If magpies cache acorns in specific sites after controlling for dispersal distance, this would support site preferences (H2). Third, our goal was to analyse whether oak seedling emergence matches the spatial pattern of acorn dispersal. Correspondence of emergence with cache distribution would support our hypothesis that caching preferences drive seedling emergence distributions (H3). The results of this study will contribute to the understanding of how scatter-hoarders shape the spatial pattern of natural forest regeneration. Further, they may provide practical lessons to assist in forest restoration.

3.2. Materials and methods

Study site

The study area is an agroforestry ecosystem in central Spain (40º 31′ 0′′ N, 3º 19′ 55′′ W), 605 m a.s.l. with continental Mediterranean climate. Mean annual temperature and precipitation are 13.8ºC and 425 mm, respectively. The soil is alluvial and deep, with a silty loam texture and high proportion of gravel and pebbles (see **Table S3.1** for stone cover) and a pH around 8.0 (Trueba et al., 1998). The area includes a 28.4 ha plantation of holm oak and Portuguese oak (*Quercus faginea* Lam.) planted in 1995, surrounded by old fields (**Figure S3.1**). Several firebreaks cross and surround the plantation and are ploughed at least once a year. Almond trees (*Prunus dulcis* (Mill.) D.A. Webb) have colonized some parts of the study area forming mixed almond tree and oak forest patches. Numerous potential acorn consumers such as rabbits (*Oryctolagus cuniculus* L.), magpies, common wood pigeons (*Columba palumbus* L.), and scarce wood mice (*Apodemus sylvaticus* L.), breed and feed in this area, while jackdaws (*Corvus monedula* L.) feed but do not breed there. Only magpies and mice are considered acorn scatter-hoarders, however, the role of mice as acorn dispersers has been argued, being considered more as an acorn consumer than as an effective disperser (Gómez et al., 2019). Additionally, the very low density of the rodents likely has a small impact on oak community dynamics in this location.

Spatial pattern of acorn dispersal

We studied the spatial pattern of acorn dispersal by magpies using radio-tagged acorns provided in six feeding stations (hereafter "feeders") in 2015-2016. Feeders consisted of a colander fixed to the top of a 60-70 cm metal rod. Feeder positions were chosen to include a range of habitat types and distances from feeders to the old fields (**Figure S3.1**). From November to December 2015, the feeders were filled repeatedly to maintain 10 acorns per feeder to attract magpies. We monitored acorn removal by magpies with trail cameras (Moultrie MCG-12634; Moultrie Products, Alabama, USA), which recorded 1-minute videos when movement was detected. Once the magpies got used to the feeders, we regularly supplied radio-tagged and untagged acorns (Martínez-Baroja et al., 2019; Pons & Pausas, 2007) from November 2015 to April 2016. Removed acorns were located on the same day to avoid post-dispersal predation or secondary dispersal. Caches of radio-tagged acorns were located in two steps; first, the caching vicinity was determined with a Yagi antenna connected to a radio receiver (Biotrack SIKA Radio Tracking Receiver, Wareham, Dorset, UK). Finally, precise locations were determined using a metal detector (White's Auto-Scan Personal Search Detector, Tulsa, Oklahoma, USA). We registered the type of habitat, sub-habitat, microsite, caching material, and coordinates of the cached acorns.

Delimitation of caching territories

To test whether magpies used caching territories, i.e. an area where only the pair that owns the territory caches acorns and prevents other magpies from caching and recovering acorns (H1), we constructed a Voronoi polygon (VP) around each active nest in the next spring to assess whether the distributions of cached acorns coincided with these polygons. VPs are often used as a model for bird territory estimations (Adams, 2001; Schlicht et al., 2014). In spring 2016, after monitoring acorn dispersal, we located all active magpie nests (Details in Supplementary Methods in Supporting Information; **Figure S3.2** and **S3.3**). VPs were drawn using Quantum GIS (Quantum GIS Development Team, 2016) by establishing perpendicular bisectors of the lines connecting each active nest to the nearest neighbouring active nests in order to equally distribute all the available space among the active territories (**Figure S3.4**). Thus, any point within each VP is closer to the nest located inside the polygon than to any other nest. We applied a 5 m buffer around each VP for territoriality deviation and GPS errors.

To qualitatively validate the pattern of caching territoriality in time and space, we sampled 18 additional nests during the period 2016-2017. To do so, 1) we captured 33 breeding magpies from 24 active nests and 136 nestlings taken from 51 active nests from May to July 2016 (details in Supplementary Methods in Supporting Information). All individuals were individually marked with field-readable combinations of coloured metal rings to the tarsus for identifications purposes. 2) We installed 24 feeders close to the nests where breeders were ringed. From December 2016 to March 2017, magpies removed acorns from 14 of 24 feeders. Each active feeder was supplied with 2–11 radio-tagged acorns (mean = 5) to study the caching behaviour of ringed individuals as described before. Finally, 3) we located all active magpie nests in spring 2017 and delimited their VPs. For the 2016-17 season, activity of ringed individuals allowed us to assess the concordance between caching territories and breeding territories in the following breeding season.

Habitats, sub-habitats, microsites, and materials for acorn caching

We assessed site preferences for acorn caching at three spatial scales. At the coarsest spatial scale, we differentiated three habitats (**Figure S3.1 C**), which were: (1) Tree plantation, dominated by planted holm oaks, spontaneous almond trees, and some planted Portuguese oaks with herbaceous vegetation in the gaps; this habitat had not been ploughed for 10 years; (2) fields that were abandoned ca. 30 yr prior to the study ("old fields" from now on), dominated by an herbaceous community with a few abandoned olive trees (tree cover <1%); this habitat surrounds the tree plantation and has not been ploughed for 29 years; and (3) Tilled areas, which are 4-7.5 m wide firebreaks within the tree plantation and between the tree plantation and the old fields; this habitat was ploughed once or twice per year.

At an intermediate spatial scale, we distinguished two sub-habitats inside the tree plantation according to plant productivity: high and low plant productivity. This was determined by the mass and cover of herbs and trees, which were defined by the presence of a streambed (high plant productivity sub-habitat) that crosses the tree plantation longitudinally *versus* outside of the streambed (low plant productivity sub-habitat; details in Supplementary Methods in Supporting Information; **Table S3.1**, **Figure S3.1**, **Figure S3.3**). Additionally, we distinguished two sub-habitats according to tree cover in the tree plantation: beneath tree canopies versus in the gaps between canopies. Location, cover, and composition of habitats and sub-habitats were determined on digitized photos using Quantum GIS.

At a fine spatial scale, we distinguished three types of microsites made by two animal species: rabbit grit mounds and latrines and ant litter mounds. We estimated the cover of these microsites around each feeder using eight radial linear transects separated by 45°. Transect length in each feeder was defined by the most remotely dispersed acorn from that feeder (mean = 83.3 m; range: 64-112 m). Microsite cover was calculated as the proportion of the transect overlapping each microsite. We also recorded three materials that magpies used to cover acorns: loose soil, plant litter, and stones. We estimated the cover of these three materials in 50 x 50 cm quadrats according to the following sampling design. We made three replicates, each one near each pair of feeders (feeders 1-2, 3-4 and 5-6; **Figure S3.1 C**, **Figure S3.3**). Each replicate included four 40-m long transects: two transects in the tree plantation (one in the high and one in the low plant productivity sub-habitats), one transect in the old fields, and finally one transect in the tilled areas between the tree plantation and the old fields. Each transect was sampled using four quadrats that were regularly placed every 10 m along the transect (**Table S3.1**, **Figure S3.3**).

Seedling emergence in different habitat types

To evaluate whether the spatial pattern of acorn caching matched the distribution of seedling emergence by habitat, we compared the density of cached radio-tagged acorns with the density of emerged seedlings in each habitat type. First, we calculated acorn caching density in each habitat by territory using data of the 2015-2016 survey. Then, in July 2016, we counted the number of emerged oak seedlings in each habitat in 200-m^2 transects (length 30-65 m and width 3-10 m) to calculate the number of seedlings ha^{-1}. We sampled 12 transects, one in each combination of habitat and territory, in the four territories where all three habitat types occurred (three territories with feeders 2, 3 and 4 and one territory with feeders 5 and 6; **Figure S3.1**, **Figure S3.3**).

Data analyses

We constructed point process models with the R spatstat package to determine whether the territorial behaviour and site preferences of magpies explained the spatial distribution of cached acorns using the data of the 2015-2016 survey (Baddeley et al., 2015; R Core Team, 2018). A point process model is a dataset of observed spatial locations of points, represented by the acorns in our study, and their relationship with other layers of spatially-explicit variables (e.g. habitat type). Distance to feeders was included as a covariate. The dependence of acorn caching density on spatial covariates was modelled as an inhomogeneous Poisson process, where the intensity of the point pattern was a log-linear function of the predictor variables (Voronoi polygons, distance, habitat and sub-habitat types). Each of the six feeders had one point pattern, one Voronoi Polygon, one habitat or sub-habitat type and one distance layer. These layers were used to construct a “hyperframe” consisting of a collection of layers that provided analogous information for each feeder. The function “mppm” was used to fit six point process models simultaneously (i.e., one model for each feeder) to obtain parameter estimates for the combination of feeders (Baddeley et al., 2015).

We analysed the point pattern generated by caching events at two spatial scales, namely habitat (coarse) and sub-habitat (intermediate) scales. First, we considered the coarse habitat scale that included the six feeders and all the caching events and fitted models to assess whether the spatial pattern of dispersal from each feeder fitted within the caching territories defined by the VP in which the feeder was located, distance to the feeder, habitat type, and all possible interactions between the layers as explanatory variables for acorn caching density. The area for the analysis (window) of these models was the “radius of action of magpie dispersal”, which was defined as a circle centred at each feeder with a radius of the maximum registered caching distance from that feeder. Second, at an intermediate spatial scale, we fitted models to assess the effect of the two sub-habitat layers within tree plantation (high *vs*. low plant productivity, and beneath canopy cover vs. in open interspaces), distance to the feeder, and all possible interactions between layers as explanatory variables for acorn caching density. The window for the analyses of these models was the tree plantation habitat contained within each nest's VP. The minimum adequate model was determined by model simplification, beginning with a global model that included all predictor variables (territory, habitat type and distance in the first model and sub-habitat type and distance in the second one), and their two- and three-way interactions. In each simplification step, the significance ($p < 0.05$) of the effect of each predictor was assessed using likelihood ratio tests until the minimum adequate model was produced, where each term was either significant or included within a significant higher-order interaction (Crawley, 2007).

We analysed magpies' preferences for the microsites and caching material by comparing their use frequency against their abundance by chi-square tests. When expected counts were too small, we estimated p-values using a Monte Carlo simulation with the "simulate.p.value=TRUE" argument on the R function "chisq.test" to properly perform chi-square tests (Verzani, 2005). Spearman's correlation was used to analyse the association between acorn caching density and seedling emergence density. All analyses were performed with R version 3.5.2 (R Core Team, 2018).

3.3. Results

Spatial pattern of caches

We monitored 260 radio-tagged acorns in 2015-2016 and 77 acorns in 2016-2017, of which 178 (range 21-41 acorns feeder^{-1}) and 42 (2–11 acorns feeder^{-1}), respectively, were cached by magpies whereas the rest were pecked open for consumption. Across both study periods, distance of cached acorns to feeders ranged 1.4-210 m (mean ± SE = 32.4 ± 1.9 m; median = 23.5 m). All acorns were cached individually in the ground.

At the coarse scale, dispersal by magpies in 2015-2016 resulted in most cached acorns (89%) occurring inside the caching territories defined by the VPs where the acorns were removed in 2016 (**Figure 3.1 a**). The effect of caching territories defined by the VPs on acorn cache density was significant after controlling for the effect of distance (**Table 3.1**, **Figure 3.1**). The distribution of the few cached acorns per feeder monitored in 2016-2017 also overlapped VPs of 2017, qualitatively supporting the territorial pattern observed in 2015-2016 (**Figure S3.4**). Between 2016 and 2017, nest displacement (several breeding magpies built new nests; 55% in 2016 and 69% in 2017) and the incorporation and disappearance of breeding pairs changed the number, size and location of VPs (**Figure S3.5**). Acorn cache density significantly differed (**Table 3.1**) among habitat types in 2015-2016 in the following order: tilled areas (100.7 acorns ha^{-1}, n = 40 acorns) > tree plantation (43.0 acorns ha^{-1}, n = 101) > old fields (10.8 acorns ha^{-1}, n = 18). These habitat differences in cache density depended on the distance to the feeders (habitat × distance interaction); thus, differences were greatest at short to medium-distances but decreased or disappeared at long-distances (**Figure 3.2**).

Table 3.1. Model selection from the global model to the minimum adequate models at the coarse (habitat) and intermediate (sub-habitat) spatial scales. Global model at the habitat scale: acorn caching density ~ territory x habitat x distance. Global model at the sub-habitat scale: acorn caching density ~ distance x plant productivity x tree cover.

Spatial scale	Parameters eliminated	Δ deviance	p-value
Coarse (habitat)	territory : habitat : distance	4.0154	0.1343
	territory : distance	2.6715	0.1022
	territory : habitat	4.9817	0.0828
	habitat : distance^{+}	**10.896**	**0.0043***
	territory^{+}	**61.571**	**< 0.001***
Intermediate (sub-habitat)	distance : plant productivity : tree cover	0.035255	0.8511
	distance : tree cover	0.26096	0.6095
	distance : plant productivity	0.50967	0.4753
	plant productivity : tree cover	0.36616	0.5451
	tree cover	1.3536	0.2446
	plant productivity^{+}	**16.2**	**< 0.001***
	distance^{+}	**77.6**	**< 0.001***

Note: $^{+}$**parameters included in the minimum adequate model**, which were either significant or included within a significant higher-order interaction. ***significant p-value**, the removed variable or interaction should not be eliminated from the minimum adequate model.

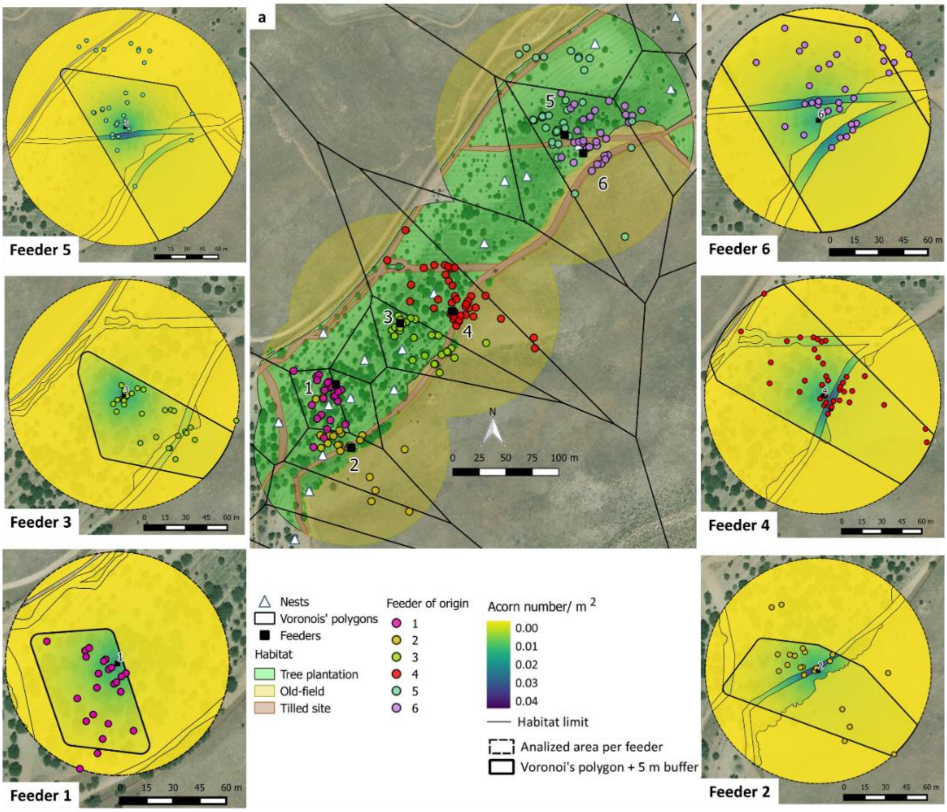

Figure 3.1. a) Voronoi polygons and dispersed acorns by magpies (dots) from the six feeders in 2015-2016. Three feeders were placed in the center of the tree plantation (numbers 1, 3 and 5) and another three at the tree plantation periphery (numbers 2, 4 and 6), near the old fields. Feeders 5 and 6 were located within the same territory. Proportions of tree plantation, old fields and tilled areas within the analyzed windows (colored circles) were 53.6%, 38.7% and 7.7%, respectively. The panels around panel a) are the spatially-explicit predictions for each feeder of acorn caching density at the habitat scale (models in **Table 3.1**). Note that the scale is different in each feeder because the radius of the maximum dispersal distance differed.

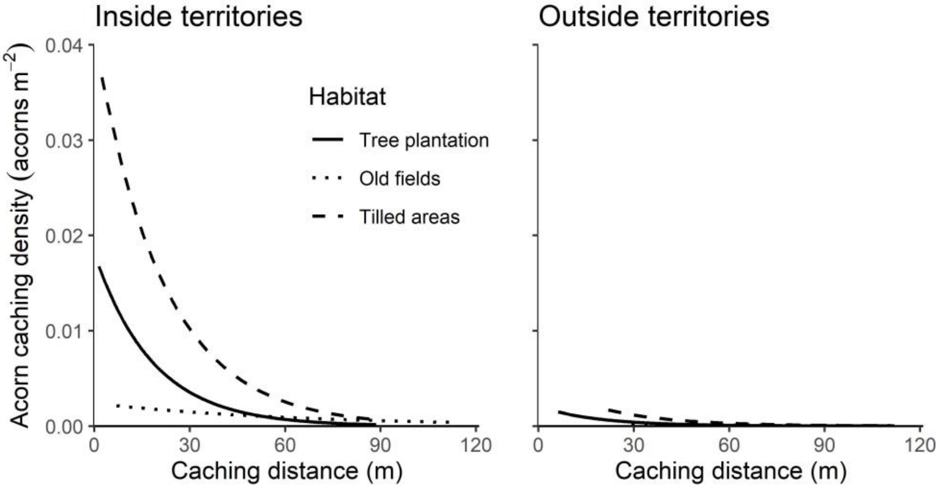

Figure 3.2. Interaction between habitat type and caching distance to the feeder on cached acorn density. Model: Acorn caching density ~ territory + habitat * distance. Model predictions for the acorns cached inside the territory (Voronoi polygon) where the feeder was (left graph) and for the acorns cached outside the territory (right graph).

At the intermediate spatial scale, acorn cache density was significantly higher in the high plant productivity sub-habitat (50.8 acorns ha^{-1}, n = 93) than in the low plant productivity sub-habitat (13.8 acorns ha^{-1}, n = 8) (**Table 3.1**, **Figure S3.6**). Acorn cache density decreased with increasing distance to the feeder in these sub-habitats (**Figure S3.7**). There were no significant differences in acorn density under tree canopies and interspaces in the tree plantation (**Table 3.1**).

Microsite and materials preferences

Most acorns (92%) were cached in microsites unrelated to the activity of other animals. However, the remaining 8% (14 out of 178 acorns) were cached in structures built by animals other than magpies: rabbit grit mounds and latrines, as well as ant litter mounds. This frequency was significantly higher than expected by chance (**Figure 3.3**), even when all animal structures were grouped ($\chi^2_{178;0.95}$ = 35.11; $p < 0.001$).

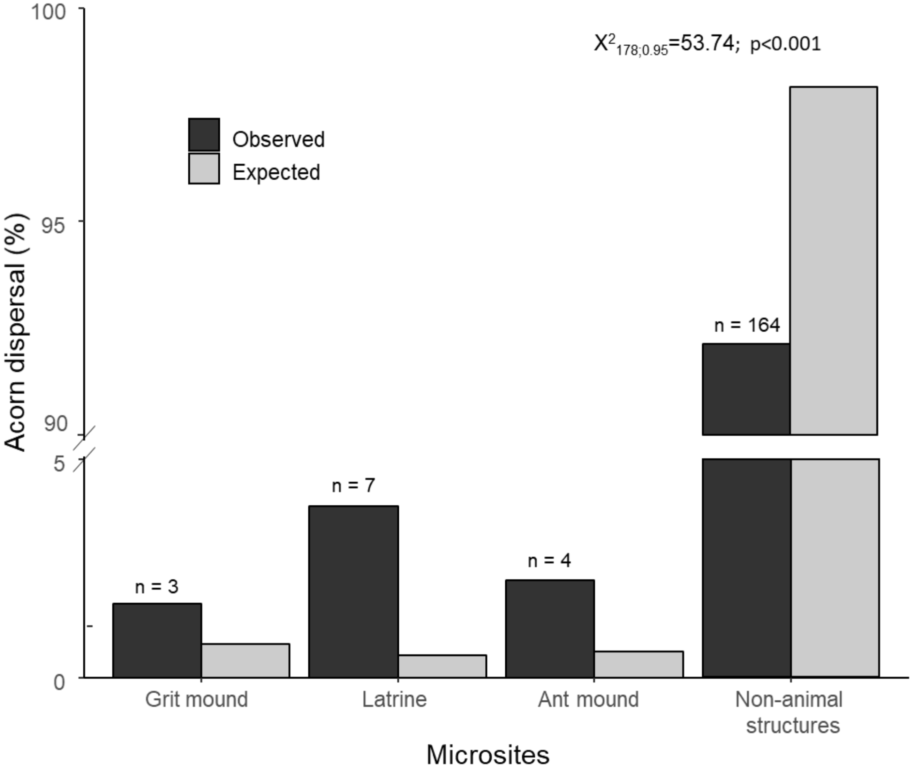

Figure 3.3. Relative frequency of observed (black) and expected (grey) cached acorns according to the microsites chosen by magpies to cache acorns. Grit mounds and latrines were made by rabbits. Total acorns n=178.

We analysed the materials used to cache the acorns in 159 out of 178 radio-tagged cached acorns. In 50% of the sites, magpies cached the acorns using the least abundant material in each site (**Figure 3.4**). In the high plant productivity sub-habitat, this corresponded to plant litter in feeders 5 and 6 and stones or litter in feeders 1 and 2. In the low productivity sub-habitat, more acorns were buried under soil than expected (feeders 5 and 6). In old fields, more acorns were cached under litter than expected (consistent for all feeders).

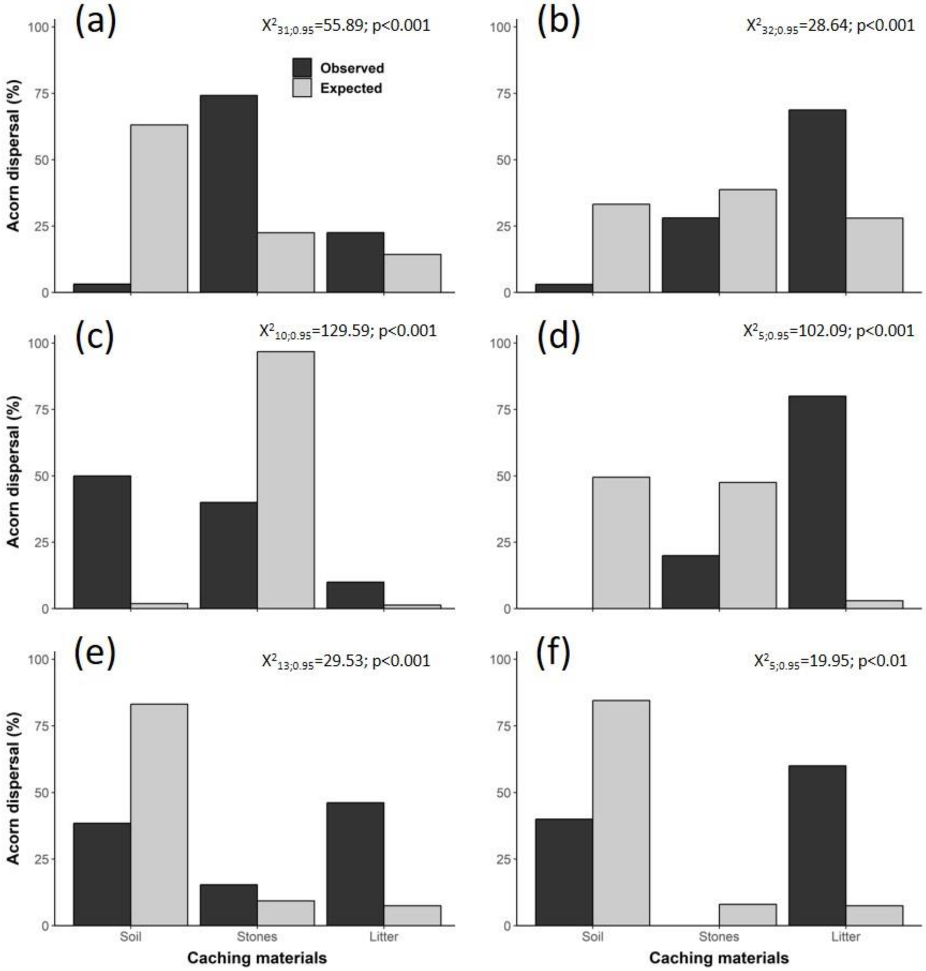

Figure 3.4. Relative frequency of observed (black) and expected (grey) cached acorns according to the caching material for the combinations of habitat or sub-habitat and feeder showing significant differences. High plant productivity sub-habitat of feeders 1 and 2 (a, n=31), and 5 and 6 (b, n=32); low plant productivity sub-habitat of feeders 5 and 6 (c, n=10) and old fields of feeders 1 and 2 (d, n=5), 3 and 4 (e, n=13), and 5 and 6 (f, n=5).

Emerged oak seedlings by habitat type

The density of emerged oak seedlings was 12 times greater in tilled areas than in the tree plantation and not a single seedling was recorded in old fields (**Figure 3.5**). Acorn caching density in the three habitat types in the fall-winter 2015-2016 was positively correlated with the density of emerged seedlings in early summer 2016 (Spearman’s rho = 0.886, $p < 0.001$, n = 4).

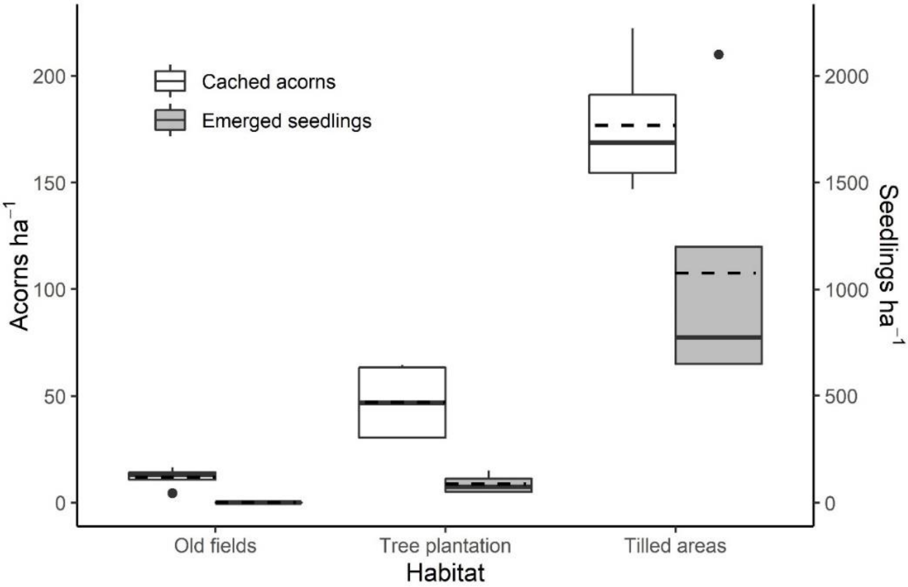

Figure 3.5. Density of cached acorns (white boxes) and emerged seedlings (grey boxes) in the three habitats (n=4). In the box plots, the solid and dashed lines are the median and mean, respectively. Boxes represent the first and third quartile. Whiskers represent the lowest and largest data point excluding outliers (points). Note that the density of cached acorns (left y-axis) is smaller than the density of emerged seedlings (right y-axis) because we used the density of cached radio-tagged acorns, which is a fraction of the cached acorn population.

