UNIVERSIDAD DE GRANADA
DEPARTAMENTO DE ECOLOGÍA

ECOLOGÍA DE LA REGENERACIÓN DE *QUERCUS ILEX* A ESCALA DE PAISAJE: IMPORTANCIA DE LOS DISPERSORES Y/O DEPREDADORES DE SEMILLAS PARA EL RECLUTAMIENTO

TESIS DOCTORAL

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Granada 2008

Editor: Editorial de la Universidad de Granada
Autor: Carolina Puerta Piñero
D.L.: Gr. 65 - 2008
ISBN: 978-84-338-4728-7

ECOLOGÍA DE LA REGENERACIÓN DE *QUERCUS ILEX* A ESCALA DE PAISAJE: IMPORTANCIA DE LOS DISPERSORES Y/O DEPREDADORES DE SEMILLAS PARA EL RECLUTAMIENTO

Memoria que la Licenciada Carolina Puerta Piñero presenta para aspirar al Grado de Doctora por la Universidad de Granada

Esta memoria ha sido realizada bajo la dirección de:
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Aspirante al Grado de Doctor

Granada, enero del 2008

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CERTIFICAN

Que los trabajos de investigación desarrollados en la Memoria de Tesis Doctoral: "Ecología de la regeneración de *Quercus ilex* a escala de paisaje: importancia de los dispersores y/o depredadores de semillas para el reclutamiento"**, son aptos para ser presentados por la Lda. Carolina Puerta Piñero ante el Tribunal que en su día se designe, para aspirar al Grado de Doctor por la Universidad de Granada.**

Y para que así conste, en cumplimiento de las disposiciones vigentes, extendemos el presente certificado a 20 de Diciembre 2007

Dr. José María Gómez Reyes **Dr. Mario Díaz Esteban**

Durante el tiempo de realización de esta Tesis Doctoral he disfrutado de dos años de Beca y dos años de contrato de investigación en prácticas, Ref. AP2003–344, del Programa Nacional de Formación de Personal Universitario del Ministerio de Educación y Ciencia.

Este trabajo estuvo financiado por el proyecto, REN2003-07048, del Ministerio de Educación y Ciencia.

La investigación presentada en esta Tesis Doctoral se ha realizado en el Departamento de Ecología de la Universidad de Granada.

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RESUMEN. Entender cuáles son los factores que modulan la regeneración natural de las poblaciones vegetales ha sido, y es, una pregunta crucial en ecología. De todos estos factores, aquellos que afectan a las primeras etapas del ciclo de vida, desde semilla hasta brinzal, son los más críticos. Por tanto, la dispersión o la depredación de semillas son determinantes para el éxito de regeneración de las especies. Mientras que los procesos de regeneración ocurren generalmente a una escala espacial pequeña las poblaciones se ubican en un rango más amplio, llegando incluso en especies leñosas a la escala regional. En esta tesis utilizo como modelo un paisaje heterogéneo de alta montaña dominado por la encina *Quercus ilex*. En este entorno estudio como la dispersión y depredación de bellotas varían entre diferentes escalas espaciales, y entre organismos mutualistas (dispersores) y antagónicos (depredadores). Vemos cómo la conectividad funcional de éste sistema está mediada por las interacciones entre plantas y animales. Así, los roedores parecen ejercer un papel dual de dispersores y depredadores de bellotas. Su actividad se localiza a escala local, pudiendo ejercer un papel efectivo en la regeneración incrementando las poblaciones preexistentes dentro de encinar; así como reestructurando la ubicación espacial de las encinas a escala fina de microhábitats. Los arrendajos son sin duda los dispersores más efectivos en este sistema. La deposición de bellotas se realiza en lugares lejanos, diferentes a los de origen (fuera del encinar generalmente) así como en hábitats y microhábitats favorables para el reclutamiento y establecimiento de plántulas y brinzales. De este modo, los arrendajos actúan como mutualistas muy eficientes, ayudando tanto a la regeneración de los encinares ya existentes como a la colonización de nuevas áreas. Los ungulados parecen jugar un papel antagonista, mermando por un lado la lluvia de semillas tras la dispersión y limitando el desarrollo de los brinzales por otro. A su vez remodelan el patrón espacial de la encina después de la dispersión, ramoneando preferentemente en ciertos hábitats y microhábitats más que en otros. Estos mecanismos diferenciales de dispersión y depredación ejercidos por parte de diferentes especies, ubicadas dentro de un mismo entorno, hacen que el patrón espacial observado en los encinares sea asimismo desigual. Así, el paisaje se constituiría como un escenario heterogéneo y dinámico en el cual ciertas áreas presentan un balance global positivo, es decir donde existe regeneración efectiva, mientras que otras tienen un balance negativo, encontrándose de este modo en sostenimiento o incluso regresión poblacional.

SUMMARY. Understanding which factors modulate natural regeneration of populations is a key question in ecology. Factors affecting the first stages, from seed to sapling, are the most critical ones. Thus, seed dispersal and predation are determinants for the success of species regeneration. While regeneration processes generally occur at small spatial scales, plant populations are found at a wider range, even at regional scales in the case of woody species. In this dissertation I use a mountainous heterogeneous landscape dominated by Holm oak, *Quercus ilex*, as model system. In this scenario I study how acorn dispersal and predation vary among spatial scales and among mutualistic (dispersers) and antagonistic (predators) species. Thus, how the functional connectivity of the system is mediated by plant-animal interactions. Hence, rodents have a dual role acting as acorn disperser and predators, focusing their activity mainly at a local scale. They can be effective dispersers by rebuilding the spatial locations of Holm oaks at fine scales (microhabitats) and by increasing preexisting populations. Jays are the most effective acorn dispersers in this system. They move acorns to far away sites, different from sources (so out of oak woodlands) and to habitats and microhabitats good for recruitment and establishment of seedlings and saplings. This way, jays are very efficient mutualists, facilitating the colonization of new areas and the establishment and regeneration of Holm oaks. Ungulates have an antagonist role; diminishing acorn rain after dispersal and restraining juvenile development. Additionally, they modify the spatial structure of acorns after dispersal, browsing mostly in some specific habitats and microhabitats. These differential mechanisms of dispersal and predation by different species, living within the same scenario, make the spatial pattern of oak woodlands also irregular. Thus, the landscape would be a heterogeneous and dynamic scenario in which some areas have a positive balance, where regeneration occurs, while others have a negative balance, being under stabilization or even regression of the populations.

INTRODUCCIÓN GENERAL

Quien se empeña en pegarle una pedrada a la luna no lo conseguirá,
pero terminará sabiendo manejar la honda."
Proverbio Árabe

La heterogeneidad espacial, definida como la complejidad y variabilidad en el espacio de las propiedades estructurales de los sistemas ecológicos, es una característica conspicua de todos los paisajes a una u otra escala espacial (Levin 1992; Li y Reynold 1995). La *teoría jerarquizada* ("Hierarchy theory") postula que los sistemas ecológicos están estructurados en *niveles de organización* discretos. Un nivel de organización puede ser examinado a diferentes *escalas*. Los procesos ecológicos en un lugar particular son el resultado de dinámicas locales y procesos actuando a escalas más amplias del paisaje circundante (Pearson 2002). Muchos aspectos de los procesos ecológicos cambian con la escala a la que son observados. Por lo tanto, cambios en la escala de observación pueden cambiar nuestra impresión de las dinámicas fundamentales de nuestras observaciones (O´Neill & Smith 2002). Como resultado, entender cómo la escala influencia nuestras observaciones es crucial para entender la ecología en general y la ecología del paisaje en particular. Muchos procesos ecológicos sólo se pueden entender, entonces, si se enmarcan explícitamente en una estructura espacial de referencia (Tilman y Kareiva 1997, Dieckmann et al. 2000). Diferentes especies, tanto vegetales como animales, se presentan a diferentes escalas espaciales. Por tanto las interacciones con otras especies también se ubican en el espacio, con cierto grado de solapamiento o escisión dependiendo del contexto ecológico. En los ecosistemas la heterogeneidad espacial es por lo tanto funcional, y no el resultado de algún proceso aleatorio o generador de ruido. Por lo tanto es importante estudiar este tipo de variabilidad por sí mismo. Una de las consecuencias en aquellos ecosistemas sin estructuración espacial serían fallos de sus funciones, por ejemplo homogeneidad a escalas amplias podría disminuir la diversidad de hábitats. A pesar de lo poco realista que puede parecer, esta es una asunción básica de muchas teorías y modelos para describir el funcionamiento de poblaciones y comunidades. La visión de un ecosistema espacialmente estructurado requiere un nuevo paradigma para los ecólogos: la estructura espacial (y temporal) es un componente fundamental de los ecosistemas (Legendre & Legendre 1998).

Muchos patrones ecológicos pueden ser descritos como parches o como gradientes. Los ecólogos examinan los patrones espaciales de las especies con objeto de entender los mecanismos que controlan la distribución de las especies. La estructura en mosaico se encuentra a todas las escalas espaciales, desde micrómetros a escalas continentales y oceánicas (Legendre & Legendre 1998). Con frecuencia aparecen contextos en mosaico con unas unidades encajadas dentro de otras: microhábitats, parches de vegetación, unidades de paisaje, paisajes, ecosistemas, biomas, etc. La mayoría de los estudios de campo cubren sólo una parte de la estructura espacial de cualquier variable. De modo que los mapas o modos de representación de los gradientes o parches pueden ser solamente interpretados con respecto a la escala de muestreo, que debería ser comparable a la escala del fenómeno de estudio. La distribución de las especies resulta de la acción combinada de diversas fuerzas, algunas externas otras intrínsecas de la comunidad. Ambos tipos de fuerzas generan un patrón espacial dentro de las especies o comunidades (Legendre y Legendre 1998).

A pesar de la gran importancia teórica de abordar estas cuestiones, aún son pocos los estudios empíricos que contemplan a la vez varias escalas espaciales y analizan los procesos que ligan la dinámica de individuos y poblaciones a escala local con las dinámicas poblaciones a escala de paisaje y las dinámicas de sucesión-colonización (Eriksson y Ehrlén 2001). Para lograr esto, es necesario generar estudios que enfaticen la relación que existe entre los patrones espaciales y los procesos ecológicos a lo largo de un amplio rango de escalas (Pickett y Cadenasso 1995).

En ambientes heterogéneos, la actividad de la mayoría de los organismos no se distribuye al azar por el paisaje, sino que depende de rasgos estructurales del espacio a varias escalas de resolución (Saab 1999, Kie et al. 2002). Diferentes organismos pueden percibir el mismo paisaje de manera muy diferente. Las interacciones planta-animal por tanto también pueden variar dependiendo de la escala espacial de acción de cada organismo. Por este motivo, la probabilidad que tiene una planta en este tipo de ambientes de interaccionar con una especie animal, y por consiguiente de sobrevivir o pasar a la siguiente fase demográfica, dependerá en gran medida de su localización espacial (Callaway 1992). Bajo estos presupuestos, es necesario considerar de forma explícita el patrón espacial de los individuos en cada fase demográfica para poder obtener una información rigurosa de la magnitud y de la identidad de los factores limitantes de la regeneración de las especies vegetales (Schupp y Fuentes 1995, Nathan y Muller-Landau 2000). La mayoría de los estudios de campo cubren sólo una parte de la estructura espacial de cualquier variable.

La ecología del paisaje es una disciplina que ha irrumpido con mucha fuerza durante las últimas décadas. Su éxito se debe a que es capaz de abordar problemas ecológicos que se desarrollan a escalas espacio-temporales amplias. Sin embargo, la inmensa mayoría de estudios desarrollados a escala de paisaje centran su atención en describir patrones ecológicos y desarrollar modelos que expliquen dichos patrones de forma rigurosa. Faltan, por el contrario estudios que imbriquen una perspectiva dinámica a los estudios demográficos, teniendo en cuenta el signo de las interacciones (mutualistas vs. antagónicas) así como su ubicación en un contexto espacial. Los patrones espaciales en el paisaje están influenciados por las interacciones entre los procesos bióticos y abióticos y viceversa (Gardner & Walters 2002). Las relaciones entre los patrones y los procesos en el paisaje son con frecuencia mejor entendidas usando modelos. Los modelos neutros, o nulos, en ecología aportan una base útil para comparar relaciones potenciales causa-efecto. Los *modelos neutros del paisaje* (modelos que no consideran los efectos ecológicos en los patrones del paisaje, Gardner et al. 1987)) ayudan a caracterizar como y qué grado de procesos ecológicos afectan a los patrones del paisaje observados. Generalmente, los modelos neutros examinan patrones del paisaje que ocurren ya sea debido a simples procesos aleatorios, o como resultado de procesos espacialmente correlacionados (Gardner & Walters 2002).

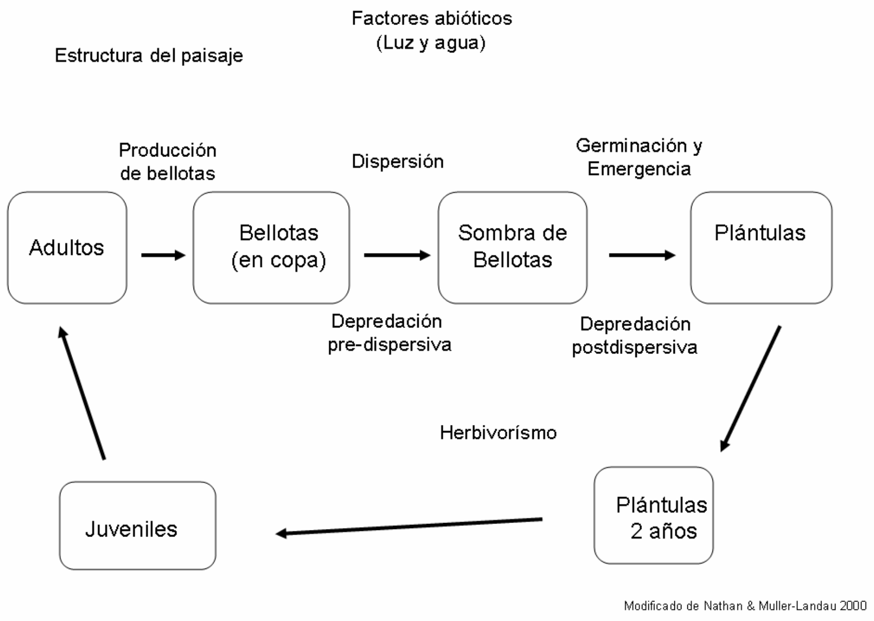
Sin embargo, es necesario estudiar no sólo los patrones sino también los procesos ecológicos que ocurren embebidos en paisajes heterogéneos (*ecología del paisaje centrada en el organismo*; Wiens et al. 1993). La mejor manera de abordar el problema de la dinámica demográfica de poblaciones vegetales en ambientes heterogéneos es mediante la comprensión mecanicista de procesos que ocurren a varias escalas, lo que requiere un diseño que contemple el incremento de escala desde los individuos, pasando por rodales o poblaciones locales y finalizando en el paisaje global. Este diseño permitiría comprobar si los procesos ecológicos varían de magnitud y signo entre diferentes estructuras espaciales, y si existe concordancia en los procesos ecológicos a diferentes escalas espaciales.

Cierto grado de *heterogeneidad estructural* puede generar diferencias en los mecanismos (tanto abióticos como bióticos) que controlan la distribución de las especies. Dado que diferentes mecanismos generan diferentes patrones demográficos, y como consecuencia de estas diferencias en el espacio (y en el tiempo), con frecuencia la heterogeneidad estructural puede desembocar en una *heterogeneidad funcional* demográfica (Gómez et al. 2004). O lo que es lo mismo, la existencia de “puntos fríos” y/o “puntos calientes” de regeneración, o puntos en retroceso o en crecimiento poblacional respectivamente. Watt (1947) fue el que primero en proponer el concepto de *mosaico espacial dinámico (dynamic spatial mosaic)*, que produce una distribución estable de los estadios sucesionales a nivel del paisaje. Considerando ésta perspectiva, la distribución espacial de las especies sería un proceso dinámico de regeneración-extinción a través del tiempo a lo largo del paisaje. Sin duda las interacciones planta-animal constituirán una pieza clave en este escenario de sucesión paisajística influyendo en la dirección e intensidad de éstas dinámicas.

En las últimas décadas se ha acumulado información empírica sobre la relación existente entre la estructura espacial del ambiente y la dinámica de reclutamiento de las plantas (Rey y Alcántara 2000, Jordano y Schupp 2000). Todos estos estudios han mostrado que en ambientes heterogéneos existen unos determinados lugares especialmente propicios para el establecimiento de la mayoría de las especies leñosas, ya sea porque son aquellos lugares donde los dispersores centran su actividad, presentan menor depredación post dispersiva, y/o mayor germinación, emergencia o supervivencia (Puerta-Piñero et al. 2007). Esto lleva a que la mayoría de las poblaciones naturales se presenten estructuradas en el espacio a varias escalas. La mayoría de estos estudios analizan, sin embargo, la heterogeneidad espacial relevante a una escala inferior a la de la propia distribución de la especie estudiada. Sin embargo, la heterogeneidad que presentan la mayoría de los ecosistemas se manifiesta a más de una escala espacial. Esto queda especialmente patente en los ambientes mediterráneos, donde el paisaje suele adoptar una estructura en mosaico, ya sea provocada por causas naturales o antrópicas. Investigar el modo en que el éxito de reclutamiento de las especies vegetales depende de características del paisaje a esta escala espacial, y cómo los organismos interactuantes modifican este proceso mediante la dispersión y/o eliminación de los propágulos colonizadores, es crucial para entender no sólo la abundancia local sino también la distribución regional de las especies (Ehrlén y Eriksson 2000, Eriksson y Ehrlén 2001).

Los primeros estadios del ciclo biológico de plantas leñosas suelen ser los más críticos en cuanto a que la mortalidad en estos momentos afectará drásticamente a la eficacia biológica de los individuos "padres" (Harper 1977; Silvertown & Charlesworth 2002?). El estudio de cómo funcionan estas etapas y su resultado para el reclutamiento temprano será por tanto decisivo para poder dar un juicio global en este tipo de sistemas. Para el caso de la encina se han estudiado algunos procesos bióticos primordiales como es el caso de la predación predispersiva y postdispersiva (Pulido & Díaz 2005; Bonal & Muñoz 2007; Gómez et al. 2008), la germinación (Gómez 2004; Puerta-Piñero et al. 2006) y la emergencia de las plántulas (Espelta et al. 1995; Puerta-Piñero et al. 2007) así como la supervivencia de plántulas y brinzales (Gómez 2004; Espelta et al. 1995; Puerta-Piñero et al. 207) . Mientras que por otro lado, se ha hecho especial énfasis a otros factores abióticos básicos como es el caso de la sequía estival y su relación con la radiación lumínica y su importancia en la supervivencia de las plántulas tras el primer verano de vida (Gómez 2004; Gómez-Aparicio et al. 2004; Pulido & Díaz 2005; Puerta-Piñero et al. 2007).

En un paisaje concreto la aparición de plántulas y su posterior supervivencia variará a su vez dependiendo de la escala espacial (micrositios, microhábitats, parches y/o unidades de paisaje). Para el caso de *Q. ilex* se ha demostrado recientemente de manera empírica que las plántulas germinan y emergen más si crecen en determinadas unidades de paisaje (Pulido & Díaz 2005) a la vez que sobreviven más y se desarrollan mejor bajo la cubierta de pinos y matorrales (Gómez 2004; Pulido & Díaz 2005; Gómez-Aparicio et al. 2005; Muñoz & Bonal 2007; Puerta-Piñero et al. 2007). Así los dispersores modulan el resultado final del ciclo biológico de la planta mediante la deposición de las semillas en lugares concretos. Para el caso de los microhábitats son muchas veces, además, favorables para su supervivencia y crecimiento de las plántulas (Puerta-Piñero et al. 2007). Esta heterogeneidad demográfica a diferentes escalas podría deberse, entre otras causas a factores intrínsecos del paisaje que quedan imbuidos en el sistema tales como radiación solar, pendiente u orientación considerando el entorno abiótico, o la estructura del hábitat o las interacciones con otros organismos si consideramos el ambiente biótico.



Modificado de Nathan & Muller-Landau 2000

Figura 1. Esquema conceptual del ciclo de vida de la encina.

Diferentes especies pueden responder de manera diferente a la pérdida de hábitat y la fragmentación. Además, las características intrínsecas de cada especie (ej, capacidad de dispersión) pueden interactuar con el patrón espacial del hábitat (fragmentado o conectado) para afectar a la dinámica poblacional en el paisaje. Deberíamos por tanto considerar el paisaje desde la perspectiva de las especies de interés.

Sistema modelo

Zona de estudio

Dentro del Parque Nacional de Sierra Nevada (Granada, España) se seleccionaron tres zonas de estudio (Figura 3). Se determinaron la cantidad de unidades de paisaje diferentes que existen en la zona de estudio así como el número de rodales de cada uno de ellos. En estas áreas georreferenciamos las principales manchas de vegetación (rodales), a la vez que las asignamos a una de estas tres categorías: matorral, pinar o encinar. Cada rodal fue caracterizado según una serie de variables estructurales abióticas (pendiente, orientación, área, etc.) y bióticas (estructura del hábitat expresado como cobertura de los principales microhábitats en diferentes estratos).
Asimismo, para cada rodal cuantificamos la producción de semillas así como la densidad de adultos, juveniles y plántulas de encina *Quercus ilex*. Igualmente, determinamos la abundancia

y actividad de depredadores (principalmente jabalí, *Sus scrofa*) y dispersores potenciales de semillas (ratón de campo, *Apodemus sylvaticus* y arrendajo *Garrulus glandarius*) así como los daños sufridos por herbivoría.