3.4. Discussion

Acorn caching is a spatially structured process resulting from a hierarchical, top-down, and selective decision-making process where the features at a coarse spatial scale determine acorn caching decisions at finer spatial scales. Magpie territoriality was crucial for acorn caching at coarse and intermediate spatial scales (H1) because territoriality constrained dispersal distance and the habitats and sub-habitats available for caching. Magpies showed marked preferences for specific habitat and sub-habitat types, caching microsites, and materials to cache acorns (H2). Importantly, habitat preference matched the distribution of oak seedling emergence (H3), so seed dispersal lays the initial template for recruitment. This study illustrates how caching territoriality and site preferences of scatter-hoarders drive the spatial pattern of seed dispersal and can affect seedling emergence.

Caching territoriality

As hypothesized (H1), the distribution of cached acorns strongly coincided with the Voronoi polygons (VPs) around the nests of the next breeding season (2016), even after controlling for the effect of distance to feeders. This supports the hypothesis that breeding magpies establish acorn-caching territories, in which most (89%) removed acorns were cached (**Figure 3.1**). While other authors have suggested that breeding magpies cache food inside their nesting territories (Birkhead, 1991; Clarkson et al., 1986), to our knowledge our study is the first one to quantify such behaviour, a detailed adjustment of acorn caching patterns to territorial boundaries (VPs), and the exclusive use of such areas by breeding individuals. Consistent with this finding, Martínez-Baroja et al. (2019) determined that magpie breeding pairs removed 89% of the acorns from the feeders located within their territories, whereas the rest of removed acorns were taken by neighbouring breeding magpies or juveniles. These “thieves” moved and cached the stolen acorns in their own caching territories in the second study period (2016-2017) (**Figure S3.4**). This suggests that the cached acorns that do not match the territorial pattern in the first study period (2015-2016) could be the result of such “theft” and of the territorial behaviour of other breeding magpies.

Our study suggests that magpies have all-purpose territories for nesting, foraging, and food caching as other authors proposed previously for other scatter-hoarders (Maher & Lott, 1995; Scofield et al., 2010). We observed that some magpies maintained their territories during the entire year, switching the territorial behaviour from caching seeds to nesting. Magpies usually remain in their nesting territory throughout the year but sometimes they move to other locations and return in spring (Birkhead, 1991; Szala et al., 2020). We showed that nest distribution varied between years, but the dispersal patterns matched the VPs derived from the nest distribution that appeared in the spring after the acorn dispersal season. Thus, food caching territories seem to affect nest location in the next breeding season (**Figure 3.1 a**). Moreover, defence of seed caching territories could be a major mechanism to avoid seed pilfering by conspecifics when seed caching is massive, which would support the social context hypothesis, i.e. different behaviour in the presence or absence of conspecifics (Kalinowski et al., 2015; Beck et al., 2020). Keeping and defending an all-purpose territory throughout the year could motivate magpies to cache acorns not only for short-term recovery (the same day or a few days later; Birkhead 1991, Zinkivskay et al. 2009), but also for long-term storage (until spring or early summer), as reported for other corvids such as the Eurasian jay (Bossema, 1979). Future studies should address the temporal pattern of acorn recovery to assess this idea.

Acorn caching territories determined the spatial pattern of acorn dispersal. First, territoriality limits dispersal distance, which is constrained by the size and shape of the territory (Beck et al., 2020). The magpie is a medium-distance seed disperser (i.e. 25-250 m, Traveset et al. 2014) according to the acorn dispersal distances we found (mean of 32 m and maximum of 210 m). However, we observed a few long-distance dispersal events in two feeders in 2016-2017, likely resulting from acorn “theft” by breeding individuals from other territories (**Figure S3.4**). Long-distance dispersal events may also occur due to food removal by non-territorial individuals (Birkhead, 1991; DeGange et al., 1989; Scofield et al., 2010). Despite their low frequency, long-distance dispersal events can play an important role in gene flow among plant populations (Cain et al., 2000; Hampe et al., 2013). Additionally, long-distance dispersal by “thieves” could be highly relevant for oak forest expansion (Jordano, 2017) when caching territories are located outside oak forest patches and magpies nest in scattered non-oak trees (**Figure S3.4**).

Secondly, acorn caching territories can affect the direction in which acorns are dispersed (Scofield et al., 2010). For instance, acorns removed from feeder 1 were mainly cached westward, likely because most of the territory was located in that direction from the feeder (**Figure 3.1** Feeder1). However, the number, size and shape of caching territories varied between years (**Figure S3.5**), which could be important for plant gene flow. Further, annual spatial dynamics of caching territories could decrease the rate of acorn retrieval of cached acorns and promote oak recruitment. Future studies should assess the generality of seed caching territories for other territorial scatter-hoarder and tree species.

Site preferences

Our results suggest that the spatial structure inside caching territories is important for the spatial pattern of seed dispersal in territorial scatter-hoarders. In accordance with our second hypothesis, magpies showed strong preferences for some habitats, sub-habitats and microsites for acorn caching. However, this site selection depended on their availability inside the caching territory. When several habitats were available inside a territory and distance to the feeder was controlled for, magpies selected mainly tilled areas, secondarily the tree plantation, and finally the old fields to cache the acorns. Habitat selection was negatively related to the time since last tilling of these habitats, which likely affects soil compaction. These findings suggest that ease of acorn caching into the ground could be an important factor for magpies. Other authors have also shown that habitat types with loose soils are highly selected by acorn scatter-hoarders (Bossema, 1979; Castro et al., 2017). The selection of specific places for acorn caching could aim to minimize the time investment, to improve efficiency of caching and subsequent retrieval, and to avoid pilfering (Bossema, 1979; Gómez, 2003; Pons & Pausas, 2007).

The interaction between habitat type and dispersal distance found here could have implications for forest regeneration. Acorn dispersal into tilled areas and oak forest patches could contribute to increase tree density closer to the seed source than farther because, within these two habitats, acorn caching density abruptly decreased with distance (**Figure 3.2**). This is usually interpreted in terms of minimized resource investment in dispersal and the natural geometric expansion of area as distance from a point-source increases (Lichti et al., 2017). However, density of caches in old fields decreased less with distance than in the other habitats, which could allow low but more homogeneous colonization in this habitat. This may be due in part to high soil compaction in the old fields that drives acorn caching mainly towards the scarce and homogeneously distributed animal structures with loose soil in this habitat (**Figure 3.3** and **Figure 3.4 d-f**). Magpies with territories located entirely within oak-forest patches can only contribute to the regeneration and persistence of such patches (**Figure 3.1**). In contrast, magpies with territories spanning oak patches and old fields can contribute to oak forest expansion into the old fields. Tilling old fields right after abandonment or strategically placing nesting sites for magpies could increase acorn arrival and, consequently, oak colonization in these open areas.

At an intermediate spatial scale, all studied magpies preferred the high-productivity sub-habitat to the low-productivity one to cache acorns. This could be associated either with the higher number and diversity of spatial cues to cache seeds (Bennett, 1993; Bossema, 1979) or with the presence of other food sources, such as invertebrates and greater plant biomass, which allows magpies to feed extensively (Birkhead, 1991).

Some features of seed dispersal events at the fine scale emerged from individual behaviour. Magpies preferred structures built by animals to cache acorns, but these structures were relatively uncommon. Similarly, magpies preferred rare covering materials such as plant litter, stones or loose soil for this process. Preference for these materials differed among caching territories, suggesting that magpies are flexible in selecting materials for acorn caching. Infrequent structures and materials could be better cues for maximizing the efficiency of seed caching and retrieval (Feenders & Smulders, 2011; Leverkus et al., 2016). Additionally, magpies could select structures built by animals because they have loose soil, which could be important in compacted soils.

Seedling emergence

As hypothesized (H3), the density of emerged seedlings across habitats matched the spatial pattern of acorn dispersal (**Figure 3.5**). Thus, habitat preferences for acorn caching by magpies could have left an imprint on oak seedling emergence density (Lenda et al., 2012). The tight relation between the density of emerged seedlings and that of cached acorns suggests that the combined outcomes of post-dispersal predation and seedling emergence rate were similar among habitat types. In addition, the differences in these rates among habitat types may not have overcome the strong differences in caching. Further research is necessary to assess whether caching territory defence and strategies for cached-acorn recovery equalize post-dispersal acorn predation across habitats. Additionally, large-seeded species such as oaks tend to have higher seedling emergence rates than small-seeded species (Lavorel & Lebreton, 1992). The differences in seedling density among habitats could result in demographic conflicts in oak recruitment across different habitat features (Leverkus et al., 2016). For instance, tilled areas are more exposed to herbivores and solar radiation than other habitats, which strongly limit oak seedling survival (Gómez-Aparicio et al., 2008; Cuesta, Villar-Salvador, Puértolas, Rey Benayas, et al., 2010), but herb competition and soil compaction are low, which can increase root growth and seedling establishment (Cuesta, Villar-Salvador, Puértolas, Jacobs, et al., 2010; Kozlowski, 1999). Future studies should address the net outcome on oak recruitment of the positive and negative effects of environmental factors on diverse ontogenetic stages in tilled and non-tilled areas, since life stage conflicts are frequent and may ultimately define the spatial patterns of recruitment (Schupp, 2007).

3.5. Conclusions

This shows that: 1) the caching animal responds to multiple aspects of the environment rather than just one feature; 2) environmental choices are applied hierarchically; and 3) animal territories can be important constraints irrespective of the quality of the environment for regeneration of the plant. Hierarchical behaviour of the caching animal will translate into structure in the plant population. This insight is demonstrated here by a territorial bird, but probably applies to a great range of other caching animals.

3.6. Acknowledgements

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3.8. Supporting information

Table S3.1. Cover of trees in each habitat type, and cover of litter, stones, bare soil, and herb biomass around each pair of feeders (1-2, 3-4 and 5-6) from which magpies dispersed acorns.

Habitat / Sub-habitat	Tree cover (%)	Feeders 1 and 2				Feeders 3 and 4			
		Litter (%)	Stones (%)	Bare soil (%)	Herb biomass (g)	Litter (%)	Stones (%)	Bare soil (%)	Herb biomass (g)
Old-field	<1	3.0	47.5	49.5	37.9	7.5	9.3	83.2	44.1
Tilled sites	0	0.0	48.7	51.3	0.0	0.0	16.9	83.1	0.0
Tree plantation:	23.5								
High plant productivity sub-habitat	27.1	14.4	22.5	63.1	32.3	33.8	53.7	12.5	36.3
Low plant productivity sub-habitat	18.1	0.5	53.7	45.8	6.5	1.0	85.3	13.7	3.8

Habitat / Sub-habitat	Feeders 5 and 6			
	Litter (%)	Stones (%)	Bare soil (%)	Herb biomass (g)
Old-field	7.5	8	84.5	67.3
Tilled sites	0.0	8.1	91.9	0.0
Tree plantation:				
High plant productivity sub-habitat	28.0	38.7	33.3	96.2
Low plant productivity sub-habitat	1.3	96.8	1.9	7.2

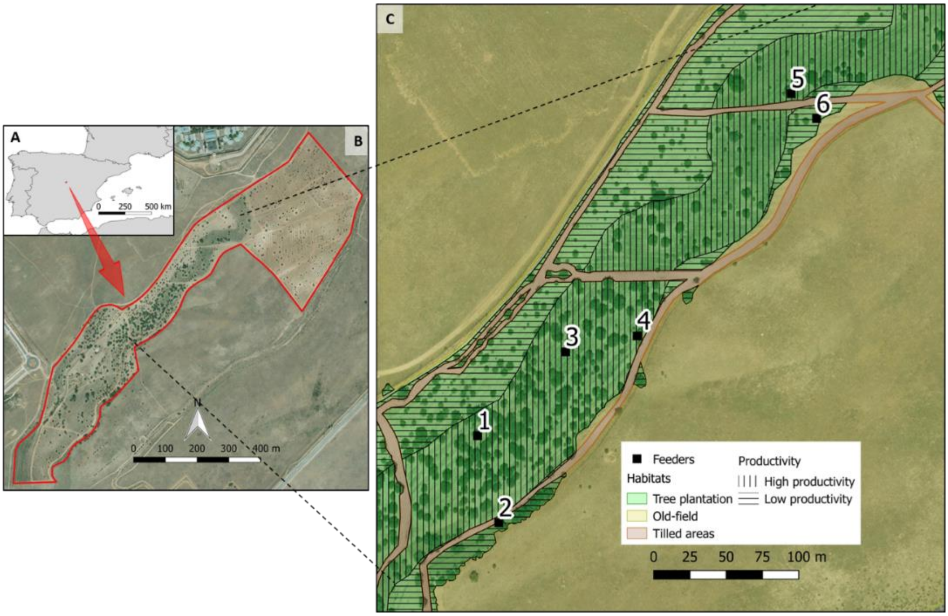

Figure S3.1. Location in the Iberian Peninsula (A) and orthophotos of the study area (B and C). The red line in panel B represents the border of the tree plantation. Panel C shows the position of the six feeders (black squares) and the three habitats considered: tree plantation, old-field and tilled areas. Inside the tree plantation habitat, we distinguished high and low plant productivity sub-habitats based on the plant community biomass productivity and the under tree and gap sub-habitats according to tree cover.

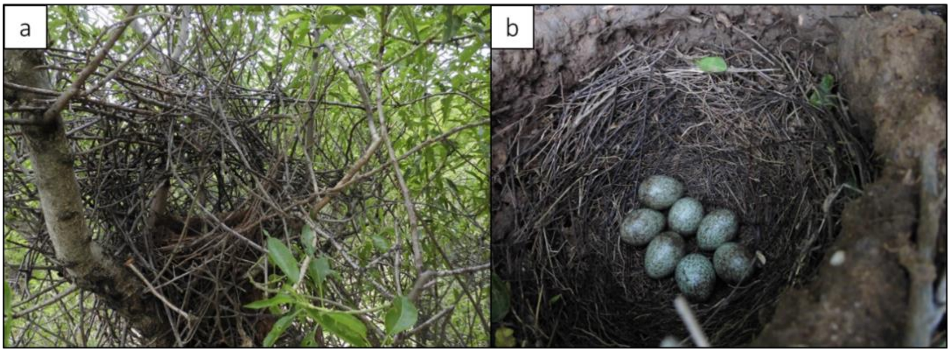

Figure S3.2. a) Outside view of a magpie nest in an almond tree with the characteristic dome made with sticks. b) Inside view of an active nest where the mud bowl is lined with plant material, such as grass, with a clutch of eggs.

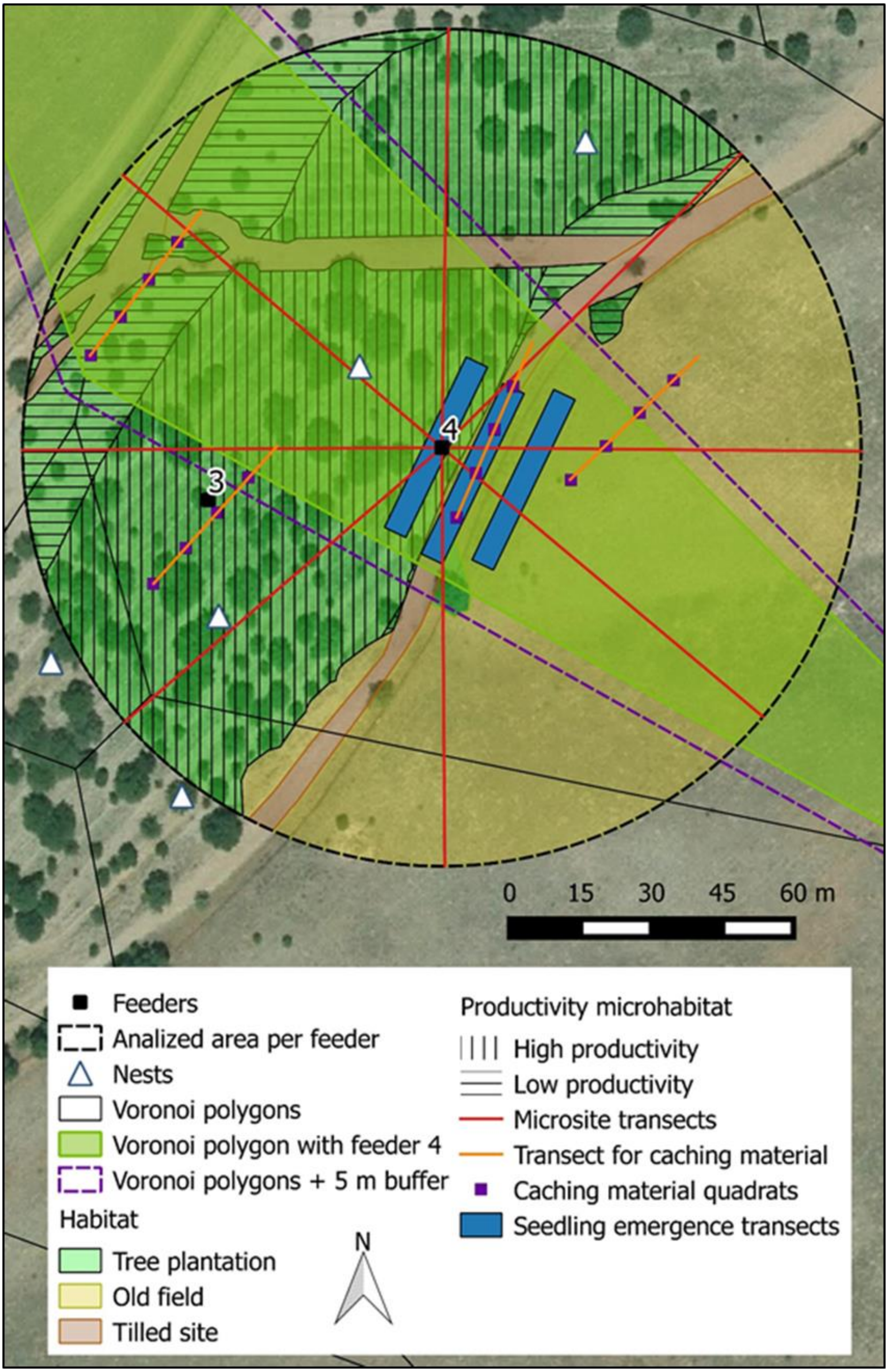

Figure S3.3. Sketch of all samplings in the study area taking the feeder 4 as an example.

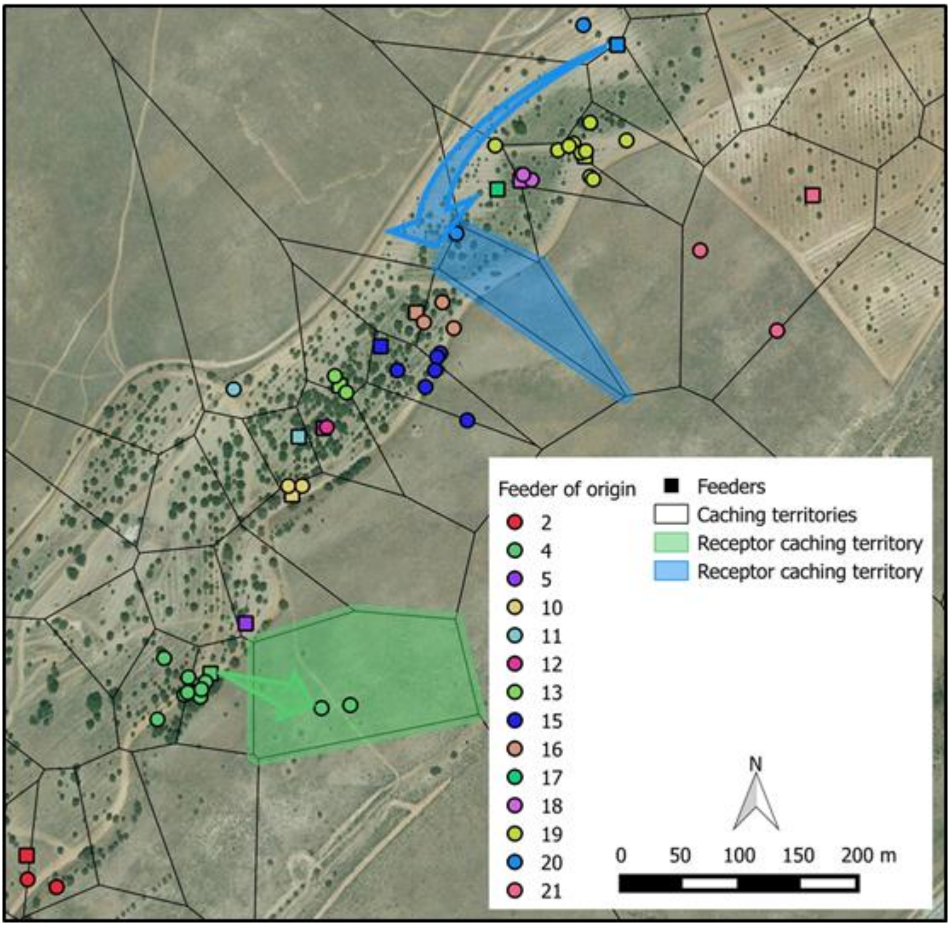

Figure S3.4. Voronoi´s polygons and cached acorns by magpies (color dots) from the feeders (color squares) in the study area in 2016-2017. The two arrows indicate long dispersal events. The blue arrow shows a cached acorn (blue dot) by a magpie that removed (i.e. stole) the acorn from a feeder (blue square) out of its caching territory (blue polygon). The green arrow shows cached acorns (green dots) by a magpie that removed the acorns from a feeder (green square inside tree plantation) out of its caching territory but returned to its caching territory (green polygon outside the tree plantation) to cache the acorns. In this green case, we only show two radio tagged acorns, but the ringed male of this caching territory stole many acorns without radio-transmitter (n=171) from the green feeder which were video-recorded by a trail camera.

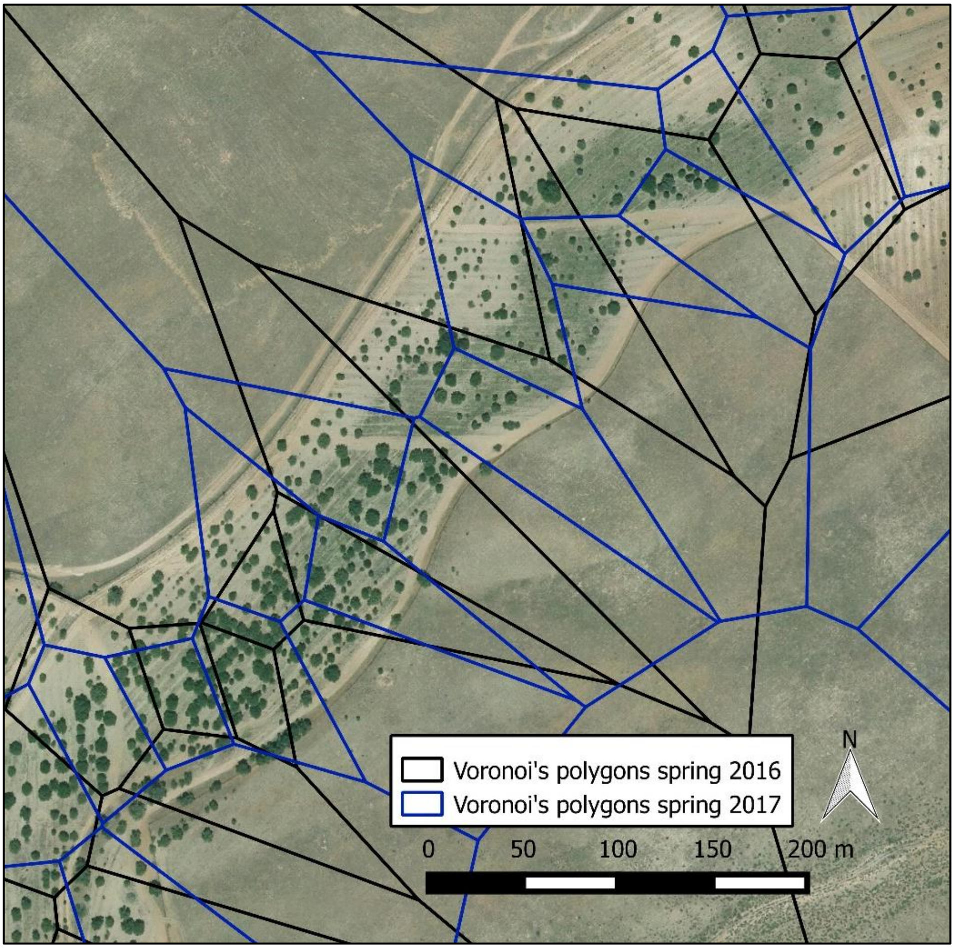

Figure S3.5. Voronoi's polygons around each active nest in spring 2016 and spring 2017, showing differences in size, shape and location between both years, due to nests displacement, incorporation and disappearance of breeding pairs.

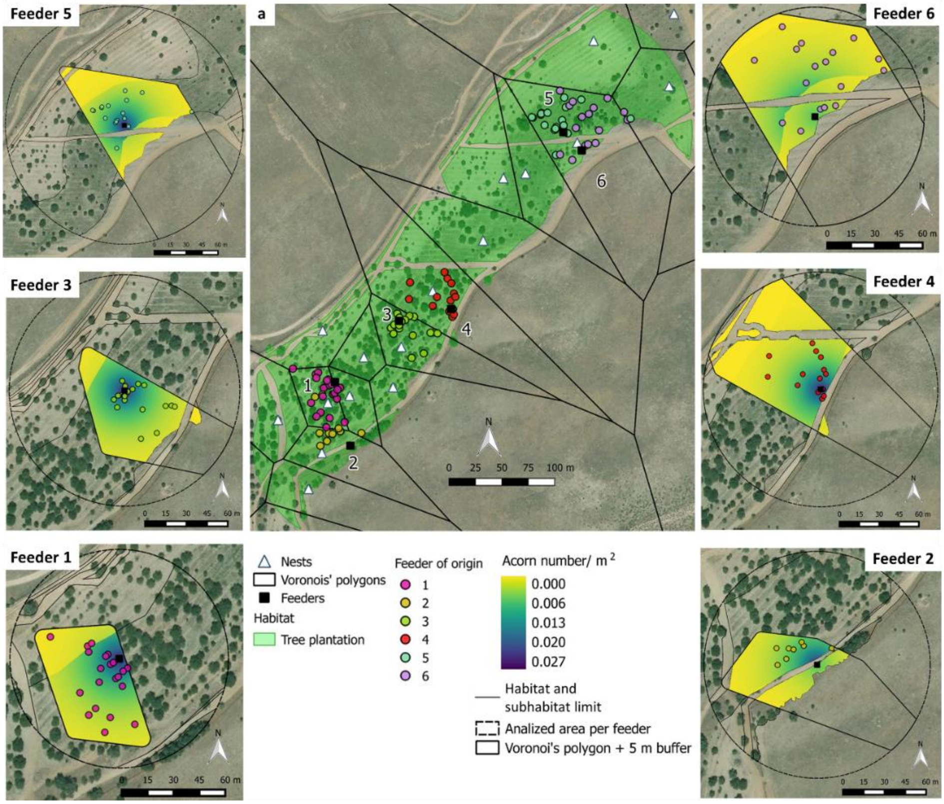

Figure S3.6. a) Voronoi´s polygons and dispersed acorns by magpies in the study area from the six feeders in 2015-2016. In the left and right columns, we show prediction maps for acorn caching density at the medium spatial scale (sub-habitat) for the feeders located in the tree plantation (feeders 1, 3 and 5, left column) and at the periphery of the tree plantation (2, 4 and 6, right column). Note that the scale is different for each feeder because the radius of the maximum dispersal distance differed among feeders. The cover of tree and gaps inside the window containing the tree plantation was 23.5 and 76.5%, respectively. The cover of the high and low plant productivity sub-habitats in the analyzed windows within the tree plantation was 59.5 and 40.5%, respectively.

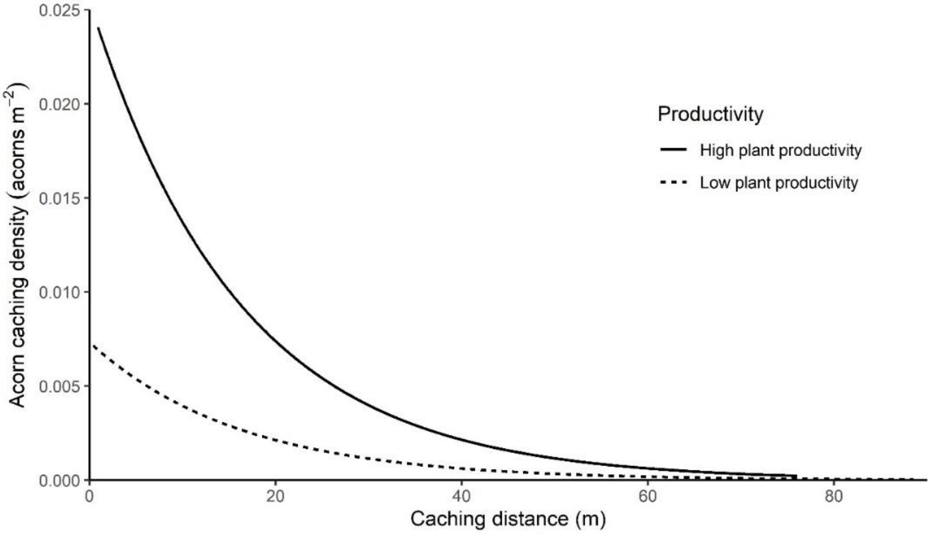

Figure S3.7. Acorn caching density with distance to the feeder in the high and low plant productivity sub-habitats. Model: acorn caching density ~ plant productivity + distance.


14
13
12
11

Imágenes de arriba a abajo y de izquierda a derecha:

Islotes forestales y encina reclutada a la izquierda de la imagen en la finca La Higueruela del CSIC (Santa Olalla, Toledo)
Protector de plástico empleado en el experimento
Protector metálico empleado en el experimento tras retirar los de plástico
Bellotas sin protector depredadas en el punto de siembra
Medida de una plántula de encina reclutada
Encina con bellotas verdes en uno de los islotes forestales
Fuente de las imágenes: L. Martínez-Baroja

Capítulo 4

Predation and aridity slow down the spread of 21-year-old planted woodland islets in restored Mediterranean farmland[8]

Abstract

Planted woodland islets act as sources of seed that may accelerate woodland development in extensive agricultural landscapes. We assessed a 1-ha plot that was planted with 16 100-m^2 islets of holm oak *Quercus ilex* subsp. *ballota* seedlings near Toledo (Spain) in 1993. In spring 2014 we measured (1) acorn predation and (2) seedling emergence from seeded acorns at different distances from and orientations around the islets with half of the acorns protected to prevent predation, (3) survival of emerged seedlings, and (4) natural tree establishment outside of the planted islets. Most (96.9%) unprotected acorns were removed or predated. Seedling emergence from protected acorns ranged from 42.9% on the northern side of the islets to 13.2% on the southern side, suggesting a less stressful microclimate on the northern side. Survival of naturally established seedlings was 28.6% by the end of first summer; seedling mortality was chiefly due to drought (45.0%) and herbivory (35.0%). Density of emerged seedlings, surviving seedlings after first dry season, and established oaks > 1-yr old was similar at different distances from the islets. Over the 21 year time period, 58 new oak individuals >1-yr old have established (an average of 3.3 established individuals per ha per year) at an average distance of 6.3 ± 5.4 m away from the closest islet. We conclude that initial oak regeneration triggered by small planted islets in Mediterranean abandoned farmland is slowed down by high acorn

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[8] This chapter fully reproduces the article:

Rey Benayas, J.M., Martínez-Baroja, L., Pérez-Camacho, L., Villar-Salvador, P., Holl, K.D., 2015. Predation and aridity slow down the spread of 21-year-old planted woodland islets in restored Mediterranean farmland. New Forests 46, 841–853. https://doi.org/10.1007/s11056-015-9490-8

predation, seedling herbivory, and stressful microclimatic conditions. Regardless, these islets are a viable tool for regeneration of Mediterranean oak woodland.

Resumen

Los islotes forestales plantados actúan como fuentes de semillas que pueden acelerar el desarrollo del bosque en paisajes agrícolas extensos. Evaluamos una parcela de 1 ha en la que se plantaron plántulas de encina (*Quercus ilex* subsp. *ballota*) en 16 islotes de 100 m^2 cerca de Toledo (España) en 1993. En primavera de 2014 medimos (1) la depredación de las bellotas y (2) la emergencia de plántulas en puntos de siembra que se realizaron a diferentes distancias y orientaciones alrededor de los islotes, con la mitad de los puntos con protectores para evitar la depredación, (3) la supervivencia de las plántulas emergidas y (4) el establecimiento natural de árboles fuera de los islotes plantados. La mayoría de las bellotas sin protector (96,9%) desaparecieron o fueron depredadas en el sitio. La emergencia de plántulas en los puntos de siembra protegidos varió desde el 42,9% en el lado norte de los islotes hasta el 13,2% en el lado sur, lo que sugiere un microclima menos estresante en el lado norte. La supervivencia de las plántulas establecidas espontáneamente fue del 28,6% al final del primer verano; la mortalidad de estas plántulas fue debida principalmente a la sequía (45,0%) y a la herbivoría (35,0%). La densidad de las plántulas emergidas, la supervivencia de las plántulas después del primer verano y el establecimiento de encinas mayores de un año fue similar a distintas distancias desde el islote. Después de 21 años, se han establecido 58 encinas de más de 1 año (3,3 encinas establecidas por ha y año en promedio) a una distancia media de 6,3 ± 5,4 m del islote más cercano. Concluimos que la regeneración inicial de encinas desencadenada por pequeños islotes plantados en campos agrícolas abandonados en ambientes mediterráneos es lenta por la alta depredación de las bellotas, la herbivoría de las plántulas y las condiciones microclimáticas estresantes. No obstante, estos islotes son una herramienta viable para la regeneración de bosques de quercíneas en ambientes mediterráneos.

4.1. Introduction

Natural forest regeneration or passive restoration of Mediterranean abandoned agricultural land is usually slow due to a number of limiting factors (Maestre et al., 2003; Bonet and G. Pausas, 2004; Vallejo et al., 2006; Rey Benayas et al., 2008a). Key constraints on the speed of regeneration include (1) dispersal limitation because seed sources are remote and dispersal vectors may be rare (Pons and Pausas, 2007a; Rey Benayas et al., 2008a; Ramos-Palacios et al., 2014; Zamora et al., 2010); (2) seed predation (Gómez, 2003; Leiva and Fernández-Alés, 2003; Gómez et al., 2008; Gómez and Hódar, 2008; Pérez-Ramos and Marañón, 2008); (3) biotic limitation such as competition from established woody vegetation and herbaceous vegetation (Rey Benayas et al., 2005; Cuesta et al., 2010b), and herbivory (Gómez, 2003; Cuesta et al., 2010a); and (4) abiotic limitation such as low water availability, extreme temperatures, poor soil structure and low nutrient availability (Rey Benayas, 1998; Cuesta et al., 2010a). Intensification of land use has brought remnant areas of natural or semi-natural vegetation into mainstream agriculture and as a result many of such areas have been lost or severely degraded. As a consequence, many agricultural landscapes, particularly those that are highly productive, lack parental trees or shrubs which severely limits seed availability, the first step for natural regeneration in circumstances where the socio-ecological dynamics promote abandonment (Pulido and Díaz, 2005; Rey Benayas and Bullock, 2012).

In actively farmed fields, strategic revegetation actions can include planting woodland islets (clusters of trees), hedgerows and isolated trees that have the potential to enhance wildlife, agricultural production, and other services at the field and landscape scales since they compete minimally for farmland use (Rey Benayas and Bullock, 2015). Rey Benayas et al. (2008) suggested a new concept for designing restoration of forest ecosystems on agricultural land, which uses small-scale active restoration as a driver for passive recovery over much larger areas. Establishment of “woodland islets” is an approach to designing restoration of woodlands in extensive agricultural landscapes where no remnants of native natural or semi-natural vegetation exist. It involves planting a number of small, dense, and sparse blocks of native shrubs and trees within agricultural land that together occupy a small fraction of the area to be restored. This approach, also called “tree islands”, “applied nucleation” (Corbin and Holl, 2012; Zahawi et al., 2013), "dispersion and attraction nuclei" (García-Martí and Ferrer, 2013), and cluster plantings (Stanturf et al., 2014), facilitates secondary succession by establishing small colonisation foci, while using a fraction of the resources required for large-scale afforestation. If the surrounding land is abandoned, colonists from the islets could accelerate woodland development through enhanced seed dispersal. Design of islets at a landscape scale benefits wildlife and provides the potential for larger-scale afforestation if the surrounding land is abandoned (Navarro and Pereira, 2012).

We have been conducting an experiment on former cropland, where we introduced holm oak (*Quercus ilex* susbsp. *ballota* (Desf.) Samp., hereafter *Q. ilex*) seedlings into 100-m^2 plots in 1993. *Q. ilex* is a late successional, slow-growing tree with high capacity of resprouting (Zavala et al., 2000). We found that, 21 years after the start of this restoration project, the planted woodland islets have grown in volume and produce large amounts of acorns (Rey Benayas et al., 2008b); however, the islets have not increased in area beyond the original planted surface of 100 m^2. Moreover, whereas a number of holm oaks of different size have established around the islets, there is a ca. 1.5-2 m wide border at the edge of the islands with minimal grass or herbs (**Figure 4.1**).

Figure 4.1. In our 21-year-old experiment, it is noticeable that the planted islets have increased in volume, exported acorns and produced new established oaks (e.g. the one with red arrow to the right of the figure) but are confined to the original planted surface. Also note the area with minimal herbaceous vegetation immediately outside the islets edge (red arrow in the centre of the figure).

In this study we assessed several demographic processes affecting early seedling recruitment around the woodland islets based on field experiments and long-term recruitment based on field observations. We hypothesized that biotic limitations (primarily acorn and seedling predation), and stressful microclimatic conditions (primarily water stress) would explain overall observed low initial natural regeneration in this system. It was difficult to predict the effect of distance to the islets on long-term oak establishment as a result of two opposing effects, namely more abundant acorn rain and facilitation but also more intense competition from established oaks for water and nutrients, as well as intense rabbit herbivory close to the islets (Bartholomew, 1970). We expected high acorn predation for unprotected acorns (H1), highest seedling emergence and survival at the northern-oriented edges of the islets due to micro-climate amelioration by islet canopy (H2), and high predation of unprotected oak seedlings (H3). Results from this study will be particularly useful to practitioners and land use planners of woodland restoration projects in agricultural landscapes.

4.2. Methods

Study site

The study site was located at “La Higueruela”, a Consejo Superior de Investigaciones Científicas research station in Toledo, central Spain (4º3'N, 4º24'W, altitude 450 m). We ran our experiment on a 1 ha field on previous cropland which had been cultivated for grain for many years until afforestation took place, and that was surrounded by rain-fed cereal crops in a highly farmed landscape context. In 1993, 1-year old *Q. ilex* seedlings were planted in 16 100-m^2 plots − the planted woodland islets− at a density of 50 seedlings per plot and a spacing of 2 m between seedlings. Mean distance separating islets is 11.8 m. Planted seedlings were subjected to experimental management summer irrigation and artificial shading for three consecutive years, after which time shading and irrigation were stopped and there was no further management (Rey Benayas and Camacho-Cruz, 2004). Whereas the initial treatments affected survival of oaks and hence the density of trees (Rey Benayas, 1998), by the time of the current data collection the overall cover of islets was similar across treatments (>90% in all islets; see aerial photo in **Figure 4.4**). At the time of the current data collection oaks in the islets were at an average density of 41.9 oaks per islet and all oaks in the periphery (i.e. at least 20 oaks in each islet) were producing abundant acorns. The climate is continental Mediterranean, characterized by a long summer drought that imposes severe water stress on the vegetation and cold winters. Total annual precipitation averaged 470.2 mm and mean temperature averaged 14.7 ºC during the 1993-2013 period. The spring of 2014 was dry and total precipitation from the initiation of the experiment (24 February) through the last spring rainfall in 22 June was 64.1 mm), whereas average precipitation for the same period since 2000 was 153.18 mm. The soil is a relatively fertile, deep luvisol type, and derives from arkoses. The use of the land in the area is mostly agricultural. Potential predators/dispersers of acorns and oak seedlings in the study area are chiefly rodents (e.g. *Apodemus sylvaticus* L. and *Mus spretus* Lataste), magpies (*Pica pica* L.), rabbits (*Oryctolagus cuniculus* L.), and hares (*Lepus granatensis* Rosenhauer) that shelter in the woodland islets. However, the European jay (*Garrulus glandarius* L.), which is and effective acorn disperser in Mediterranean forests (Gómez, 2003) is absent in this highly deforested area.

Predation and germination of seeded acorns

We seeded holm oak acorns in our experimental field around the 16 planted woodland islets on 24 February 2014. All acorns were from the Leonesa provenance region (NW Spain) and acquired at the Centro Nacional de Mejora Forestal "El Serranillo" (MAGRAMA). Prior to seeding, acorns were submerged in water for 12 hours and floating acorns were eliminated, as they were assumed to be dead or unfilled. A posteriori test resulted in 71.4% of acorn emergence. A total of 386 points were seeded, with five acorns buried at a depth of 3 cm at each seeding point. Seeding points were located along two 10-m long transects extending out from each of the four corners of every woodland islet (**Figure S4.1**). Most seeding points were located at 0, 1, 5 and 10 m from the woodland islet edge. However, in some cases the distance between adjacent islets and between islets and nearby active crop fields impeded seeding at the 5 and 10 m distances; consequently, for these cases seeding points were located either equidistant between adjacent islets or at the edge of the experimental field. In total, 36 points were located between 1 and 5 m, 23 between 5 and 10 m, and 9 points were at 10 m.

One of the two seeding points located at the same distance of each woodland islet side was protected (**Figure S4.1**) with a 25 cm plastic tree shelter buried 10 cm and topped with a 15-mm wire mesh to prevent access by acorn predators. This resulted in 193 protected seeding points and 193 unprotected ones. The protection of seeding points at the same distance from each woodland islet side was randomly assigned. Three protected and three unprotected seeding points were accidentally ploughed and lost from the experiment. We buried a 7-cm iron nail together with the unprotected seeding points to facilitate later detection with a metal detector. We monitored seeding points five times on 14 May, 4-6 June, and on 1, 6 and 19 July for acorn predation and seedling emergence. One third of emerged seedlings occurred after a late spring rain event (18 mm). As seeded acorns were not marked for radio-tracking, we were not able to assess where moved acorns were placed by dispersers.

Seedling survival

On 22 June, after seedling emergence ended, we carefully removed the plastic protectors at half of the seeding points that contained at least one emerged seedling to leave them unprotected from herbivores. For the other half of seeding points with emerged seedlings, the tree shelter was replaced by a wire cage to prevent the micro-climate effects by tree shelters on seedling performance (Puértolas et al., 2010; Oliet et al., 2012). We monitored seedling survival six times, once every ca. 10 days starting at the beginning of July and ending at the end of August, and a final time on 19 October 2014.

Natural early establishment of holm-oak

To assess natural establishment of holm oak seedlings during the 2014 growing season, i.e. not from our experimental acorn seeding, we sampled 192 rectangular plots and nine squared plots between the islets or between the islets and nearby active crops to count seedling emergence in the spring of 2014 and monitor their survival through the end of summer (mid-October). The rectangular plots were placed at the edge of the woodland islets in all four orientations, two at each corner and one between them (**Figure S4.1**). These plots were 1 × 5 m between adjacent islets or 1 × 10 m between islets and active crop fields. The squared plots between islets were 5 × 5 m. The 201 plots, which covered a total area of 1474.9 m2 (i.e. 17.6% of the experimental field area that was not occupied by woodland islets), were initially surveyed once between May 17 and June 22 and later on July 6 and October 19 due to rain events after the start of the first seedling counting and to account for final survival after summer, respectively. The emerged seedlings in all plots were tagged for easy later localization. The density of both dead and surviving seedlings in bands at different distance to the islets (0-2, 2.01-4, 4.01-6, 6.01-8, 8.01-10 and > 10 m) was measured. Recruitment within the islets was not measured as this study focuses on regeneration outside the islets; additionally, the islets were very dense and shaded and visual inspection hinted new established oaks in them were sprouts.

Mapping and size measurement of naturally established holm oak since islet planting

All naturally established holm oaks, i.e. those at least 1-yr old, were located, positioned with a GPS (Garmin DAKOTA 20) and mapped using high resolution imagery taken by a drone-borne visible camera of 2 × 2 cm spatial resolution pixel that produced an ortho-photo of the 1-ha experimental field. We measured their density in the bands explained above and, for illustrative purposes, their height, basal diameter and crown projected area (Rey Benayas, 1998; Rey Benayas and Camacho-Cruz, 2004).

Data analyses

Acorn removal at unprotected seeding points was so high (H1, see below) that we could not statistically test the effects of orientation and distance to the woodland islets on this rate. All subsequent statistical analyses of seedling emergence and survival in relation to orientation and distance (H2) to the islets are thus only based on the protected seeding points.

We analyzed differences in seedling emergence using generalized linear mixed-effects model (GLMM) with a binomial error distribution and a logit link function to test the effects of the woodland islets (random effect), orientation and distance to the islets and their interaction (fixed effects). Akaike's (1987) information criterion (AIC) was calculated for each model; a smaller AIC indicates a better-fitting model as determined from the parsimony in the number of parameters. We used the cutoff of ΔAIC < 2 units to differentiate models with better explanatory power (*sensu* Burnham and Anderson, 2002). Likewise, we performed a binomial generalized linear model including orientation, distance and their interaction based on previous results from the GLMM to test specific hypotheses in relation to these factors (H2).

Seedling survival from seeded acorns (H3) or naturally established in the Spring of 2014 was assessed by survival analysis based on a Cox's Proportional Hazards semi-parametric model using the maximum partial likelihood as the estimation method (Allison, 1995; Fox, 1993). We correlated the volume (i.e., height ×crown projected area) and distance to the closest planted woodland islet of the naturally established oaks > 1 yr old since 1993. Finally, we tested the density distribution of naturally emerged and surviving seedlings after the first dry season and of established oaks > 1 yr old at the bands of different distance to the islets using contingency analysis. GLMM analysis was performed with packages stats (R Core Team, 2014) lme4 (Bates et al., 2014) and MuMIn (Barton, 2014) with R software v. 3.1.2. GLMs and survival analysis were carried out with Statistica 7.0 (Statsoft. Tulsa, Oklahoma, USA).

4.3. Results

Predation of seeded acorns

Acorns were not found in 83.7% of the unprotected seeding points; these acorns could have been moved or predated. Of the rest of the acorns, 13.2% were predated *in situ* and only six (3.1%) out of the 190 unprotected seeding points remained with acorns at the end of the spring.

Seedling emergence

At least one seedling emerged at 51 seeding points (13.5%), 49 of which were protected and two were unprotected. However, only 6.7% of all seeded acorns with protection produced a seedling. The two GLMMs that best explained seedling emergence included the interaction between orientation and distance from the woodland islet (AIC = 212.6; χ^2_3 = 14.12, p = 0.0028) and the orientation relative to woodland islet (AIC = 213.9; χ^2_6 = 21.26, p = 0.0016), respectively, but distance by itself did not have any effect χ^2_3 = 3.07, p = 0.38). Seedling emergence was highest (42.9%) on the northern side and lowest on the southern side (13.2%) of islets.

We found 28 naturally established oak seedlings that emerged in 2014 (189.8 seedlings ha^{-1}). Mean distance of these seedlings to islets was 4.1 ± 2.7 m. Density distribution of these seedlings did not show any significant pattern at different distance to the islets (χ^2_5= 10.16, p = 0.07) (**Figure 4.2**).

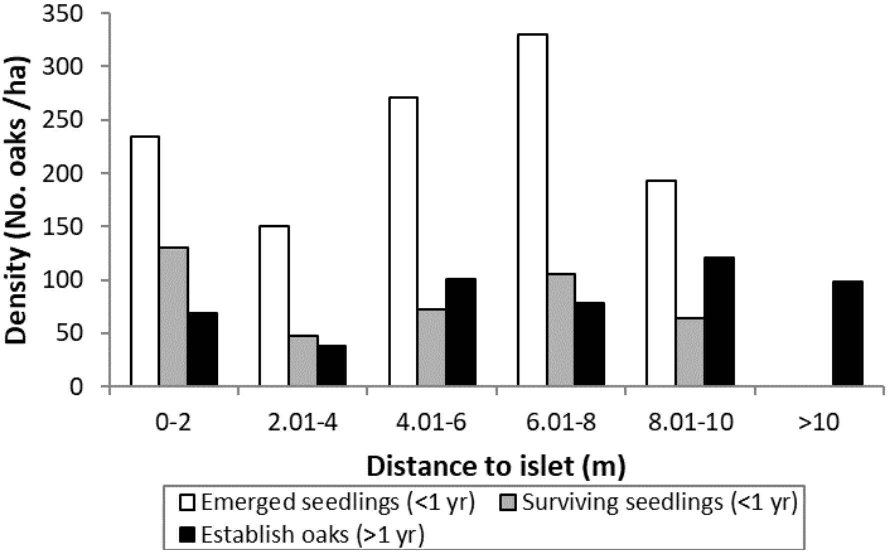

Figure 4.2. Oak density (emerged seedlings in 2014, surviving seedlings after the first dry season, and established oaks > 1-year old) in 2-m width bands at different distance to the woodland islets

Early seedling survival

All emerged unprotected seedlings were predated (i.e. they were found with no aerial organs) while survival of protected seedlings at the end of the first growing season was 33.3% (protection effect χ^2_1= 13.33, p = 0.0003; **Figure 4.3**). There was a peak of mortality at days 41 to 51 that was much higher for unprotected than for protected seedlings. Neither orientation (χ^2_3 = 3.03, p = 0.39) nor distance (χ^2_3 = 2.1, p = 0.83) affected seedling survival, but sample size was low (n = 49) and the design was highly unbalanced.

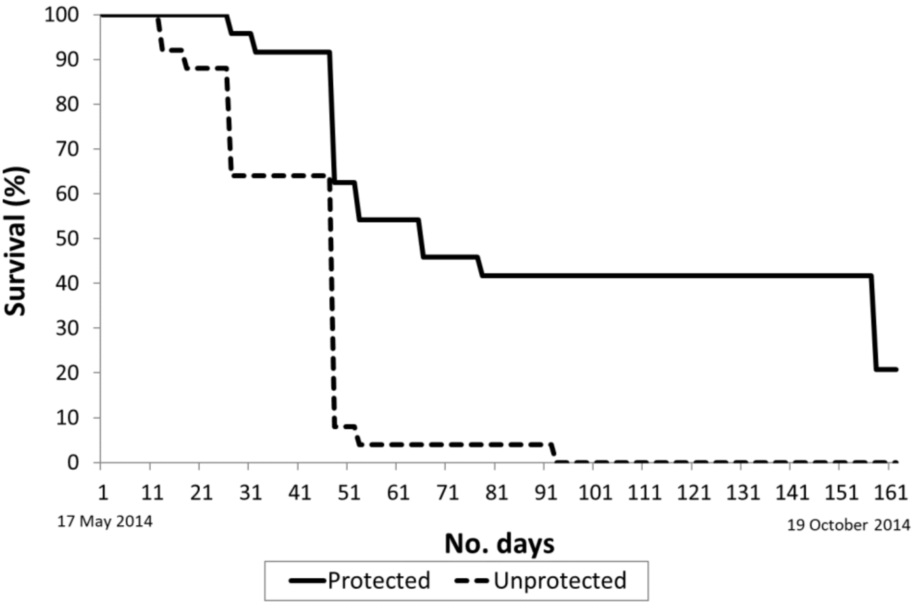

Figure 4.3. Changes in survival probability of protected and unprotected *Q. ilex* seedlings through the summer and early fall of the first growing season. These *graphs* refer to the 31 emerged seedlings from seeded acorns that were monitored since May 17 2014 plus the 18 seedlings that emerged later

Survival of the 28 naturally established oak seedlings that emerged in 2014 was 28.6% by the end of summer (54.2 seedlings ha^{-1}), and it was independent of orientation (χ^2_3 = 1.81, p = 0.77) or distance (χ^2_4 = 2.97, p = 0.56) according to the survival analysis. Mean distance of surviving and dead seedlings to islets was 3.0 ± 3.0 m and 4.6 ± 2.5 m, respectively (differences in these distances were not significant, t-test p = 0.15). Density distribution of emerged seedlings that survived after first dry season did not differ among distance bands (χ^2_5= 7.92, p = 0.16). Thirty per cent of dead seedlings dried out, 35% were predated when they were alive and 15% once dry, and for the remaining 20% dead seedlings we could not conclude the cause of death.

Oak establishment after 21 years

Fifty-eight holm oak individuals >1-yr old that were developed from dispersed acorns outside the planted islets have established in the experimental field after 21 years (**Figure 4.4**), resulting in a density of 65.1 oaks per ha excluding the area occupied by the islets with an average establishment rate of 3.3 oaks ha^{-1} yr^{-1}. Average distance of these to the closest islet was 6.3 ± 5.4 m (5.8 ± 3.7 m excluding an outlier oak located at 35.7 m from the closest islet), which is similar to half the average distance among islets (5.9 m). The density distribution of these established oaks did not differ among distance bands (χ_5^2 = 5.75, p = 0.33; **Figure 4.2**). Height, basal diameter and crown projected area of the established oaks averaged 49.2 ± 64.3 cm, 20.1 ± 31.3 mm, and 0.44 ± 1.09 m^2, respectively.