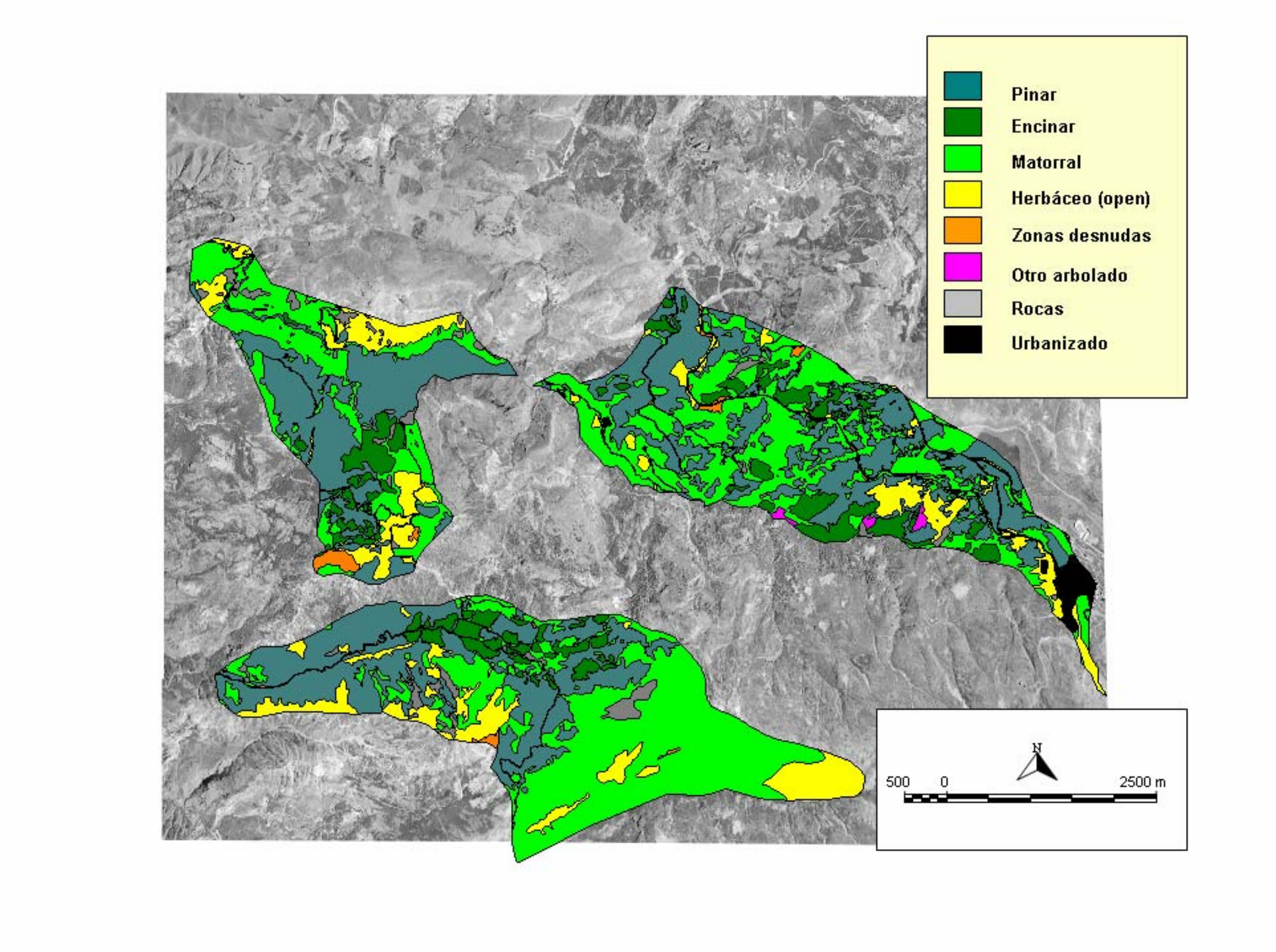


Figura 3. Mapa de las zonas de estudio y correspondencia de las principales unidades de paisaje.

Por otro lado, dentro del valle del Huenes se marcaron cinco parcelas de 50x50m para la realización de estudios intensivos (capítulos 1 y 2), dos de ellas valladas para impedir el acceso a ungulados (principalmente jabalís) y las tres restantes permanecerán sin vallar para permitir el paso de estos herbívoros. Cada parcela fue muestreada igualmente para determinar la distribución espacial y el porcentaje de cobertura de cada microhábitat (diferenciando entre suelo descubierto o con herbáceas, roca, cobertura arbórea y cobertura por cada una de las especies de matorral existente en la zona). Cada parcela fue georreferenciada en un mapa con el objeto de obtener su localización espacial exacta, para su posterior uso en estadística espacial.

Especies modelo

Quercus ilex

La encina se encuentra en muchas regiones de España formando bosques que presentan gran heterogeneidad espacial, ya sea porque se presentan en forma de bosques fragmentados, como los bosques islas, o en forma de bosques mixtos formando un mosaico de rodales. Algunos estudios pioneros han documentado que en este tipo de ambientes la heterogeneidad espacial afecta a la propia probabilidad de reclutamiento de la encina, bien directamente o mediante el concurso de los organismos claves (Gómez 2003; Muñoz & Bonal 2007; Pausas & Pons 2007; Pons & Pausas 2007; Puerta-Piñero et al. 2007). Los fragmentos forestales pequeños presentan también déficits de regeneración, aparentemente ligados a los bajos tamaños finales de cosecha y a la concentración invernal de roedores, que pasan de comportarse como dispersantes a adquirir importancia como depredadores postdispersivos (Tellería et al. 1991, Santos y Tellería 1994, 1997). Finalmente, en los bosques mixtos existe posibilidades de regeneración dentro de rodal pero también posibilidad de movimiento hacia rodales dominados por otras especies debido al comportamiento de algunos dispersores (Lookingbill y Zavala 2000, Zavala et al 2000, Gómez et al. 2001c; Purves et al. 2007), aunque no hay información rigurosa de la probabilidad que tiene esta colonización incipiente de traducirse en establecimiento real y posterior sustitución de la vegetación dominante en dichos rodales.

Toda esta información preliminar sugiere que la distribución espacial de los elementos del paisaje a varias escalas espaciales puede condicionar el éxito de la regeneración del arbolado, sobre todo porque, debido a que los organismos que interaccionan con la encina son tan distintos entre si en tamaño y morfología, también difieren en la escala a la que perciben el paisaje. Así, el área de campeo de los ratones de campo es significativamente menor (≈ 0.5 ha, Jensen y Nielsen 1986; Muñoz & Bonal 2007) que el de los arrendajos (≈ 14 ha, Rolando 1998; Pons & Pausas 2007) y el de éstos menor que el de los jabalíes (≈ 135 ha de área de campeo mensual, Masseis et al. 1997; Meriggi & Sachi 2000). Es esperable por tanto que la estructuración espacial manifiesta a diferentes escalas en estos bosques mixtos afecte de forma diferencial a la interacción que mantiene la planta con cada uno de estos organismos. Los patrones de actividad y la distribución espacial a varias escalas de los organismos que interactúan con los árboles durante el proceso de regeneración determinará no sólo el resultado final de dicho proceso sino también la configuración paisajística del mosaico de vegetación.

En el caso de los bosques mediterráneos, dominados mayoritariamente por la encina *Quercus ilex* en España (Blanco et al. 1997), hay ya un conocimiento suficientemente profundo de varios aspectos de su ecología de la regeneración (Pulido 1999, Rodà et al. 1999). Estos estudios han mostrado la existencia de aspectos cruciales de la ecología de la encina que la hacen atrayente para su uso como especie modelo:

Varios agentes bióticos inciden sobre estas fases demográficas de la encina, jugando un papel relevante en el resultado final del proceso de regeneración, y comportándose como organismos clave para la regeneración de los encinares (Gómez et al. 2001, Pulido 2002). Esto conlleva que el éxito de reclutamiento de la encina, como el de la mayoría de los árboles del género *Quercus* en ambientes mediterráneos, dependa de la acción de un conjunto diverso de agentes bióticos claves que actúan sucesivamente, cuyos efectos son positivos o negativos y que se diferencian bastante entre sí en rasgos ecológicos cruciales. En los bosques ibéricos, las dos especies principales de dispersores son el ratón de campo *Apodemus sylvaticus* y el arrendajo *Garrulus glandarius* (Gómez 2003, Pulido 2002, Pulido y Díaz 2002; Gómez et al. 2008; Capítulo 1 de esta tesis), dos especies que acumulan bellotas en otoño para su posterior consumo. El papel de estos vertebrados es doble, actuando como depredadores o como dispersores. El balance neto final depende de la capacidad que tenga cada especie de relocalizar las bellotas guardadas así como de la escala de su área de campeo y actividad.

Tras la germinación y emergencia de las plántulas, una gran mayoría de ellas mueren bien porque no han sido colocadas en micrositios adecuados para soportar la intensa sequía estival o bien porque son dañadas por organismos que buscan las bellotas o que ramonean en sus hojas (Gómez et al. 2001b, 2002, Pulido y Díaz 2002b; Espelta et al. 1995). Como consecuencia, las probabilidades de supervivencia de los propágulos aumentan mucho cuando se encuentran ubicados en determinadas unidades del paisaje o al amparo de algunas especies de matorrales que actúan como nodriza, facilitando la regeneración de las encinas (Callaway 1992, Callaway y Davis 1998, Gómez et al. 2001a, Pulido y Díaz 2002b; Gómez-Aparicio et al. 2004).

De suma importancia es el hecho de que todos estos organismos claves para la regeneración natural de la encina no actúan de forma independiente, sino que pueden interactuar entre sí, de manera que los efectos espaciales sobre cada uno de ellos pueden compensarse, atenuarse o amplificarse dependiendo de la magnitud y signo de la interacción con otros elementos (Figura 3).

Sus scrofa

Los jabalís, *Sus scrofa*, se constituyen como unos de los principales consumidores de bellotas y plántulas de los sistemas ibéricos (Gómez 2004; Muñoz & Bonal 2007). Se ha comprobado que los jabalís centran su actividad principalmente bajo encinas y pinos (Meriggi and Sacchi 2000) y pueden tener un área de campeo y actividad que incluya varias hectáreas (Masseis et al. 1997; Meriggi and Sacchi 2000). Estas características los hacen interesantes para su inclusión como especie clave en interacción con la encina previsiblemente con balance negativo a modo de depredación pre y post-dispersiva de bellotas. Presumiblemente, su actividad depredadora podría cambiar a lo largo del paisaje, variando entre unidades de paisaje y/o entre rodales de vegetación.

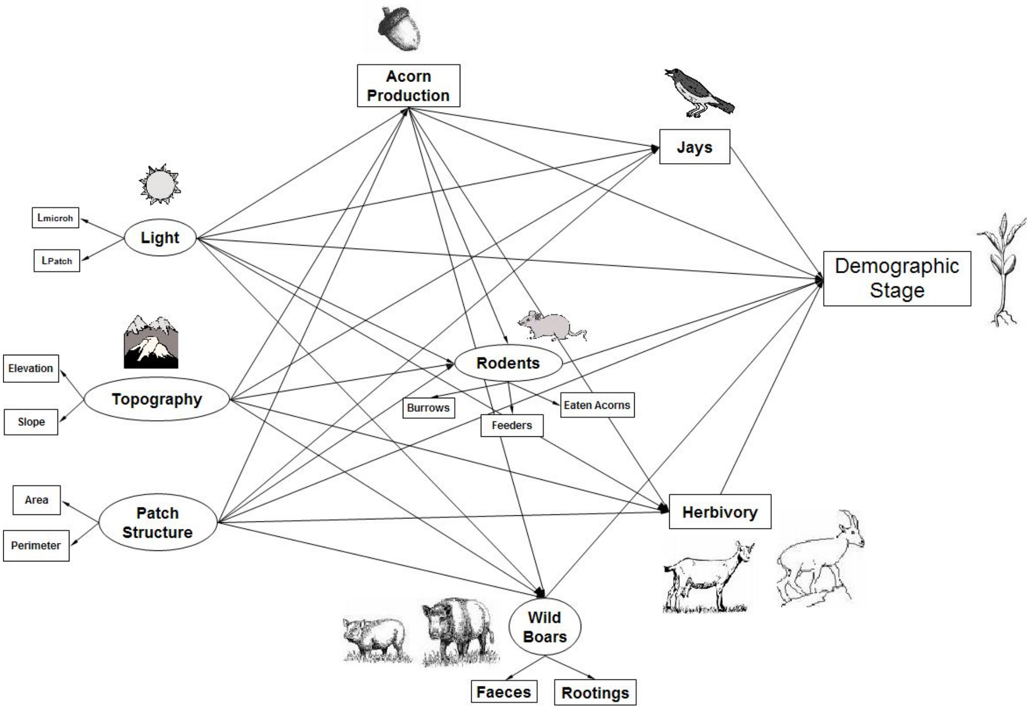


Figura 3. Esquema hipotético teórico de factores abióticos y bióticos sobre el reclutamiento de la encina *Quercus ilex*.

Apodemus sylvaticus

Los roedores constituyen una pieza decisiva en cuanto a dispersión y depredación de bellotas de *Quercus ilex* se refiere (Pulido & Díaz 2005; Muñoz & Bonal 2007; Pons & Pausas 2007). Por tanto, establecer cuál es el signo de esta interacción (mutualista cuando ejercen de dispersores) o antagonista (si se trata de depredación) es fundamental para conocer la dinámica de regeneración natural de los encinares. En la Península Ibérica se ha establecido un marco comparativo entre diferentes especies de roedores (Muñoz 2005) y diferentes unidades de paisaje y regiones (Gómez et al. 2003; Muñoz 2005; Gómez et al. 2006).

Para el caso del ratón de campo *Apodemus sylvaticus* se ha demostrado un comportamiento centrado en los encinares y dirigido a determinados microhábitats dentro del conjunto de todos los microhábitats disponibles (Muñoz & Bonal 2007). Así en encinares de Dehesa su actividad se concentra bajo las encinas (Pulido & Díaz 2005; Muñoz & Bonal 2007), mientras que, cuando se trata de zonas montanas su actividad dispersora se focaliza bajo a los matorrales (Gómez et al. 2003; Muñoz 2005; Gómez et al. 2006). Se observa además en ambos casos una importante tendencia a permanecer ligados a las encinas que le suplen de alimento (ya sean de dentro o de fuera de su territorio). Esto nos llevaría en principio a considerar que el papel final de los roedores en la dinámica demográfica de la encina será el de establecimiento o incremento de poblaciones ya consolidadas en un espacio dado (Gómez et al. 2006).

Garrulus glandarius

Se ha comprobado que la actividad de deposición de bellotas de los arrendajos se centra principalmente bajo la unidad de paisaje “pinar” y bajo pinos dispersos y matorrales (“microhábitats”) en otras unidades de paisaje (Gómez 2003). Su área de campeo y actividad parece variar dependiendo del hábitat (Gómez 2003; Pons & Pausas 2007). Además las distancias medias de dispersión de las bellotas observadas oscilan entre decenas de metros en zonas altamente fragmentadas de cultivos (Pons & Pausas 2007) a cientos de metros en áreas de bosques en mosaico (Gómez 2003). La distancia máxima de dispersión oscila entre cientos de metros a pocos kilómetros (Bossema 1979; Gómez 2003; Pons & Pausas 2007). Esto hace pensar que los arrendajos tienen la posibilidad de moverse a escalas interrodales y paisajística actuando como importantes mutualistas para la encina en cuanto a colonización de nuevas áreas (Gómez et al. 2006), así como al mantenimiento de una estructura genética equilibrada de las poblaciones (Grivet et al. 2005).

Objetivo General

Dentro de este marco conceptual, el objetivo general de la tesis que aquí se presenta sería el de determinar el papel que juega la heterogeneidad espacial en las interacciones que mantiene la encina con determinados organismos claves. Así como las consecuencias derivadas para su regeneración natural y para la dinámica a largo plazo de los bosques de encina y los paisajes en que se integran. La idea es comprobar si sobre el patrón de heterogeneidad estructural típico del paisaje mediterráneo se superpone un patrón de heterogeneidad funcional a través de las interacciones planta-animal.

En este aspecto, la originalidad científica de esta tesis se fundamenta en 1) afrontar el estudio de las interacciones entre plantas y animales a más de una escala espacial (microhábitat, rodal y paisaje), sabiendo que la mayoría de los trabajos han intentado estudiar esta cuestión centrándose exclusivamente en las diferencias entre microhábitats dentro de población (Gómez-Aparicio et al. 2004; Quero et al. 2007) o descripción de patrones en el paisaje (Turner 2000); 2) Investigar el efecto del patrón espacial sobre los procesos demográficos de la encina, siguiendo una aproximación netamente mecanicista (Levin 1992) y 3) Incorporar la dimensión espacial de las interacciones no sólo a escala local sino también a escala más amplia. En este contexto el presente proyecto de tesis pretende investigar la dinámica demográfica de la encina y las interacciones que mantiene con depredadores y dispersores, desde una perspectiva paisajística. La principal finalidad del proyecto es la de investigar el efecto que tiene para la dinámica demográfica de la encina a escala de paisaje la percepción diferencial de la heterogeneidad espacial por parte de los organismos que determinan su reclutamiento. Este objetivo general se concreta en los siguientes objetivos parciales para cada capítulo:

Objetivos parciales

Capítulo 1. Dispersión por roedores 1. Determinar la escala de percepción que los roedores tienen del paisaje. Se persigue saber cual es la capacidad que tienen de moverse entre microhábitats y elementos paisajísticos, y de utilizar cada uno de ellos como lugar de predación o deposición de semillas. Asimismo, también se pretende indagar si su actividad predominante es dispersora o depredadora de semillas.

Capítulo 2. Dispersión por roedores 2. Se pretende descubrir qué patrón de movimiento de bellotas generan los roedores en el proceso de dispersión de la encina. Asimismo se indagarán los efectos de ese patrón de distribución espacial en relación con respecto al posterior reclutamiento.

Capítulo 3. Depredación. Se persigue saber la capacidad que tiene cada especie predadora de semillas de moverse entre elementos paisajísticos, así como de utilizar cada uno de ellos como lugar de predación de semillas. Asimismo, también se pretende saber si cada especie animal desarrolla su actividad preponderantemente en algún hábitat específico así como qué probabilidades de supervivencia al ataque de los depredadores tienen las bellotas y plántulas dependiendo del contexto espacial donde se localicen.

Capítulo 4. Global. Analizar todos los resultados de los objetivos parciales anteriores interconectando unos resultados con otros para poder así obtener una visión global del estado de regeneración natural de la encina en los primeros estadios de su ciclo de vida.

Referencias

Blanco E, Casado MA, Costa M, Escribano R, García M, Génova M, Gómez A, Gómez F, Moreno JC, Morla C, Regato P, Sáinz H. 1997. Los bosques ibéricos. Una interpretación geobotánica. Planeta, Madrid, Spain.

Blondel J, Aronson J. 1999. Biology and wildlife of the Mediterranean Region. Oxford University Press.

Bonal R. 2005. Consecuencias sobre la eficacia biológica de las interacciones entre *Quercus ilex* y un consumidor especialista de sus bellotas, *Curculio elephas.* Tesis Doctoral.

Callaway RM. 1992. Effect of shrub on recruitment of *Quercus douglasii* and *Quercus lobata* in California. Ecology 73: 2118-2128.

Callaway RM, Davis FW. 1998. Recruitment of *Quercus agrifolia* in central California: the importance of shrub-dominated patches. Journal of Vegetation Science 9: 647-656.

Díaz M. 1992. Rodent seed predation in cereal crop areas of Central Spain: effects of physiognomy, food availability, and predation risk. Ecography 15: 77-85.

Díaz M, Alonso CL. 2002. Individual and population responses to food supplementation in wintering wood mice *Apodemus sylvaticus*: abundance, body condition, reproduction, and parasites. Enviado a Ecology.

Díaz M, Campos P, Pulido FJ. 1997. The Spanish dehesa: a diversity in land-use and wildlife. Pages 178-209 in D.J. Pain and M.W. Pienkowski, editors: Farming and birds in Europe. Academic Press, London.

Díaz M, Santos T, Tellería JL. 1999. Effects of forest fragmentation on the winter body condition and population parameters of an habitat generalist, the wood mouse *Apodemus sylvaticus*: a test of hypotheses. Acta Oecologica 20: 39-49.

Dieckmann U, Law R, Metz JAJ. 2000. The geometry of ecological interactions: simplifying spatial complexity. Cambridge University Press, Cambridge.

Ehrlén J, Eriksson O. 2000. Dispersal limitation and patch occupancy in forest herbs. Ecology 81: 1667-1674.

Eriksson O, Ehrlén J. 2001. Landscape fragmentation and the viability of plant populations. Páginas 157-175 en Silvertown J. y J. Antonovics (eds) Integrating ecology and evolution in a spatial context. Blackwell.

Fernández C, Acosta FJ, Abellá G, López F, Díaz M. 2002. Complex edge effect fields as additive processes in patches of ecological systems. Ecological Modelling 00: 000-000.

Gardner RH, Walters S. 2002. Neutral landscape models. En: Learning Landscape ecology. A practical guide to concepts and thechniques. Sarah E. Gergel & Monica G. Turner (editoras). Springer-Verlag. New York, Inc.

Gergel SE, Turner, MG (editoras). 2002. Learning Landscape ecology. A practical guide to concepts and thechniques. Springer-Verlag. New York, Inc.

Gómez JM. 2003. Spatial patterns in long-distance of *Quercus ilex* acorns by jays in a heterogeneous landscapes. Ecography 26:1573-1584.

Gómez JM, García D, Zamora R. 2003. Impact of vertebrate acorn- and seedling-predators on a Mediterranean *Quercus pyrenaica* forest. Forest Ecology and Management.