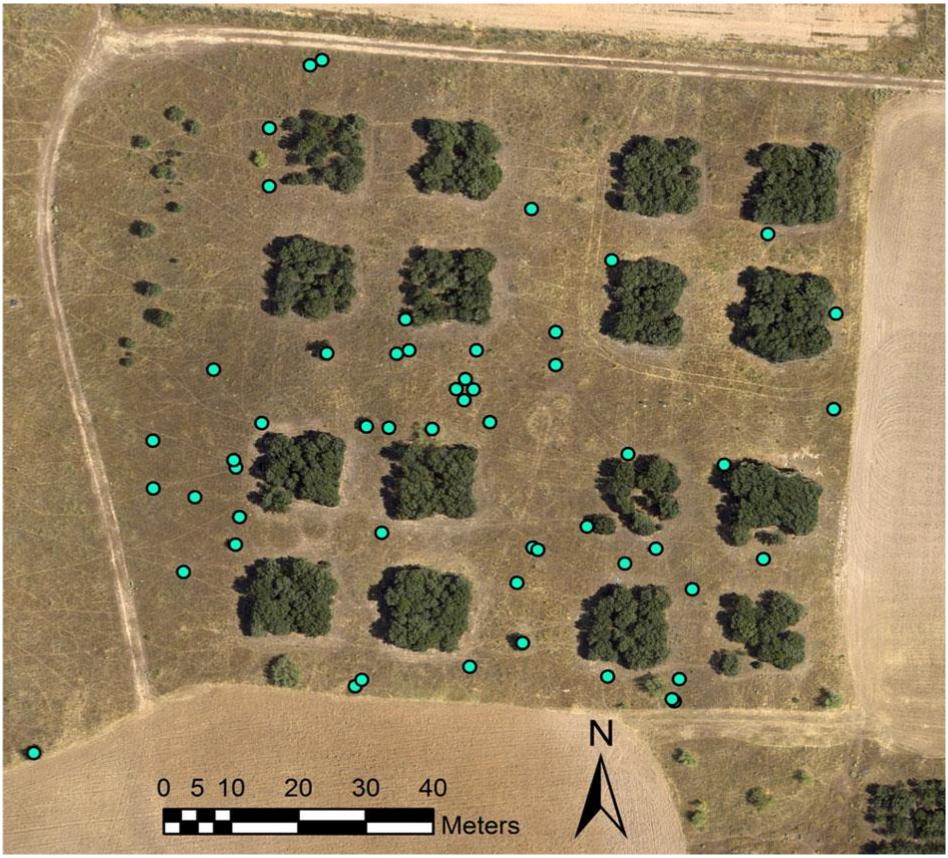

Figure 4.4. Position of the 58 naturally established oaks > 1 year old in the experimental field

4.4. Discussion

High acorn predation and low seedling survival

Our results clearly show that acorn predation is a major bottleneck for holm oak recruitment, consistent with our first hypothesis. Similar to our findings, Leiva and Fernández-Alés (2003) reported that only 0-2.4% of acorns escaped from predation in an oak savanna located in southern Spain, and Pons and Pausas (2007b) found that 98.7% of acorns were removed and/or predated by rodents in eastern Spain. Rodents and magpies are both predators and dispersers of acorns (Waite, 1985), but rabbits and hares, which are abundant in our field site, are only predators (Zamora et al., 1985; Díaz et al., 1996; Leiva and Fernández-Alés, 2003; Guzmán et al., 2008). We have clear evidence of acorn predation *in situ* for a small fraction of the unprotected acorns but suspect that most of the unfound acorns were either entirely consumed immediately after removal or re-cached and consumed later in other sites (Perea et al., 2011), as the farmland environment where our woodland islets are embedded may exacerbate predation. For instance, Gómez et al., (2008) found in the Sierra Nevada Mountains (SE Spain) that most caches were recovered and consumed, and only 1.3% of the original experimental acorns were found alive in caches the following spring. Likewise, in another experiment that we conducted for three years in old fields in central Spain with tagged acorns, we found that 100% of remobilized acorns were finally predated (Villar-Salvador and Pérez-Camacho, *unpublished data*). Other studies, however, have documented the spatial patterns and effects of long-distance oak dispersal at the landscape scale and hence the importance of isolated oaks as seed sources (Gómez, 2003; Purves et al., 2007). Acorn physical protection against predators is needed in Mediterranean environments to ensure oak establishment after seeding (Adams et al., 1992; Castro et al., 2015), as other methods such as chemical repellents have been shown to be unsuccessful (Leverkus et al., 2013).

We found low rates of seedling survival, consistent with previous studies on *Quercus* establishment in Mediterranean environments (Rey Benayas et al., 2005; Castro et al., 2006; Valdecantos et al., 2006; del Campo et al., 2010; Cuesta et al., 2010a, 2010b). As we anticipated (H3), most of this mortality was a consequence of seedling predation; all of unprotected seedlings in the seeding experiment and at least 50% of the naturally established seedlings (which were not protected) were predated by the end of the first growing season. On the other hand, two-thirds of our caged seedlings and at least one third of the new naturally established seedlings dried out probably reflecting mortality due to summer drought, which occurred quickly (**Figure 4.3**). The natural establishment rate we recorded in 2014 (54.2 seedlings ha^{-1}) is lower than those we estimated from data reported by Pulido and Díaz (2005) in oak woodland (132 seedlings ha^{-1} yr^{-1}) and by Garcia-Barreda and Reyna (2013) in gaps of a planted pine forest (120 seedlings ha^{-1} yr$^{-1)}$, but higher than that found by Pulido and Díaz (2005) in an oak savanna (2.8 seedlings ha^{-1} yr^{-1}). Gómez et al. (2003) also found that 98% of the 1000 experimental seedlings were killed by herbivores, notably wood mice, wild boar, and domestic and wild ungulates.

Low seedling emergence

Seedling emergence was low when compared with results in previous studies of holm oak. For instance, Smit et al. (2009) observed emergence values >90% while Pulido and Díaz (2005) observed 73% emergence in their study. Low emergence values in our study are probably a consequence of the dry spring, particularly in the few weeks after seeding. This idea is supported by the emergence peak after a late spring rainy event and by the fact that emergence was highest at the sites with northern exposure where soil desiccation is ameliorated in agreement with our H2 (Montero et al., 2008). Acorns are recalcitrant seeds with their viability dependent upon relatively high water content (Villar-Salvador et al., 2013); hence, *in situ* desiccation is an important cause of acorn mortality (Joët et al., 2013).

Lack of distance effects

The distance to woodland islets at small scales did not affect acorn predation and seedling performance. Lack of distance effect on acorn predation is probably due to the fact that our longest seeding distance (10 m) can be easily reached by all dispersers/predators that may shelter in the islets (Pons and Pausas, 2007b; Gómez et al., 2008). Similarly, we did not find higher seedling emergence at closer distances to the islets where we expected higher emergence due to micro-climate amelioration by islet canopy shade. This contrasts with results in Smit et al. (2009) showing higher emergence in shaded microsites than in open microsites and suggests a lack of "safe" microsites for recruitment in our experimental field (Pulido and Díaz, 2005). It is possible that microclimatic amelioration by islet canopy was not enough to maintain high soil moisture during the dry spring, but we did not measure soil water content to assess this explanation. The lack of distance effect on seedling mortality from herbivory could be due to the fact that separation between islets is too small to detect a difference in rabbit and hare movement (Gómez et al., 2008), but our observations suggest that consumption of herbs by rabbits is much higher within 0-2 m of the edge of the islets (**Figure**

4.1). It is possible that there is a neutral balance between counteracting effects of established islets on seedling establishment, namely microclimate amelioration facilitating establishment near islets and competition with mature trees and herbivory favoring establishment further away. A final possible explanation for lack of distance effect on seedling emergence and early seedling survival is that we had insufficient power to detect interactive effects between distance and orientation due to low sample size and unbalanced design, due to high predation

Initial woodland regeneration

We recorded a natural establishment rate of 3.3 oaks ha^{-1} yr^{-1} along the 21 years of our experiment, which in comparison with the figure of natural establishment found after the first dry season suggests strong future mortality of recently established seedlings in our field site. However, our woodland islets started to produce acorns seven years after oak seedling plantation and seed production in the first reproductive years was small. This means that the rate above will likely be higher and increase in the future. (Leverkus et al., 2014) found a natural establishment rate of 4.18 oaks ha^{-1} yr^{-1} at a post-fire regeneration site in a Mediterranean mountainous environment with higher precipitation.

We have investigated one case study to address the complex issue of outcomes of relevant techniques, methods and approaches for large scale and long-term efforts for landscape forest restoration (Stanturf et al., 2014). Three limitations of this study are that it was conducted in only one site of 1 ha with planted oak islets, included only one year of monitoring acorn removal/predation and seedling emergence/survival ,and did not assess dispersal. On the other hand, the age of the introduced islets, the set of recruitment stages and processes studied, and the singularity of the experimental design provide relevant lessons for woodland restoration.

Acorn availability is a bottle-neck that limits vegetation establishment in agricultural landscapes (Rey Benayas et al., 2008a; Rey Benayas and Bullock, 2012, 2015), and this limitation was clearly overcome by the introduction of small woodland islets that established successfully in our experimental field. These islets have triggered holm oak regeneration that would have been high unlikely without nearby seed sources (Gómez-Aparicio et al., 2009), but the rate of recruitment is limited by high acorn predation, seedling herbivory, and stressful microclimatic conditions. Using tree shelters against herbivores that also ameliorate climate harshness (Puértolas et al., 2010) of the naturally established seedlings from acorns dispersed from planted woodland islets would accelerate passive restoration of former cropland and pastureland. Thus, planting woodland islets without further intervention seems not be sufficient to catalyze "fast" initial recovery of Mediterranean woodland on abandoned farmland and restoration will be resource intensive. "Success" or "failure" in restoration efforts like the one investigated here nonetheless depends on the time frame of evaluation, particularly in Mediterranean ecosystems where recruitment is notoriously episodic (Moreno et al., 2011). Overall, we suggest that the woodland islet approach is a low cost and useful technique to speed up woodland restoration in agricultural landscapes.

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4.7. Supporting information

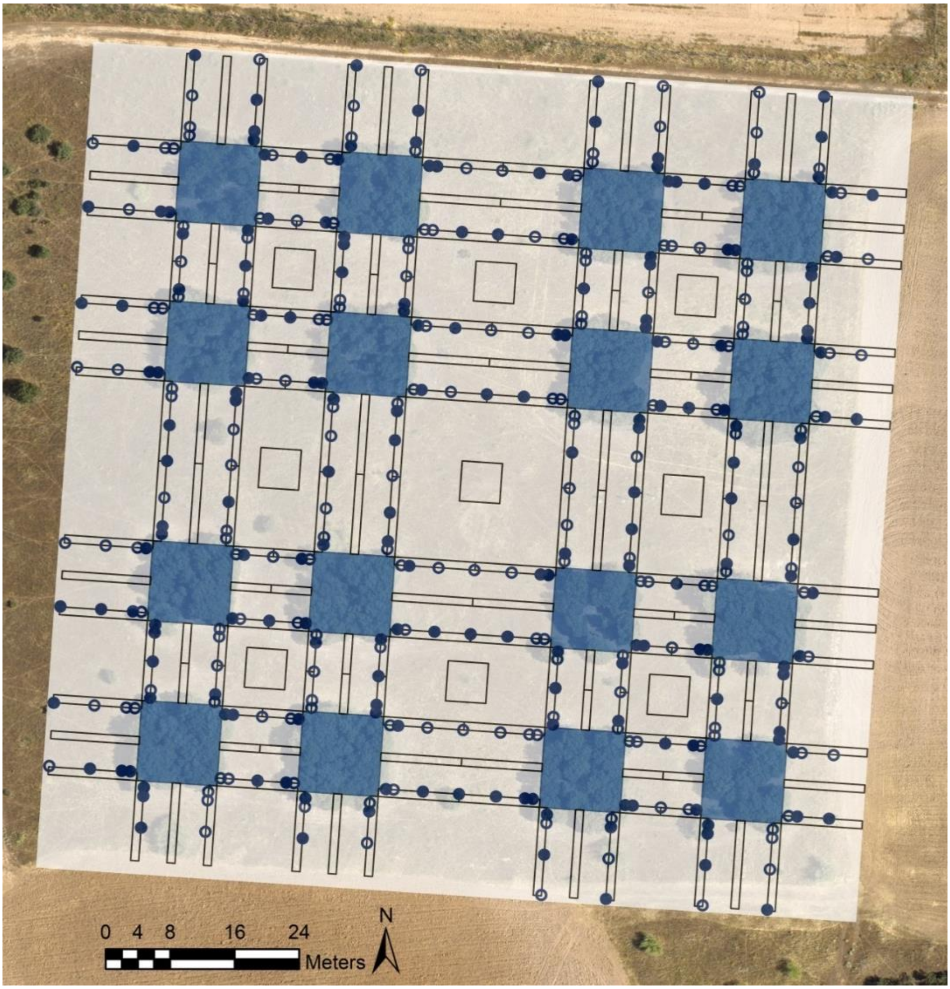

Figure S4.1. Design of the seeding experiment and sampling for assessment of early natural establishment of oak seedlings. Position of (a) 386 acorn seeding points located along two 10-m long transects in each of the four corners of every woodland islet. Open and solid blue circles indicate unprotected and protected seeded acorns, respectively, at 0, 1, 5 and 10 m from the islet edge (see text for a few exceptions to these seeding distances); and (b) 192 rectangular plots and nine squared plots between the islets or between the islets and nearby active crops to count and monitor natural seedling emergence and early survival.


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Imágenes de arriba a abajo y de izquierda a derecha:

Islotes forestales y encina reclutada a la derecha de la imagen en la finca La Higueruela del CSIC (Santa Olalla, Toledo)
Encina de uno de los islotes con bellotas
Protector metálico con plántula emergida
Esquina de uno de los islotes forestales con puntos de siembra
Jaula de exclusión de herbívoros antes de la recogida de la biomasa dentro y fuera
Plántula de encina reclutada desde los islotes forestales con etiqueta para el seguimiento
Juvenil de encina reclutada desde los islotes forestales
Fuente de las imágenes: L. Martínez-Baroja

Capítulo 5

Drivers of oak establishment in Mediterranean old fields from 25-year-old woodland islets planted to assist natural regeneration[9]

Abstract

Plantation of woodland islets can provide seeds for restoring forest ecosystems in Mediterranean old fields lacking seed sources, but other factors than seed arrival can hinder the establishment of woody species in those fields. Here we experimentally examined factors affecting the emergence of *Quercus ilex* L. (holm oak) seedlings as well as the survival, growth, and recruitment of juveniles from 25-year-old 100-m^2 oak woodland islets planted in a Mediterranean old field. Damage by wild boar reduced seedling emergence. Oak seedling emergence and early survival were increased in wet springs and summers as well as in microsites close to the islets in less sun-exposed orientations of the islets and far from the islets in more sun-exposed orientations; these factors did not, however, affect oak annual growth. Survival of seedlings was 26% lower without shelter than with shelter, reflecting herbivory. Herb community biomass and light extinction increased with distance from nearest islet; the sparse herb cover around islets was due to competition from woodland islets, not to herbivory. Variation of the abundance of naturally regenerated oak juveniles with distance from nearest islet did not match the way that seedling survival varied with distance, suggesting that other drivers such as acorn dispersal can counteract seedling survival. We conclude that natural regeneration of holm oak in old fields from planted woodland islets is slow (5.7 seedlings ha^{-1} yr^{-1}) due to acorn and seedling predation, as well as drought during spring and summer. Despite their small size,

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[9] This chapter fully reproduces the following manuscript under review:

Martínez-Baroja, L., Rey-Benayas, J. M., Pérez-Camacho, L. and Villar-Salvador P. In first review. Drivers of oak establishment in Mediterranean old fields from 25-year-old woodland islets planted to assist natural regeneration. *Forest Ecology and Management*.

planted islets affected survival of oak juveniles depending on the orientation and distance relative to the islets.

Resumen

La plantación de islotes forestales puede proporcionar semillas para restaurar los ecosistemas forestales en campos abandonados en ambientes mediterráneos que carecen de fuentes de semillas, pero otros factores además de la llegada de semillas pueden obstaculizar el establecimiento de especies leñosas en esos campos. En este estudio evaluamos experimentalmente los factores que afectan a la emergencia de las plántulas de *Quercus ilex* L. (encina), así como a la supervivencia, al crecimiento y al reclutamiento de los juveniles a partir de islotes forestales de quercíneas de 100 m^2 plantados hace 25 años en un campo abandonado mediterráneo. El daño causado por el jabalí redujo la emergencia de plántulas. La emergencia y la supervivencia temprana de las plántulas de encina aumentaron en primaveras y veranos húmedos, así como en micrositios cercanos a los islotes en las orientaciones de los islotes menos expuestos al sol y lejos de los islotes en las orientaciones más expuestas al sol; sin embargo, estos factores no afectaron el crecimiento anual de encinas. La supervivencia de las plántulas fue un 26% menor en los puntos de siembra sin protector frente a aquéllos que sí lo tenían por efecto de la herbivoría. El patrón espacial de la supervivencia de las plántulas con la distancia no coincidió con la distribución de los juveniles de encina procedentes de la regeneración natural, lo que sugiere que otros procesos como la dispersión de bellotas podrían superponerse al efecto de la supervivencia de las plántulas y contrarrestarlo. Concluimos que la regeneración natural de encinas asistida mediante islotes forestales plantados en campos agrícolas abandonados es lenta (5,7 plántulas ha^{-1} $año^{-1}$) debido a la depredación de las bellotas y las plántulas y a la sequía durante la primavera y el verano. A pesar de su pequeño tamaño, los islotes afectaron a la supervivencia de los juveniles en función de la orientación y la distancia a los islotes.

5.1. Introduction

Natural regeneration, also called passive restoration, has restored many woodland and forest areas (Chazdon et al., 2020); for instance, 133 million ha in Europe have been recovered through natural regeneration up to 2010 (FAO, 2015). It has been estimated that 0.9 billion ha of woodlands and forests can still be restored globally (Bastin et al., 2019). Passive restoration can help to meet international forest restoration goals such as the 2011 Bonn Challenge and the 2014 UN Declaration on Forests (Crouzeilles et al., 2016; Meli et al., 2017).

However, insufficient seed dispersal reduces the effectiveness of passive forest restoration (Jordano et al., 2008; Navarro and Pereira, 2012; Rey-Benayas and Bullock, 2012). Vegetation remnants in the landscape export seeds to the surrounding areas, making them important foci of forest regeneration (Andivia et al., 2017; Cruz-Alonso et al., 2019a). Various strategic revegetation actions have been applied to reintroduce natural vegetation to areas without forest remnants, such as farmed landscapes (Rey-Benayas and Bullock, 2015). These actions include planting tree clusters, hedgerows and even isolated trees, all of which not only promote natural regeneration but also enhance wildlife, agricultural production, and other ecosystem services (Manning et al., 2006; Rey-Benayas et al., 2008; Van Vooren et al., 2017).

The introduction of tree clusters (“woodland islets”) to assist natural regeneration was first suggested by Rey-Benayas et al., (2008) - the woodland islets approach - as a new action for restoring forests on old fields. Several small, dense blocks of native shrubs and trees are sparsely planted in agricultural land to trigger secondary succession over larger areas (Navarro and Pereira, 2012). Later researchers have referred to this approach as “tree islands” or “applied nucleation” (Corbin and Holl, 2012; Piiroinen et al., 2015; Zahawi et al., 2013), "dispersion and attraction nuclei" (García-Martí and Ferrer, 2013), or “tree clumps” (Stanturf et al., 2014). This approach has been implemented in various restoration actions (Corbin et al., 2016; Dendy et al., 2015; Ramírez-Soto et al., 2018; Shaw et al., 2020), yet few studies have addressed the long-term effectiveness of woodland islets for facilitating forest restoration or the factors that may compromise that effectiveness (Holl et al., 2020; Rey-Benayas et al., 2015; Rey-Benayas and Bullock, 2015).

In Mediterranean old fields, numerous factors have already been shown to slow down passive restoration (Cruz-Alonso et al., 2019a; Martínez-Muñoz et al., 2019; Rey-Benayas et al., 2015); these include seed dispersal, seed predation, competition by herbs (Cuesta et al., 2010b; Rey Benayas et al., 2005), herbivory (Gómez et al., 2003; Puerta-Piñero et al., 2012), and harsh abiotic conditions

(Andivia et al., 2017; Cuesta et al., 2010a; Martínez-Muñoz et al., 2019). Summer drought and high inter-annual climate variation can also strongly affect plant performance (Forner et al., 2018); therefore, running multi-year experiments are needed to capture the potential effects of climate variability on dynamics of recruited tree species (Cuesta et al., 2010b; Pérez-Camacho et al., 2012).

Studies of woodland islets should also take into account how their effects on restoration vary with distance from nearest islet, as the woodland-herb edge creates a heterogeneous environment for new plants (Benítez-Malvido et al., 2018; Holl et al., 2020; Rey-Benayas et al., 2015), and factors may operate differently at locations near or far from islets. For example, seeds produced by islets can be dispersed at a wide range of distances from them (Corbin et al., 2016). However, the effect of planted woodland islets on the distribution of recruits from the islets depend on the net outcome of several ecological processes, which intensity can change with the distance and orientation from the islets. At short distances, islets may compete against new woody plants directly (Gavinet et al., 2020; Morán-López et al., 2018). At the same time, the islets can facilitate indirectly the establishment of woody plant recruits by reducing the competition of herbs on oak recruits (Cuesta et al., 2010b). Islet competition against oak recruits may be stronger in sun-exposed orientations than in shady orientations, which may have a less harsh abiotic micro-environment (Pérez-Ramos et al., 2013). Finally, islets can provide mycorrhizae to nearby open areas, which further promotes the establishment of new plants (Dickie et al., 2007).

The goal of the present study was to assess the spatial effects of holm oak (*Quercus ilex* L.) woodland islets on oak establishment 25 years later in Mediterranean old fields in Toledo, central Spain, and to identify factors that have influenced that restoration. *Quercus ilex* is a late successional, slow-growing tree with high resprouting capacity (Villar-Salvador et al., 2013). Since their plantation in 1993, the woodland islets have grown in volume, they produce large amounts of acorns (Rey-Benayas et al., 2008), and some holm oaks of different sizes have become established around the islets (Rey-Benayas et al., 2015). However, the islets have not grown beyond their original limits. Moreover, a strip approximately 1.5-2.0 m wide around the islets show minimal herbs, suggesting that plant development near the islets may be limited by competition from islets and from herbivory.

In a previous study (Rey-Benayas et al., 2015), we analysed long-term recruitment at this site, and we identified several demographic processes that may have affected early seedling recruitment around the woodland islets based on field experiments. We showed that high acorn predation or removal, seedling herbivory and stressful microclimatic conditions have slowed down oak regeneration from the woodland islets. The present study continued these investigations over multiple years in order to verify our earlier findings as well as capture potential effects of inter-annual climate variability. In addition, we looked more closely at how processes involving the islets and surrounding herb matrix interact at the edge of islets.

In this study, we hypothesised that seedling emergence and survival would be highest in years with a less stressful climate, particularly with rainier springs and milder summers (H1); seedling emergence and survival would be higher at northern, less sun-exposed edges of the islets, where the islet canopy improves the microclimate (H2); and competition by the islets, surrogated by distance from nearest islet, and herbivory will reduce seedling emergence and survival and herb growth near the islets (H3). Our data spanning a quarter-century identify mechanisms affecting the success of applied nucleation, which may help guide natural woodland regeneration of Mediterranean old fields and other regions of low productivity.

5.2. Material and methods

Study site

The study was conducted at “La Higueruela”, a research station in Santa Olalla, Toledo, Spain (40º3'N, 4º24'W, elevation 450 m), managed by the Consejo Superior de Investigaciones Científicas. We ran our experiments on an old field of 1 ha that had been cultivated for grain for many years, until woodland islets were planted there in 1993. In that year, 16 oak woodland islets of 100 m^2 were established at a density of 50 seedlings per islet, with a mean distance of 11.8 m between the islets. The woodland islets are embedded in a grassland matrix dominated by annuals that have remained from when the islets were planted (**Figure S5.1**). The field is surrounded by rain-fed cereal crops in a highly farmed landscape context. More details about islet establishment and analyses of management and outcomes through 2014 have been described elsewhere (Rey

Benayas, 1998; Rey Benayas and Camacho-Cruz 2004; Rey Benayas et al. 2015). In 2014, the mean height of trees in the islets ranged between 3 and 4 m.

The climate is continental Mediterranean, characterised by cool winters and a long summer drought that imposes severe water stress on the vegetation. During 1993-2018, annual precipitation averaged 468.2 mm and mean temperature averaged 15.5 °C. Daily climate data were obtained from an *in situ* weather station. During the period 2000—2018, precipitation and temperature in spring (24 February-14 May) and summer (15 May – 31 August), the number of days with high temperature (maximum >36 °C) and the length of the longest heatwave (defined as consecutive days with maximum temperature >36 ºC) differed substantially across the years. Springs in 2014 and 2017 were particularly dry and hot, spring precipitation in 2015 was close to the average for the period 2000-2018, and spring precipitation in 2016 was higher than the average. The summer of 2014 and of 2016 were dry. Summer precipitation in 2015 was similar to the average for the period, and that of 2017 was higher than the average (**Table 5.1, Figure S5.2**).

Table 5.1. Spring and summer precipitation, mean temperature, number of days with maximum temperature >36 ºC and consecutive days with maximum temperature >36 ºC per year. Red background indicates a dry season (below-average precipitation) or hot season (above-average temperature). Blue background indicates a wet season (above-average precipitation) or a cool season (below-average temperature). White background indicates seasons with average precipitation or temperature. Green background represents the spring when we irrigated acorn seeding points to achieve the precipitation equal to the average spring precipitation for the period 2000-2014.

Year	Precipitation (mm)			Mean temperature (°C)			No. days	
	Spring	First summer	Second summer	Spring	First summer	Second summer	T>36 ºC	Longest heatwave
2014	45.8	38.1	47.1	14.1	23.4	25.7	26	7
2015	109.2	47.1	19.8	13.8	25.7	25.3	57	47
2016	184.8	19.8	138.7	10.9	25.3	25.9	61	7
2017	56.6	138.7	54.4	13.8	25.9	24.1	51	15
Mean for entire period (2000-2018)	132.03	51.6	51.6	12.5	24.5	24.5	41	16

The soil is a relatively fertile, deep luvisol type, and it is derived from arkoses. The major potential predators/dispersers of acorns and oak seedlings in the study area are rodents (e.g. *Apodemus sylvaticus* L. and *Mus spretus* Lataste), Eurasian magpies (*Pica pica* L.), and wild boars (*Sus scrofa*), as well as rabbits (*Oryctolagus cuniculus* L.) and hares (*Lepus granatensis* Rosenhauer) that shelter in the woodland islets.

Experimental design to identify factors affecting seedling emergence and survival

We seeded holm oak acorns around woodland islets on 24 February 2014, 31 January 2015, 8 February 2016, and 23 February 2017. Acorns were from Mediterranean continental-climate provenances from inland Spain acquired in the Centro Nacional de Recursos Genéticos Forestales “El Serranillo”. Prior to seeding, acorns were submerged in water for 12 h. The floating acorns, which had been partially eaten or rotten, were discarded. Mean emergence of acorn lots under laboratory conditions was 79.4% across studied years.

A total of 169 points were seeded and protected in 2014, 206 points in 2015, 198 points in 2016 and 209 points in 2017. The number of protected seeding points was smaller in 2014 because of a different acorn predation experiment. Each point had five acorns buried at a depth of 3 cm, which were protected with wire shelters to avoid changing the microclimate around the seeded acorns and emerged seedlings (**Figure S5.1**). We used the same type of wire shelters in 2014, 2015 and 2016 (**Figure S5.3 a**), and the shelters were nailed to the ground. Due to high acorn predation by wild boars in 2016 (see below; **Figure S5.3 c**), we used another type of wire shelter in 2017 that was designed to deter predation by wild boars (Reque and Martin 2015; **Figure S5.3 b**).

In all years, seeding points were located along two, 10-m long transects extending out from each of the external corners of every group of four woodland islets (**Figure S5.1**). Only in 2014, some seeding points were placed among the four islets. Seeding points were located at 0, 1, 5 and 10 m from the woodland islet edge. However, proximity between adjacent islets and nearby active crop fields or trails prevented seeding at some distances of 5 and 10 m. Our analyses did not include equidistant seeding points between adjacent islets because they were not independent of the orientation of the two islets.

We assessed seedling emergence at four times during spring, early summer and fall in each year. When a cluster of five acorns at the same seeding point produced more than one seedling, only one seedling was left to avoid conspecific competition, and the other emerged seedlings were removed by excising the stem at the root collar level to prevent resprouting. Survival of the remaining seedlings was monitored 4-16 times from emergence until the end of the experiment in March 2019.

To assess the importance of seedling herbivory at one year after emergence, we removed the shelters from 40 of the 88 seeding points in 2015 that had alive seedlings on 12 May 2016.

Dynamics of natural establishment

To assess natural establishment of holm oak seedlings during 2014-2017, we counted the emerged seedlings and monitored their survival in 192 rectangular plots and nine square plots located between the islets as well as between the islets and the edge of the study site. The rectangular plots were located along the edges of the woodland islets in four orientations: two at each corner and one halfway between them (**Figure S5.1**). Sampling took place in July 2014, 2016 and 2017, but it was delayed until November in 2015 because of logistical problems. The size of the plots between islets was 1 × 5 m; those between islets and active crop fields or trails measured 1 × 10 m. Square plots between islets measured 5 × 5 m. The 201 sampling plots covered a total area of 1,474.9 m^2 or 17.6% of the experimental field area not occupied by woodland islets. Emerged seedlings in all plots were tagged for later localisation.

We monitored the plots to assess survival of emerged seedling in October or early November, i.e. after the summer dry period and at the start of each autumn. We measured the size of all living seedlings on 14 March 2019.

Holm oak recruitment and growth assessment

We thoroughly prospected the entire study site to find all naturally established holm oaks with a minimum height of 5 cm, which were positioned on an ortho-photo. These individuals represent long-term recruitment after woodland islets had started to produce acorns. We measured the distance of each juvenile to the nearest islet; from 2014 to 2019, we also measured their height, basal diameter and calculated the projected crown area.