Gómez JM, Márquez R, Puerta-Piñero C. 2003. Interacciones entre la encina *Quercus ilex* y el ratón de campo *Apodemus sylvaticus* ¿mutualismo o antagonismo? Actas del VII Congreso de la AEET (Ed AEET). Barcelona, España, pp. 14-24

Gómez JM, Puerta-Piñero C, Schupp EW, Huertas Martínez ML. 2006. Dispersión de *Quercus ilex* por roedores y arrendajos: consecuencias demográficas a escala de paisaje. Actas del VIII Congreso de la AEET (Ed AEET). Lisboa, Portugal.

Gómez JM, Hódar JA, Zamora R, Castro J, García D. 2001a. Ungulate damage on Scots pines in Mediterranean environments: effects of association with shrubs. Canadian Journal of Botany 79: 739-746.

Gómez JM, Valladares F, Puerta-Piñero C. 2004. Differences between structural and functional environmental heterogeneity caused by seed dispersal. Functional Ecology 18: 787- 792.

Gomez JM. 2004. Importance of microhabitat and acorn burial on *Quercus ilex* early recruitment: non-additive effects on multiple demographic processes. Plant Ecology, 172: 287-297.

Herrera CM, Jordano P, López-Soria L, Amat JA. 1994. Recruitment of a mast-fruiting, bird-dispersed tree: bridging frugivore activity and seedling establishment. Ecological Monographs 64: 315-344.

Iniesta Marín C. 2006. Estado de las poblaciones de Encina *(Quercus ilex)* en el Parque Nacional de Sierra Nevada desde una perspectiva paisajística. Proyecto Fin de Carrera. Licenciatura en Ciencias Ambientales.

Jensen TS, Nielsen OF. 1986. Rodents as seed dispersers in a heath-oak wood succession. Oecologia 70: 214-221.

Jones CG, Lawton JH, Schachak M. 1994. Organisms as ecosystem engineers. Oikos 69: 373-386.

Jordano P, Schupp EW. 2000. Seed disperser effectiveness: the quantity component and patterns of seed rain for *Prunus mahaleb*. Ecological Monographs 70: 591-617.

Kie JG, Bowyer RT, Nicholson MC, Boroski BB, Loft ER. 2002. Landscape heterogeneity at differing scales: effects on spatial distribution of mule deer. Ecology 83: 530-544.

Kiviemi K, Eriksson O. 1999. Dispersal, recrutiment and site occupancy of grassland plants in fragmented habitats. Oikos 86: 241-253

Legendre P, Legendre L. 1998. Numerical Ecology, second edition. Developments in Environmental Modelling 20. Elsevier.

Li H, Reynolds JF. 1995. On definition and quantification of heterogeneity. Oikos 73: 280-284.

Lookingbill TR, Zavala MA. 2000. Spatial pattern of *Quercus ilex* and *Quercus pubescens* recruitment in *Pinus halepensis* dominated woodlands. Journal of Vegetation Science 11: 607-612.

Massei G, Genov PV, Staines BW, Gorman ML. 1997. Factors influencing home range and activity of wild boar (*Sus scrofa*) in a Mediterranean coastal area. Journal of Zoology 242: 411-423.

Meriggi A, Sacchi O. 2000. Habitat requirements of wild boars in the northern Appennines (N Italy): a multi-level approach. Italian Journal of Zoology 68: 47-55.

Muñoz A. 2005. Análisis ecológico del comportamiento depredador y dispersante de semillas de encina (*Quercus ilex*), por el ratón moruno (*Mus spretus*) y el ratón de campo (*Apodemus sylvaticus*). Tesis Doctoral. universidad complutense de Madrid.

Nathan R, Muller-Landau HC. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. Trends in Ecology and Evolution 15: 278-285.

O´Neill, RV, Smith MA. 2002. Scale and hierarchy theory. En: Learning Landscape ecology. A practical guide to concepts and thechniques. Sarah E. Gergel & Monica G. Turner (editoras). Springer-Verlag. New York, Inc.

Pearson S. 2002. Interpreting landscape patterns from organism-based perspectivas. En: Learning Landscape ecology. A practical guide to concepts and thechniques. Sarah E. Gergel & Monica G. Turner (editoras). Springer-Verlag. New York, Inc.

Pickett STA, Cadenasso ML. 1995. Landscape ecology: spatial heterogeneity in ecological systems. Science 269: 331-334.

Plieninger T, Pulido FJ, Konold W. 2003. Effects of land-use history on size structure of holm oak stands in Spanish dehesas: implications for conservation and restoration Emvironmental Conservation 30: 61-70.

Plieninger T, Pulido FJ, Schaich H. 2004. Effects of land-use and landscape structure on holm oak recruitment and regeneration at farm level in *Quercus ilex* L. dehesas. Journal of arid environments 57: 345-364.

Puerta Piñero C, Gómez Reyes JM, Iniesta Marín C. 2006. "Poniendo los pies en la tierra: Estructura espacial de patrones demográficos en la encina *Quercus ilex*". Actas del VIII Congreso de la AEET (Ed AEET). Lisboa, Portugal.

Pulido F, Díaz M. 2005. Regeneration of a Mediterranean oak: a whole-cycle approach. Écoscience 12: 92-102.

Pulido FJ. 1999. Herbivorismo y regeneración de la encina (*Quercus ilex* L.) en bosques y dehesas. Tesis Doctoral.

Pulido FJ. 2002. Biología reproductiva y conservación: el caso de la regeneración de los bosques templados y subtropicales de robles (*Quercus* spp.). Revista Chilena de Historia Natural 75: 5-15.

Rey P, Alcántara JM. 2000. Recruitment dynamics of a fleshy-fruited plant (*Olea europaea*): connecting patterns of seed dispersal to seedling establishment. Journal of Ecology 88: 622-633.

Rodà F, Retana, J, Gracia C, Bellot J. 1999. Ecology of Mediterranean evergreen oak forests. Springer Verlag.

Rolando A. 1998. Factors affecting movements and home range in the jay (*Garrulus glandarius*). Journal of Zoology 246: 249-257.

Saab V. 1999. Importance of spatial scale to habitat use by breeding birds in riparian forests: a hierarchical analysis. Ecological Applications 9: 135-151.

Santos T, Tellería JL. 1994. Influence of forest fragmentation on seed comsumption and dispersal of Spanish Juniper *Juniperus thurifera*. Biological Conservation 70:129-134.

Santos T, Tellería JL. 1997. Vertebrate predation on Holm oak, *Quercus ilex*, acorns in a fragmented habitat: effects on seedling recruitment. Forest Ecology and Management 98:181-187.

Schupp EW. 1995. Seed-seedling conflicts, habitat choice, and patterns of plant recruitment.American Journal of Botany 82: 399-409.

Schupp EW, Fuentes M. 1995. Spatial patterns of seed dispersal and the unification of plant population ecology. Ecoscience 2: 267-275.

Tellería JL, Santos T, Alcántara M. 1991. Abundance and food searching intensity of Wood Mice (*Apodemus sylvaticus*) in fragmented forests. Journal of Mammalogy 72: 183-187.

Tilman D, Kareiva P. 1997. *Spatial ecology: the role of space in population dynamics and interspecific interactions*. Princeton University Press, Princeton.

Vander Wall SB. 1990. Food hoarding in animals. University of Chicago Press, Chicago.

Vázquez FM. 1998. Semillas de *Quercus*. Biología, ecología y manejo. Consejería de Agricultura y Comercio. Badajoz.

Wiens JA, Stenseth NC, Van Horne B, Ims RA.1993. Ecological mechanisms and landscape ecology. Oikos 66: 369-380.

Zavala MA, Espelta JM, Retana J. 2000. Constraints and trade-offs in Mediterranean plant communities: the case of Holm oak-Aleppo pine forests. Botanical Review 66: 119-149

Zavala MA, Zea E. 2004. Mechanisms maintaining biodiversity in Mediterranean pine-oak forests: insights from a spatial simulation model. Plant Ecology 171: 197-207.

CHAPTER 1

Effectiveness of rodents as local seed dispersers of an oak with a stratified dispersal system

Quien cede el paso se ensancha el camino

Proverbio Chino

Gómez JM, Puerta-Piñero C, Schupp EW. 2008. Oecologia. *In press.*

Capítulo 1

Abstract. Oaks have a stratified dispersal system; jays move acorns long distances and contribute to regional dynamics while rodents move acorns short distances and contribute to local dynamics. Here we assess the effectiveness of rodents as dispersers of *Quercus ilex* in a patchy landscape in southeastern Spain. We followed the fates of 3200 marked and weighed acorns from fall through the period of germination in the spring in experiments initiated over three years. 99% of acorns were handled by rodents. Of these, 67% were dispersed. We relocated 74% of the dispersed acorns and of these 7.4% were initially cached. Most caches were recovered and consumed, however, and only 1.3% of the original experimental acorns were found alive in caches the following spring. Dispersal distances were short (mean = 356.2 cm, median = 157 cm) and strongly right skewed. Heavier acorns were dispersed further and were more likely to be cached and to survive in caches than lighter acorns. Most acorns were dispersed to oak and shrub microhabitats with fewer to pine, open, and rock. Based on microhabitat cover, dispersed acorns were found more often than expected in oak, as often as expected in pine, and less often than expected in other microhabitats. Those acorns dispersed to pine were the most likely to be cached, but the least likely to survive. Surviving caches were more frequent than expected in oak, as frequent as expected in shrub, and less frequent than expected in other microhabitats. Overall, most surviving acorns were either in oak, because of the disproportionate number of acorns dispersed there, and in shrub, because the shrub microhabitat is by far the most abundant. Using our results and published information on the suitability of different microhabitats for oak recruitment in the region we determined that rodents are effective dispersers of *Q. ilex*.

Keywords: Acorn dispersal, *Apodemus sylvaticus*, Disperser effectiveness, *Quercus ilex*, *Sciurus vulgaris*

Capítulo 1

Introduction

Seed dispersal is a critical process that has dramatic consequences for individual fitness and population dynamics of most plant species (Schupp and Fuentes 1995; Nathan and Muller-Landau 2000; Forget et al. 2005). Of particular interest in studies of the consequences of seed dispersal is the effectiveness of dispersal provided by the dispersal agents. Disperser effectiveness, a measure of the contribution of a disperser to the recruitment of a plant, is determined first by the quantity of seeds dispersed and second by the quality of dispersal provided each seed (Schupp 1993). Because effectiveness is determined by, among others, morphology, physiology, and behavior, different dispersal agents are expected to differ at least to some degree in effectiveness, and thus in their contributions to the dynamics of plant populations they interact with.

Oaks (*Quercus* spp.) are generally dispersed by two very different types of organisms, rodents and birds (Bossema 1979; Vander Wall 1990; Vander Wall and Longland 2004; den Ouden et al. 2005). These animals differ in microhabitat use, home range size, movement patterns, and caching and food relocation behavior, all of which potentially affect patterns and consequences of dispersal (Bossema 1979; den Ouden et al. 2005). For example, birds tend to move seeds longer distances than do rodents (Darley-Hill and Johnson 1981; Sork 1984). In addition, because of smaller home ranges rodents appear to relocate a higher proportion of cached acorns than do jays (Darley-Hill and Johnson 1981; Santos and Tellería 1997; den Ouden et al. 2005; Iida 2006). In general, because birds and rodents use the landscape very differently, the total dispersal kernel and seed shadow of an oak is likely composed of two very distinct partial kernels, one dominated by short-distance dispersal by rodents and the other dominated by long-distance dispersal by birds. We refer to this as a stratified dispersal system. A consequence of such stratified dispersal is that oak dispersal kernels – and the outcomes of dispersal – are perhaps more complex than those of many other animal-dispersed plants.

The ultimate consequences of being dispersed by two such different vectors for the dynamics and spatial structure of plant populations are presumed to be very intricate (Vander Wall and Longland 2004). While birds appear be important for the regional dynamics of oaks (Darley-Hill and Johnson 1981; Gómez 2003; Purves et al. 2007), rodents are presumably involved primarily in the local regeneration of oak populations (Jensen and Nielsen 1986; Iida 1996; 2006). Importantly, though, regional- and local-scale dispersal likely interact, with effective local dispersal increasing population size and the quantity of seed produced, resulting in more longer-distance dispersal events (Clark et al. 1998).

However, while many studies have addressed patterns of acorn dispersal by rodents (Vander Wall and Longland 2004; Den Ouden et al. 2005; Cheng et al. 2005 and references therein), none to our knowledge have attempted to address the effectiveness of rodent dispersal for oaks, and thus their potential contribution to local population or subpopulation dynamics.

The Holm oak, *Quercus ilex* L., is a Mediterranean evergreen tree that is dispersed both by rodents, mostly woodmice (*Apodemus sylvaticus*) and to a lesser extent red squirrels (*Sciurus vulgaris*), and by Eurasian jays (*Garrulus glandarius*) (Gómez 2003; Pulido and Díaz 2005; Purves et al. 2007). Jays disperse and cache acorns in excess of 300-400 m from source trees, mostly outside oak woodlands in shrublands and pine woods (Gómez 2003). This aspect of jay behavior has consequences for oak metapopulation dynamics at the landscape scale (Gómez 2003; Purves et al. 2007). In contrast, rodents have limited movement relative to jays and appear to forage for acorns primarily within oak woodlands (Gómez 2004a, b; Pulido and Díaz 2005). It is likely, therefore, that jays and rodents have very different roles in population and metapopulation dynamics of Holm oak. Our main goal in this study is to preliminarily assess the effectiveness of rodents as acorn dispersers of Holm oak. This involves quantifying (1) the numbers of acorns dispersed, cached, and surviving in caches, and (2) the spatial pattern of acorn dispersal focusing on distance dispersed and microhabitat destination. In addition, we address the effects of acorn weight and of microhabitat in which an acorn is encountered on patterns and consequences of dispersal.

Materials and Methods

Study species and sites

Quercus ilex is a sclerophyllous evergreen tree abundant in the Mediterranean region. Acorns are consumed during late October-early December by several vertebrate species, especially the Eurasian jay, wood pigeon (*Columba palumbus*), wild boar (*Sus scrofa*), red deer (*Cervus elaphus*), woodmouse, and red squirrel (Gómez 2003; 2004a, b; Pulido and Díaz 2005). Jays and rodents are also seed dispersers, caching acorns and failing to relocate some. Jay-dispersed acorns are usually transported far from adult oaks, and cached beneath shrubs or trees (Gómez 2003).

The study site is located in the upper reaches of the Huenes River valley (Sierra Nevada Protected Area, SE Spain, 37° 5' N, 3° 28' W) and ranges from 1550 to 1800 m a.s.l. Climate is continental Mediterranean, with cold winters, hot summers, and severe summer drought (July–August). The mean minimum temperature of the coldest month

(January) is -0.9°C, the mean maximum of the hottest month (July) is 29.0°C, and the mean annual temperature is 11.5°C. Precipitation, mostly as rain, is concentrated in autumn and spring, with an annual total of 825 mm (mean 1990–1998; data from a climate station in the center of the study site at 1650 m a.s.l.).

The landscape is a mosaic of mixed oak-pine woodlands, several dense pine afforestations, and extensive shrub stands (see Gómez 2003 for a detailed description). Within this landscape we focused on "oak woodlands," comprised of small patches of oak clones or clumps intermingled with isolated pines, tall shrubs (>0.5 m tall), sub-shrubs (≈ 30 cm high), and open areas. Although oak woodlands as a unit are easily distinguished on the landscape, they vary considerably in size, density of oaks, quantity and identity of shrubs, proximity to pure pine stands, and other characteristics. We considered five microhabitat types within oak woodlands: (1) "oak," under the canopy of *Q. ilex*; (2) "pine," under the canopy of a pine tree, whether isolated (typical) or within an adjacent pure stand (occasional); (3) "shrub," under the canopy of any of a variety of shrub species; (4) "open," bare soil with relatively sparse herbaceous cover; and (5) "rock," with rocks > 0.25 m^2.

Experimental design

Experiments were set up in each of three years, 2002, 2003, and 2004; 2002 and 2003 had abundant and relatively equivalent acorn production while 2004 had extremely low acorn production (J.M. Gomez, C. Puerta-Piñero and E.W. Schupp, personal observation). Experimental acorns were pierced with a dissecting needle at the base. This allowed us to attach a metal wire (8 cm long, 0.6 mm diameter) to which we tied individually numbered colored plastic flagging (10 cm long) that facilitated relocating acorns and allowed individual identification (Zhang and Wang 2001b; Li and Zhang 2003; Xiao et al. 2004). We used short wires to reduce interference with vegetation. The weight of the wire with flagging averaged approximately 100 mg (N=500), about 5-10 % of the total weight of the acorns. We individually weighed the entire experimental acorn (acorn + wire + flag) and used this value as "acorn weight" in all analyses since it is the weight rodents perceived. When rodents buried experimental acorns in the soil the flagging was nearly always exposed on the surface making them easy to relocate (Xiao et al. 2004). Xiao and coauthors (2006a) demonstrated that marking acorns with wire tags does not significantly affect the patterns of seed dispersal by rodents.

Experiments were initiated in November during the natural dispersal period. In 2002 we placed five groups of experimental acorns (25 acorns/group) in each of the four main microhabitats (oak, pine, shrub, and open; rock excluded) in an approximately 2-ha plot inside a large fenced exclosure (N=500 acorns in total). In 2003 we increased the number of experimental acorns, placing five groups of acorns in each microhabitat in two separate plots within the large exclosure; one of these plots was the same one used in 2002. In addition, we placed eight groups of acorns in the oak microhabitat in a third, unfenced plot (N=1200 acorns). In 2004, we placed 10 groups of acorns (30 acorns/group) under oaks only (the natural situation) in each of five plots, two fenced and three unfenced (N=1500 acorns); fenced plots were those used the year before while unfenced were new. In all cases acorns were placed on the ground within an area of about 15 cm diameter with wire markings pointing outwards to reduce interference with handling and moving acorns. We refer to this as a supply point.

Each year we began censusing experimental acorn fate one week after initiating the experiment, and continued censusing on an irregular basis until the following spring when seedling emergence naturally occurs. Because of slopes and frequently thick, loose litter acorns can easily move short distances over the winter without being carried by an animal; therefore, we conservatively considered an acorn to be dispersed only when it was relocated >50 cm from the original supply point.

A census began at the supply point, where we recorded the identifying number of each undispersed acorn and whether the acorn had been consumed *in situ* or was unconsumed. We then searched outwards from the supply point in expanding circles. When we located a dispersed acorn, we recorded the distance (in cm) from the supply point, the microhabitat in which it was located, and whether it had been consumed or cached (initial fate); note that the category "dispersed" is independent of the fate of the acorn. During each recensus we relocated previously cached acorns and recorded whether they had been recovered or robbed by rodents and consumed or were still surviving. In the last census we noted which caches survived to spring (final fate).

In order to determine whether the distributions of dispersed, cached, and surviving acorns were random with respect to microhabitat, we estimated the proportional cover of each of the five microhabitats in experimental plots at two spatial scales in 2004. We sampled at a small, 5-m scale around each acorn supply point (oak microhabitat only in 2004) to investigate microhabitat patterns of dispersal and of fate. For example, within the range of typical dispersal movements are acorns preferentially dispersed to some microhabitats at the expense of others? This scale was chosen because most dispersal was short distance (both mean and median <5 m, see results below). We also sampled at a larger, whole-plot scale in order to investigate microhabitat patterns of acorn arrival, caching, and survival at the population level. For example, at the level of the entire plot, are acorns arriving in some microhabitats more often than expected by chance?

We quantified microhabitat cover at the small scale using four primary transects radiating from each oak supply point (0º, 90º, 180º, and 270º) and another four secondary transects in between (45º, 135º, 225º, and 315º). We then recorded the microhabitat every 0.5 m from 0.5 – 5.0 m on primary transects and from 3.0 – 5.0 m on secondary transects; this scheme was used to reduce the overemphasis of microhabitat cover near supply points, which tended to be oak. We used these data to compare to the microhabitat distribution of acorns (as well as caches and surviving caches) dispersed by rodents up to 5 m, excluding acorns dispersed further. We quantified microhabitat cover at the larger whole-plot scale using three 50-m transects randomly positioned within each plot. We recorded the microhabitat at three points at each meter starting at 1.0 m: on the transect and 1.0 m to each side of the transect (150 points/transect, 450 points/plot). These data were used to compare with microhabitat distributions of all dispersed acorns, caches, and surviving caches at the entire plot level.

Data analysis

We used Generalized Linear Mixed Models (GLMM) to explore the spatio-temporal patterns of acorn fate. Year and Plot were random variables, with plot nested within year. Response variables (e.g. initially cached versus consumed) were fit to a binomial distribution with logit as the link function. To explore the effects of different variables on dispersal distance we performed Linear Mixed Models (LMM), fitting the dependent variable distance to a normal distribution and building the same type of model as above. Finally, the microhabitat distribution of dispersed acorns was analyzed with log-linear models, fitting the dependent variables to a multinomial distribution and again using the same model approach as in the previous analyses. GLMMs were performed using lme4 package in R (Bates 2005; R Development Core Team 2006), whereas LMMs and log-linear models were performed using JMP 6.0 (SAS 2005).

The observed and expected microhabitat distributions of acorns were contrasted by means of contingency table analyses using JMP 6.0 (SAS 2005). The expected distributions were from the proportional microhabitat cover data described above.

Results

Overall patterns of acorn handling, dispersal, and caching

Considering all data from the three years, approximately 99% (N=3155) of acorns were handled by rodents (Fig. 1). Of handled acorns, rodents dispersed 65.7% (N=2061) and consumed the rest at the supply points (Fig. 1). We relocated 1522 of the dispersed acorns (74%). Of these relocated acorns, 7.4% (N=113 acorns) were cached while the rest were quickly consumed at the point to which they were dispersed. Rodents, however, recovered many of the cached acorns and by the following spring only 1.3% (N=42) of the initially placed experimental acorns were alive in caches.