On 14 March 2019, we measured the size of all living seedlings and naturally established holm oaks (experiments and observation described in sections 2.2 and 2.3) and calculated annual growth rate as:

$$\frac{\text{(Plant final size - Plant initial size)}}{\text{Number of years}} \qquad (1)$$

When calculating the initial size of the naturally emerged seedlings and established seedlings from sowing points, we assumed the initial height to be 0.5 cm and the initial projected crown to be 0.78 cm^2. For the naturally established holm oaks, initial size was calculated from the first measurement data.

Microsite environment around islets

To assess whether islets reduced the growth of the herb community and therefore its competition with oak seedlings, we measured the development of the herb community in two ways. The first was to measure light extinction by the herb community at all seeding points containing emerged seedlings (**Figure S5.1**) at the end of the dry period in November 2015 and on 1 June 2016. The second was to measure herb biomass in May 2016 in quadrats of 40 x 40 cm located 1 m away from the point where we measured soil moisture (see below). Herbs were dried in an oven at 60 ºC for at least 48 h and weighed.

We also studied whether soil moisture differed with orientation and distance from the islet edge by inserting PVC tubes at 45 points in May 2016 (**Figure S5.1**). Soil moisture was measured at depths of 10, 20, 30 and 40 cm and at 1, 5 and 10 m from the islet edge in all orientations. Measurements were made with a moisture sensor (Profile Probe Type PR2, Delta-T Devices, Cambridge, UK) connected to a moisture meter (HH2, Delta-T Devices). In some cases, moisture could not be measured at 10 m due to the presence of cropped fields or trails. Measurements were made several times from May 2015 to May 2017.

To ascertain whether strips of sparse herb vegetation around the islet edge were the result of competition from islets or from herbivores living inside the islets (mainly rabbits), we placed on 5 November 2016 a total of 32 wire cages (60 cm deep, 38 cm wide and 29 cm tall) on the ground to exclude herbivores (**Figure**

S5.3 e). One cage was placed at 1 m from each islet edge on the northern and southern sides. On 7 June 2017, i.e. after maximum herb growth in the spring and before senescence in the summer, we harvested the herb biomass within the cages and in paired plots measuring 60 x 38 cm (**Figure S5.1**), then processed it as described above.

Data analysis

Generalised linear models (GLMs) with a binomial distribution and a logit-link function were used to analyse seedling emergence at the experimentally seeded points, as well as the survival of seedlings that had emerged from seeded acorns or were naturally established. We included the year as a categorical variable to test the effect of inter-annual variation in the initial model (fixed effect; H1). The initial model contained orientation, distance from nearest islet, their interaction (H2 and H3) and damage by wild boar (yes or no) nested within the year as fixed effects. Plot (four groups of four closest woodland islets) was also included as a fixed effect, because our data were spatially aggregated and the plot factor showed only four levels (Crawley, 2007). To analyse the effect of seedling herbivory, we added the presence or absence of seedling shelter in 2015 seeding points and its interaction with distance from nearest islet as a fixed effect.

We analysed light extinction by herbs and herb biomass near the points where soil moisture was measured. Orientation, distance from nearest islet, their interaction, and plot were included as fixed effects. We also analysed the differences in herb biomass at the islet edges to test the effect of orientation and herbivory exclusion (fixed effects; H3). We used linear models for all analyses except for light extinction by herbs, for which we used GLMs with a gamma error and an inverse link function. We used linear mixed models (LMMs) to analyse the effects of orientation, distance from nearest islet, depth and their double interactions on soil moisture; these models included position and measurement date as random effects. Akaike's (1987) information criterion (AIC) was calculated for each model. We used the cut-off of ΔAIC < 2 units to identify models with better explanatory power that followed the principle of parsimony (Burnham and Anderson, 2002; Crawley, 2007).

We used the chi-squared test to analyse whether the proportion of the established oaks differed between expected and observed values for strips of land at different “distance bins” from the islets. Expected values were calculated by taking into account the proportion of area covered by each strip of land. We used GLM with a gamma error and an inverse link function and LM to analyse the fixed effects of orientation and distance from nearest islet on annual growth rate of living seedlings. These analyses were performed separately for experimentally seeded acorns (with year as fixed effects) and for naturally established oaks. All analyses were performed with R software version 3.5.2 (R Core Team, 2018) using the packages *lme4* (Bates et al. 2014), *MuMIn* (Barton 2014), *ggplot2* (Wickham, 2016), *effects* (Fox and Weisberg, 2018), and *heatwaveR* (Schlegel and Smit, 2018).

5.3. Results

Seedling emergence

At least one seedling emerged at 41 (24.3%) seeding points in 2014, 134 (65.0%) in 2015, 27 (13.6%) in 2016 and 46 (22.0%) in 2017. For all years, the model that best explained seedling emergence was the one that included the orientation × distance interaction and its main effects, as well as sowing year, damage by wild boar, and plot (**Table 5.2**). Emergence averaged 43.1% on the northern side and 19.8% on the southern side. It increased with distance from nearest islet in the southern orientation, while the opposite was observed in the northern orientation (**Figure 5.1**). Distance had a negligible effect on emergence in the western and eastern orientations. Emergence was higher at seeding points that were undamaged by wild boar than at points that were damaged (42.6 vs. 5.6%).

We found 28 naturally emerged oak seedlings in 2014, corresponding to a density of 190 seedlings ha^{-1}. The corresponding values in other years were as follows: 40 seedlings and 271 seedlings ha^{-1} in 2015, 152 and 1030 in 2016, and 42 and 285 in 2017. Across the four study years, these seedlings were located a mean (SE) of 4.9 ± 0.18 m from nearest islets, and mean distance ranged annually from 4.1 to 5.3 m (**Figure S5.4**).

Table 5.2. Selection of models of seedling emergence from seeding points and of survival of seedlings that emerged from seeding points or that were naturally established. Tested initial model of seeding points: **seedling emergence** ~ orientation * distance + year / wild boar damage + plot; **seedling survival** ~ orientation * distance + year + plot. Tested initial model of natural regeneration: **seedling survival** ~ orientation * distance + year + plot. **Bold**: model parameters in the final model.

Study	Sampling time	Model parameters	df	AICc	ΔAICc	R2
Experimental seeding	Seedling emergence	Orientation * distance + year / wild boar damage + plot	16	747.74	0.00	0.28
		Orientation + year / wild boar damage + plot	12	750.54	2.80	0.27
		Orientation * distance + year / wild boar damage	13	750.74	3.00	0.28
		Null model	1	979.02	231.29	0
	Seedling survival after first summer	Orientation * distance + year	11	273.62	0	0.175
		Distance + year	5	276.48	2.86	0.112
		Null model	1	293.67	20.06	0
Naturally emerged seedlings	Seedling survival after first summer	Orientation * distance + year + plot	17	289.25	0	0.213
		Orientation * distance + year	13	290.07	0.81	0.183
		Distance + year + plot	9	292.24	2.99	0.148
		Null model	1	317.58	28.32	0
	Seedling survival after second summer	Distance + year	5	82.41	0	0.352
		Distance	2	84.51	2.1	0.272
		Null model	1	106.57	24.16	0

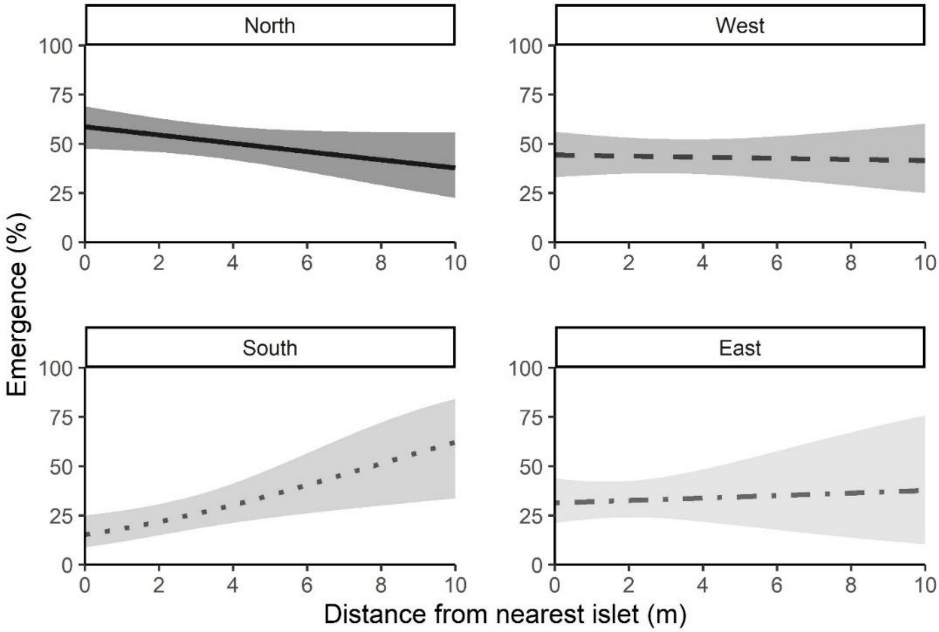

Figure 5.1. Predicted values of emergence of holm oak seedlings as a function of orientation with respect to the woodland islet and of distance from nearest islet. Shaded areas represent the 95% confidence interval.

Seedling survival

After excluding the seeding points damaged by wild boars, survival at the end of the first growing season of the herbivory-protected seedlings was 33.3% (n=7) in 2014, 69.4% (n=93**)** in 2015, 28.0% (n=7) in 2016, and 54.3% (n=19) in 2017. The model that best explained seedling survival after the first summer included the sowing year and the interaction between orientation and distance from nearest islet (**Table 5.2**). Survival increased with distance from nearest islet in the southern orientation, but it decreased with distance in the remaining orientations, especially the northern one (**Figure 5.2 a**). At the last sampling on 14 March 2019, we counted 71 living seedlings at the seeding points, comprising 6 at points seeded in 2014, 47 at sites seeded in 2015, 2 at sites seeded in 2016, and 16 at sites seeded in 2017.

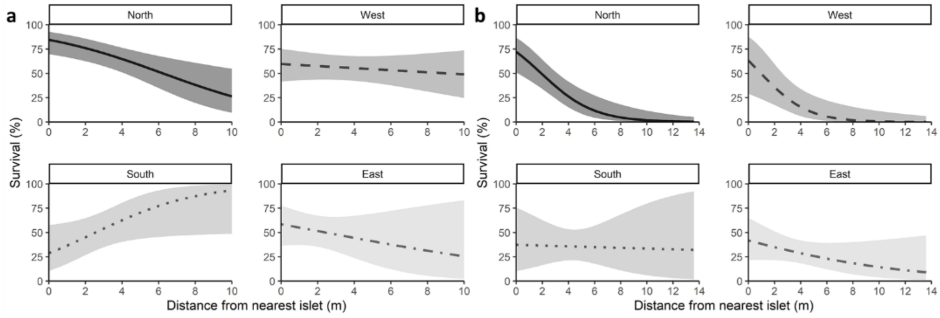

Figure 5.2. Predicted values of survival of emerged seedlings after the first summer in relation to orientation and distance from nearest islet in the case of (a) experimentally seeded acorns and (b) natural regeneration. Values are means ± CI (shaded areas represent the 95% confidence interval).

For naturally-established seedlings, survival at the end of the first summer were 28.6% for those that emerged in 2014, 50.0% for those that emerged in 2015, 21.7% for those that emerged in 2016, and 35.7% for those that emerged in 2017 (**Figure S5.5**). The model that best explained the survival of these seedlings included the year of emergence and the interaction between orientation and distance from nearest islet (**Table 5.2**). In general, seedling survival was higher nearer rather than farther from the islets, especially in the northern and western orientations (**Figure 5.2 b**). At the end of the second summer, survival rates were 14.1% for seedlings that emerged in 2014, 7.5% for those that emerged in 2015, 9.2% for those that emerged in 2016, and 31.0% for those that emerged in 2017 (**Figure S5.5**). The model that best explained seedling survival after the second summer included distance from nearest islet and year of emergence (**Table 5.2**). Seedling survival decreased with distance from nearest islet. At the last sampling, we counted 24 living seedlings on the sampled plots, comprising 0 that emerged in 2014, 2 that emerged in 2015, 10 that emerged in 2016, and 12 that emerged in 2017.

In the 2015 experiment designed to assess seedling herbivory, survival after the end of the second summer was higher for protected seedlings (81.2%) than for unprotected ones (55.0%). Survival was lowest in the eastern orientation, and it decreased with distance from nearest islet similarly for protected and unprotected seedlings (**Table S5.1, Figure S5.6**).

Light extinction, herb biomass and soil moisture

The model that best explained light extinction in autumn included the plot and the interaction between orientation and distance from nearest islet. In contrast, the model that best explained light extinction in spring included only distance from nearest islet (**Table 5.3 a, b**). Light extinction in autumn and spring increased with distance from nearest islet; in autumn, it was highest in the northern orientation (**Figure 5.3 a, b**).

Table 5.3. Selection of models of light extinction, herb biomass, and soil moisture. The initial model: **light extinction** ~ orientation x distance + plot; **herb biomass** ~ orientation * distance + plot; **soil moisture** ~ orientation + distance + depth + (orientation : distance) + (orientation : depth) + (distance : depth) + plot + (1|partial_n) + (1|date). **Bold**: model parameters in the final model.

Microsite environment characteristic	Model parameters	df	AICc	ΔAICc	R^2
(a) Light extinction in autumn (November)	Orientation * distance + plot	12	1292.8	0	0.32
	Orientation * distance	9	1295.3	2.470	0.28
	Null model	2	1338.81	45.99	0
(b) Light extinction in spring (June)	Distance	3	759.18	0	0.299
	Orientation * distance	9	762.35	3.17	0.386
	Null model	2	786.56	27.38	0
(c) Herb biomass near the points of soil moisture measurements	Distance + plot	6	386.59	0	0.764
	Orientation + distance + plot	9	394.10	7.51	0.771
	Null model	2	441.64	55.05	0
(d) Soil moisture	Orientation * depth + distance * depth + plot + (1|partial_n) + (1|date)	18	6001.05	0.00	0.581
	Orientation * depth + plot + (1|partial_n) + (1|date)	14	6006.85	5.80	0.577
	Null model	4	6857.08	856.03	0.261

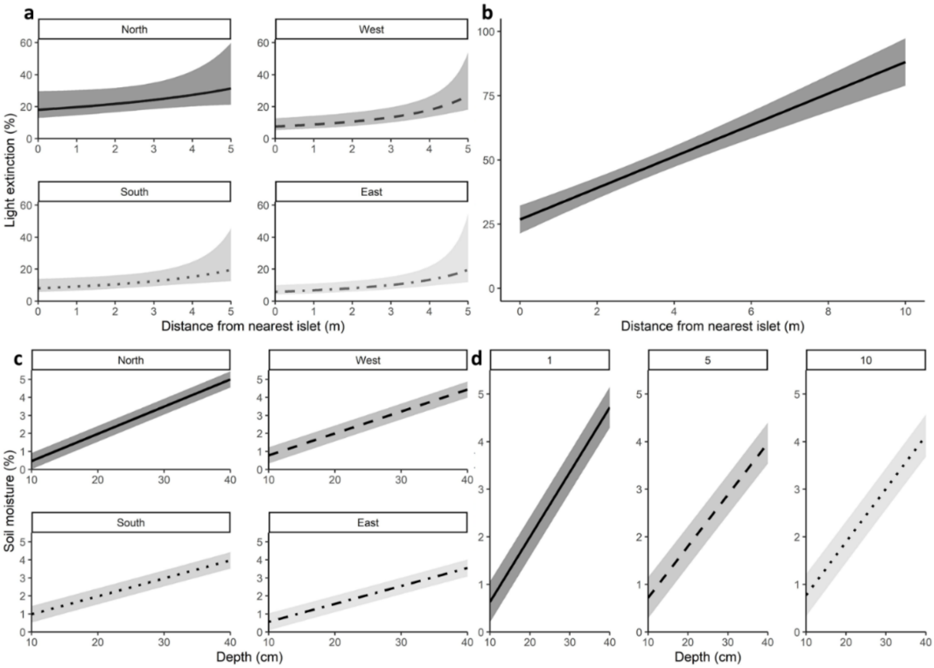

Figure 5.3. Predicted values of light extinction in (a) autumn 2015 in relation to orientation and distance form nearest islet, and in (b) spring 2016 in relation to distance. Soil moisture in relation to (c) orientation and depth and (d) distance and depth. Shaded areas represent the 95% confidence interval.

Herb biomass was similar inside and outside the herbivore exclusion cages and was unaffected by orientation or plot (**Table S5.2, Figure S5.7**). Herb biomass close to the points where soil moisture was measured increased with distance from nearest islet (**Table 5.3 c, Figure S5.8**).

Soil moisture was affected by the interaction between orientation and depth: it increased with depth, especially in the northern orientation. Soil moisture was also affected by the interaction between distance from nearest islet and depth, increasing with depth especially near the woodland islets, and the plot (**Table 5.3 d, Figure 3 c-d**).

Long-term natural regeneration

At 25 years after islet planting, 92 holm oak individuals taller than 5 cm had become established naturally near the islets (**Figure 5.4**). This resulted in a density of 103.3 oaks ha^{-1} in areas outside the islets, with an average establishment rate of 4.1 oaks ha^{-1} yr^{-1} on the islets since 1993 or 5.7 oaks ha^{-1} yr^{-1} since the oaks planted in the islets started to produce acorns at the age of seven years. Height, basal diameter and crown projected area of the established oaks averaged 67.2 ± 81.2 cm, 26.4 ± 46.4 mm and 0.90 ± 2.66 m2, respectively. The recruits were located an average of 6.8 ± 4.8 m to the closest islet, and each defined strip within different distance bins from the islets contained significantly different proportions of all recruits (χ^2_5 = 21.89, p < 0.001; **Figure S5.9**).

Figure 5.4. Positions of the 92 spontaneously established holm oaks taller than 5 cm in the experimental field.

Oak growth

At the last sampling in 14 March 2019, the 95 living seedlings that had emerged either at the seeding points or were naturally established were 9.1 ± 0.46 cm tall, with a basal diameter of 2.8 ± 0.18 mm and a crown projected area of 25.6 ± 1.95 cm^2. Their annual growth rate did not vary with orientation or distance from nearest islet (**Table S5.3 a**). In fact, the annual growth rate of the 92 naturally established individuals taller than 5 cm (0.34 ± 0.15 m^3 yr^{-1}) did not vary significantly with any variable analysed (**Table S5.3 b**).

5.4. Discussion

This study of natural oak regeneration from woodland islets planted 25 years ago shows that regeneration progresses slowly and is influenced by inter-annual climate variation and herbivory. It also provides evidence of "islet edge" effects that affect oak seedling emergence and early survival and that depend on orientation and distance from nearest islet.

Influence of inter-annual climate variation and microsite characteristics on seedling establishment

We observed marked inter-annual variation in seedling emergence and survival, suggesting an important role of climate variability on oak establishment, consistent with previous studies in Mediterranean old fields (Cruz-Alonso et al., 2019b). For instance, emergence was notably higher in 2015 (65.0%) than in 2014 (24.3%), mostly due to inter-annual climate differences in spring (H1). The spring of 2014 was particularly dry and hot, whereas spring precipitation in 2015 was close to the average for the period 2000-2018 (**Table 5.1, Figure S5.2**). Acorns seeded in 2015 were irrigated in spring to the same level as the historical mean spring precipitation. Our results are consistent with the fact that acorns are recalcitrant seeds (Villar-Salvador et al., 2013) and quite sensitive to spring drought, which hinders seedling emergence (Joët et al., 2013). In addition, holm oak is a masting species, and acorn production depends strongly on inter-annual weather variation (Bogdziewicz et al., 2017). Consequently, inter-annual climate variation can affect acorn availability and seedling emergence on particular years (**Figure S5.4**).

Seedling survival was higher in years in which both summer and spring were wet (**Table 5.1, Figure S5.2;** H1). Similar to emergence, survival after the first summer showed the trend 2015 > 2017 > 2014 > 2016 for seedlings that emerged from experimentally seeded acorns and for naturally emerged seedlings. Seedling survival was lower in the drier summers of 2014 and especially in that of 2016 than in the summers of 2015 and 2017, which were comparatively wetter (**Figure S5.2**). The spring of 2017 was drier than the spring of 2015, but the summer of 2017 was much wetter than the summer of 2015, suggesting that spring rainfall can be as critical as summer rainfall for oak survival in Mediterranean environments, as suggested by others (Castro, 2006). It is possible that seedlings that emerge in spring with average or above-average rainfall may be more drought-resistant than seedlings that emerge in a dry spring (Castro, 2006; Cuesta et al., 2010a; De Luis et al., 2008).

Woodland islets improved early performance of seedlings established in their proximity, but this effect depended on orientation. Emergence and survival decreased with distance from nearest islet in less sun-exposed orientations, especially the northern orientation (**Figure 1-2**). These results support H3 only in the most sun-exposed orientation. A similar pattern was shown by O’Donnell et al. (2020), who reported increased seedling emergence and survival up to 3 m from the forest edge. We observed the opposite trend in the most sun-exposed orientation, the southern orientation. This supports our H2 and implies that seedlings did not tolerate the combination of higher insolation and water competition from islets in the southern orientation.

The decrease in seedling establishment with distance from nearest islet and toward northern orientation was opposite to the trends observed for the development of herb community. The lower herb development reflected competition from islets in their proximity, in support of H3 and consistent with previous studies in other Mediterranean old-fields (Cuesta et al., 2010a; Rey-Benayas et al., 2005). This suggests that better early seedling performance close to islets in less sun-exposed orientations could be due, in part, to lower competition from herbs, an indication of indirect facilitation by the islets. Two results support this idea. First, herb biomass increased with distance from nearest islet, especially in less sun-exposed orientations; similarly, light extinction, a surrogate of herb biomass, increased with distance from nearest islet. Second, the herbivore-exclusion experiment (see section 2.5) demonstrated that the sparsity of herb vegetation in a strip surrounding the islets resulted from competition from islets rather than from herbivory. Low development of herbs close to islets in the less sun-exposed orientations may be due to shading by the islets during the winter and spring (Kunstler et al., 2006), as well as to allelopathy induced by ectomycorrhizal fungi associated with holm oak roots (Menta et al., 2014; Saitta et al., 2018).

Lower development of herb community and shading close to islets was associated with increased soil moisture in the northern and western orientations, mainly in the deepest soil layers (Rey Benayas et al., 2007, 2005, 2002). Higher soil moisture with depth, especially near woodland islets, may help explain the better early seedling performance in less sun-exposed orientations.

Notably, the spatial pattern of seedling survival relative to islets that was measured after experimental acorn seeding or in naturally emerged seedlings did not match the spatial distribution of naturally recruited holm oaks. Naturally recruited oak juveniles were more abundant at intermediate distances from nearest islet than close to the islets (**Figure S5.9**). Nevertheless, the variation in the proportion of naturally emerged seedlings with distance from the islet edge matched the pattern observed for juvenile oaks > 5 cm, which represent long-term recruitment (**Figure S5.4** and **S5.9**). This suggests that other main processes involved in the recruitment of oak seedlings are overriding the seedling survival. We can envisage at least three processes explaining the mismatch between the variation of survival and the proportion of naturally recruited oaks with distance from nearest islet. One is the pattern of acorn dispersal. Scatter-hoarders may prefer to cache their acorns at intermediate distances rather than close or far from islet edges (Gómez et al., 2019), where emergence and seedling survival would therefore be more likely. Consistent with this possibility, rodents disperse acorns a mean distance of 4-5 m (Morán-López et al., 2018; Pons and Pausas, 2007), close to the average distance of natural regeneration (6.8 m) observed in our study. A second one is acorn predation, which may be higher close to islet edges than in open areas (Villalobos et al., 2020). A third process that may counteract seedling survival is variation in the interaction between holm oak juveniles and herbs from negative to neutral along oak ontogeny, due to increased stress resistance of oak juveniles (Andivia et al., 2020; Cavender-Bares and Bazzaz, 2000).

Our results showed slow natural oak regeneration in old fields from planted woodland islets, despite the fact that islets provided acorns to accelerate secondary succession. This slowness presumably reflects high acorn predation at the study site, documented here and in a previous analysis (96.9% of unprotected acorns seeded in 2014 were predated; Rey-Benayas et al., 2015), as well as low seedling emergence and survival. The rate of natural establishment in our study was 4.1 oaks ha^{-1} yr^{-1} since plantation of the islets 25 years ago, and 5.7 oak ha^{-1} yr^{-1} in the 18 years since the oaks in the islets attained the ability to reproduce sexually. These rates are higher than recruitment rates reported for another Mediterranean old field near a forest edge without planted woodland islets (2 oaks ha^{-1} year^{-1}; Cruz-Alonso et al., 2019b), and similar to the rate of natural regeneration at a Mediterranean mountainous site after a major fire (4.1 oaks ha^{-1} year^{-1}; Leverkus et al., 2014). The differences and similarities among these various studies may depend on distances between the forest edge and open old fields, as well as on abundances of predators and acorn dispersers. Regardless of these variations across studies of forest regeneration, they make clear that such regeneration is a multi-decade process, even when assisted by woodland islets and even in forests of high primary productivity, such as tropical forests, which show recruitment rates of 100 seedlings ha^{-1} yr^{-1} (Holl et al., 2020, 2017).

Lessons to improve assisted natural forest regeneration using planted woodland islets

Our long-term experiments provide useful insights for assisting natural forest regeneration based on planted woodland islets. Despite acorn protection in our study, wild boars strongly predated in two of the four sowing years (**Figure S5.3 d**). The shelters used in 2017, which were specifically designed against ungulates (Reque and Martin, 2015), usually protect acorns from wild boar predation, but they actually destroyed some seeding points by excavating the soil and exposing acorns to the air. Wild boar damage probably reflected the increase in the local boar population (Massei et al., 2015), particularly after 2016 (unpublished data). Methods to protect acorns in direct acorn seeding projects need to be improved (Löf et al., 2019).

Another insight from our study is that shelters should be maintained during the early plant stages. Herbivory reduced early survival of holm oak seedlings: thus, survival was substantially higher for seedlings protected with wire shelters than for unprotected seedlings. On the other hand, survival was higher nearer rather than farther from the islets, even though rabbits built their burrows under the islets to take advantage of oak roots. The apparent lack of a distance effect on herbivory may reflect that the home range of rabbits is larger than the distances between islets in our study site (Lombardi et al., 2007). Future studies should clarify the interaction of herbivory and distance from woodland islets by using larger plots and increasing the distance between planted islets.

The low oak colonization of the abandoned field matrix from planted woodland islets and the fact that islets did not grow beyond their original size of 100 m^2 (data not shown) at the study site may argue against using woodland islets to restore old fields in dry Mediterranean climate regions and other low-productivity environments. However, we believe that certain interventions can accelerate natural regeneration based on planted and natural woodland islets. Rather than planting mono-specific islets of only one slow-growing, late successional tree species such as oaks, we suggest planting multi-specific islets that are more attractive to a greater richness of dispersers, including species of shrubs or trees with fleshy fruits (Martínez and García, 2017; Martínez-López et al., 2019). Some shrub species such as *Retama sphaerocarpa* (L.) and fleshy fruit species colonise old fields faster than oaks and can facilitate oak establishment at latter stages (Cruz-Alonso et al., 2019b; Debussche and Lepart, 1992). Additionally, shrub species can be planted around the islets to act as “nurse shrubs” that facilitate recruitment of later successional species (Andivia et al., 2017; Cruz-Alonso et al., 2019b; Gómez-Aparicio et al., 2008). Conserving isolated nesting trees or placing new nesting sites for seed dispersers such as the magpie inside the old fields and near islets can increase seed arrival and consequently recruitment (Martínez-Baroja et al., under review).

5.5. Conclusion

Plantation of oak woodland islets can provide acorns for forest restoration, but the success of this approach depends on inter-annual climate variation. In our study, wet springs were especially important for enhancing emergence and first summer survival of seedlings. Emergence and seedling survival were higher nearer rather than farther from the islet edges in less sun-exposed orientations, whereas the opposite was observed in the most sun-exposed orientation. The herb community was less developed closer to the islets than farther away, which may reflect competition from islets that indirectly facilitates seedling emergence and survival. The pattern of seedling survival with distance from nearest islet did not match the distance profile of naturally regenerated oak juveniles, suggesting that other drivers of oak recruitment such as acorn dispersal, acorn predation and competition between oak seedlings and herbs could override the effect of seedling survival. This study may help increase the effectiveness of woodland islet plantation for restoring Mediterranean old fields and other areas with harsh climates.

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5.8. Supporting information:

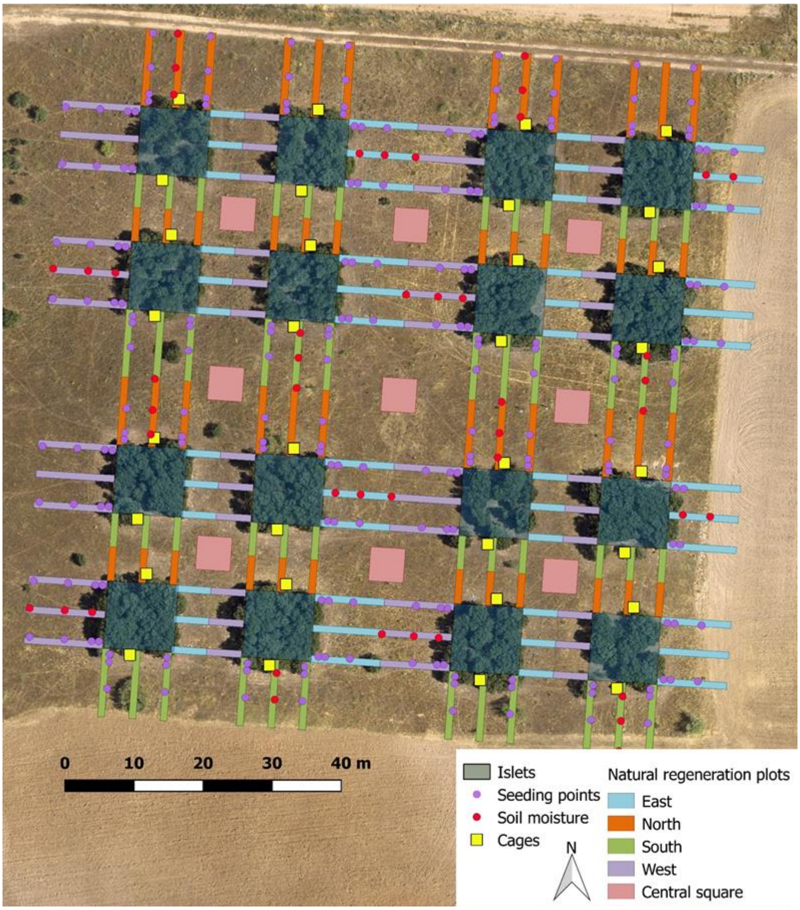

Figure S5.1. Design of the seeding experiments performed in 2015-2017, and of the sampling of early naturally established oak seedlings during 2014-2017. The figure shows the location of (1) acorn seeding points (purple dots, n = 222) placed along transects 10-m long in each corner of every group of four woodland islets (plots) at 0, 1, 5 and 10 m from the islet edge. At these points, we assessed seedling emergence and survival and light extinction in the herb community. (2) The 192 rectangular plots and nine square plots between the islets or between the islets and nearby active crop fields, where the emergence and survival of naturally regenerated seedlings were monitored. (3) The 45 points where soil moisture and herb biomass were measured (red dots). (4) The 32 cages used to exclude herbivores from predating the herb community (yellow squares). This picture was taken on 17 June 2014, after the surrounding crops had been tilled, using a visible-light camera with spatial resolution of 2 x 2 cm attached to a drone.

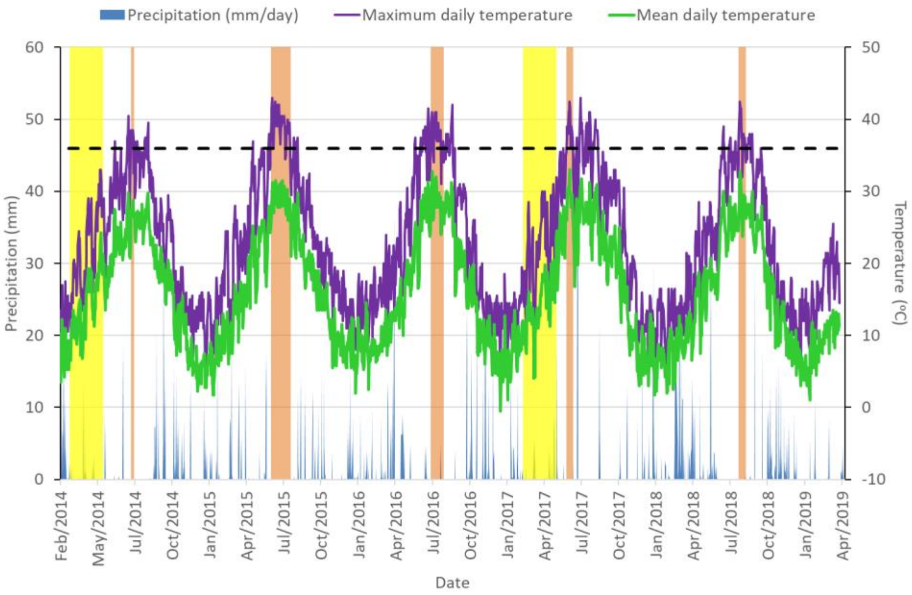

Figure S5.2. Precipitation and temperature registered at the climate station of the study site during the study period. The dashed line indicates the 36 ºC threshold that was used to quantify the number of hot days and the length of heatwaves. Yellow bands indicate dry and hot springs, which occurred between Feb 24 and May 14. The width of brown bars corresponds to heatwave length.

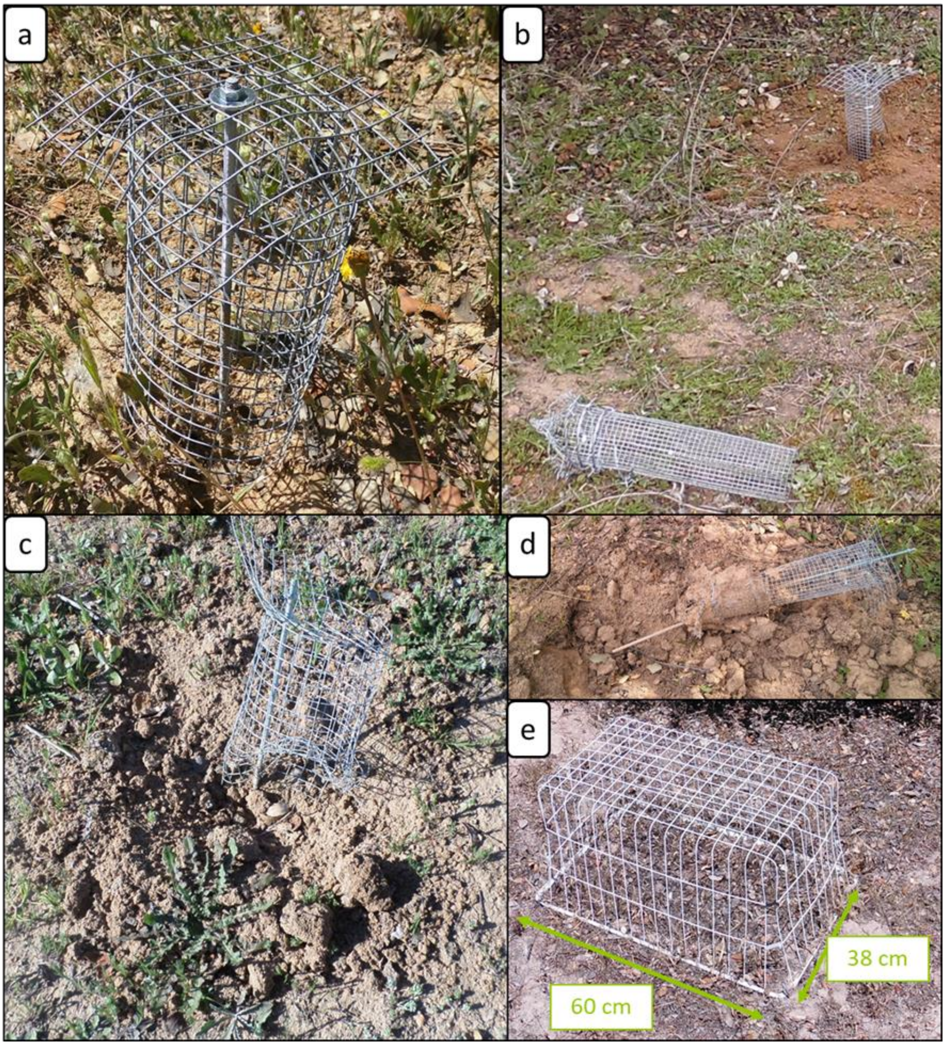

Figure S5.3. (a) Wire shelters used to protect acorns sown in 2014, 2015 and 2016. (b) Wire shelters against wild boars used in 2017, modified from the original design by Reque and Martin (2015). (c-d) Examples of seeding points destroyed by wild boars in (c) 2016 and (d) 2017. The wild boars could not eat the acorns with the shelters used in 2017, but some shelters were disturbed, and acorns were exposed to the air and dried up. (e) Wire cage used to assess the effect of herbivory, chiefly by rabbits, on herb biomass at the edge of woodland islets.

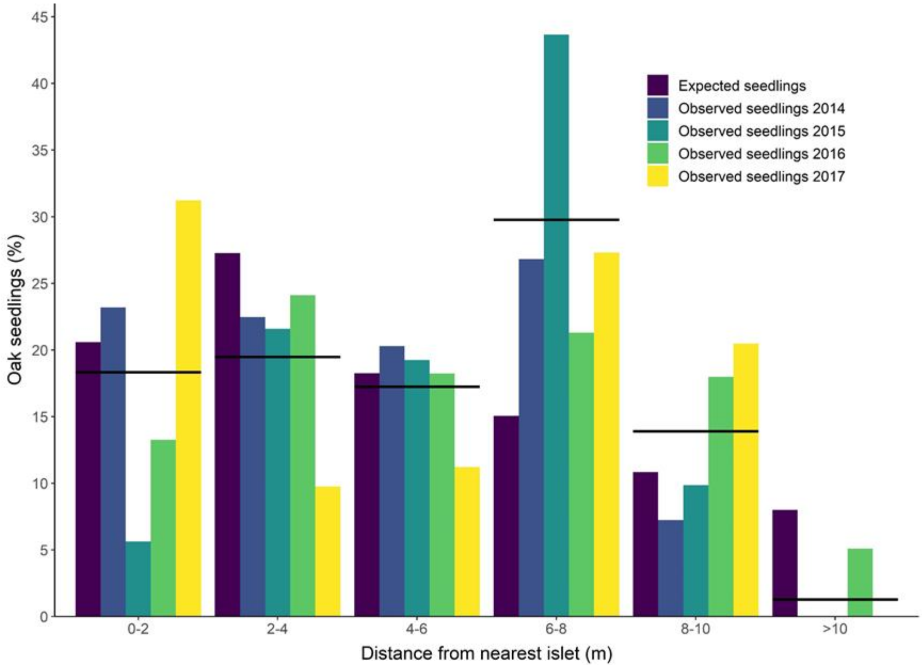

Figure S5.4. Distribution of naturally emerged oak seedlings during the 2014 to 2017 period along a distance gradient from the woodland islet edge. The numbers of emerged seedlings each year was 28 in 2014, 40 in 2015, 152 in 2016, and 42 in 2017. Black lines represent the mean proportion of observed seedlings in all study years in each distance category. The expected proportion of oak seedlings was calculated after taking into account the proportion of area covered by each distance bin from the islet edge.

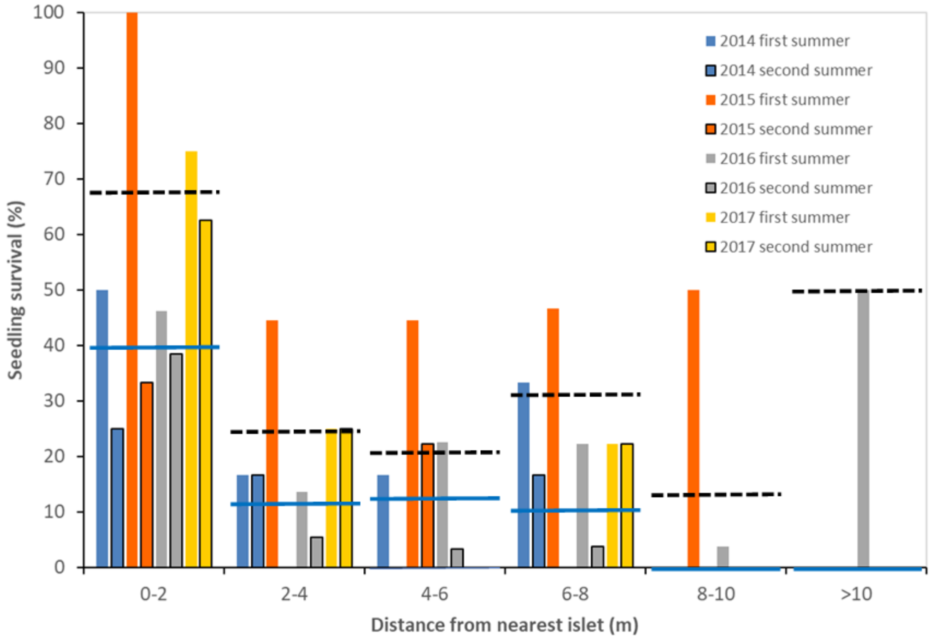

Figure S5.5. Survival of naturally established seedlings at the end of the first and second summers. The numbers of seedlings alive at the end of the first summer were 8 in 2014, 20 in 2015, 33 in 2016, and 15 in 2017. Black dashed and blue solid lines represent mean survival after the first and second summers, respectively, by distance category across the entire period 2014-2017.

Table S5.1. Selection of models to test the effect of plant protection against herbivores on seedling mortality after the second summer, based on seedlings that emerged from acorn seeding in 2015.Tested initial model: seedling survival ~ orientation * distance + distance * shelter + plot. Selected final model and its parameters are shown in **bold**.

Model parameters	df	AICc	ΔAICc	R^2
Orientation + distance + shelter	**6**	**87.80**	**0.00**	**0.318**
Orientation * distance + shelter	9	88.71	0.91	0.366
Orientation + distance * shelter	7	89.42	1.62	0.324
Orientation * distance + plot + shelter	12	89.70	1.89	0.414
Orientation + distance + plot + shelter	9	90.59	2.78	0.352
Null model	1	110.56	22.75	0.000

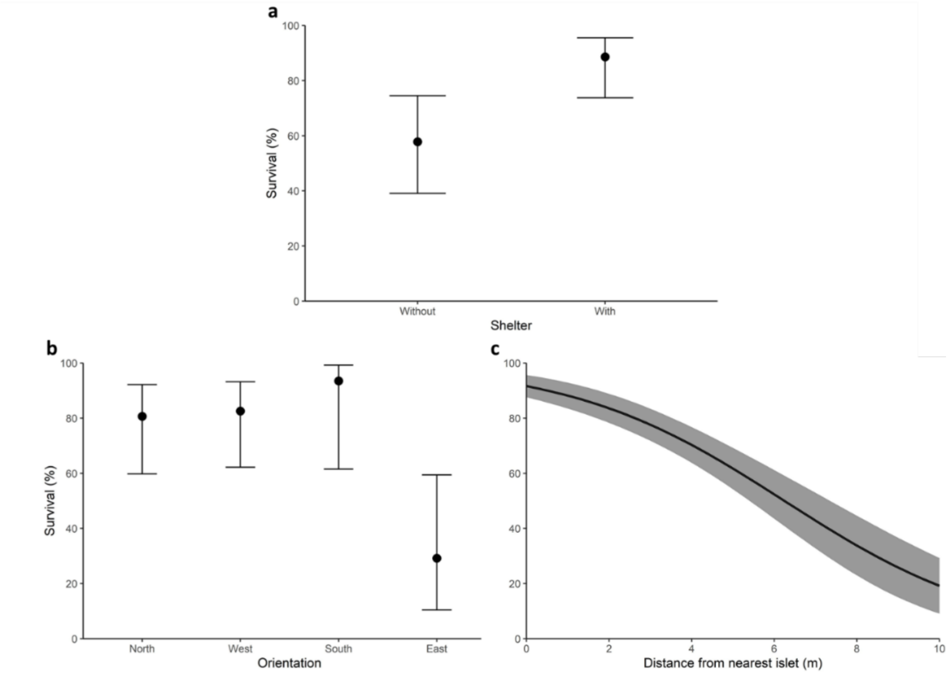

Figure S5.6. Predicted values of survival after the second summer in seedlings emerged from seeding points in 2015 in relation to (a) the presence of shelter against herbivores, (b) orientation relative to the islet, and (c) distance from the closest islet edge. Shaded area represents the 95% confidence interval.

Table S5.2. Selection of models to test the effect of herbivore exclusion on herb biomass. Tested initial model: herb biomass ~ orientation * exclusion + plot. Selected final model and its parameters are shown in **bold**.

Model parameters	df	AICc	ΔAICc	R^2
Exclusion + plot	6	377.051	0	0.156
Plot	5	377.803	0.75	0.113
Exclusion	3	378.036	0.99	0.043
Null model	**2**	**378.655**	**1.60**	**0**
Orientation * Exclusion + plot	8	378.968	1.92	0.198
Orientation + Exclusion + plot	7	379.142	2.09	0.162

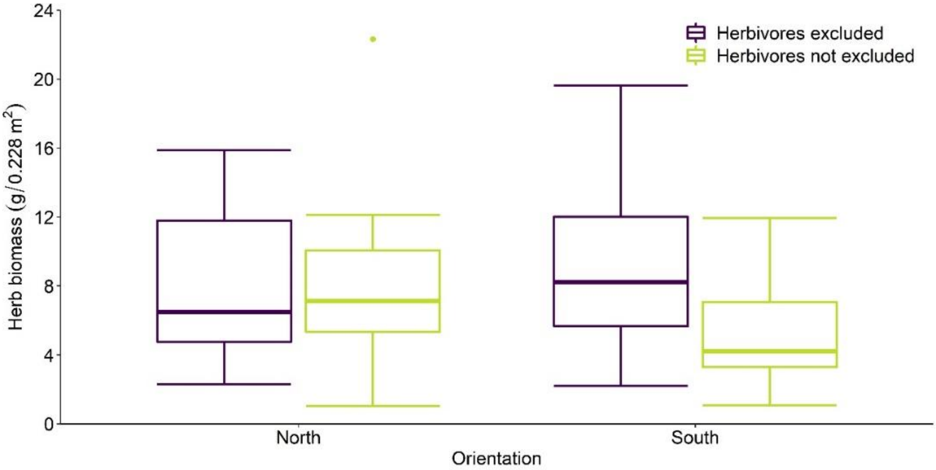

Figure S5.7. Differences in herb biomass at the islet edge due to herbivore exclusion and orientation with respect to the woodland islet.

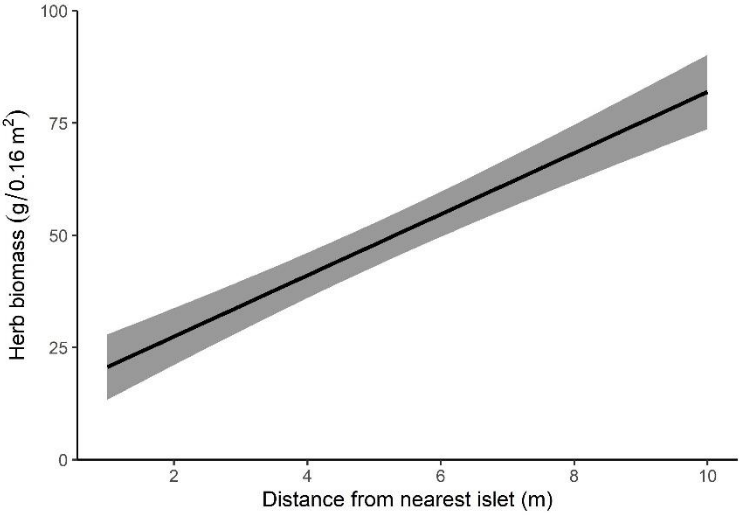

Figure S5.8. Predicted herb biomass with distance from the nearest islet. Herb biomass was measured near the 45 points where soil moisture was measured in May 2016. Shaded area represents the 95% confidence interval.

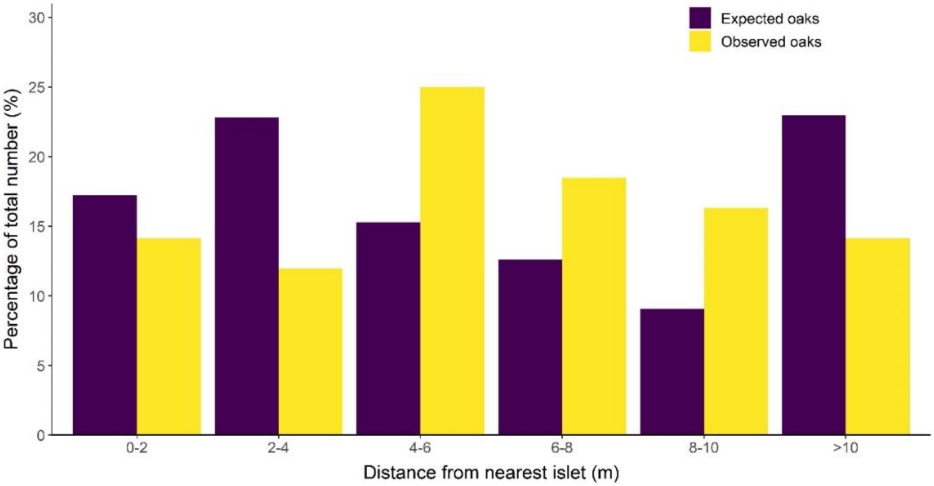

Figure S5.9. Proportion of the 92 juvenile oaks > 5 cm in height established at different class distances from the closest woodland islet. The expected number of oaks were calculated considering the proportion of area covered by each distance band from the islet edge.

Table S5.3. Selection of models to test the annual growth rate (AGR) of seedlings (emerged both from experimentally seeding and natural regeneration during 2014-2017) or juveniles (natural regeneration after 25 years). Tested initial model for seedlings: AGR ~ Orientation * distance + origin + plot + year. Tested initial model for juveniles: AGR ~ Orientation * distance + plot. Selected final model and its parameters are shown in **bold**.

	Model parameters	df	AICc	ΔAICc	R^2
(a) Seedlings	**Null model**	**2**	**828.99**	**0**	**0**
	Distance	3	829.05	0.06	0.028
	Orientation	5	829.95	0.96	0.074
	Orientation + distance	6	831.188	2.2	0.087
(b) Juveniles	**Null model**	**2**	**285.93**	**0**	**0**
	Orientation	5	287.17	1.24	0.063
	Distance	3	287.77	1.84	0.004
	Orientation + distance	6	288.88	2.95	0.07

Imágenes de arriba a abajo y de izquierda a derecha:

Vista general de la finca El Carmen en la que se observa tanto el bosquete como una zona arada dentro de ese bosquete
Encina con bellotas
Detalle de dos bellotas
Urraca cogiendo una bellota de encina
Urraca anillada con bellota en el pico en el suelo
Plántula de encina reclutada marcada para el seguimiento
Vista general de los islotes forestales en la finca La Higueruela del CSIC (Santa Olalla, Toledo)
Fuente de las imágenes: L. Martínez-Baroja y grupo de investigación SERAVI

Capítulo 6

Discusión general:

El **objetivo general** de esta Tesis Doctoral fue evaluar el efecto de la dispersión de bellotas por urracas (**Capítulos 2 y 3**) y de algunas etapas post-dispersivas, como la emergencia y la supervivencia de las plántulas (**Capítulos 4 y 5**), que determinan el reclutamiento natural de las encinas en campos agrícolas abandonados en ambientes mediterráneos. Para ello hemos analizado algunos de los factores determinantes de la regeneración de las encinas que actúan en esas etapas dispersivas y post-dispersivas del reclutamiento. Los resultados de esta Tesis Doctoral pueden contribuir a diseñar actuaciones que mejoren y aceleren la restauración de campos agrícolas abandonados en ambientes mediterráneos.

A continuación, se discuten transversalmente los principales resultados de los capítulos de investigación (**Tabla 6.1**) para tener una perspectiva global de los fenómenos y procesos investigados, identificar las aplicaciones principales del conocimiento generado y proponer futuras líneas de investigación. Se trata de poner en valor la importancia de las actuaciones de restauración para establecer fuentes de semillas, fomentar las interacciones planta-animal dispersor y proveer sitios adecuados para las semillas para la restauración de los campos agrícolas abandonados en ambientes mediterráneos.

Tabla 6.1. Hipótesis y resultados principales de los capítulos de investigación de la Tesis Doctoral. ✓ Se cumple la hipótesis de partida. ≈ Se cumple parcialmente la hipótesis de partida.

Capítulo	Título	Hipótesis		Resultados principales
2	Massive and effective acorn dispersal into agroforestry systems by an overlooked vector, the Eurasian magpie (*Pica pica*) (Martínez-Baroja et al., 2019)	1. Las urracas son dispersoras masivas de bellotas a distancias relativamente largas (decenas de metros).	✓	Las urracas retiraron más de la mitad de la producción anual de bellotas de los árboles. Un individuo puede remover hasta 1500 bellotas en 6 semanas. La mayoría de las bellotas removidas (86%) fueron almacenadas individualmente en el suelo con distancias de dispersión entre 1,4 y 210 m.
		2. El estatus reproductor y el sexo de los individuos determinan la capacidad de dispersión de bellotas.	✓	Los individuos reproductores fueron los que removieron más bellotas (169–1372 bellotas). Los juveniles tuvieron un papel marginal. Los machos removieron casi el doble de bellotas (219-1595) que las hembras (197-747).
		3. Las urracas son dispersoras efectivas de bellotas.	✓	El 0,6-2,4% de las bellotas escondidas acabaron en plántulas emergidas, lo que produjo una alta densidad de plántulas a principios de verano (56–439 plántulas/ha).
3	Caching territoriality and site preferences by a scatter-hoarder drive the spatial pattern of seed dispersal and affect seedling emergence (Martínez-Baroja et al., en segunda revisión en *Journal of Ecology*)	1. Existencia de territorios de almacenamiento.	✓	Las parejas reproductoras almacenaron las bellotas dentro de sus territorios.
		2.Las urracas tienen preferencias espaciales para esconder bellotas a distintas escalas espaciales.	✓	Independientemente de la distancia al comedero las urracas seleccionaron las zonas aradas más que la plantación forestal y más que el herbazal. Dentro de la plantación seleccionaron las zonas más productivas. Seleccionaron los micrositios (estructuras hechas por animales como escarbaduras) y los materiales menos comunes.
		3. La preferencia espacial para esconder bellotas se corresponde con diferencias de densidad de plántulas emergidas.	✓	La densidad de plántulas emergidas está correlacionada con el patrón espacial de la dispersión de bellotas en los hábitats.