Based on a binomial model using all handled acorns, the proportion of acorns that were dispersed versus consumed *in situ* differed among years (LR $\chi2$= 357.07, N=3155, p<0.0001, GLMM). In 2002 and 2003 roughly 80% of the acorns were dispersed but in 2004, the year of extremely low acorn production, only 48% were dispersed.

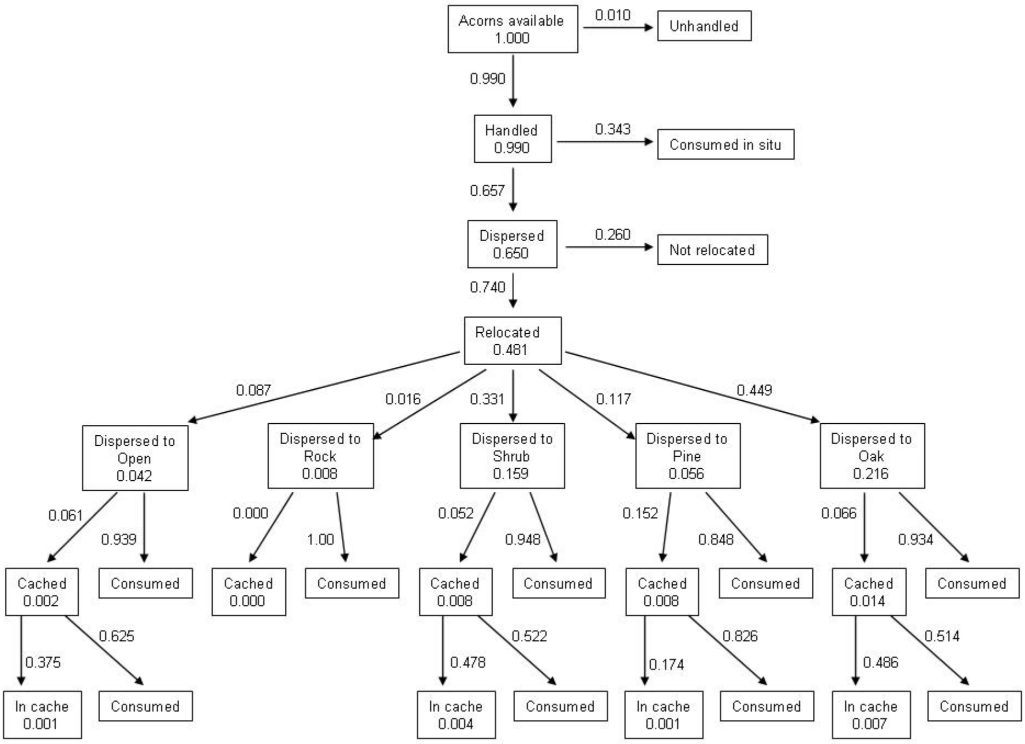


Figure 1. Acorn fate diagram showing the proportion of acorns moving from one stage, or fate, to the next (transition probabilities, values beside the arrows) and the proportion of the initial experimental acorn crop still alive at each stage, or fate (values inside the boxes).

Dispersal distances

Overall, acorns were dispersed relatively short distances and dispersal curves were strongly right-skewed [356.2±15.5 cm (mean±1 SE), range=50-7450 cm, median=157 cm, N=1522 relocated acorns] (Fig. 2). We found marginal among-year differences in dispersal distances, however (Table 1). In 2002 dispersal distances were relatively longer (median dispersal = 336.5 cm [30.1-2426.3]) and had lower skewness (1.90) and kurtosis (4.75). In 2003 and 2004, the median dispersal distances were relatively shorter (2003: 136.0 cm [25.4-1006.6]; 2004: 136.0 cm [39.0-3277.0]) and the distributions had higher skewness (4.39 and 4.24, respectively) and kurtosis (28.47 and 22.07, respectively). There were significant effects of plot and, more interestingly, acorn weight on dispersal distance (Table 1). Heavier acorns were dispersed further than lighter acorns, although acorn weight explained very little of the variance (Log [dispersal distance] = 1.805 + 0.590*Log [acorn weight], t=6.58, $P<0.0001$, $R^2=0.03$).

Table 1. Summary of the Linear Mixed Model testing the factors affecting dispersal distance (Log-transformed). Year and Plot were considered random factors. Bold type highlights significant effects.

Source	DF	F Ratio	P-values
Year	1	3.22	0.14
Plot[Year]	7	**4.20**	**0.02**
Microhabitat	3	**4.02**	**0.007**
Acorn weight	1	**15.76**	**0.0001**
Year*Acorn weight	1	2.01	0.19
Acorn weight*Plot [Year]	7	**11.07**	**0.0001**

Note: Non-significant interactions were pooled with main terms. N=1522 acorns. R^2=0.14

Microhabitat destination of dispersed, cached, and surviving acorns

Of the 1522 dispersed acorns that were relocated, 44.9% were dispersed to oak, 33.1% to shrub, 11.7% to pine, 8.7% to open, and 1.6% to rock (Fig. 1). Microhabitat destination was not affected by either year or acorn weight; only plot affected the distribution of dispersed acorns among microhabitats (Table 2).

At the local scale around individual acorn supply points (within 5.0 m) originally placed beneath oaks, the microhabitat destination differed from the expected based on microhabitat cover ($\chi2 = 202.9$, $p<0.0001$; using only 2004 data and only acorns dispersed ≤ 5.0 m)

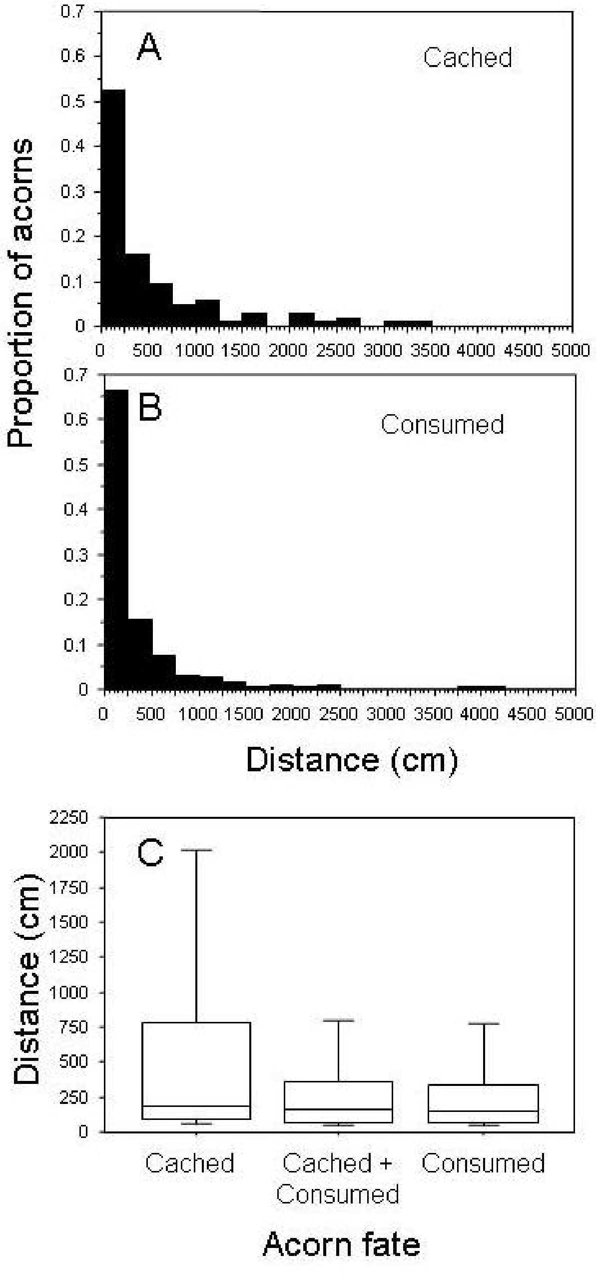


Figure 2. The frequency distributions of acorns (A) dispersed and (B) cached at different distances from the supply point, and (C) box-plots showing the median (horizontal lines), 25-75% quantiles (boxes), and the 10-90% (whiskers) of acorns that were cached and survived, acorns that were cached but recovered and consumed, and acorns that were consumed immediately after dispersal.

Dispersal to the oak microhabitat was considerably greater than expected while dispersal to open and shrub was substantially less than expected (Table 3). The spatial pattern of cached acorns also differed from expected ($\chi2 = 14.5$, $P<0.0001$). Rodents cached acorns more frequently than expected in oak and pine and less frequently than expected in open (Table 3). The distribution of surviving caches could not be analyzed because only a single cached acorn ≤ 5.0 m from a supply point survived; this surviving acorn was in the oak microhabitat. Thus, at the local scale it appears that rodent behavior disproportionately put potential recruits in oak and pine microhabitats.

At the whole-plot scale (again using only 2004 data, but all acorns) the distributions of dispersed acorns ($\chi2$ = 186.6, P<0.0001), cached acorns ($\chi2$ = 45.2, P<0.0001), and surviving acorns ($\chi2$ = 40.4, P<0.0001) all differed from the expected. Acorns were dispersed more frequently than expected to oak and less frequently than expected to open, rock, and shrub (Table 3). Results were very similar for cached acorns except at this stage there were also more acorns in pine than expected (Table 3). Surviving caches were found only in the shrub microhabitat, at about the frequency expected, and in the oak microhabitat, much more frequently than expected (Table 3). At the whole plot scale it appears that rodent behavior again disproportionately moved potential recruits to the oak and pine microhabitats, but the low survival in pine means realized recruitment was only disproportionately frequent beneath oaks. This result is similar to that of the overall analysis in the previous section as seen in the fate diagram (Fig. 1); more surviving caches were found in oak than any other microhabitat. This analysis also gives insight into why the shrub microhabitat had the second most surviving caches (Fig. 1). Shrubs had roughly as many recruits as expected, which is better than all microhabitats except oaks, and shrubs comprised the most abundant microhabitat type. Although rodents do not disproportionately move acorns to shrubs, the sheer abundance of shrubs means that a lot of acorns are dispersed to and survive in the shrub microhabitat.

Note that these observed versus expected results are based only on 2004 data and that we demonstrated that years differ in the microhabitat destination of dispersed acorns (see above). A higher proportion of acorns was dispersed to shrubs in 2004 than in the other two years yet still fewer than expected arrived beneath shrubs. Thus, year-to-year differences do not appear to greatly alter the overall pattern of results presented in this analysis.

Effects of microhabitat of origin

We used data from the first two years (2002 and 2003) to assess the extent to which the microhabitat in which acorns are discovered by rodents (microhabitat of origin) affects seed handling, dispersal, and fate. Acorns differed in the probability of being handled depending on the microhabitat of origin (LR $\chi2$=70.2, p<0.0001). Rodents handled 100% of the acorns placed in shrub, oak, and open microhabitats, but left 5.2% of the acorns placed in pine untouched.

Table 2. Summary of the log-linear models testing the factors affecting the microhabitat destination of dispersed acorns. A) Including all three years, but only acorns supplied in the oak microhabitat (N=822 dispersed acorns). B) 2002+2003 data in order to assess the effect of microhabitat of origin on the microhabitat destination of dispersed acorns (N= 692 dispersed acorns). Bold type highlights significant effects.

Source	DF	Wald χ^2	P value
A)			
Year	4	7.13	0.13
Plot[Year]	28	**63.27**	**0.0002**
Acorn weight	4	1.51	0.82
Year* Acorn weight	4	0.01	0.99
Acorn weight *Plot[Year]	28	15.57	0.97
Total	68	334.96	0.00001
R^2	0.24		
B)			
Microhabitat of origin	12	**135.863**	**0.0001**
Acorn weight	4	3.258	0.5156
Microhabitat* Acorn weight	12	12.116	0.4364
Plot	12	15.166	0.2325
Total	40	1011.408	0.0001
R^2	0.57		

Note: Some interactions were pooled with the error term because they created unstable models.

The percentage of handled acorns that were dispersed also differed among microhabitats of origin in both years (LR $\chi2=58.65$, N=466, $p<0.0001$ for 2002; LR $\chi2=41.55$, N=1173, $p<0.0001$ for 2003), although the pattern differed between the two years. Of acorns handled in 2002, rodents dispersed 97% of those in oak, 91% of those in pine, 83% of those in shrub, and only 64% of those in open. In contrast, of the acorns handled in 2003 rodents dispersed 91% of those in open, approximately 80% of those in oak and pine, and 70% of those in shrub.

Table 3. Observed and expected proportions of acorns being dispersed to, cached in, and surviving in different microhabitats in 2004, where expected values are based on proportional cover of the given microhabitat (see text for methods). Local scale refers to the 5.0 m radius around individual supply points that were located beneath oaks; whole plot scale refers to the entire approximately 2-ha plots.

	Local scale				**Whole plot scale**			
Microhabitat	**Expected**	**Observed dispersed (n=1097)**	**Observed cached (n=32)**	**Observed surviving (n=1)**	**Expected**	**Observed dispersed (n=1522)**	**Observed cached (n=113)**	**Observed surviving (n=9)**
Open	0.27	0.06	0.07	0.00	0.38	0.07	0.12	0.00
Rock	0.03	0.01	0.00	0.00	0.08	0.02	0.00	0.00
Shrub	0.21	0.10	0.19	0.00	0.40	0.11	0.22	0.33
Pine	0.03	0.05	0.16	0.00	0.09	0.11	0.19	0.00
Oak	0.45	0.78	0.58	1.00	0.05	0.68	0.47	0.67

Microhabitat of origin also affected the microhabitat destination of dispersed acorns (Wald $\chi2$= 135.86, df=12, P<0.0001, N=692 acorns; Table 2). Rodents tended to disperse acorns primarily to the same microhabitat type in which they initially found the acorns; 84% of acorns collected in oak were moved to oak, 94% of acorns collected in shrub were moved to shrub, and 52% of acorns collected in pine were moved to pine. The only exception was for acorns located in open, which were mostly dispersed to shrub (65%), although open (28%) was the second most frequent destination.

Lastly, microhabitat of origin affected the probability of an acorn being cached (LR $\chi2$=29.2, p<0.00001). Of acorns initially handled, about 3% of those initially placed in shrub, oak, and open microhabitats were cached, but 12% of those in pine were cached.

Initial and final fate of dispersed acorns

Plots differed greatly in initial fate but not in final fate, while years did not differ in either (Table 4). There was a significant relationship between the microhabitat to which an acorn was dispersed and initial fate (Table 4). Between 5.2 and 6.6% of the acorns dispersed to open, shrub, and oak were cached, while no acorns dispersed to rock and 15.2% of acorns dispersed to pine were cached (Fig. 1). This relationship disappeared, however, for final fate (Table 4); although the probability of a cached acorn surviving to the spring following dispersal varied across microhabitats from 17.4 to 48.6%, this difference was not significant, likely due to the small numbers at this stage (Fig. 1).

The cumulative effects of among-microhabitat differences in the probabilities of being dispersed, being cached, and surviving in a cache resulted in differences among microhabitats in the proportion of the initial experimental acorns that survived in a cache as a potential recruit. This proportion was highest in oak (0.7%), intermediate in shrub (0.4%) and extremely low in open, pine, and rock (0.0-0.1%; Fig. 1). The relatively high potential seedling recruitment in oak was due mostly to high levels of dispersal and of survival in caches, while the lower recruitment in shrub was mostly a result of slightly lower rates of dispersal and of caching of dispersed acorns. Causes of very low recruitment in the other microhabitats varied. Open and rock had low rates of dispersal and, in the case of rock, of caching. Pine had moderate rates of dispersal and of caching, but had by far the lowest survival of caches.

Acorn weight significantly affected both initial and final fate (Table 4). The probability of an acorn being initially cached increased with acorn weight (0.28±0.05, $\chi2$=34.37, p<0.0001, Univariate Logistic Regression), and the same relationship was still evident for final fate (0.28±0.09, $\chi2$=10.22, p=0.0014).

Lastly, distance affected the initial fate of acorns (Table 4). Although acorns were both cached and consumed near and far, a higher proportion of cached than of consumed acorns were moved longer distances (Fig. 2). This effect disappeared for final fate, however (Table 4).

Table 4. Summary of the Generalized Linear Mixed Models testing the factors affecting the initial fate (the number cached vs. the number consumed) and the final fate (the number of cached acorns that were recovered and consumed vs. the number surviving in a cache) of dispersed acorns. Year and Plot were included as random factors. Bold type highlights significant effects.

	Initial Fate			Final Fate		
Source	**DF**	χ^2	**P value**	**DF**	χ^2	**P value**
Year	1	0.98	0.32	1	0.001	0.97
Plot[Year]	7	**31.95**	**0.0001**	7	11.24	0.13
Microhabitat	4	**16.53**	**0.002**	4	1.21	0.88
Acorn weight	1	**1.88**	**0.05**	1	**1.87**	**0.04**
Dispersal distance	1	**2.63**	**0.0084**	1	0.37	0.71

Note: Non-significant interactions were pooled with main terms. N=1522 acorns. Initial Fate: AIC=616.8, Deviance=604.8; Final Fate: AIC=211.2, Deviance=199.2

Discussion

We relocated about 75% of the dispersed acorns, or about 83% of the total initial acorns counting the high number consumed at the supply point and relocated. This relocation rate was extremely high compared with other studies using similar methods. Sork (1984) and Iida (1996; 2004; 2006) used metal to tag acorns and metal detectors to locate them and relocated 28-46% and 59-63% of tagged acorns, respectively. Xiao et al. (2004; 2006a). Li and Zhang (2003) used tin tags externally attached to acorns and visually searched for them as we did; they relocated 50% and 32-60%. A very important consequence of our higher success in relocating acorns is that we can be relatively confident in our interpretations of patterns of dispersal, caching, and survival.

Our results suggest that rodents, probably mostly *A. sylvaticus*, acted mainly as seed predators of Holm oak in the study site, since only around 1% of the experimental acorns survived to the spring following dispersal. This outcome agrees with many studies that have shown rodents to be important post-dispersal seed predators of oaks (Pulido 2002; Gómez et al. 2003; Cheng et al. 2005; Haas and Heske 2005; Iida 2006; Takahashi et al. 2006; Xiao et al. 2006b), including *Quercus ilex* (Santos and Tellería 1997; Leiva and Fernández-Alés 2003; Pulido and Díaz 2005). A high proportion of acorns were consumed *in situ* beneath the parent trees. Competition for acorns is severe in Holm oak woodlands where a diverse group of organisms, including wild boars and other ungulates, usually outcompete rodents (Focardi et al. 2000; Gómez 2004a; Pulido and Diaz 2005). Under these circumstances, rodents may benefit from consuming acorns immediately when encountered rather than dispersing them away from the parent to consume or cache, although this benefit may be countered to some extent by increased predation risk. In fact, rodents even climb trees to gather acorns before they fall to the ground (Santos and Tellería 1997). Nevertheless, given the incredibly large numbers of acorns handled by rodents, the small proportion surviving likely contribute significantly to local dispersal and population regeneration of Holm oaks in the study site (see below).

Rodents generally moved holm oak acorns only short distances – median dispersal was less than 2 m and mean dispersal was around 3 m. This is compatible with most published studies (e.g. Sork 1984; Jensen and Nielsen 1986; Li and Zhang 2003; Cheng et al. 2005). Interestingly, rodents dispersed heavier acorns further than lighter acorns. Heavier acorns represent a better food item, and rodents are known to disperse more valuable resources further in order to reduce klepto-parasitism by conspecifics or other acorn consumers like jays (Stapanian and Smith 1978; 1984). Indeed, some studies have found that with increasing distance from source trees acorns are increasingly likely to survive secondary predation (Li and Zhang 2003). We found that heavier acorns had a higher probability of surviving in caches. Furthermore, rodents were more likely to initially cache heavier acorns than lighter ones, suggesting that they try to maximize the quality of food cached for the winter. This outcome is interesting because acorn weight has been shown to be positively related to recruitment probability in several *Quercus* species (Tripathi and Khan 1990; Bonfil 1998; Seiwa 2000; Gómez 2004b). Thus, those acorns with intrinsically greater probabilities of producing seedlings are more likely to be dispersed further, more likely to be cached, and more likely to survive in caches. In addition, the act of caching is in itself beneficial since acorns left on the surface suffer greater predation and reduced germination and seedling establishment relative to buried acorns (García et al. 2002; Gómez 2004a). This suite of behaviors is clearly beneficial to oak recruitment.

The seed shadow generated by rodents was not homogeneous. Acorns were dispersed to oaks more often than expected by chance; to pines as often as expected; and to shrubs, rocks, and open less often than expected. This was somewhat surprising since most studies on the behavior and seed consumption of *A. sylvaticus*, the rodent we presume to be the major disperser/predator in our site, have shown that these rodents prefer to forage under shrubs where they are well protected from predators rather than under trees (Jensen and Nielsen 1986; Alcántara et al. 2000; Rey et al. 2002; Díaz et al. 2005; Fedriani and Manzaneda 2005). The initial non-random seed shadow created by dispersal was then altered by caching behavior; for example, while all acorns dispersed to rocks were consumed immediately about 15% of those dispersed to pines were cached. Lastly, secondary seed predation further altered the microhabitat distribution of acorns, with mortality in caches ranging from about 50% in shrubs and oaks to >80% in pines. Interestingly, there was no secondary caching of acorns in this study; all acorns that were recovered were consumed. Changes in the spatial distribution of seeds due to post-dispersal seed predation have been shown in a number of other systems (Rey and Alcántara 2000; Tomita et al. 2002; Traveset et al. 2003) and promote spatial discordance between sequential life-cycle stages.

The non-random patterns of acorn dispersal, caching, and recovery have important consequences for Holm oak recruitment. Despite extensive overall acorn mortality in all microhabitats, a relatively high proportion of the many acorns dispersed to oaks were cached and a relatively high proportion of these caches survived. In addition, early seedling survival appears to be relatively high beneath oaks in this system (Gómez 2004a). Ultimately, however, the oak microhabitat is unlikely to be very suitable for oak recruitment due to high intraspecific competition with the adults and perhaps due to soil pathogens (Gómez 2004a; Puerta-Piñero et al. 2006). In stressful environments parents may often facilitate early stages of juvenile recruitment by ameliorating the harsh abiotic environment, but begin to interfere with recruitment as the juveniles grow and the strength of competition increases; that is, the net effect of parents on recruitment can switch ontogenetically from positive to negative (Ibáñez and Schupp 2001; Miriti 2006; Schupp *in press*).

A moderate number of acorns were dispersed to pines. These acorns had by far the greatest probability of being cached, but this advantage was counteracted by these caches also having the lowest probability of surviving. Those surviving, however, appear to be in a favorable microhabitat for the recruitment of oak seedlings. Acorns under pines have relatively high rates of germination and emergence and produce seedlings with good survival and rapid growth, probably due both to amelioration of the stressful microclimatic and improvement of soil physical-chemical conditions (Espelta et al. 1995; Retana et al. 1999; Gómez 2004a; Puerta-Piñero et al. 2006).

Although acorns were dispersed to shrubs less frequently than expected, it is important to note that still one third of all dispersed acorns were moved into this microhabitat due to the overwhelming abundance of shrub cover as a microhabitat. A relatively high number of these acorns were cached and nearly half of these caches survived. Similar to pines, shrubs facilitate Holm oak recruitment in the study site, mostly due to improvement of microclimatic conditions (Gómez 2004a; Gómez-Aparicio et al. 2004; 2005a,b).

Relatively few acorns were dispersed to microhabitats without woody plant cover (open and rock). No acorns dispersed to rocks were cached, but a relatively high proportion of those dispersed to open sites were cached and survived in caches; in fact, there were about as many surviving acorns in open as there were beneath pines. However, the open microhabitat appears to be unsuitable for oak recruitment at the study site due to heat and water stress (Gómez 2004a; Gómez-Aparicio et al. 2004; 2005a,b).

The tendency for rodents to disperse acorns to the same microhabitat type in which they initially found the acorns may be due to a variety of causes. It may be a consequence of the very short dispersal distances; short-distance movements are less likely to result in crossing into a new microhabitat. It might also result from among-species (e.g. Vieira et al. 2005) and/or among-individual (e.g. Scheibe and O'Farrell 1995) differences in microhabitat use. Insufficient data exist to evaluate the potential causes of these patterns, however. In contrast, it appears straightforward why acorns originally encountered in the pine microhabitat were the acorns most likely to be cached; acorns encountered in pine were mostly dispersed to pine, and acorns dispersed to pine were more likely to be cached than acorns dispersed to other microhabitats.

So are rodents effective dispersers of Holm oak acorns? Based on our results, out of every thousand acorns falling to the ground we would expect only about five surviving caches in the more suitable microhabitats of shrub and pine and only about eight surviving caches in the less suitable microhabitats. While on the surface this appears to be incredibly ineffective dispersal, it is an inherent outcome of seed dispersal systems where the major dispersers are also major consumers. Looking at the results from a different perspective, the two most suitable microhabitats received about 45% of the dispersed acorns, 50% of the initial caches, and 38% of the surviving caches. In addition, by caching acorns beneath litter and in the ground rodents greatly increase the probabilities of germination and of seedling emergence. Lastly, rodent responses to acorn size appear to further benefit oak recruitment; larger acorns that are inherently more likely to successfully produce seedlings are dispersed further from the parent and are more likely to be cached and to survive in caches than smaller acorns. Combined with the very large number of acorns handled by rodents, this preliminary assessment suggests that rodents at the very least are moderately effective local dispersers of Holm oak acorns at our study site.

In fact, rodents play a critical role in the population dynamics of Holm oaks. While jays move acorns long distances, carrying them outside oak woodlands and caching them in very suitable microsites (Gómez 2003), rodents move seeds only very short distances and almost exclusively within the same oak woodland. Indeed, rodents are virtually the only local-scale dispersal agents. The two distinct types of dispersal agents create a stratified dispersal system for Holm oak metapopulations in our study site, with jays promoting the colonization of new patches and rodents promoting local subpopulation regeneration and dynamics. Such a stratified dispersal system is probably typical of oaks and many other nut-bearing trees dispersed by both jays and rodents.

Acknowledgments

Janis Boettinger, Manuel Huertas, Rocío Márquez, Ángel Navarra and Joaquín Sánchez provided important help in the field. Financial support was provided by the Spanish Ministry of Science and Education grant REN2003-07048 and a doctoral fellowship AP2003-2444. Red de Jardínes Botánicos de Andalucía (Junta de Andalucía) and the headquarters of the Sierra Nevada National Park gave constant support and facilities for field work.

References

Alcantara JM, Rey PJ, Sánchez-Lafuente AM, Valera F. 2000. Early effects of rodent post-dispersal seed predation on the outcome of the plant-seed disperser interaction. Oikos 88: 362-370.

Bates D. 2005. Fitting linear mixed models in R. R News 5: 27-30.

Bonfil C. 1998. The effect of seed size, cotyledon reserves, and herbivory on seedling survival and growth in *Quercus rugosa* and *Q. laurina* (Fagaceae). American Journal of Botany 85: 79-87.

Bossema I. 1979. Jays and oaks: an eco-ethological of a symbiosis. Behavior 70: 1-117.

Cheng J, Xiao Z, Zhang Z. 2005. Seed consumption and caching on seeds of three sympatric tree species by four sympatric rodent species in a subtropical forest, China. Forest Ecology and Management 216: 331-341.

Clark J, Fastie C, Hurtt G, Jackson S, Johnson C, King G, Lewis M, Lynch J, Pacala S, Prentice C, Schupp EW, Webb III T, Wyckoff P. 1998. Dispersal theory offers solutions to Reid's paradox of rapid plant migration. BioScience 48: 13-24.

Darley-Hill S, Johnson WC. 1981. Acorn dispersal by the blue jay (*Cyanocitta cristata*). Oecologia 50: 231-232.

Den Ouden J, Jansen PA, Smit R. 2005. Jays, mice and oaks: predation and dispersal of *Quercus robur* and *Q. petraea* in north-western Europe. In: Forget P-M, Lambert JE, Hulme PE, Vander Wall SB (eds) Seed Fate: predation, dispersal and seedling establishment. CABI International. Wallingford, Oxfordshire, UK. pp 223 – 240.

Díaz M, Torre I, Peris A, Tena L. 2005. Foraging behavior of wood mice as related to presence and activity of genets. Journal of Mammalogy 86: 1178-1185.

Espelta JM, Riba M, Retana J. 1995. Patterns of seedling recruitment in west Mediterranean coppiced holm-oak (*Quercus ilex* L.) forests as influenced by canopy development. Journal of Vegetation Science 6: 465-472.

Fedriani JM, Manzaneda A. 2005. Pre- and postdispersal seed predation by rodents: balance of food and safety. Behavior Ecology 16:1018-1024

Focardi S, Capizzi D, Monetti D. 2000. Competition for acorns among wild boar (*Sus scrofa*) and small mammals in a Mediterranean woodland. Journal of Zoology 250: 329-334

Forget PM, Lambert JR, Hulme PE, Vander Wall SB. 2005. Seed fate: predation, dispersal and seedling establishment. CABI Publishing. Wallingford, Oxfordshire, UK.

García D, Bañuelos MJ, Houles G .2002. Differential effects of acorn burial and litter cover on *Quercus rubra* recruitment at the limit of its range in eastern North America. Canadian Journal of Botany 80: 1115-1120

Gómez JM. 2003. Spatial patterns in long-distance dispersal of *Quercus ilex* acorns by jays in a heterogeneous landscape. Ecography 26: 573–584

Gómez JM. 2004a. Importance of microhabitat and acorn burial on *Quercus ilex* early recruitment: non-additive effects on multiple demographic processes. Plant Ecology 192: 287-297

Gómez JM. 2004b. Bigger is not always better: Conflicting selective pressures on seed size in *Quercus ilex*. Evolution 58:71-80

Gómez JM, García D, Zamora R. 2003. Impact of vertebrate acorn- and seedling-predators on a Mediterrean *Quercus pyrenaica* forest. Forest Ecology and Management 180: 125-134

Gómez-Aparicio L, Zamora R, Gómez JM, Hódar JA, Castro J, Baraza E. 2004. Applying plant facilitation to forest restoration: a meta-analysis of the use of shrubs as nurse plants. Ecological Applications 14: 1128–1138

Gómez-Aparicio L, Gómez JM, Zamora R, Boettinger JL. 2005a. Canopy vs. soil effects of shrubs facilitating tree seedlings in Mediterranean montane ecosystems. Journal of Vegetation Science 16: 191-198

Gómez-Aparicio L, Valladares F, Zamora R, Quero JL. 2005b. Response of tree seedlings to the abiotic heterogeneity generated by nurse shrubs: an experimental approach at different scales. Ecography 28: 757-768

Haas JP, Heske EJ. 2005. Experimental study of the effects of mammalian acorn predators on red oak acorn survival and germination. Journal of Mammalogy 86: 1015-1021

Ibáñez I, Schupp EW. 2001. Positive and negative interactions between environmental conditions affecting *Cercocarpus ledifolius* seedling survival. Oecologia 129: 543–550

Iida S. 1996. Quantitative analysis of acorn transportation by rodents using magnetic locator. Vegetatio 124: 39–43

Iida S. 2004. Indirect negative influence of dwarf bamboo on survival of *Quercus* acorns by hoarding behavior of wood mice. Forest Ecology and Management 202:257-263

Iida S. 2006. Dispersal patterns of *Quercus serrata* acorns by wood mice in and around canopy gaps in a temperate forest. Forest Ecology and Management 227: 71-78

Jensen TS, Nielsen OF. 1986. Rodents as seed dispersers in a heath-oak wood succession. Oecologia 70: 214-221

Leiva MJ, Fernández-Alés R. 2003. Post-dispersive losses of acorns from Mediterranean savanna-like forests and shrublands. Forest Ecology and Management 176: 265-271

Li HJ, Zhang ZB. 2003. Effect of rodents on acorn dispersal and survival of Liaondong oak (*Quercus liatungensis* Koidz.). Forest Ecology and Management 176: 387-396

Miriti MN. 2006. Ontogenetic shift from facilitation to competition in a desert shrub. Journal of Ecology 94: 973-979

Puerta-Piñero C, Gómez JM, Zamora R. 2006. Species-specific effects on topsoil development affect *Quercus ilex* seedling performance. Acta Oecologica 29:65-71

Pulido FJ. 2002. Biología reproductiva y conservación: el caso de la regeneración de bosques templados y subtropicales de robles (*Quercus* spp.). Revista Chilena de Historia Natural 75: 5-15

Pulido FJ, Díaz M. 2005. Regeneration of a Mediterranean oak: a whole-cycle approach. EcoScience 12: 92-102

Purves DW, Zavala MA, Ogle K, Prieto F, Rey Benayas JM. 2007. Environmental heterogeneity, bird-mediated directed dispersal, and oak woodland dynamics in Mediterranean Spain. Ecological Monographs In press.

R Development Core Team. 2006. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Retana J, Espelta JM, Gracia M, Riba M. 1999. Seedling recruitment. In: Rodá F, Retana J, Gracia CA, Bellot J (eds) Ecology of Mediterranean Evergreen Oak Forests. Springer-Verlag, Berlin, Germany, pp 89-103

Rey P, Alcántara JM. 2000. Recruitment dynamics of a fleshy-fruited plant (*Olea europaea*): connecting patterns of seed dispersal to seedling establishment. Journal of Ecology 88:622-633

Rey P, Garrido JL, Alcántara JM, Ramírez JM, Aguilera A, García L, Manzaneda AJ, Fernández R. 2002. Spatial variation in ant and rodent post-dispersal predation of vertebrate-dispersed seeds. Functional Ecology 16: 773-781

Santos T, Tellería JL. 1997. Vertebrate predation on Holm oaks, *Quercus ilex*, acorns in a fragmented habitat: effects on seedling recruitment. Forest Ecology and Management 98: 181-187.

SAS Institute Inc. (2005) SAS/STAT Software: changes and enhancements through release 6.12. Cary, NC, USA.

Scheibe JS, O'Fasrrell MJ. 1995. Habitat dynamics in *Peromyscus truei*: eclectic females, density dependence, or reproductive constraints. Journal of Mammalogy 76: 368-375

Schupp EW. 1993. Quantity, quality and the effectiveness of seed dispersal by animals. Vegetatio 107/108: 15-29

Schupp EW Suitable sites for dispersal are context dependent. In: Dennis A, Schupp EW, Green R, Westcott D (eds) Seed Dispersal: Theory and Its Application in a Changing World. CABI International, Wallingford, UK, in press.

Schupp EW, Fuentes M . 1995. Spatial patterns of seed dispersal and the unification of plant population ecology. Écoscience 2: 267–275

Seiwa K. 2000. Effects of seed size and emergence time on tree seedling establishment: importance of developmental constraints. Oecologia 123: 208-215

Sork VL. 1984. Examination of seed dispersal and survival on red oak, *Quercus rubra* (Fagaceae), using metal-tagged acorns. Ecology 65: 1020-1022

Stapanian MA, Smith CC. 1978. A model for seed scatter-hoarding: coevolution of fox squirrels and black walnuts. Ecology 59: 884–898

Stapanian MA, Smith CC. 1984. Density-dependent survival of scatterhoarded nuts: an experimental approach. Ecology 65: 1387–1396

Takahashi K, Sato K, Washitani I. 2006. The role of the wood mouse in *Quercus serrata* acorn dispersal in abandoned cut-over land. Forest Ecology and Management 229: 120-127

Tomita M, Hirabuki Y, Seiwa K. 2002. Post-dispersal changes in the spatial distribution of *Fagus crenata* seeds. Ecology 83: 1560-1565

Traveset A, Gulias J, Nieras N, Mus M. 2003. Transition probabilities from pollination to establishment in a rare dioecious species (*Rhamnus ludovici-salvatoris*) in two habitats. Journal of Ecology 91: 427-437

Tripathi RS, Khan ML. 1990. Effects of seed weight and microsite characteristics on germination and seedling fitness in two species of *Quercus* in a subtropical wet hill forest. Oikos 57: 289-296

Vander Wall SB. 1990. Food hoarding in animals. The University of Chicago Press, Chicago, USA.

Vander Wall SB, Longland WS. 2004. Diplochory: are two seed dispersers better than one? Trends in Ecology and Evolution 19: 155-161

Vieira EM, Iob G, Briani DC, Palma ART. 2005. Microhabitat selection and daily movements of two rodents (*Necromys lasiurus* and *Oryzomys scotti*) in Brazilian Cerrado, as revealed by a spool-and-line device. Mammalian Biology 70: 359-365

Xiao Z, Zhang Z, Wang Y. 2004. Dispersal and germination of big and small nuts of *Quercus serrata* in a subtropical broad-leaved evergreen forest. Forest Ecology and Management 195: 141–150.

Xiao Z, Zhang Z, Wang Y. 2005. Effects of seed size on dispersal distance in five rodent-dispersed fagaceous species. Acta Oecologica 28: 221-229

Xiao Z, Jansen PA, Zhang Z. 2006a. Using seed-tagging methods for assessing post-dispersal seed fate in rodent-dispersed trees. Forest Ecology and Management 223: 18-23

Capítulo 1

Xiao Z, Wang Y, Harris M, Zhang Z. 2006b. Spatial and temporal variation of seed predation and removal of sympatric large-seeded species in relation to innate seed traits in a subtropical forest, Southwest China. Forest Ecology and Management 222: 46-54.

CHAPTER 2

Spatial patterns of acorn dispersal by rodents: Does the environment matter?

Si supiese que es lo que estoy haciendo,

no lo llamaría investigación, ¿verdad?

A. Einstein

Puerta-Piñero C, Gómez JM, Schupp EW. In preparation.

Capítulo 2

Abstract. The spatial distribution of dispersed seeds is a factor highly influencing their establishment probability. Thereby, seed disperser effectiveness may depend on the seed shadow they create. Any factor affecting the spatial distribution of seeds may also modify the disperser effectiveness. In this study, we investigate whether the seed shadow created by seed-caching dispersers depends on the presence of other competitors, the type of microhabitat and the future seed fate. For this study, we used as study system Holm-oaks Quercus ilex, a Mediterranean tree dispersed by rodents and birds. Our experiments were conducted within oak woodlands in two contrasting acorn crop years and both inside and outside enclosures of ungulate acorn consumers that compete with rodents. There were clear differences in spatial patterns between years and enclosure treatments. During large crop years seed dispersal is more clumped than in lower crop years. In the presence of competing ungulates seed dispersal was sparser than in their absence. Interestingly, we found strong effect of acorn fate and microhabitat of destination on dispersal pattern. Acorns cached for future consumption are distributed in less density and with bigger distances between them than acorns eaten immediately. In addition, rodents aggregated the acorns with different intensity in different microhabitats. This will entails important differences in the quality component of the dispersal effectiveness between years, exclosure traits, microhabitats and acorn fate and will have important consequences for further oak recruitment and establishment.

Keywords: Diggle´s G, masting, point patterns statistic, *Quercus ilex,* Ripley´s K, risk aversion, seed shadow, disperser effectiveness.

Introduction

Dispersal effectiveness, defined as the contribution of a disperser to the recruitment of a plant, has both a quantitative and a qualitative component (Schupp 1993; Jordano and Schupp 2000). Quantitatively, a disperser is effective if it disperses many seeds. Qualitatively, an effective disperser is that increasing recruitment probability of dispersed seeds. Several aspects of the qualitative component of dispersal effectiveness have been emphasized in empirical studies. Of these, the dispersal distance (e.g. Vander Wall 1990; Jordano and Schupp 2000; Forget et al. 2005; Jordano et al. 2007, Spiegel and Nathan 2007, Gómez et al. 2008), and the microsite, microhabitat, or habitat deposition (e. g. Jordano and Schupp 2000; Wenny 2001; Vander Wall 2001, 2002; Hollander and Vander Wall 2004; Muñoz and Bonal 2007; Gómez et al. 2008), have probably received the most attention. In contrast, a variety of potentially important measures of the quality of dispersal have received much less consideration. Among these, the spatial pattern of the deposited seeds, in terms of aggregation or segregation among dispersed propagules (e. g. Russo and Augspurger 2004) has only begun to be assessed quantitatively (Moore et al. 2007). Whether seed deposition has a clumped, random or homogeneous distribution will have important consequences for plant fate (Satterthwaite 2007). For example, seeds deposited in clumps are more likely to suffer from several hazards, like intraspecific competition, post-dispersal seed and seedling predation, pathogen attack, and allelopathy, (Augspurger and Kelly 1984; Howe 1989; Inderjit 1999; Harms et al. 2000; Schupp et al. 2002; Callaway and Howard 2006). However, if the habitat is intrinsically heterogeneous in conditions and resources, clumped dispersal to favorable microsites could benefit establishment (Grubb 1977; Muller-Landau et al. 2000). Thus, the population-level spatial pattern of seed dispersal is potentially a critical determinant of disperser effectiveness. In addition, because the potential negative effects of clumping are driven by near-neighbor interactions and small-scale density dependence, it is important to consider the distances between dispersed propagules independent of the type of dispersal kernels generating them.

Seed-caching rodents and birds tend to distribute the seeds at random or sparsely, in order to impede the pilfering of caches by other seed consumers (Stapanian and Smith 1978, 1984; Vander Wall 1990; Male and Smulders 2007). Neither the spatial patterns of dispersal nor the distances between dispersed seeds are fixed characteristics of a species of disperser, however, so it is also important to consider the ecological context in which dispersal occurs. Thus, the spatial pattern of seed dispersal might vary greatly depending on the abundance and composition of the community of competitors potentially pilfering caches, although to our knowledge this has been poorly investigated (but see Muñoz and Bonal 2007). Dispersal behavior can also differ depending on whether the seed is going to be immediately consumed or will be cached for later consumption (Vander Wall 1990; Li and Zhang 2003; Jansen et al. 2004). Furthermore, dispersers often forage for and cache seeds in specific locations, and rarely use all the available microhabitats at random (Schupp 1993; Giannoni et al. 2001; Vander Wall 2002; Gómez 2003; Pearson and Theimer 2004; Muñoz and Bonal 2007; Pons and Pausas 2007b; Gómez et al. 2008). In heterogeneous systems those sites to which seeds are disproportionately dispersed are themselves sited in a specific spatial location that normally entail different microhabitats. Different microhabitats frequently differ in seedling emergence and performance (Vander Wall 2002; Gómez 2004; Puerta-Piñero et al. 2007; Schupp 2007). So, it would be essential to know if the spatial patterns of seed deposition differs among microhabitats (Muñoz and Bonal 2007). Finally, in masting species the size of the seed crop can affect seed dispersal (see references in Vander Wall 1990). Effects of seed crop size on dispersal have been principally reported in terms of number of seeds dispersed (Schnurr et al. 2002; Jansen et al. 2004), the speed of dispersal (Vander Wall 2002; Jansen et al. 2004), and the distances dispersed (Vander Wall 2002; Xiao et al. 2005; Moore et al 2007). To our knowledge few studies have focused on the effects of differences in crop size on the spatial pattern of dispersed seeds (but see Moore et al. 2007).

The degree to which the study of spatial patterns allows the inference of underlying processes has been widely discussed (Levin 1992). Plant spatial patterns results from many processes that can operate simultaneously and even interact with each other (Harper 1977). Seed dispersal is the first process that creates the template for plant spatial distributions (Schupp and Fuentes 1995; Schupp et al. 2002; Russo and Augspurger 2004). After seed deposition, other processes such as intra- and interspecific competition, post dispersal predation, secondary dispersal, herbivory, pathogens, etc. can moderately or radically restructure this primary spatial distribution (Jordano and Herrera 1995; Schupp and Fuentes 1995; Muller Landau et al. 2000). Many of these interacting processes can lead to the same or at least very similar final observed spatial pattern. Thus, it is necessary considering the mechanisms producing the spatial patterns. The seed dispersal kernel has been extensively investigated in a wide variety of systems (Nathan and Muller-Landau 2000; Jordano and Godoy 2002; Nathan et al. 2002; Kwit et al. 2007; Nathan 2007). However, even as the amount of information increases on the mechanisms underlying seed dispersal, there has been little success linking the spatial pattern of the seed shadow with the plant spatial distribution (but see Russo and Augspurger 2004).