Capítulo	Título	Hipótesis		Resultados principales
4	Predation and aridity slow down the spread of 21-year-old planted woodland islets in restored Mediterranean farmland (Rey-Benayas et al., 2015)	1. Alta depredación de las bellotas sembradas sin protector.	✓	El 96,9% de las bellotas sin protector fueron depredadas.
		2. Mayor emergencia de plántulas en las orientaciones con menor insolación.	✓	La emergencia fue mayor en el lado norte (42,9%) que en el lado sur (13,2%) de los islotes forestales.
		3. Alta depredación de las plántulas sin protector.	✓	Todas las plántulas emergidas a las que se les quitó el protector fueron depredadas.
5	Drivers of oak establishment from 25-year-old woodland islets planted to assist natural regeneration in Mediterranean old fields (Martínez-Baroja et al., en revisión en *Forest Ecology & Management*)	1. La emergencia y la supervivencia de plántulas es mayor en años con primaveras húmedas y veranos suaves.	✓	Marcada variación interanual en la emergencia y supervivencia. Las primaveras lluviosas incrementan ambos procesos. La supervivencia se incrementa más si la primavera lluviosa es seguida por veranos también lluviosos.
		2. La emergencia y la supervivencia de plántulas es mayor en las orientaciones de los islotes forestales menos expuestas a la insolación.	✓	La emergencia y la supervivencia es mayor en orientaciones menos expuestas a la insolación (norte y oeste).
		3. La competencia de los islotes, teniendo en cuenta la distancia y la herbivoría, reducen la emergencia y la supervivencia de las plántulas y el crecimiento de la hierba cerca de los islotes.	≈	En las orientaciones menos expuestas a la insolación, la emergencia y la supervivencia fue mayor cerca de los islotes, al contrario de lo que ocurrió en las más expuestas. Este patrón no coincidió con la distribución de la abundancia de juveniles establecidos espontáneamente. La menor presencia de herbáceas se debe a la competencia de los islotes, pero no a la herbivoría.

6.1. El desconocido papel de la urraca como dispersora de bellotas

Nuestros resultados han demostrado que la urraca es una **dispersora masiva y efectiva** de bellotas de encina en campos agrícolas abandonados mediterráneos (**Capítulo 2**). También evidenciamos que dispersa bellotas de quejigo. A pesar del solapamiento de las distribuciones de las quercíneas y las urracas en Eurasia (**Figure 2.6**) y de los indicios de la dispersión de bellotas de otras quercíneas (Waite, 1985; Clarkson et al., 1986; Birkhead, 1991; den Ouden et al., 2005), hasta esta Tesis Doctoral no se había evaluado la capacidad de las urracas como dispersoras de bellotas. Hemos observado que algunas urracas pueden dispersar hasta 1.300 bellotas en 6 semanas con distancias de dispersión desde 1,4 m hasta 210 m y con grandes diferencias entre individuos según su estatus reproductor y sexo. La población de urracas esconde más de la mitad de la producción anual de bellotas de encina en el sistema estudiado, lo que la sitúa cerca del nivel de otros grandes dispersores de bellotas mejor conocidos como son el arrendajo euroasiático (*Garrulus glandarius*) o ciertas especies de córvidos americanos como los arrendajos azules (*Aphelocoma coerulescens* y *A. insularis*) (Bossema, 1979; DeGange et al., 1989; Pesendorfer, Sillett, Morrison, et al., 2016).

La eficacia de la dispersión, entendida como la emergencia de plántulas a partir de las bellotas escondidas por urraca, es baja en nuestro sistema (2%), debido en gran medida a la depredación de bellotas por el conejo. La importancia de la depredación post-dispersiva de bellotas también se evidenció experimentalmente en la parcela de los islotes de encina (**Capítulos 4 y 5**). Esto no resta mérito a la urraca como dispersora efectiva de bellotas. Gómez et al. (2019) sostienen que la capacidad dispersora debe ser evaluada independientemente del devenir final de la bellota dispersada, es decir, independientemente del contexto del dispersor. La densidad de plántulas recién emergidas fue media o alta dependiendo de los años y los hábitats. Sin embargo, en nuestro contexto de alta densidad de conejos y aridez ninguna plántula sobrevivió al año siguiente.

Hemos demostrado también que la urraca establece un **territorio de almacenamiento** para esconder las bellotas que dispersa (**Capítulo 3**). Este territorio tiene límites claros, que coinciden bien con la mediatriz de la línea entre los nidos más cercanos, y aparentemente sin solapamiento con territorios vecinos. Otros autores han sugerido que la urraca esconde alimentos en sus territorios de nidificación (Clarkson et al., 1986; Birkhead, 1991), pero nosotros hemos demostrado que el territorio de almacenamiento establecido por la urraca en otoño e invierno condiciona la posición del nido en la primavera siguiente. Todo esto señala el papel multipropósito que el territorio tiene en esta especie. Otras evidencias refuerzan esta idea: las parejas reproductoras de urraca fueron los individuos que se llevaron la mayoría de las bellotas de los comederos del territorio y ambos miembros de la pareja esconden bellotas respetando dichos límites territoriales (**Capítulo 3**). Además, el 10% de las bellotas que se escondieron fuera de los territorios (**Capítulo 3**) coincide con el mismo porcentaje de las bellotas que se llevaron los individuos que no pertenecían al nido del territorio en el que se instaló el comedero (**Capítulo 2**). Esto sugiere que las urracas esconden dentro de sus territorios también las bellotas que “roban” en otros territorios, como se confirma en el experimento con individuos de urraca anillados (**Capítulo 3**, **Figure S3.4**).

La urraca podría ser crucial en la expansión de las encinas hacia campos agrícolas abandonados por la **selección espacial** para almacenar las bellotas dispersadas (**Capítulo 3**). Los territorios limitan las preferencias espaciales a distintas escalas (hábitat, sub-hábitat y micrositio). Dentro de los territorios, cuando la urraca puede elegir, prefiere dispersar las bellotas en zonas aradas antes que en las plantaciones de leñosas, mostrando baja preferencia por los herbazales, lo que podría ser una respuesta relacionada con la compactación del suelo. Este comportamiento, junto con una gestión adecuada (ver el apartado 6.5), contribuirían a la densificación de las plantaciones o a la colonización de campos de cultivo abandonados en función de dónde se realice el arado del suelo.

Creemos que **cambiar la visión negativa** sobre esta especie de ave por parte de algunos sectores de la población (Madden et al., 2015) sería beneficioso para fortalecer esta interacción planta-animal que puede ayudar a la restauración forestal de los campos agrícolas abandonados (**Capítulos 2 y 3**). Este beneficio para la regeneración forestal se ha demostrado e incluso cuantificado económicamente con otras especies de córvidos dispersores de bellotas (Hougner et al., 2006; Pesendorfer, Sillett, Koenig, et al., 2016). Teniendo en cuenta el papel de la urraca como “sembradora de bosques de quercíneas” por la dispersión masiva y efectiva de bellotas, la amplia y solapada distribución de las urracas y las quercíneas y el escenario de abandono agrícola actual en Europa (Navarro y Pereira, 2012; FAO, 2020) y el hecho de que parece ser una dispersora facultativa de frutos carnosos (Martínez-López et al., 2019), parece justificado cambiar esta visión hacia una más positiva, como proveedor de un servicio ecosistémico relevante.

6.2. La importancia del destino de las bellotas en las etapas post-dispersivas del ciclo de regeneración de las encinas

La **depredación de las bellotas** ha demostrado ser uno de los factores limitantes más determinantes en el reclutamiento de encinas en campos agrícolas abandonados en ambientes mediterráneos. La mayoría de las bellotas sembradas sin proteger fueron retiradas de los puntos de siembra o depredadas *in situ* (**Capítulo 4**). Incluso muchas de las bellotas protegidas resultaron afectadas por los jabalíes que depredaron las bellotas protegidas u hozaron alrededor de los puntos de siembra, lo que desenterró y desecó las bellotas limitando la emergencia de las plántulas (**Capítulo 5**). Otro resultado que apoya esta limitación de la depredación de bellotas fue la baja tasa de emergencia anual de las bellotas dispersadas por las urracas, que varió entre el 0,6 y el 2,4 % (**Capítulo 2**). Estas bellotas también fueron depredadas en el sitio en el que las escondieron las urracas, pero es posible que otra fracción fuera trasladada a otros lugares por las urracas u otros animales y depredadas o escondidas de nuevo (Emery y Clayton, 2001; Wang et al., 2019). Este tipo de dispersión que realizan los animales desde el lugar en el que se dispersaron inicialmente se denomina dispersión secundaria (Gómez et al., 2019), y es uno de los grandes procesos desconocidos en los estudios de dispersión con córvidos. Unas tasas altas de dispersión secundaria podrían incrementar la distancia o desdibujar el patrón espacial de dispersión mostrado en esta Tesis, dependiendo también de si el dispersor secundario es otra especie dispersora, otra urraca de un territorio vecino o la pareja de urracas del territorio.

Otro de los cuellos de botella del reclutamiento de encinas en campos agrícolas abandonados en ambientes mediterráneos es la **depredación de las plántulas**. El 35% de las plántulas que emergieron de manera espontánea y todas las plántulas a las que se les quitaron los protectores durante el primer año fueron depredadas

(**Capítulo 4**). La supervivencia de las plántulas a las que se les retiró el protector fue un 26% menor por la depredación que a las que no se les retiró el protector (**Capítulo 5**). Además, hay que destacar que en el área de estudio donde se realizaron los experimentos de dispersión, las plántulas emergidas no sobrevivieron al año siguiente, posiblemente por la depredación de la densa población de conejos (**Capítulo 2**). Por estas razones tanto la depredación de las bellotas como la de las plántulas depende del contexto, por lo que la cantidad de depredadores de unas y otras en cada lugar limitan en mayor o menor medida el reclutamiento de quercíneas pudiendo llegar a bloquearlo (Pesendorfer, Sillett, Morrison, et al., 2016).

Como se ha mostrado en esta Tesis, **el micrositio al que llegan las bellotas es esencial en las etapas iniciales del reclutamiento de encinas** por la competencia con la vegetación tanto herbácea como leñosa (Cuesta et al., 2010; Morán-López et al., 2018; Gavinet et al., 2020), por el efecto facilitador de la sombra sobre las nuevas plántulas (Pérez-Ramos et al., 2013) y por la protección frente a la herbivoría (Gómez-Aparicio et al., 2008). En nuestro caso, las diferentes características del micrositio se han analizado a través de las diferencias respecto a la orientación y la distancia a los islotes forestales plantados que afectaron a la emergencia y la supervivencia de las nuevas plántulas (**Capítulos 4 y 5**). En los lugares con menor insolación, tanto la emergencia como la supervivencia fue mayor y decreció con la distancia a los islotes forestales plantados. Sin embargo, en la orientación con mayor insolación, ambas aumentaron con la distancia y el reclutamiento de juveniles fue mayor a distancias intermedias. Estos resultados sugieren que las condiciones estresantes ligadas a una alta insolación junto con la competencia de los islotes forestales, demostrada experimentalmente por la disminución del desarrollo de la comunidad herbácea cerca de los mismos, limitan la supervivencia de las nuevas encinas.

La **variabilidad climática interanual** propia de climas mediterráneos también resultó determinante en las tasas de emergencia y supervivencia de plántulas a lo largo de los años de estudio (**Capítulo 5**), como se ha observado previamente en otros estudios en ambientes mediterráneos (Castro, 2006; De Luis et al., 2008; Cuesta et al., 2010; Cruz-Alonso et al., 2019). Las primaveras secas disminuyeron la tasa de emergencia de plántulas y estas plántulas mostraron una baja supervivencia estival, independientemente de la intensidad de la aridez del verano, lo que sugiere que las plántulas nacidas en primaveras secas son menos resistentes a la sequía estival.

Los islotes de encinas plantados hace 25 años han permitido sortear la falta de propágulos, una limitación clave para la regeneración de encinares en campos agrícolas abandonados. La **provisión de bellotas** por los islotes ha resultado en tasas de reclutamiento de hasta 5,7 encinas ha^{-1} año^{-1}. Esta tasa resulta baja comparándola con otros ecosistemas más productivos como los tropicales en los que las tasas de reclutamiento de leñosas pueden ser mayores de 100 plantas ha^{-1} año^{-1} (Holl et al., 2020). Sin embargo, en el contexto mediterráneo, se trata de una tasa relativamente elevada si se compara con los datos reportados por otros autores, que varían entre 2 y 4,1 encinas ha^{-1} año^{-1} (Leverkus et al., 2014; Cruz-Alonso et al., 2019). No obstante, hay que tener en cuenta que la superficie del área abarcada en esos estudios, que afecta a la distancia a las fuentes de bellotas, fue manifiestamente mayor que la de nuestra zona de estudio (1 ha).

6.3. Los beneficios conjuntos de la dispersión de bellotas por urracas y los islotes forestales

Las plantaciones de islotes forestales podrían ser beneficiosas para la **conectividad de la comunidad de animales dispersores de semillas** y, a través del servicio de dispersión que prestan estos animales, influir en el reclutamiento de juveniles y la regeneración del bosque en campos agrícolas abandonados mediterráneos (Manning et al., 2006; Martínez y García, 2017; Martínez-López et al., 2019). En zonas de bosques tropicales húmedos, los islotes forestales tienen una abundancia de dispersores de semillas grandes y de aves frugívoras similar al de las plantaciones convencionales. Esto resultó en una abundancia y riqueza de especies vegetales dispersadas por esos animales y en un reclutamiento de plántulas similar para ambas estrategias de revegetación (Holl et al., 2020). Es decir, con una inversión económica menor dirigida a proporcionar las fuentes de semillas por medio de islotes forestales plantados allí donde no existen parches forestales remanentes, se podrían obtener unos resultados similares de restauración forestal de los campos agrícolas abandonados que con las estrategias convencionales de restauración reconstructiva (**Capítulo 1, Figura 1.2**).

Los islotes forestales de encina proporcionan **estructuras adecuadas para la nidificación**. En la finca La Higueruela se han observado en las encinas de los islotes forestales nidos de urracas. De igual modo, en la finca El Carmen, el 49% de los nidos de urraca se construyeron sobre encinas. Los nidos son necesarios para el establecimiento de territorios multipropósito (nidificación, alimentación y almacenamiento) por las urracas. Utilizando como referencia el patrón espacial y la distancia de dispersión de las bellotas (entre 1,4 y 210 m, 118 m considerando solo las dispersiones dentro del territorio de la fuente de bellotas, **Capítulo 3**) así como la distancia entre nidos vecinos (media = 60,1 m, rango = 15,1 – 276,8 m) observada en esta Tesis, se podrían espaciar los islotes forestales alrededor de 250 m en una distribución regular, que corresponde aproximadamente con la distancia máxima entre nidos vecinos tratando de reducir la competencia por los recursos. Hay que tener en cuenta que la densidad de urracas en nuestra zona de estudio era muy alta, por lo que esta distancia podría aumentarse con densidades menores. De esta manera se optimizaría el área de dispersión de bellotas por urracas: 1) por su reducido tamaño cada islote albergaría solo un nido de urraca; 2) este sería el centro de su territorio de almacenamiento rodeado por campo de cultivo abandonado; 3) maximizaría el área de dispersión de cada pareja reproductora evitando conflictos territoriales; y 4) toda la superficie de campos de cultivos sería susceptible de albergar dispersiones, debido a que la mediatriz entre islotes vecinos estaría a 125 m de cada islote, siendo esta distancia aproximadamente igual a la distancia máxima de dispersión observada dentro del territorio (118m).

6.4. Aplicaciones para la restauración forestal de campos agrícolas abandonados

Del conocimiento generado por esta Tesis doctoral, hemos aprendido las siguientes lecciones prácticas para la restauración forestal de campos agrícolas abandonados.

1. **Fomentar las poblaciones de urracas** para maximizar su papel como “sembradoras de quercíneas”. Mediante el establecimiento de árboles aislados o islotes forestales de quercíneas o de otras especies, pero cercanos a otras quercíneas, se podría favorecer la nidificación y por lo tanto el establecimiento de territorios multipropósito que son usados como

territorios de almacenamiento en los que las urracas dispersan las bellotas. También pueden instalarse estructuras o aprovechar las ya existentes con diseños que faciliten su nidificación (por ejemplo, las urracas nidifican habitualmente en ciertos tipos de torretas eléctricas en campos de cultivos deforestados). En los lugares en los que ya existen urracas, habría que mantener o promover sus poblaciones, así como divulgar el servicio ecosistémico que brindan para el hombre, además de prohibir su captura como se hace en numerosos cotos de caza.

2. **Instalar comederos** adecuados para las urracas y que eviten el acceso a animales terrestres depredadores de bellotas, como los ratones y los conejos (Gómez et al., 2003, 2019), con las bellotas y frutos de otras plantas que se deseen establecer (Homet-Gutiérrez et al., 2015; Castro et al., 2017; Martínez-López et al., 2019), puede asistir y acelerar la restauración de los campos agrícolas abandonados. Este tipo de acciones se ha utilizado con éxito en Brasil con animales frugívoros en lugares donde la falta de semillas o la escasez de dispersores limita la regeneración forestal (Silva et al., 2020). A priori se trata de una actuación de bajo coste comparada con otras técnicas de restauración activa habituales como las plantaciones, aunque, al mismo tiempo, habría que analizar la relación coste/efectividad de estas medidas para valorar su eficacia.

3. **Arar los campos agrícolas antes del abandono** podría ser una buena práctica para favorecer la llegada de nuevos propágulos puesto que las urracas seleccionaron con mucha intensidad las zonas aradas para dispersar las bellotas (**Capítulo 3**). Otra opción, con la que se reducirían costes, es arar solo algunas zonas, en lugar de los campos abandonados completos. Para optimizar y enfocar esta actuación de manera adecuada, el estudio de las zonas aradas a distintas distancias, posiciones, etc., propuesto en la sección de futuras líneas de investigación, supondría un salto cualitativo importante para optimizar las dimensiones y las posiciones más adecuadas de esas zonas aradas.

4. **Controlar las densidades de conejos**, que depredan tanto las bellotas como las plántulas (Zamora et al., 1985; Leiva y Fernández-Alés, 2003), **y de**

jabalíes, que depredan principalmente las bellotas pero también dañan las plántulas (Gómez y Hódar, 2008), puede tener efectos positivos en el reclutamiento de encinas en los campos agrícolas abandonados en ambientes mediterráneos. Se ha observado que el éxito en el reclutamiento de las encinas es dependiente del contexto dado que los depredadores afectan distintas fases del ciclo de regeneración. Teniendo en cuenta el cuello de botella que supone la depredación, establecer fuentes de bellotas y fomentar sus dispersores son medidas estériles si la depredación de bellotas y plántulas es muy alta. El control de las densidades de los depredadores ha demostrado tener efectos positivos en el reclutamiento de otras quercíneas dispersadas por otro córvido con un comportamiento de almacenamiento de bellotas similar a la urraca (Pesendorfer et al., 2017).

5. **Realizar riegos de emergencia en los puntos de siembra** en años con sequía primaveral puede garantizar los resultados de proyectos que impliquen siembras de bellotas que, de no hacerlo, resultarían un fracaso. No se puede controlar ni prever si el año en el que se realizan las siembras será suficientemente lluvioso para una buena emergencia y supervivencia de las plántulas de encina; sin embargo, con los datos de precipitación mensuales del año de la siembra y de los años anteriores se pueden planificar riegos si no se alcanza la lluvia media mensual para ese lugar.

6.5. Futuras líneas de investigación

Finalmente, los resultados de esta Tesis doctoral dejan abiertas algunas cuestiones que invitan a investigar en las siguientes líneas en el futuro.

1. **Replicar los experimentos de dispersión de bellotas de encina por urraca en otros lugares** y con otras quercíneas y otras especies de semillas grandes, incluso en agroecosistemas con remanentes forestales mixtos. La metodología empleada en esta Tesis Doctoral, combinando el foto-trampeo de los comederos con el marcaje de los individuos, el radio-seguimiento de las bellotas removidas y la monitorización de bellotas escondidas, ha demostrado ser eficaz en el estudio de la dispersión de bellotas por urracas, brindando una gran cantidad de información valiosa e inaccesible hasta el desarrollo de estas tecnologías.

2. **Evaluar el coste del servicio de la dispersión**, como se ha hecho con los arrendajos en otros sistemas (Hougner et al., 2006; Leverkus y Castro, 2017), contribuiría a mejorar la percepción que se tiene de las urracas en ciertos sectores de la población.

3. Conocer las **tasas de reclutamiento de las encinas en los diferentes ambientes seleccionados por las urracas** para esconder las bellotas, sin el condicionante de la herbivoría, aportará información adicional acerca de la efectividad de la dispersión de las urracas. En esta Tesis se han puesto de manifiesto las preferencias de las urracas a la hora de seleccionar los lugares de almacenamiento de las bellotas. Algunos de esos destinos pueden ser determinantes para el reclutamiento por sus condiciones microclimáticas, como hemos observado con el estudio de la orientación y la distancias a los islotes forestales. La importancia del destino de la dispersión, en términos de condiciones microclimáticas, se observa, por ejemplo, en las mayores tasas de reclutamiento de encinas bajo arbustos facilitadores (Cuesta et al., 2010; Andivia et al., 2017; Cruz-Alonso et al., 2019). Esto es especialmente interesante porque hay que tener en cuenta que las urracas almacenan más bellotas en zonas aradas donde la vegetación es prácticamente inexistente. Además, será interesante analizar si los ambientes seleccionados por las urracas para esconder las bellotas muestran diferencias de depredación por otros animales, así como la recuperación de las bellotas por las urracas tanto para consumirlas como para la dispersión secundaria (Gómez et al., 2019). Si la depredación y la recuperación de bellotas es distinta en los distintos ambientes, también la tasa de reclutamiento variará en los diferentes ambientes.

4. Evaluar el efecto del **arado de áreas de campos agrícolas abandonados** de diferentes tamaños y a distintas distancias de las fuentes semilleras sobre la efectividad de la dispersión de bellotas por la urraca. Esto podría hacerse mediante el diseño de experimentos en los que se aren distintas superficies combinando distintas distancias a las fuentes de bellotas teniendo en cuenta la distancia de dispersión de bellotas por la urraca. Los experimentos deberían tener bandas alrededor de las fuentes de bellotas localizadas entre

el valor medio y el más alto de la distancia de dispersión observada en esta Tesis para favorecer la llegada de bellotas más lejos. Otra opción a estudiar sería arar transectos radiales y/o sectores partiendo de la fuente de semillas, con una superficie relacionada con la distancia a la fuente para mantener el esfuerzo de muestreo teniendo en cuenta el aumento de la superficie a estudiar en función del aumento de la distancia a la fuente de semillas. Asimismo, este tipo de diseño podría servir para evaluar la emergencia y la supervivencia de las plántulas y los juveniles en esas bandas o transectos, profundizando en el efecto del micrositio relacionado con la distancia y la orientación a otras plantas, analizando el efecto a distancias más largas y a escalas temporales más amplias a las consideradas en esta Tesis.

5. La información de esta Tesis también permite crear **modelos predictivos de la expansión de encinares** que ayuden en la gestión de la restauración de campos agrícolas abandonados. Para ello, además de los datos que se presentan en esta Tesis, es necesario cuantificar otros procesos como la producción de bellotas, la proporción de bellotas que caen al suelo y las densidades de dispersores y depredadores de bellotas, e integrar esta información en modelos predictivos a largo plazo. La información sobre la supervivencia y el crecimiento de los juveniles aparecidos en distintos ambientes es importante para dichos modelos. Será interesante realizar simulaciones con distintas densidades de dispersores y depredadores de bellotas y plantas para comprender su papel e identificar densidades de depredadores críticas que bloqueen el reclutamiento y las etapas del ciclo de reclutamiento más críticas. Este tipo de modelos se han hecho con otras especies de aves dispersoras de bellotas en islas próximas a la costa de California y han destacado la importancia de la recuperación del mutualismo planta-animal dispersor para acelerar la regeneración de las quercíneas y los beneficios del control de la herbivoría en ambientes mediterráneos (Pesendorfer et al., 2017).

6. Analizar la **preferencia** de las urracas **por bellotas de diferentes tamaños y de distintas especies y por otros frutos** que se puedan almacenar como almendras y nueces. En esta Tesis se ha observado que las urracas también almacenan bellotas de quejigo y almendras (**Capítulo 2**), aunque no se ha

cuantificado, y en otros trabajos hemos demostrado que almacenan nueces (Castro et al., 2017). Sin embargo, desconocemos la preferencia que tienen por cada una de estas semillas y sus diferentes tamaños y cómo estas preferencias pueden afectar a la proporción que almacenan de cada uno de ellos.

7. Evaluar la efectividad de **distintos tamaños de islotes forestales** en el reclutamiento de encinas en campos agrícolas. Idealmente, sería útil conocer el tamaño que optimice el coste de la actuación y el reclutamiento de las encinas, es decir, que aporten los propágulos suficientes, atraigan los dispersores más eficaces y exporten las bellotas a más larga distancia para desencadenar la restauración del campo agrícola.

8. Analizar el efecto **de distintas especies vegetales plantadas en los islotes forestales**. Sobre todo podría ser interesante introducir especies de frutos carnosos y otras especies pioneras en la sucesión forestal que además de atraer a dispersores de semillas (Camargo et al., 2020) también pueden facilitar a especies tardías de la sucesión. Algunas de las especies que podrían cumplir esta función en ambientes mediterráneos son los enebros (*Juniperus oxycedrus y J. communis*), los rosales (*Rosa* sp.), el majuelo (*Crataegus monogyna*), el endrino (*Prunus spinosa*), las zarzas (*Rubus* sp.) y la retama (*Retama sphaerocarpa*), entre otras.

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Imágenes de arriba a abajo y de izquierda a derecha:

Portada del capítulo 2: Massive and effective acorn dispersal into agroforestry systems by an overlooked vector, the Eurasian magpie (*Pica pica*)
Portada del capítulo 3: Caching territoriality and site preferences by a scatter-hoarder drive the spatial pattern of seed dispersal and affect seedling emergence
Portada del capítulo 4: Predation and aridity slow down the spread of 21-year-old planted woodland islets in restored Mediterranean farmland
Portada del capítulo 5: Drivers of oak establishment in Mediterranean old fields from 25-year-old woodland islets planted to assist natural regeneration

Capítulo 7

Conclusions:

This section reports the main conclusions of this Thesis. Conclusions 1 and 2 are related to the acorn dispersal capacity by magpie (**Chapter 2**). Conclusions 3 to 5 are linked to the spatial preference to cache the acorns by magpie (**Chapter 3**). Conclusions 6 to 9 are concerned with different factors that determine the seedling emergence and survival in Mediterranean abandoned farmland and conclusion 10 is related to recruitment rate of holm oak from oak islets (**Chapter 4 and 5**). Finally, conclusion 11 highlights helpful information for future research of oaks recruitment in agroforestry systems.

1. Magpies removed more than a half of the annual acorn production from trees. One individual removed up to 1500 acorns in 6 weeks. Most of the removed acorns (86%) were cached, and the rest were consumed immediately after removal. The dispersal distance ranged between 1.4 and 210 m and the mean was 32,5 m. Up to 2.4% of cached acorns resulted in emerged seedlings which yielded a high seedling density, 56–439 seedlings/ha. The massive and effective dispersal capacity makes magpie a key species for the regeneration of oak agroforestry systems in analogy to jays' role in forests.

2. The breeding status and gender of the magpies determined acorn dispersal activity. Breeding magpies were the main scatter-hoarders. Breeding males dispersed around twice as many acorns as breeding females. Juveniles dispersed a small fraction of acorns, but they dispersed them farther than adults.

3. Scatter-hoarding by magpie is a hierarchical selective decision-making process at different spatial scales, driven by territoriality and cache site preferences. Caching territories constrained dispersal distance and the habitats and sub-habitats available for acorn caching.

4. Magpies preferred tilled areas over tree plantations and tree plantations over old fields to cache acorns. These differences were maximized at relatively short to medium dispersal distances, where most acorns were cached. Within tree plantations, magpies preferred high plant-productivity sites over low productivity ones. At the smallest spatial scale, magpies preferred structures built by animals and selected uncommon materials for acorn caching.

5. Habitat preference for acorn caching matched the density of emerged seedlings across habitats, meaning that magpie territoriality indirectly drives oak seedling emergence and can determine oak recruitment and forest regeneration.

6. Predation of acorns and emerged seedlings strongly limits holm oak recruitment in Mediterranean abandoned farmland, being one of the major limiting factors. Most (97%) unprotected acorns were removed or predated and half of the unprotected emerged seedling were predated. Even protected acorns were affected by wild boar in two of our four sowing experiments.