There are four fundamental hypotheses in this study. First, in tree species with masting reproduction, strong differences among years in seed production translate into different spatial patterns of seed dispersal. Second, due to risk aversion, rodents will alter the spatial pattern of acorn dispersal (caching) depending on the presence or absence of competing acorn consumers such as large ungulates. Third, rodents will disperse acorns in different patterns depending on whether they are going to cache the acorn or consume it immediately. Fourth, the pattern of acorn dispersal by rodents will be affected by the microhabitat to which they disperse the acorns. Under these hypotheses, our main objectives were to determine: 1) the spatial pattern of seed dispersal by rodents in a heterogeneous system; 2) whether the patterns differ among years with different crop sizes and among enclosure treatments that alter the community of competitors for acorns, and 3) whether rodents create different spatial patterns of dispersed acorns depending on the microhabitat to which acorns are dispersed and whether the acorns are cached or consumed. For these purposes, as most statisticians suggest (Ripley 1981, Diggle 1979; Barot et al. 2004), we have used two functions simultaneously. First, Ripley´s K function (Ripley 1981) tests the spatial distribution by counting the number of points within an area (density) at different radii from the origin. Second, the Diggle´s G function (Diggle 1979) considers the distance between each point and its nearest neighbor. As a model system, we consider a heterogeneous landscape composed of oak woodland patches (*Quercus ilex* L.; the Holm oak) intermingled with pine woodlands (*Pinus* spp.) and shrubland patches. Oak woodland patches, the focus of this study, are internally heterogeneous with *Q. ilex* clumps or clones mixed together with different species of shrubs, pines, and open spaces. *Quercus ilex* are dispersed by rodents (Muñoz and Bonal 2007; Pons and Pausas 2007a), mainly the woodmouse *Apodemus sylvaticus* (Gómez et al. 2008), and the Eurasian jay *Garrulus glandarius* (Gómez 2003; Pons and Pausas 2007b). Our experiments were conducted within oak woodlands in two contrasting acorn crop years and both inside and outside of enclosures that exclude ungulate acorn consumers that compete with rodents.

Materials and Methods

Study species and sites

Quercus ilex is a masting evergreen tree abundant in the Mediterranean region. From late October through early December acorns are consumed by a number of vertebrate species, including the Eurasian jay, wild boar (*Sus scrofa*), woodmouse, and red squirrel (*Sciurus vulgaris*) (Gómez 2003; 2004; Pulido and Díaz 2005; Muñoz and Bonal 2007, Gomez et al. 2008). Jays and rodents are also seed dispersers; whereas rodents move the seeds at local, small spatial scales, jays tend to move the seeds at larger spatial scales (Gómez 2003, Muñoz and Bonal 2007, Gómez et al. 2008).

The study site is located in the Sierra Nevada protected area, SE Spain (37° 5' N, 3° 28' W), from 1550 to 1800 m a.s.l. Climate is continental Mediterranean, with cold winters, hot summers, and severe summer drought. Mean annual temperature is 11.5°C. Precipitation, mostly as rain in autumn and spring totals 825 mm/year. The landscape is a mosaic of mixed oak-pine woodlands, several dense pine afforestations, and extensive shrublands (see Gómez 2003 for a detailed description). Within this landscape we focused on “oak woodlands,” comprised of small patches of oak clones or clumps intermingled with isolated pines, tall shrubs

(>0.5 m tall), sub-shrubs (about 30 cm high), and open areas. We considered four microhabitat types within oak woodlands: (1) “oak,” under the canopy of *Q. ilex*; (2) “pine,” under the canopy of a pine tree; (3) “shrub,” under the canopy of any of a variety of shrub species; and (4) “open,” bare soil with relatively sparse herbaceous cover.

Experimental design

We haphazardly selected a sample of 68 Holm oaks trees (hereafter called acorns supply points) to monitor the spatial pattern of acorn dispersal by rodents. Some of supply points (40) were located inside a 12- ha exclosure made in 1982 with a fence of 2-m height to exclude ungulates while allowing the passage of rodents predators. This fact is important to allow assigning any effect of the exclosure to the absence of ungulates without any confounding effect of a parallel decrease in predation pressure.

Experiments were set up in 2003, a year with abundant acorn production and in 2004, a year with low acorn-production. We used a semi-quantitative scale, ranging from 0 (no acorns) to 4 (more than 90% of the branches full with acorns) in a subset of 50 trees in 2003 and 250 trees in 2004. The year 2003 had values of 1.83±1.25,Mean±SD, Median=2, skewness= 0.20, kurtosis= -0.97 while 2004 had values of 0.85±0.58, Median= 1, skewness=0.31, kurtosis= 1.06; being both years statistically different (p=0.009, χ^2 = 26.452; U=0.32) in acorn production. Experiments were initiated in November during the natural dispersal period and lasted until the following spring when seedling emergence occurs. In 2003, we monitored a total of 450 acorns in 18 supply points, 10 inside the exclosure and eight outside the enclosure (25 acorns/supply point). In 2004 we monitored 1500 acorns, in 50 supply points (30 acorns/supply point) 20 inside the enclosure and 30 outside the enclosure. Acorns were placed on the ground and covered with a metal cage of 1cm^2 sieve of 0.5 x 1.0 x 0.1 m (wide x length x height dimensions), open on two opposing sides to allow the entrance of rodents but not ungulates or jays. Acorns were individually numbered and attached to a metal wire (8 cm long, 0.6 mm diameter) with a flag (see Gómez et al. 2008 for a complete description of the methods). This marking method does not affect seed dispersal by rodents (Xiao et al.2006a).

When rodents buried acorns in the soil, the flagging remained exposed on the surface making easy their relocation (Xiao et al. 2004). We conservatively considered an acorn to be dispersed only when it was moved >50 cm from the original supply point. We began censuses at supply points and searched outwards in expanding circles. When finding an acorn, we recorded (1) the distance (in cm) and direction (in degrees) from the supply point, (2) the microhabitat of deposition (oak, pine, shrub, open), and (3) its fate, considering two categories (eaten, cached).

Quantification of acorn spatial pattern

We firstly determined the position (in a cartesian coordinate system) of each dispersed acorn in the appropriate circular plot that corresponded to a given supply point (N=68) (see Fig. 1 for an example and appendix A for all the maps). For each plot we considered a radius equal to the maximum dispersal distance from that supply point observed in the field, so each plot had a different radius and area. With this approach each plot included the total dispersed acorns found in the field.

We therefore fitted the spatial trend of each supply point (see Fig. 1 on the right for an example of this trend) and used this trend to compute the inhomogeneous Ripley´s K and Diggle´s nearest neighbor G for the total observed acorns at each supply point (Ripley 1973; 1981; Diggle 1979; Baddeley and Turner 2005). The tests involve two complementary functions based on: (1) the average number of points located within an area for a given distance from the supply point (Ripley´s K function, K(r) hereafter) and (2) the distance between each point of the observed sample and its nearest neighbor (Diggle´s G function, G(r)). As we considered all the acorns per supply points we did not compute any edge correction (Wiegand et al. 2007).

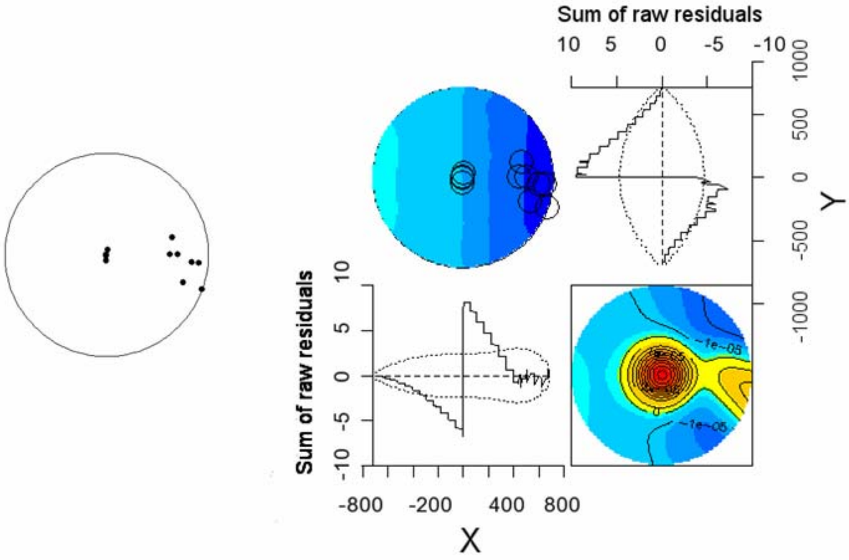


Figure 1. Example of the observed acorn dispersal pattern in a supply point (left) and its correspondent fitted trend (right). Note that the sums of raw residuals on both dimensions (X and Y) are cumulative.

We then compared each observed distribution to an inhomogeneous Poisson process with the same area and number of acorns (H0: complete spatial randomness, CSR) to see if the spatial pattern followed a random, clumped or homogeneous distribution. Tests of significance were estimated by a Monte Carlo procedure using 200 permutations (Wiegand et al. 2007). Rejection limits were estimated as the envelopes of the simulation. If the observed distribution was above the confidence intervals the distribution was considered as clumped, within the confidence intervals as random, and below the intervals as homogeneous. The two tests have different sensitivities to different types of spatial distributions (Diggle 1979); G(r) is a better detector of regularity while K(r) has the advantage of being density-independent (Barot et al. 1999). Because it is highly recommended to use various methods simultaneously (Ripley 1981, Diggle 1979) we performed all the analyses for both K (r) and G(r) and then compared the results.

Finally, when the null hypothesis (CSR) was rejected, we followed Barot et al. (1999) suggestions and computed the maximum discrepancy distance (*dmax*) between the theoretical and observed Ripley´s K and Diggle´s G functions (*dmax K* and *dmax G*, respectively) and subsequently used them as dependent variables. For clumped patterns, *dmax* is an indication of clump “compactness”. For example in the case of G(r), it measures the average distance between points within a clump (Barot et al. 1999). Thus, the larger the value of *dmax* the less “compact” the spatial distribution of the acorns and vice versa (Barot et al. 1999).

We performed all the spatial computations using spatstat (Baddeley and Turner 2005).

Statistical analysis

General Linear Mixed Models (GLMM) were used to explore the effects of enclosure and year on the spatial pattern of the acorns as measured by *dmax*. Year was considered as a random factor and enclosure as fixed factor. Response variables were previously transformed to improve normality using log or arcsin(square root). Significance of the random factor was calculated by comparing models with and without the random factor (Pinheiro and Bates 2000). Data were analyzed using R (R development core Team 2007).

Afterward, we used the information of the fate and the microhabitat destination (namely marks) of each acorn to fit two different models using the trends of the marks. After that, we calculated Ripley´s inhomogeneous K and the maximum discrepancy distance for acorn fate (*dmax KF*) and microhabitat (*dmax KM*), and fitted the same GLMM as described above.

Finally, we divided the acorns per supply point into eaten vs. cached acorns and separately computed the inhomogeneous K(r) and G(r) functions and separately calculated *dmax K* and *dmax G* for each of these categories. After that, we fitted models considering fate as independent variable and *dmax K* and *dmax G* as dependent variables.

Results

Spatial pattern of acorn dispersal

All the point patterns presented per supply points had a clumped spatial distribution (see Appendix A for visual inspection of the patterns). Results were the same, thus clumped spatial patterns, considering the Ripley´s K or the Diggle´s G function ($p<0.05$ in all the cases).

Differences among years and enclosure effects

Both K (r) and G (r) functions showed analogous results. There were significant differences between years in *dmax K* (Table 1, Fig. 2), being higher in 2004 (1209.0±167.5, mean ± SE) than in 2003 (212.0±273.5). That is to say, in 2004 the spatial pattern of dispersed acorns was less compactness that in 2003. The same pattern was found considering *dmax G* with higher values in 2004 (0.80±0.02) than in 2003 (0.68±0.03). Thus, 2004 had less compactness distances between nearest neighbors than 2003 (See Fig 2).

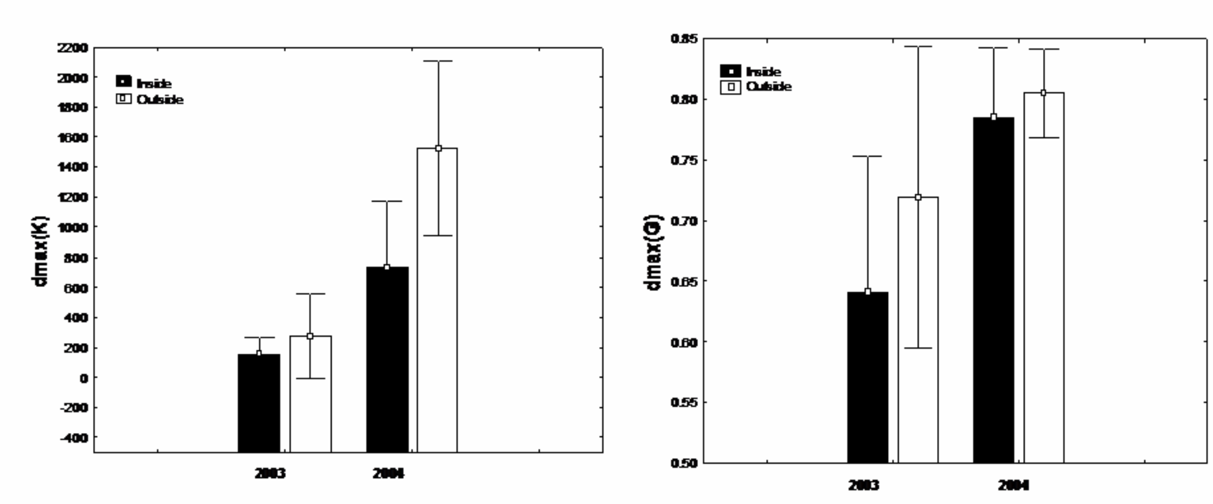


Figure 2: Mean values and Standard error between years and exclosure treatments (inside vs. outside the exclosure). Bars indicate the maximum discrepancy distance between the observed and theorethical spatial pattern (dmax) for Ripley´s K (left) and Diggle´s G (right).

Although there were differences in mean values inside and outside the exclosures both for *dmax G* (with mean values of 0.74±0.06 and 0.79±0.06 for *dmax G*) and *dmax K*, respectively), results were only marginally significant for *dmax K* (Table 1). Inside the exclosure mean *dmax K* was 555.6±484.2, whereas outside the exclosure mean *dmax K* was 1261.6±477.1. In other words, the density of the acorns was higher inside than outside the exclosure. Thus, outside the enclosure the dispersed acorns were more sparsely distributed than inside the enclosure.

The percentage of variance of the model explained by the random factor (year) for *dmax K* and *dmax G* was 20.5% and 29.7%, respectively.

Effects of acorn fate and microhabitat destination

Surprisingly, for the model fitting considering the mark of acorn fate there were strong mean differences between years and exclosure. In 2004 *dmax KF* was 1208.8±167.5, while in 2003 it was 354.4±268.2. Thus, 2004 had a less compactness distribution of the acorns than 2003. Inside the exclosure *dmax KF* was 602.2±420.94 while outside was 1289.4±418.60. Hence, the distribution of acorns was sparer in the presence than in the absence of ungulates. However, after fitting the model there was no significant effect either of year or exclosure (Table 1).

Table 1. Dispersal spatial patterns and year and exclosure treatments.

		dmax (K)		**dmax(G)**		**dmax(KF)**		**dmax(KM)**	
	df	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**
Year	1		<0.05		<0.05		ns		<0.05
Exclosure	1	3.793	0.056	1.207	0.276	2.586	0.113	2.605	0.111
R^2_{adj}	66	0.146		0.155		0.118		0.097	

Result of the general linear mixed model. Response variables were previously log or arcsin transformed. The factor Year was considered as random and Enclosure as fixed. In all the cases the best model in terms of Akaike Information Criterion (AIC) was the model containing the random factor (p<0.05 contrasting models with and without the random factor).

There were significant between-year differences in *dmax* considering the microhabitat destination of the acorns. In 2003 the observed spatial pattern of the dispersed acorns was on average more compactness (*dmax KM* = 261.0±656.3, mean ± SE) than in 2004 (*dmax KM* = 2334.6±409.4). Although *dmax KM* was smaller inside than outside the exclosure (1011.0±1038.8 and 2417.0±1033.2, respectively), indicating less compactness in ungulate absence than in presence of ungulates, there was no significant effect of exclosure (Table 1). Then again, considering the AIC, in all cases the best models were those containing the random factor (year). The percentage of the variance of the model explained by the random factor (Year) was 14.6% for *dmax KF* and 14.9% for *dmax KM*.

There was a strong correlation between *dmax KF* and *dmax KM*, suggesting some sort of spatial relationship between acorn fate and microhabitat destination (Fig 2).

Finally, there were significant differences of eaten vs cached acorns in *dmax G* (R^2= 0.22, P<0.001) (Table 2). The distance between neighbor cached acorns was higher than the distance between eaten acorns (Table 2), as indicated by the *dmax G* values (cached acorns= 0.73± 0.03, eaten acorns= 0.38 ±0.03). Despite of the noticeable differences between *dmax K* for eaten (1185.9 ± 163.7, Mean ± SE) and cached acorns (967.4 ± 117.5, Mean ± SE), the model for *dmax K* considering the fate of the acorns was not significant (Table 2) .

Table 2. Seed fate and spatial dispersal pattern.

		dmax(K)		dmax(G)	
	df	**F**	**p**	**F**	**p**
Fate	1	1.18	0.28	76.19	<0.0001
R^2_{adj}		0.001		0.22	

Results of the general linear model including the fate of the acorns (eaten vs. cached) as predictor variable and the spatial pattern as response variables.

Discussion

There were clear differences in spatial patterns between years and exclosure treatments. Our results suggest that during large crop years seed dispersal is more clumped than in small crop years. On the other hand, in the presence of competing ungulates seed dispersal was sparser than in the absence of them. There are many studies showing that different seed crops can lead into differences in seed dispersal patterns (Janzen 1970; see references in Herrera et al. 1998 and Kelly 1994). Those differences have been reported in a variety of ecosystems from tropics (Wilson and Janzen 1972; Li and Zhang 2007) to temperate forests (Jordano and Schupp 2000; Vander Wall 2002; Moore et al.2007). Masting events have been reported to influence the rate of seed dispersal (number of seed dispersed from the total seed crop), the dispersal distance (Vander Wall 2002; Moore et al.2007) and even the velocity of dispersal (Vander Wall 2002) or the microsites of deposition of the seeds (Jordano and Schupp 2000). Though, to our knowledge, this is a pioneer study finding differences in the spatial pattern of seed dispersal using distance between neighbor seeds and density-dependence spatial patterns.

As far as we know, the risk aversion hypothesis (Safir et al. 1999) by far has been less explored in terms of its consequences on seed dispersal patterns. Foraging by frugivores has rarely been studied within the framework of foraging theory (Fedriani and Boulay 2006; Ohgushi et al. 2007). It has been suggested that the foraging behavior is highly correlated with coefficients of variation and the unpredictability of the food supply (Safir 2000). And thus, lead to a risk sensitive foraging in the majority of the cases studied (Safir et al. 1999; Roche et al. 1997; Safir 2000), including Apodemus sylvaticus (Fedriani and Boulay 2006; Díaz et al. 2005) with a tendency to avoid the risk (Wirsing et al. 2007) and preferences for constant food rather than variable food patches (Roche et al. 1997). In our study, it appears that rodents sparse the acorns more in the presence of big ungulates. Recent studies have reported that ecological factors can change *Apodemus sylvaticus* foraging behavior (Díaz et al. 2005; Fedriani and Boulay 2006). Wood mice showed spatial and temporal changes in foraging behavior under predation risk affecting decisions about how often and how long to forage (Díaz et al. 2005). On the other hand, the abundance and distribution of resources determined foraging in terms of microhabitats used (Fedriani and Boulay 2006). Our results support these findings and extrapolated these foraging decisions s*ensu lato* to their acorn caching behaviour. In our system, rather than escaping from predators, rodents try to avoid the risk of loosing their food item by other acorn consumers. So, as Díaz et al. (2005) and Fedriani and Boulay (2006) found that *A. sylvaticus* changed their foraging tactic in the presence of predators or food availability, we found, that rodents modified their caching behavior to avoid competitors steal their valuable food for scarcer seasons.

More interestingly, we found strong effect of acorn fate and microhabitat of destination on dispersal pattern. Rodents dispersed the acorns in a different way whether they were to consume or cache them. Acorns for future consumption will be distributed in less density and with bigger distances between them than acorns eaten immediately. This behavior will have important consequences for further oak fitness. In addition, rodents aggregated the acorns with different intensity in different microhabitats. Unfortunately, our analysis cannot distinguish between different microhabitats because in many supply points the majority of the acorns were disperse to the same microhabitat. But, it is certain that our results showed that the marks of the microhabitat had clear influences on both Ripley´s inhomogeneous K and on Diggle´s G. Many studies have shown different dispersal patterns among microhabitats in terms of rate of dispersal (Jordano and Herrera 1995; Castro et al. 1999; García et al. 2000; Rey and Alcántara 2000; Gómez-Aparicio et al. 2005; Russell and Schupp 1998; Jordano and Schupp 2000; Muñoz and Bonal 2007; Gómez et al. 2008). Our results support these studies and add further differences in densities and distances between neighbor acorns.