7. Climate inter-annual variation determined the emergence and survival of oak seedling. Seedlings emerged in wet springs had higher survival after summer drought than seedlings emerged in dry and hot springs. This indicates that spring precipitation was as important as summer precipitation for emergence and those seedlings emerged in average and wet spring are more drought resistant than seedlings emerged in a dry spring.

8. Oak islets planted to assist natural regeneration in old fields affected the performance of the oak seedlings emerged around them. This effect, however, depended on the orientation and distance to the islet. Seedling emergence and survival were the highest in the less sun-exposed sites and near than far from the islet edges in contrast to the most sun-exposed one where were higher far than near. However, despite these effects in early stages of holm oak recruitment, more naturally established oak juveniles were found at intermediate distances from the islets. This decoupling

between seedling performance and abundance of recruits indicates that other ecological drivers and processes (e.g. seed dispersion) override the effect of seedling survival in the recruitment of oak juveniles.

9. Oak islets but not herbivory reduced herb growth. The competitive effect of islets against the herb community decreased with distance to the islet likely facilitating indirectly seedling emergence and early survival near the islets.

10. Recruitment rate of holm oak from oak islets planted to assist natural regeneration in old fields was 5.7 plants ha^{-1} year^{-1}. This indicates that planted oak islets are an effective acorn source in Mediterranean abandoned farmland where there are no remnants of natural vegetation.

11. Future research on oak recruitment in agroforestry systems should analyse recruitment rates in selected sites by magpies to cache the acorns, perform parametrised models to predict long term spatial recruitment, and evaluate the suitability of different sizes and more diverse woodland islets.

Conclusiones

Esta sección expone las conclusiones principales de esta Tesis Doctoral. Las conclusiones 1 y 2 está relacionadas con la capacidad de dispersión de bellotas de la urraca (**Capítulo 2**). Las conclusiones de la 3 a la 5 están vinculadas a la preferencia espacial de la urraca para almacenar bellotas (**Capítulo 3**). Las conclusiones de la 6 a la 9 se refieren a diferentes factores que determinan la emergencia y la supervivencia de plántulas en ambientes mediterráneos y la conclusión 10 hace referencia a la tasa de reclutamiento de encinas desde islotes forestales (**Capítulos 4 y 5**). Finalmente, la conclusión 11 destaca información útil para futuras investigaciones sobre el reclutamiento de quercíneas en sistemas agroforestales.

1. Las urracas retiraron más de la mitad de la producción anual de bellotas de los árboles. Un individuo removió hasta 1500 bellotas durante seis semanas. La mayoría de las bellotas que se llevaron (86%) fueron escondidas y el resto fueron depredadas inmediatamente después de removerlas. Las distancias de dispersión fueron desde 1,4 a 210 m con una media de 32,5 m. Hasta el 2,4% de las bellotas escondidas resultaron en plántulas emergidas lo que produjo una alta densidad de plántulas, 56–439 plántulas / ha. La capacidad de dispersión de bellotas masiva y efectiva hace que la urraca sea una especie clave en la regeneración de quercíneas en sistemas agroforestales de manera análoga al rol de los arrendajos en bosques.

2. El estatus reproductor y el género de las urracas determinó la actividad dispersora de bellotas. Las urracas reproductoras fueron las principales dispersoras. Los machos reproductores dispersaron alrededor del doble de bellotas que las hembras reproductoras. Los juveniles dispersaron una pequeña fracción de bellotas, pero las dispersaron más lejos que los adultos.

3. El almacenamiento de bellotas por urraca siguió un proceso jerárquico de toma de decisiones a diferentes escalas espaciales dirigido por la territorialidad y la preferencia de sitios para esconderlas. Los territorios de almacenamiento restringieron la distancia de dispersión y los hábitats y sub-hábitats disponibles para esconder las bellotas.

4. Las urracas prefirieron las zonas aradas antes que la plantación arbórea y estas antes que el herbazal. Estas diferencias fueron mayores a distancias de dispersión relativamente cortas y medias, donde se escondieron la mayor parte de las bellotas. Dentro de las plantaciones las urracas prefirieron las zonas con alta productividad vegetal antes que las de baja productividad. A una escala menor, las urracas prefirieron las estructuras hechas por otros animales y seleccionaron los materiales menos comunes para esconder las bellotas.

5. La preferencia de hábitats para esconder las bellotas coincidió con la densidad de plántulas emergidas en los distintos hábitats. Esto significa que la territorialidad de la urraca dirige indirectamente la emergencia de plántulas de quercíneas y puede determinar su reclutamiento y la regeneración del bosque.

6. La depredación de las bellotas y de las plántulas emergidas limita fuertemente el reclutamiento de encinas en campos agrícolas abandonados en ambientes mediterráneos, siendo uno de los mayores factores limitantes. La mayoría de las bellotas que no se protegieron fueron removidas o depredadas en el sitio y la mitad de las plántulas no protegidas también. Incluso las bellotas protegidas sufrieron daños por jabalíes durante dos de los cuatro años de experimentos con siembras.

7. La variabilidad climática interanual determinó la emergencia y la supervivencia de plántulas de encina. Las plántulas emergidas en primaveras húmedas sobrevivieron más después de sequías estivales que las emergidas en primaveras secas y calurosas. Esto indica que la precipitación de primavera fue tan importante como la precipitación de verano y que esas plántulas emergidas en primaveras con precipitaciones medias o húmedas son más resistentes a la sequía que las emergidas en primaveras secas.

8. Los islotes de encinas plantados para asistir la regeneración natural en campos agrícolas abandonados afectaron a la emergencia de las plántulas de encinas a su alrededor. Este efecto dependió de la orientación y la distancia

a los islotes. La emergencia y la supervivencia de las plántulas de encina fue mayor en la orientación menos expuesta al sol y cerca mayor que lejos del borde de los islotes al contrario que en las orientaciones más expuestas donde fue mayor lejos que cerca. Sin embargo, a pesar de estas diferencias en las etapas tempranas del reclutamiento de encinas, se encontraron más encinas juveniles establecidas naturalmente a distancias intermedias de los islotes. Este desajuste entre las plántulas y la abundancia del reclutamiento indica que otros factores y procesos ecológicos (como la dispersión de semillas) anulan el efecto de la supervivencia de plántulas en el reclutamiento de juveniles de encina.

9. Los islotes forestales pero no la herbivoría redujeron el crecimiento de herbáceas. El efecto de la competencia de los islotes sobre la comunidad herbácea disminuyó con la distancia a los islotes posiblemente facilitando indirectamente la emergencia de plántulas y la supervivencia temprana cerca de los islotes.

10. La tasa de reclutamiento de encinas desde los islotes de encinas plantados para asistir la regeneración natural en campos de cultivo abandonados fue de 5,7 encinas ha^{-1} año^{-1}. Esto indica que los islotes de encinas plantados son una fuente efectiva de bellotas en campos agrícolas abandonados en ambientes mediterráneos donde no hay remanentes de vegetación natural.

11. Las futuras investigaciones sobre el reclutamiento de encinas en sistemas agroforestales deberían analizar las tasas de reclutamiento en los lugares seleccionados por las urracas para esconder las bellotas, realizar modelos parametrizados para predecir el reclutamiento espacial a largo plazo y evaluar la idoneidad de islotes forestales de diferentes tamaños y más diversos.

Imagen:

Urraca y plántula de encina
Fuente de la imagen: Daniel Gómez-Sánchez y Pablo Quiles

Agradecimientos[10]

Tenía muchas ganas de que llegara este momento y poder expresar mi agradecimiento a todas las personas que han estado ahí durante estos años de Tesis Doctoral. Espero acordarme de todas las que han colaborado tanto en el campo como viendo vídeos y muchas otras que han dado el apoyo que hace falta siempre que se quieren llevar a cabo grandes proyectos.

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[10] Todos los capítulos de investigación contienen una sección de agradecimientos a las personas e instituciones que han contribuido en cada trabajo.

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Por último, quería agradecer muy especialmente a mi familia todo el apoyo, la ayuda y la compresión a lo largo de estos años de Tesis. Algunos se han “dejado engañar” para venir al campo alguna vez, como mis tíos, Itzi y Josetxu, que vinieron a sembrar bellotas junto con mis padres, y que me acogen con cariño por el norte, ¡gracias! A mi padre, Patxi, por su optimismo, por confiar en mí más que nadie y por su apoyo incondicional siempre. Ha sido la persona que más ha venido a divertirse (el marketing es importante) conmigo a La Higueruela, incluso a pesar de la oferta gastronómica, ya sabes 😊. ¡Gracias, aita, sin ti esto no sería posible! A mi madre, Mercedes, por todo el interés, la preocupación a veces y el apoyo siempre y por ayudarme para que pudiera dedicar el mayor tiempo posible a terminar. ¡Mamá, ahora sí! A mis hermanos, Javier y Leire, por compartir buenos momentos y por estar ahí en los no tan buenos, por vuestro apoyo, vuestro cariño, por los viajes que hemos hecho y los que nos quedan por hacer, pero sobre todo por las risas y porque sé que puedo contar con vosotr@s.

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Anexo fotográfico[11]

Capítulos 2 y 3

Figura A.1. Material para el anillamiento de aves. A) Alicates para colocar las anillas. B) Anillas de aluminio lacadas con distintos colores para la identificación de las aves en los vídeos y de acero inoxidable con numeración del ministerio. C) Urraca adulta anillada en el momento previo a la liberación.

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[11] Fuente de las imágenes: L. Martínez-Baroja y grupo de investigación SERAVI

Figura A.2. Anillamiento de pollos de urraca. A) Anillamiento de un pollo de urraca en el tarso con anillas de colores y una anilla numerada del ministerio. B) Detalle de las anillas de un pollo anillado. C) Pollos de un mismo nido anillados.

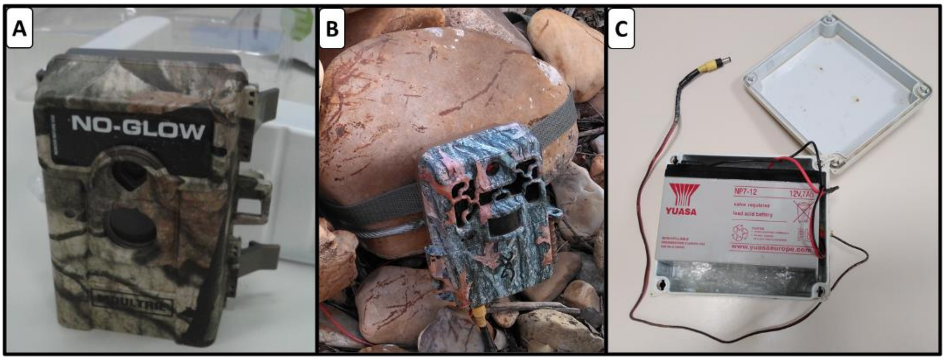

Figura A.3. Material para fototrampeo. Los dos tipos de cámaras empleadas: A) cámara antes de la instalación (Moultrie MCG-12634; Moultrie Products, Alabama, USA) y B) cámara instalada en el campo (Browning Dark Ops HD Elite, Browning Trail Cameras, USA). C) Batería externa para las cámaras.

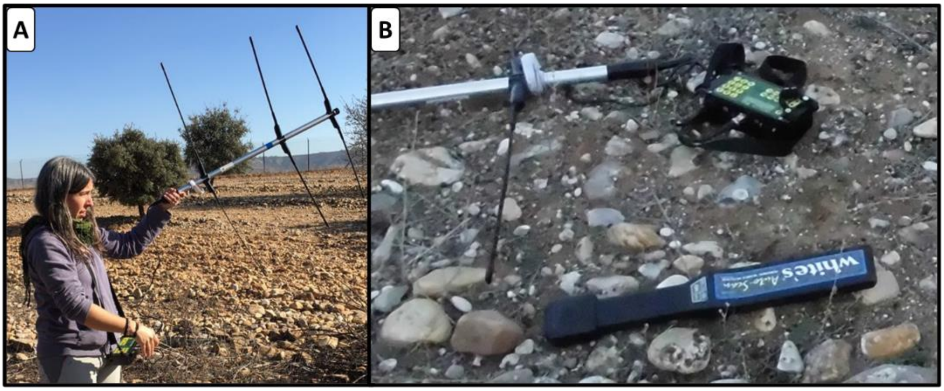

Figura A.4. A) Radioseguimiento de una bellota con el receptor y la antena. B) Detalle del receptor y parte de la antena en la parte superior de la imagen y detector de metales de mano en la parte inferior.

Figura A.5. A) Rama con bellotas con radiotransmisor pegadas para colocarla en una encina. B) Misma rama ya adherida a la encina.

Figura A.6. Muestreo de materiales para esconder las bellotas (cobertura de piedras, suelo desnudo y necromasa) y recogida de biomasa. A) Cuadrado de muestreo de 50 x 50 cm y cintra métrica marcando el transecto. B) Cuadrado de muestreo antes de recoger la biomasa. C) Mismo cuadrado de muestreo después de recoger la biomasa.

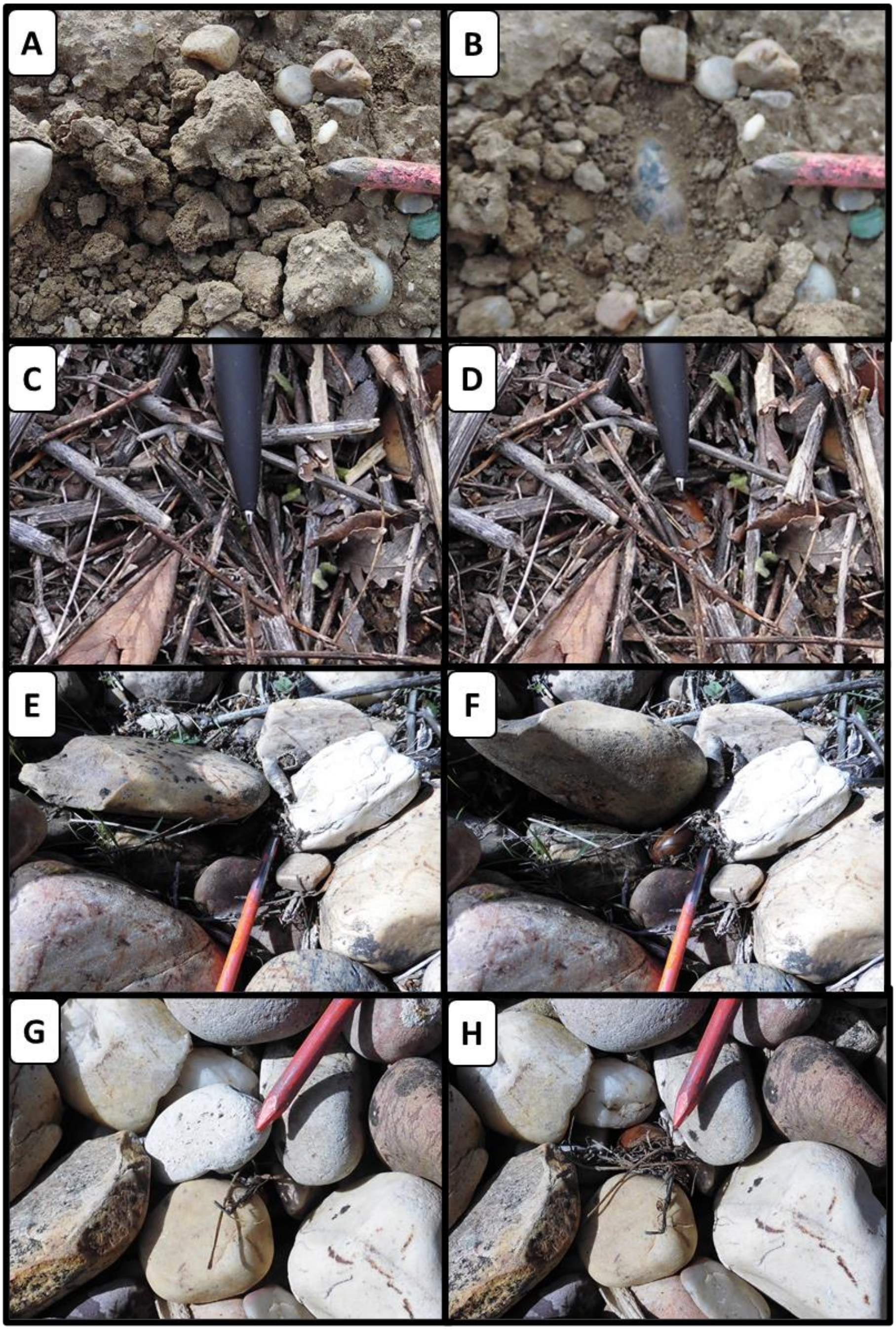

Figura A.7. Bellotas escondidas en los distintos materiales del área de estudio. Figuras de la izquierda antes de retirar el material sobre la bellota y figuras de la derecha después de quitar el material. A-B) Suelo desnudo. C-D) Necromasa. E-F) Incrustada bajo una piedra (sin moverla). G-H) Debajo de varias piedras de menor tamaño moviendo al menos una de ellas para cubrir la bellota.

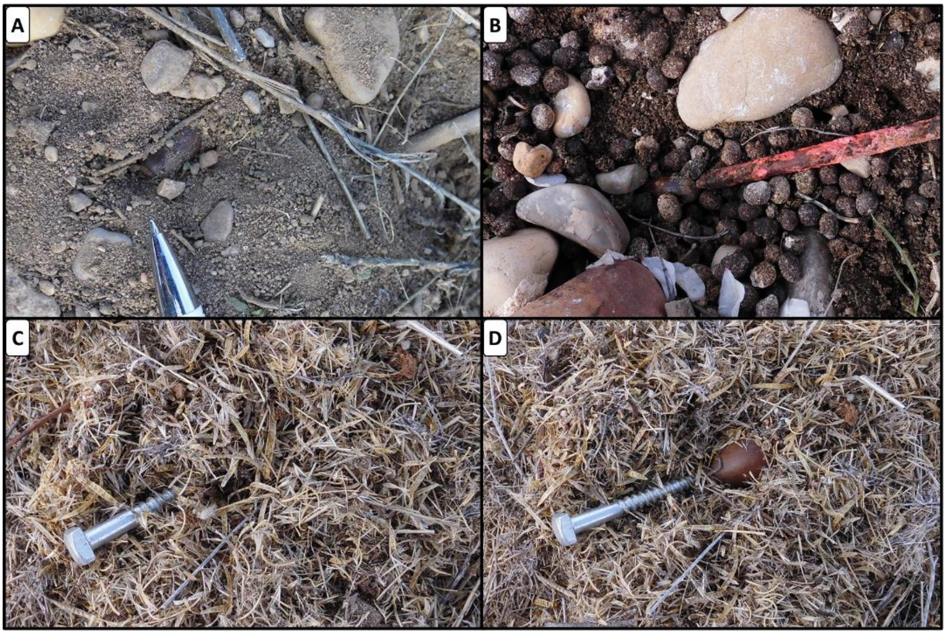

Figura A.8. Bellotas con radiotransmisor escondidas en estructuras hechas por animales. A) En escarbadura de conejos. B) En letrina de conejos. C) Entre los restos vegetales de desecho de un hormiguero antes de retirar los restos sobre la bellota. D) Después de retirar los restos sobre la bellota.

Figura A.9. Marca para el seguimiento de una bellota con radiotransmisor dispersada por urraca en la zona de estudio y sustituida por una bellota sin radiotransmisor.

Capítulos 4 y 5

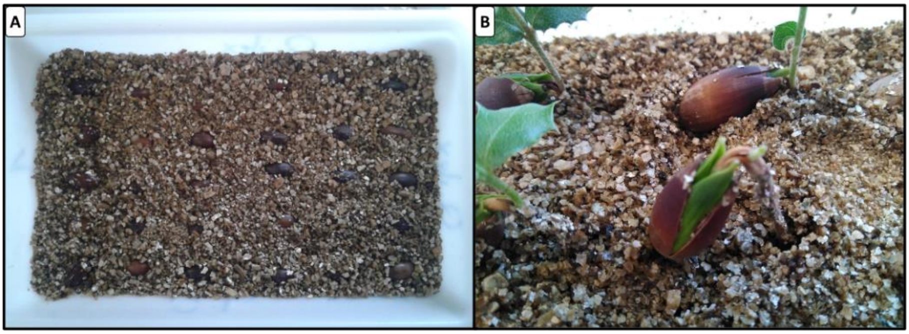

Figura A.10. A) Experimento de germinación y emergencia de bellotas en vermiculita para obtener las tasas de ambos procesos. B) Detalle bellotas emergidas.

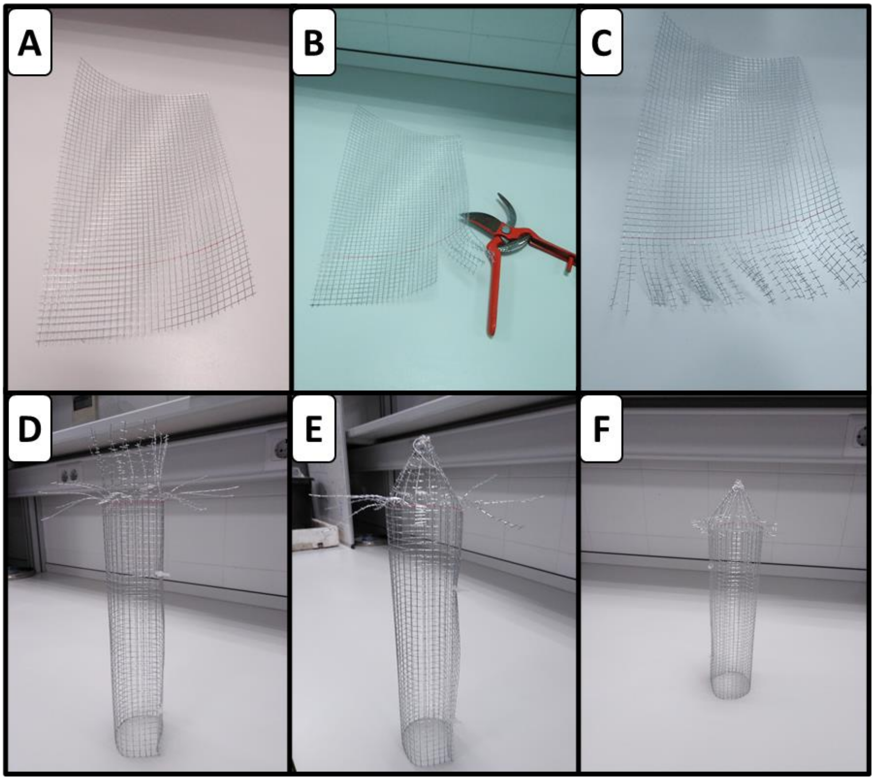

Figura A.11. Secuencia del montaje de los protectores de bellotas frente a jabalís. Más detalles y medidas en el artículo de Reque y Martin (2015).

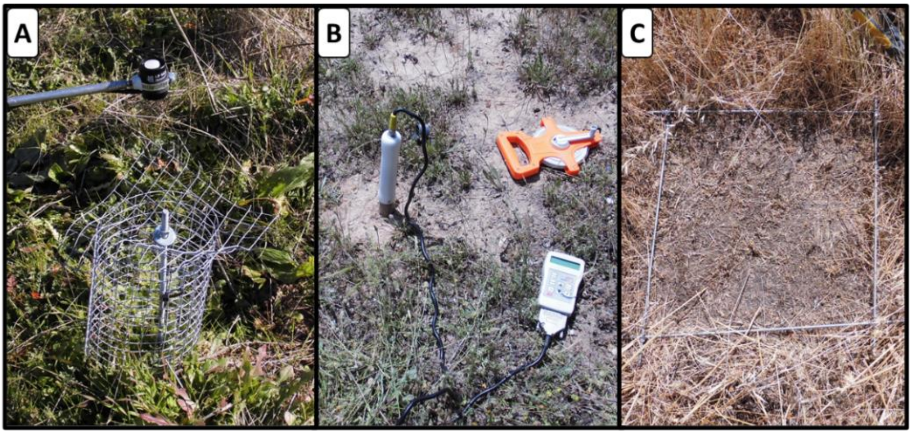

Figura A.12. A) Medida de extinción de luz. B) Medida de humedad del suelo dentro de tubo de 45 cm enterrado en el suelo. C) Recogida de biomasa cerca de un punto de medida de humedad del suelo.

Figura A.13. Evolución de la biomasa herbácea dentro y fuera de las Jaulas de exclusión de herbívoros. A) Instalación. B) Intermedio. C) Recogida. En ninguno de los casos se observan diferencias en la cantidad de biomasa dentro y fuera de las jaulas (resultado en el capítulo 5).

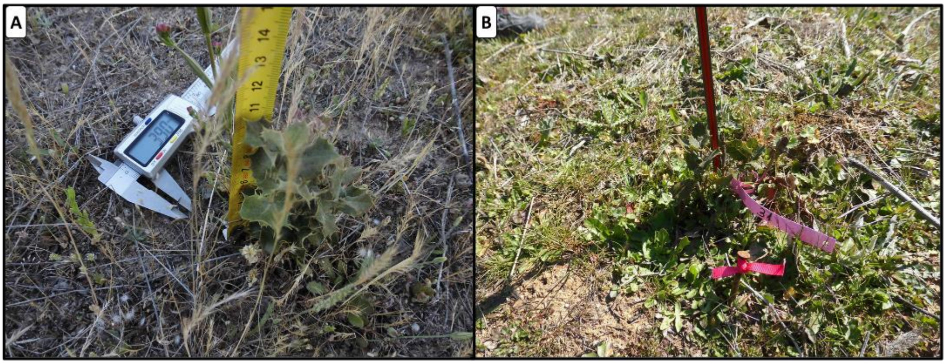

Figura A.14. Seguimiento y medida de las plántulas mayores de 5 cm. A) Medida de la altura y diámetro del tallo de la plántula. B) Plántula marcada con etiqueta numerada para el seguimiento.

Estancia de investigación en el extranjero

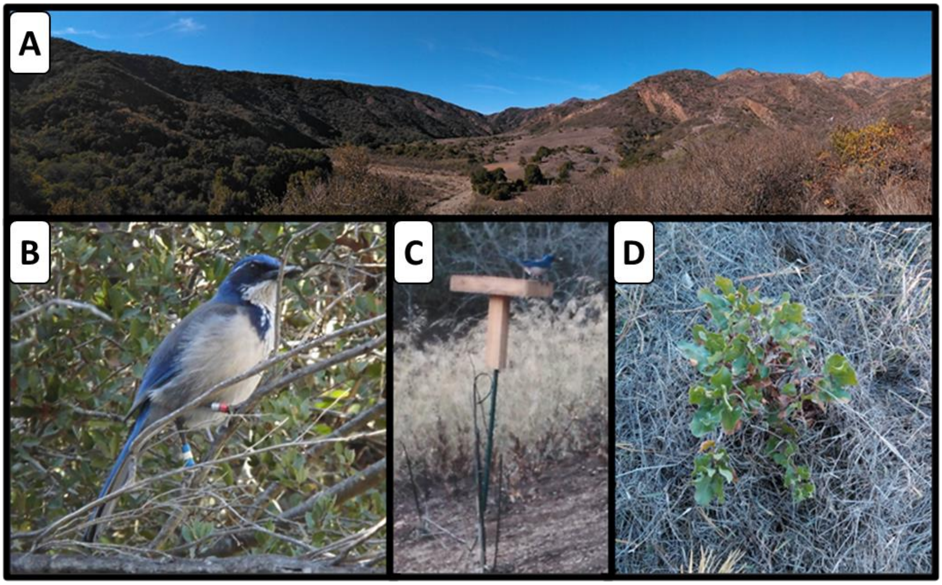

Figura A.15. Fotografías tomadas durante la estancia en la isla Santa Cruz, frente a la costa de California, que ilustran una interacción córvido-quercíneas similar a la presentada en esta Tesis con la urraca y la encina. A) Vista general de la zona de estudio. B) Ejemplar de Island Scrub-Jay (*Aphelocoma insularis*) anillado, dispersor de bellotas en ese sistema. C) Island Scrub-jay con bellotas en el pico sobre uno de los comederos. D) Quercínea reclutada.

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