Seed dispersal effectiveness, in terms of spatial dispersed pattern, was associated on the one hand with crop and risk aversion by rodents and on the other hand with microhabitat of destination and the fate of the seedlings. This will entails important differences in the quality component of the dispersal effectiveness between years, exclosure effects, microhabitats and acorn fate. Thus, according to our estimates, we will expect having high-quality dispersal (so, less acorn density and more distance between dispersed acorns) during low crop years, in presence of competitors and when acorns are cached for future consumption. From the acorn/seedling viewpoint we can report that there were differences in the distances between neighbor seeds between microhabitats. Different microhabitats have been widely reported to entail differences in terms of abiotic characteristics such as soil, moisture, light, etc., (Gómez 2004; Gómez-Aparicio et al. 2005; Puerta-Piñero et al. 2007). Those features often translate into differences in oak recruitment (Puerta-Piñero et al. 2007). Our results suggest that different microhabitats will also present contrasting intensity of biotic interactions such as competition or post-dispersal seed and seedling predation (Russell and Schupp 1998; Satterthwaite 2007; In fact, in the study site there are many studies supporting our findings (Castro et al. 1999; Gómez 2004; Gómez et al. 2003; Gómez-Aparicio et al. 2005; García et al. 2000; García 2001). On the other hand, from the population viewpoint we would like to account two main concerns. First, cached acorns are dispersed sparser than eaten acorns suggesting the possibility of the spread of the population. It is also appealing that acorns were dispersed sparser in the presence of higher competitors. Second, there are some microhabitats with more success than others, so changes in the spatial distribution of the species can occur in the long term.

Acknowledgements

We deeply appreciate the guidance of Marcelino de la Cruz through the statistical analysis of spatial point patterns. Janis Boettinger, Manuel López de las Huertas, Ángel Navarra and Joaquín Sánchez provided important help in the field. Financial support was provided by the Spanish Ministry of Science and Education grant REN2003-07048 and a doctoral fellowship AP2003-344. Red de Jardínes Botánicos de Andalucía (Junta de Andalucía) and the headquarters of the Sierra Nevada National Park gave constant support for field work.

References

Augspurger CK, Kelly CK. 1984. Pathogen mortality of tropical tree seedlings - experimental studies of the effects of dispersal distance, seedling density, and light conditions. Oecologia 61: 211-217.

Baddeley A, Turner R. 2005. Spatstat: an R package for analyzing spatial point patterns. Journal of Statistical Software 12 (6), 1-42. ISSN: 1548-7660. URL: www.jstatsoft.org

Barot S, Gignoux J, Menaut JC. 1999. Demography of a savanna palm tree: predictions from comprehensive spatial pattern analyses. Ecology 80: 1987-2005.

Callaway RM, Howard TG. 2006 Competitive networks, indirect interactions, and allelopathy: a microbial viewpoint on plant communities. Progress in Botany 68: 315-335.

Castro J, Gómez JM, García D, Zamora R, Hódar JA. 1999. Seed predation and dispersal in relict Scots pine forests in southern Spain. Plant Ecology 145: 115-123.

Diaz M, Torre I, Peris A, Tena L. 2005. Foraging behavior of wood mice as related to presence and activity of genets. Journal of Mammalogy 86: 1178-1185.

Diggle PJ. 1979. On parameter estimation and goodness-of-fit testing for spatial point patterns. Biometrics 35: 87-101.

Fedriani JM, Boulay R 2006. Foraging by fearful frugivores: combined effect of fruit ripening and predation risk. Functional Ecology 20: 1070-1079.

Forget PM, Lambert JR, Hulme PE, Vander Wall SB. 2005. Seed fate: predation, dispersal and seedling establishment. CABI Publishing. Wallingford, Oxfordshire, UK.

García D. 2001. Effects of seed dispersal on Juniperus communis recruitment on a Mediterranean mountain. Journal of Vegetation Science. 12: 839-848.

García D, Obeso JR, Martínez I. 2000. Spatial concordance between seed rain and seedling establishment in bird-dispersed trees: does scale matter? Journal of Ecology 93: 693-704.

Gómez JM, García D, Zamora R. 2003. Impact of vertebrate acorn- and seedling-predators on a Mediterranean *Quercus pyrenaica* forest. Forest Ecology and Management 180: 125-134.

Gómez JM, Puerta-Piñero C, Schupp EW. 2008. Effectiveness of rodents as local seed dispersers of an oak with a stratified dispersal system. Oecologia, In press.

Gómez JM. 2003. Spatial patterns in long-distance dispersal of *Quercus ilex* acorns by jays in a heterogeneous landscape. Ecography 26: 573–584

Gómez JM. 2004. Importance of microhabitat and acorn burial on *Quercus ilex* early recruitment: non-additive effects on multiple demographic processes. Plant Ecology 192: 287-297.

Gómez-Aparicio L, Gómez JM, Zamora R. 2005. Microhabitat shift rank in suitability for seedling establishment depending on habitat type and climate. Journal of Ecology 93: 1194-1202.

Harms KE, Wright SJ, Calderon O, Hernandez A, Herre EA. 2000. Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. Nature 404: 493-495

Herrera CM, Pellmyr O. 2001. Plant-Animal Interactions. Blackwell Science, Oxford, UK.

Hollander JL, Vander Wall SB. 2004. Effectiveness of six species of rodents as dispersers of singlleaf piñon pine (*Pinus monophylla*). Oecologia 138: 57-65.

Howe HF, Smallwood J. 1982. Ecology of seed dispersal. Ann. Rev. Ecol. Syst. 13: 201-228.

Howe HF. 1989. Scatter-dispersal and clump-dispersal and seedling demography: hypothesis and implications. Oecologia 79: 417-426

Jordano P, García C, Godoy JA, García-Castaño JL. 2007. Diferential contribution of frugivores to complex seed dispersal patterns. Proc. Natl Acad. Sci. U S A, 104, 3278–3282.

Jordano P, Herrera CM. 1995. Shuffling the offspring - uncoupling and spatial discordance of multiple stages in vertebrate seed dispersal. Ecoscience 2: 230-237.

Jordano P, Schupp, EW. 2000. Seed disperser effectiveness: the quantity component and patterns of seed rain for Prunus mahaleb. Ecological Monographs 70: 591–615.

Levin SA. 1992. The problem of pattern and scale in ecology: the Robert H. MacArthur award lecture. Ecology 73: 1943-1967.

Li HJ, Zhang ZB. 2003. Effect of rodents on acorn dispersal and survival of Liaondong oak (*Quercus liatungensis* Koidz.). Forest Ecology and Management 176: 387-396

Moore JE, McEuen AB, Swihart RK, Contreras TA, Steele MA. 2007. Determinants of seed removal distance by scatter-hoarding rodents in deciduous forests. Ecology 88: 2529-2540.

Muñoz A, Bonal R. 2007. Rodents change acorn dispersal behaviour in response to ungulate presence. Oikos 44: 157-164.

Nathan R, Muller-Landau H. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. Trends in Ecology and Evolution 15: 278- 285.

Ohgushi T, Craig T P, Price PW. 2007.Ecological communities: Plant mediation in indirect interaction webs. CUP.

Pinheiro J, Bates D, DebRoy S, Sarkar D. 2006. nlme: Linear and nonlinear mixed effects models. R package version 3.1-79.

Pinheiro JC, Bates DM. 2000. "Mixed-Effects Models in S and S-PLUS", Springer.

Pons J, Pausas JG. 2007a. Rodent acorn selection in a Mediterranean oak landscape. Ecological research 22: 1440-1703.

Puerta-Piñero C, Gómez JM, Zamora R. 2006. Species-specific effects on topsoil development affect *Quercus ilex* seedling performance. Acta Oecologica 29:65-71

Pulido FJ, Díaz M. 2005. Regeneration of a Mediterranean oak: a whole-cycle approach. EcoScience 12: 92-102

R Development Core Team. 2007. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Rey PJ, Alcántara JM. 2000. Recruitment dynamics in a fleshy-fruited plant (Olea europaea ar.sylvestris): connecting patterns of seed dispersal to seedling establishment. Journal of Ecology 88: 622-633.

Ripley BD. 1981. Spatial Statistics. Wiley Series in probability and statistics. Wiley-IEEE. USA.

Roche JP, Timberlake W, McCloud C. 1997. Sensitivity to variability in food amount: Risk aversion is seen in discrete-choice, but not in free-choice, trials. Behaviour 134: 1259-1272.

Russo SE, Augspurger CK. 2004. Aggregated seed dispersal by spider monkeys limits recruitment to clumped patterns in Virola calophylla. Ecology letters 7: 1058-1067.

Safir SB, Wiegman DD, Smith BH, Real LA. 1999. Risk-sensitive foraging: choice behaviour of honeybees in response to variability in volume reward. Animal behaviour 57: 1055-1061.

Safir SB. 2000. Risk-sensitive foraging: the effect of relative variability. Oikos 88: 663-669.

Schnurr JL, Ostfeld RS, Canham CD. 2002. Direct and indirect effects of masting on rodent populations and tree seed survival. Oikos 96: 402-410.

Schupp EW, T. Milleron, and S.E. Russo. 2002. Dissemination limitation and the origin and maintenance of species–rich tropical forests. *In*: D.J. Levey, W.R. Silva, and M. Galetti, eds. Seed dispersal and frugivory: Ecology, evolution and conservation. CABI Publishing, Wallingford, Oxfordshire, UK.

Schupp EW. 1993. Quantity, quality and the effectiveness of seed dispersal by animals. Vegetatio 107/108: 15-29

Spiegel O, Nathan R. 2007. Incorporating dispersal distance into the disperser effectiveness framework: frugivorous birds provide complementary dispersal to plants in a patchy environment. Ecology letters 10: 718-728.

Vander Wall SB, Kuhn KM, Beck MJ. 2005. Seed removal, seed predation, and secondary dispersal. Ecology 86: 801-806.

Vander Wall SB. 1990. Food hoarding in animals. The University of Chicago Press, Chicago, USA.

Vander Wall SB. 2002. Masting in animal-dispersed pines facilitates seed dispersal. Ecology 83: 3508-3516.

Wiegand T, Gunatilleke S, Gunatilleke N, Okuda T. 2007. Analyzing the spatial structure of a Sri Lankan tree species with multiple scales of clustering. Ecology 88: 3088-3102.

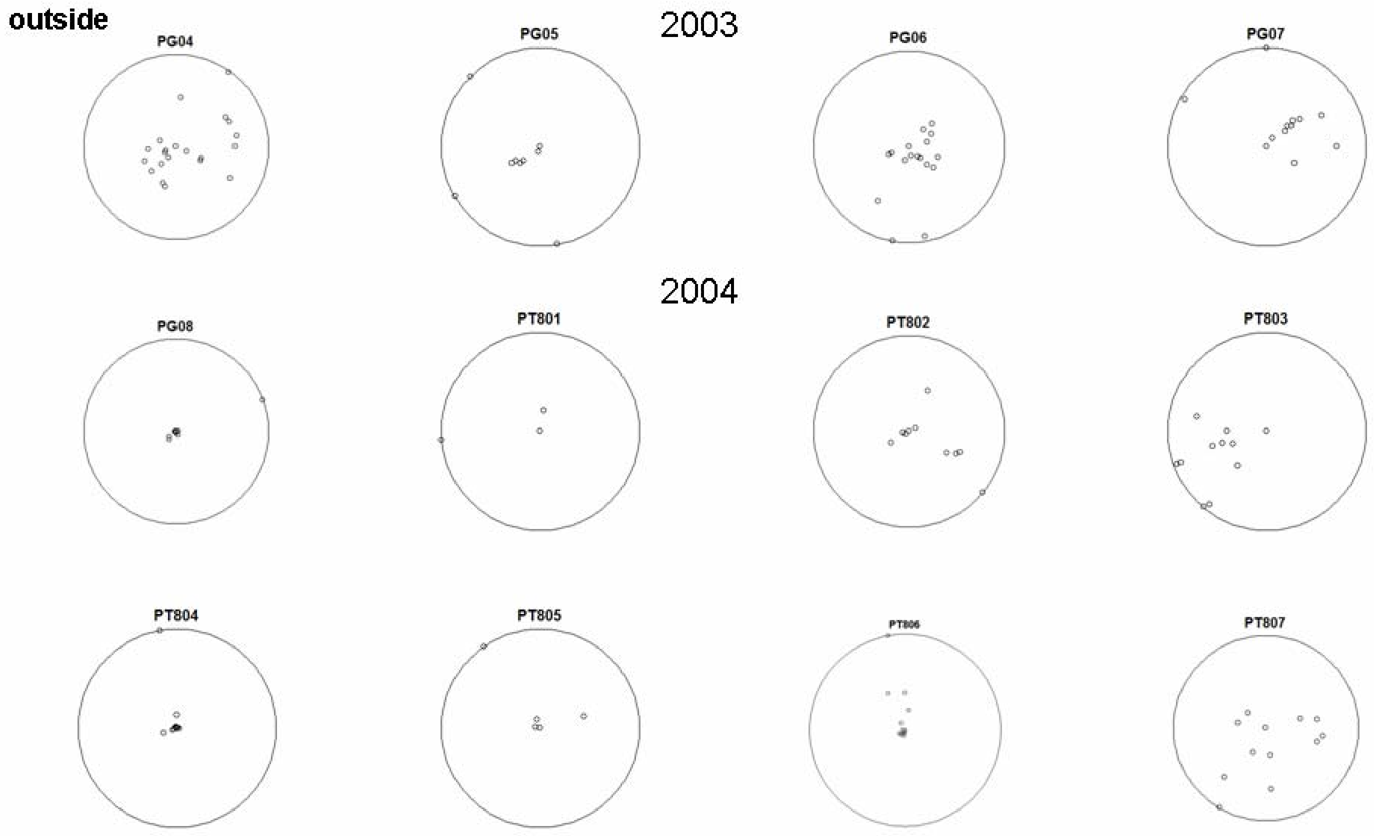
Wirsing AJ, Heithaus MR, Dill LM. 2007. Can you dig it? Use of excavation, a risky foraging tactic, by dugongs is sensitive to predation danger. Animal behaviour 74: 1085-1091.

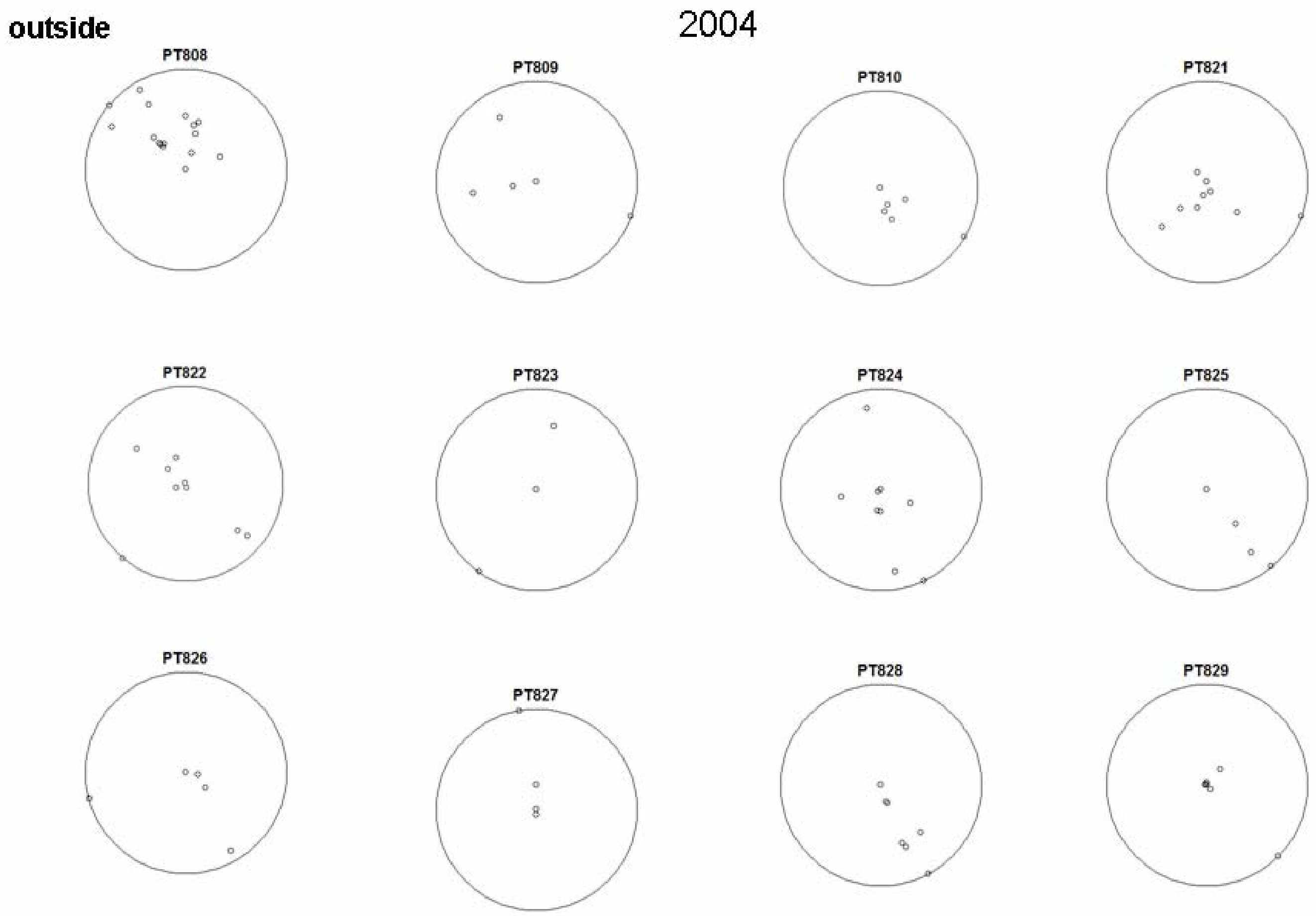
Wolf JO. 1996. Population fluctuations of mast-eating rodents are correlated with production of acorns. Journal of mammalogy 77: 850-856.

Xiao Z, Zhang Z, Wang Y. 2004. Dispersal and germination of big and small nuts of *Quercus serrata* in a subtropical broad-leaved evergreen forest. Forest Ecology and Management 195: 141–150.

Xiao Z, Zhang Z, Wang Y. 2005. Effects of seed size on dispersal distance in five rodent-dispersed fagaceous species. Acta Oecologica 28: 221-229.

Appendix A. Maps of all the supply points showing the position of the dispersed acorns. Note that each supply point has different radius and area.

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PT821
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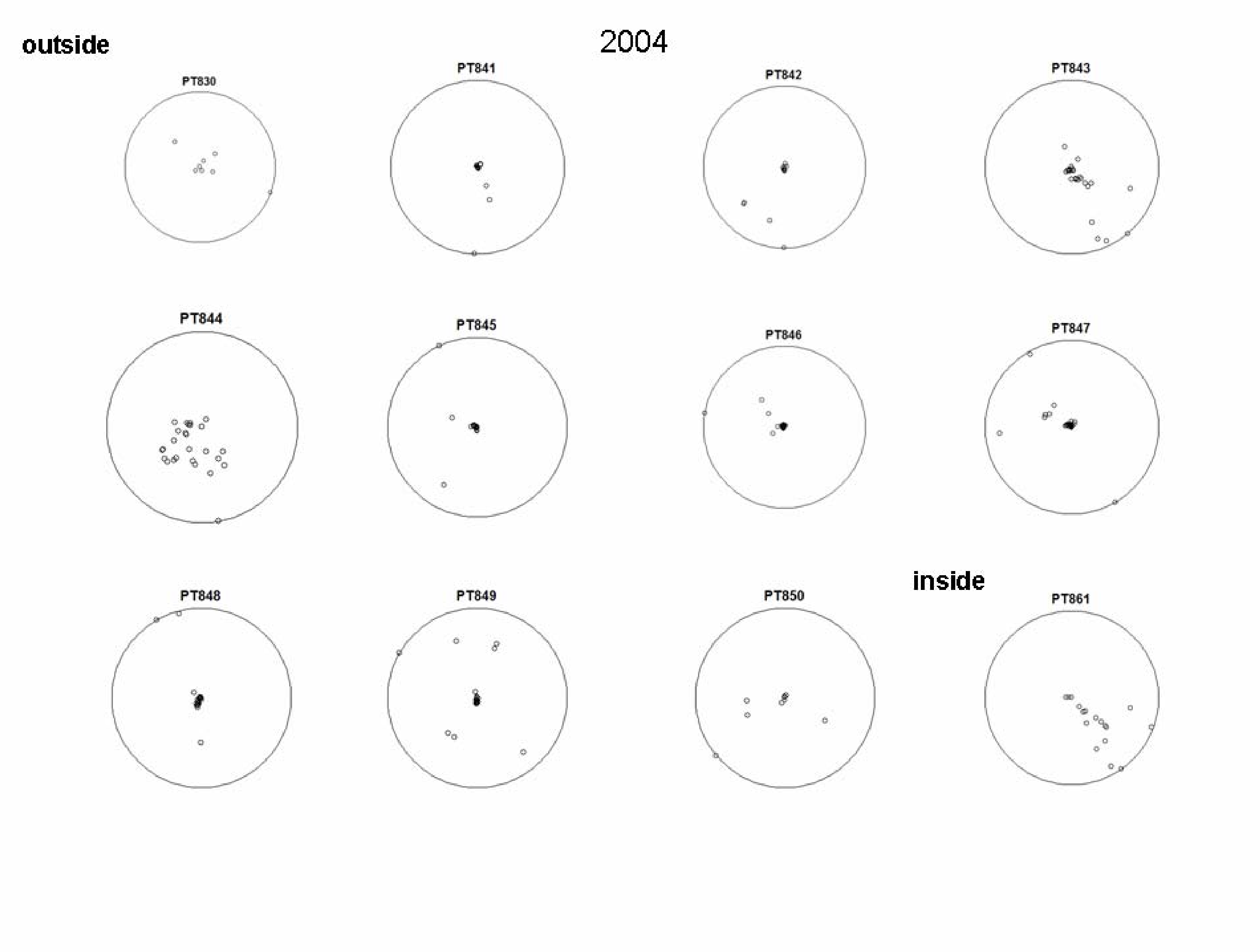
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PT850
inside
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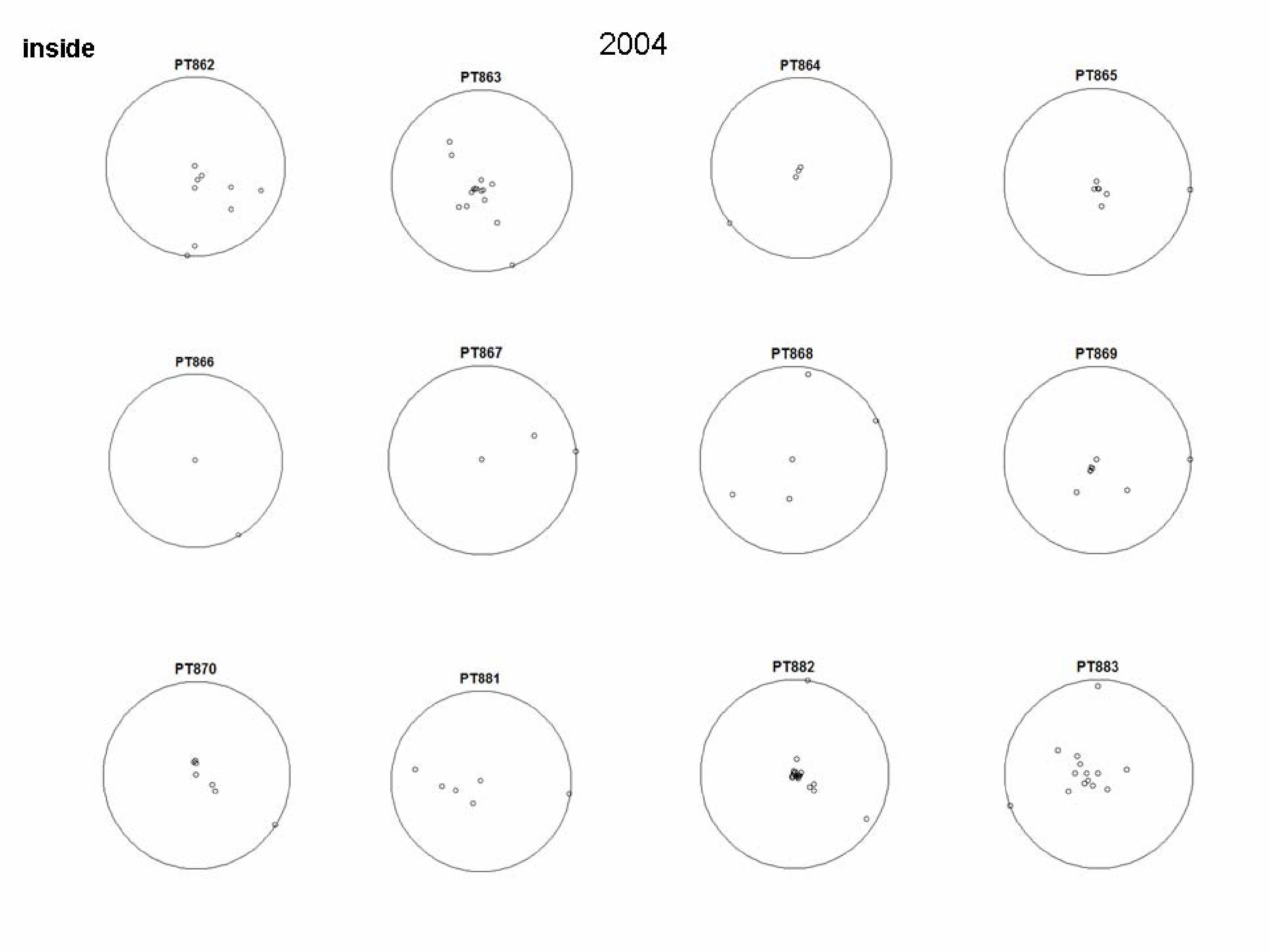
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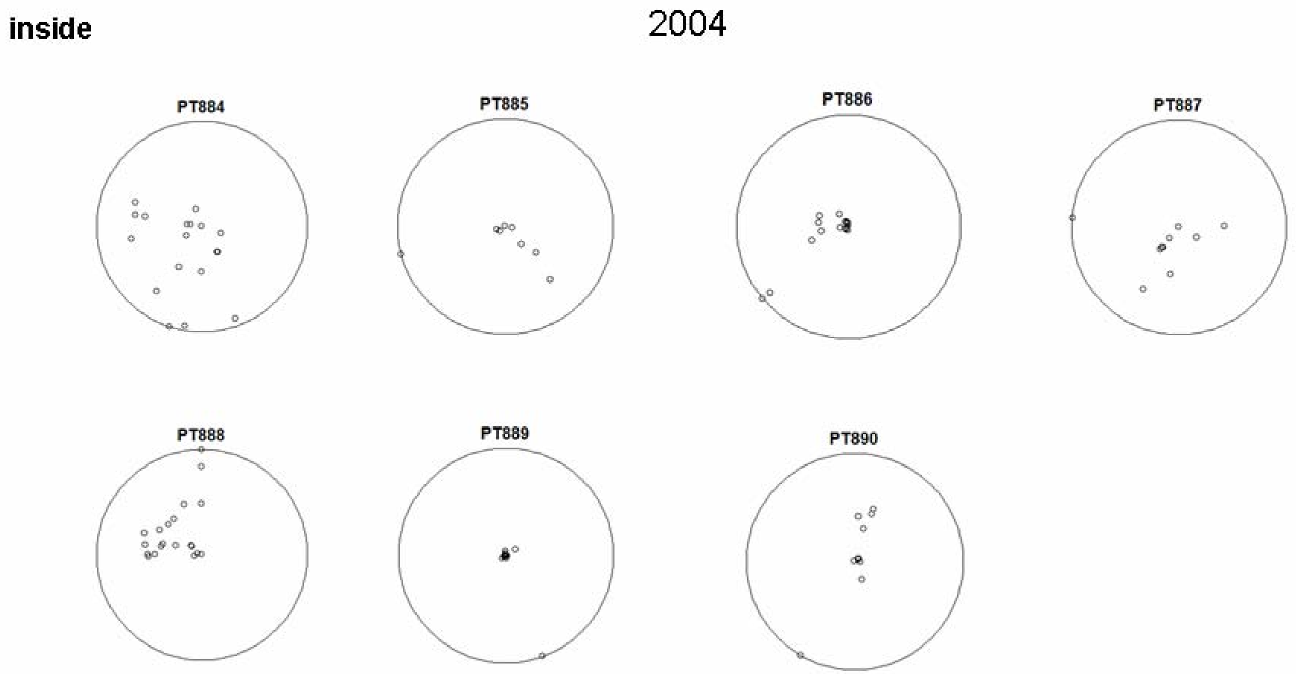
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CHAPTER 3

Post dispersal seed removal near and far: differences among spatial scales in a heterogeneous landscape

> *Si buscas resultados distintos,*
>
> *no hagas siempre lo mismo.*
>
> *A. Einstein*

Carolina Puerta-Piñero. In preparation.

Abstract. Seed dispersal and seed predation and their consequences for plant recruitment have been the focus of plant ecologists since decades. There is an emerging interest of analyzing the effects of seed removal among different spatial levels or structures within the landscape. The spatial distribution of seeds is influenced by the behavior of seed dispersers and subsequent seed-killing agents. Animal activity can vary from a few squares meters to hundreds hectares interacting at different spatial levels with the plants. The main goals of this study are to assess 1) whether seed predation vary among spatial levels of the landscape, and 2) whether these differences were due to different predator species acting at different spatial scales. As a model system I used a landscape composed of a mosaic of patches and microhabitats, using different spatial levels: landscape, landscape unit, trees; and three spatial scales: valley, patch and microhabitat. The presence and activity of the main acorn predators (rodents and boars) vary within the landscape. Different spatial levels showed differences in pre and post-dispersal acorn removal. The patch scale consistently appears to be a key explanatory variable. The microhabitat or the landscape unit did not have substantial importance in terms of seed removal and/or seedling emergence after dispersal. Wild boar rooting activity was mainly focused on pine woodlands while rodents feeding activity was mainly centered on oak woodlands. Post-dispersal seed removal at different spatial levels translates into different quality sites for future plant recruitment. The post-dispersal seed removal and emergence also varied spatially. Within the same landscape unit, different microhabitats did not show significant results in germination or emergence. These results suggest that seed predators influence the spatial distribution of *Q. ilex* populations by reshaping the seed distribution along the landscape, especially by variations among patches. So, considering heterogeneity explicitly in the design and analysis of these interactions become crucial to understand the entire picture.

Keywords: *Apodemus sylvaticus,* landscape ecology, Mediterranean Region, *Quercus ilex*, recruitment, postdispersal seed predation, Sierra Nevada, spatial analysis, *Sus scrofa*.

Capítulo 3

Introduction

Seed dispersal and seed predation have been the focus of plant ecologists since decades (Janzen 1971; Forget and Milleron 1991). Their consequences for plant recruitment have also gained numerous studies all over the world (see references in Howe and Smallwood 1982; Vander Wall 1990; Herrera & Pellmyr 2001 and Levey et al. 2002). However, whether seed consumers affect plant recruitment is still an important unresolved question (Maron and Simms 1997; García et al. 2005, Maron and Crone 2006).

On the other hand, there is an emerging interest of analyzing the effects of seed removal at a landscape level (Clark et al. 1998) and, even among different spatial levels or structures within the same landscape (Williams et al. 2006; García and Chacoff 2007). In addition, seed removal experiments have been often conducted in single populations, over short distances and without considering the microhabitat or the landscape unit in which seeds are deposited (Hulme 2002). Structural heterogeneity of habitats is thought to influence spatial patterns of seed dispersal and seed survival, two critical processes influencing seedling recruitment (Russell and Schupp 1998; Gómez et al. 2004). In fact, the effect of spatial heterogeneity on postdispersal seed predation is often considerable and rarely a mere function of the distance from the nearest fruiting adult (Hulme 1998). As different species perceive the landscape from a different perspective, it is logical to assume that their activity can also vary throughout a heterogeneous landscape (Wiens et al. 1993; Wiens 2000). And thus, different processes can operate over different ranges of distances. Animal activity can vary from a few squares meters to hundreds hectares implying that, from the plant's viewpoint, they interact at different spatial levels such as trees, patches, or even among populations or communities. Therefore, considering different spatial scales simultaneously is becoming crucial for understanding the effects of these animals on plant recruitment (Schupp 1992).

The spatial distribution of seeds is influenced by the behavior of seed dispersers and subsequent seed-killing agents (Wiens et al. 1993; Tomita et al. 2002). Seed dispersers are thought to influence plant recruitment by creating initial seed deposition templates. However, post-deposition processes (e.g. seed predation) may alter these initial patterns (Balcomb and Chapman 2003). Thus, the principal role of post-dispersal seed predators in the plant-disperser interaction is to act as a filter on the resultant seed shadow, modifying seed densities and/or distributions (Rey and Alcantara 2000). So, in animal-dispersed plants it is also interesting to compare seed removal before and after seed dispersal. According to the Janzen & Conell hypothesis (1970-1971), one of the principal advantages of being dispersed is to escape seed predation . The model hypothesizes that mortality near parents is virtually complete and recruitment is limited to areas at some distance from conspecifics (Schupp 1992; Forget et al. 1999). So, it is expected to find higher removal rates around the parental trees while less seed predation in other microhabitats or landscape units. In addition, there are many studies that suggest that local dispersal to different microhabitats can improve microclimatic conditions (Schupp 1992; Jordano & Schupp 2000 and references therein), provide less post-dispersal predation (Forget et al. 1999; Rey and Alcantara 2000; Nathan and Neemann 2004), pathogens and/ or herbivory decline (Conell 1970), or reduction of intra-competition with the mother tree (Nathan and Neemann 2004). The establishment of plants depends crucially on the environment where seeds are deposited (Erikson and Erhlén 2000; Muller-Landau et al. 2000; García et al. 2005). So, at a local scale, the results of being buried under different microhabitats, even within small distances, can be extremely positive for further establishment. However, process-oriented studies assessing seed predation beneath and beyond canopies of fruiting trees tend to control, rather than account for, microhabitat variation (Hulme 2002). At a landscape perspective, seed dispersal to different habitats (here called landscape units) could also provide the advantages described above and, supply the extra advantage of potential colonization of new areas (Colonization hypothesis in Howe and Smallwood 1982). However, this may also implies that the same species can act in a different way (Gómez 2003; Williams et al. 2006), or even that different species are implied in this plant-animal interaction (Nathan & Muller- Landau 2000). There are some studies that consider the landscape experimentally to check for the advantages of long distance seed dispersal (Schupp 1992; Kunstler et al. 2007). However, some of them consider the landscape as a continuum or a gradient of environmental conditions (Clark et al 1998) rather than as a heterogeneous scenario where the processes can considerably vary spatially (but see Williams et al. 2006). Subsequently, we need larger spatial scales as well as crossing-scales experiments to better determine which features are most important for seed removal.

Within the present work I wanted to disentangle if seed predation over the landscape may modulate the demography of the Holm oak *Quercus ilex* (L.) found in the field (Author´s unpublished data). As a model system I used a landscape composed of a mosaic of patches and microhabitats. This scenario constitutes a heterogeneous arena which implies differences in rates of seed dispersal (Gómez 2003; Gómez et al. submitted) and posterior seedlings emergence (Gómez 2004) and survival (Gómez et al. 2004; Puerta-Piñero et al. 2007) through the landscape. The main goals of this study are to assess 1) whether seed predation vary among spatial levels of the landscape, and 2) whether these differences were due to different predator species acting at different spatial scales.

Material and Methods

Study site and species

The study site is located within the Sierra Nevada Protected Area, Southeastern Spain (Fig. 1). The three valleys selected for this study range between 1500-2000 m a. s. l. Climate in the area is typically continental Mediterranean with hot and dry summer and cold winters and precipitation mainly during spring and fall. In the study area, oak woodlands appear in a mosaic landscape intermingled with pine woodlands and shrublands as well as other minor landscape units. Within oak woodlands, the predominant tree is *Q. ilex*, which appears together with different species of tall shrubs (>0.5 m tall) and misdstory cover (scrubs ≈ 30 cm high). For this study the following functional groups were selected, integrating all the nearby microhabitats in the area 1) Oak, 2) Pine, 3) Open areas, 4) Rock, 5) Broom, 6) Scrub, 7) Shrub, 8) Spiny scrub, 9) Spiny shrub and 10) Tussock (see Gómez et al. 2004 for a better description of each category of microhabitat). *Quercus ilex* is a sclerophyllous evergreen tree very abundant in the Mediterranean region. Acorns are dispersed during fall abiotically and biotically mainly by jays and rodents (Pulido 1999; Gómez 2003; Gómez et al. 2003; Muñoz and Bonal 2007; Pausas et al. 2007). Biotic dispersal is usually far from adult oaks, and buried 1-2 cm under shrubs or trees, mostly under *Pinus* sp. (Gómez 2003; Gómez et al. 2008). Postdispersal seed predation is mainly due to rodents and wild boars in the study site (Gómez 2004; Gómez et al. 2008). Rodents are basically represented in the area by the woodmouse *Apodemus sylvaticus* and the red squirrel, *Sciurus vulgaris*. Both rodents have home ranges of a maximum wide distance of dozens square meters (Muñoz and Bonal 2007; Gómez et al. 2008). Woodmice are associated only to oak woodlands patches (Gómez et al. submitted), while squirrels are also associated to pine woodlands (López de las Huertas 2005; Gómez et al. 2006). Wild boars, *Sus scrofa*, focus their activity mainly under oaks and pines (Meriggi and Sacchi 2000) and can have a home and activity range of several hectares (Meriggi and Sacchi 2000). Natural *Q. ilex* seedlings appear mostly under shrubs and pines (Gómez et al. 2004); sites that also have the highest emergence and survival (Espelta et al. 1995; Retana et al. 1999; Gómez 2004; Puerta- Piñero et al. 2007).

Sampling design and data analysis

The sampling followed a hierarchical design with three high mountain upper river valleys (Huenes, Barranco Seco and Dornajo, hereafter), tree landscape units within each valley (*Quercus ilex* woodlands, *Pinus spp.* woodlands, and shrublands) and the total number of the available patches per landscape unit and valley. This implies a total of 21 patches of *Q. ilex* woodlands, seven patches of *Pinus* woodlands and six shrubland patches in the Huenes Valley; A total of 12 patches of *Q. ilex* woodlands, two patches of *Pinus* woodlands and two patches of shrublands in Barranco Seco and, finally, six patches of *Q. ilex* woodlands, three patches of *Pinus* woodlands and three patches of shrublands in Dornajo Valley. These patches were selected because they included high-quality representations of the landscape as well as having fine accessibility to data collection.

At each *Q. ilex* patch five Holm-oak adults were permanently marked with metal tags (see Fig. 1 for individual tree positions).

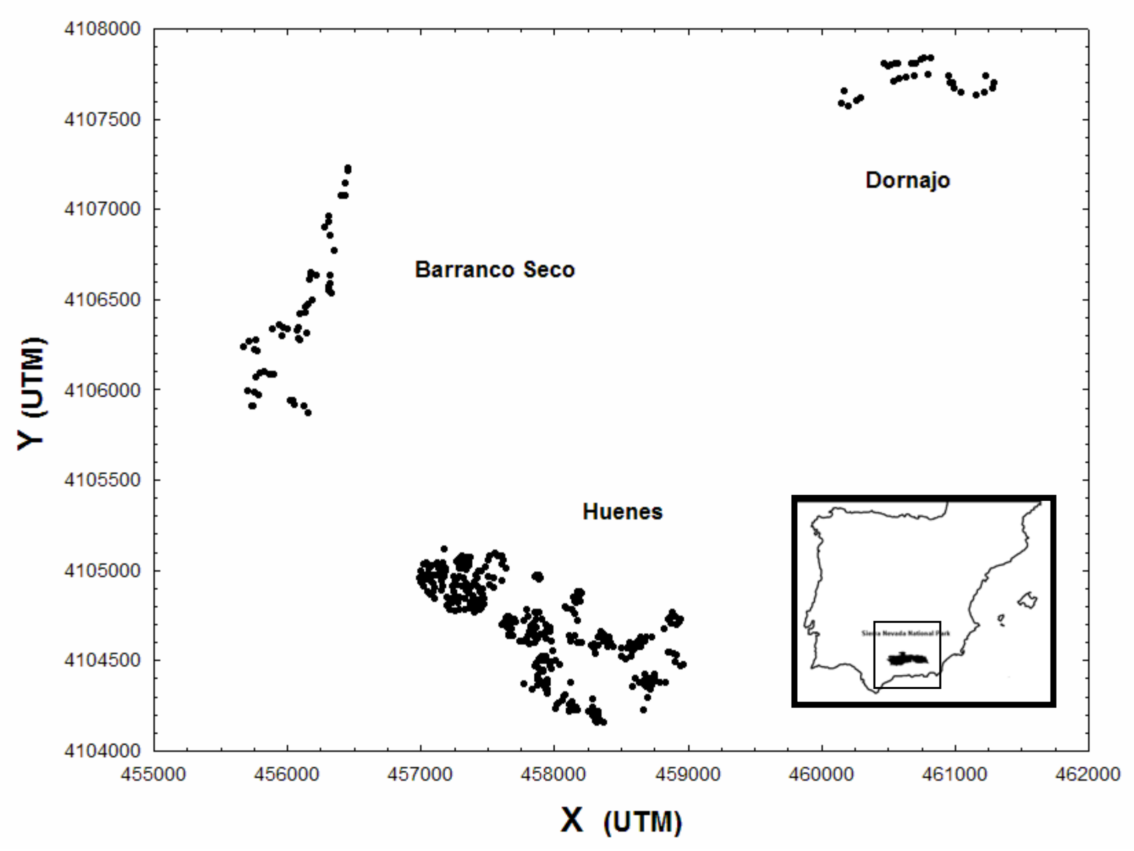


Figure 1. Figure 1. Geographic position (in UTM) of the study sites. Black dots indicate the position of individual trees.

Seed predation on Q. ilex woodland patches

For the first surveillance all the *Q. ilex* woodlands patches in the three valleys were delimitated and five Holm-oak adults per patch were used. This implies a total of 36 *Q. ilex* woodland patches and 261 adult trees. *Quercus ilex* acorns were harvested under different trees and stored in cold room (2-4ºC) until the beginning of the experiment. Acorns were additionally marked with two dots of white painting to facilitate identification. During fall 2004, ten acorns were set under the canopy of each tree, just underneath the metal tag. The fate of the acorns (whether staying in the original place or not) was recorded at the end of the dispersal period (late winter 2004). At this time, 100% of the acorns were lost so no subsequent statistical analysis was done.

In fall 2004 the same design was used to record the proportion of acorns eaten by woodmice under oaks. To complete our goal the same *Q ilex* trees, oak woodland patches and the three valleys described above were used. Two 1-m^2 plots were randomly located under each tree. At each plot I counted the number of total present acorns and the number of acorns eaten by woodmice. Acorns eaten by woodmice were easily identifiable by clear clean gnaws compared to other rodents. To improve normality I added 0.5 to the counts of total acorns and to the number of eaten acorns (Quinn and Keough 2002) and the proportion of eaten acorns from the total was arcsin (square root) transformed (Sokal and Rohlf 1995). In order to check for autocorrelation in the data among spatial locations, I computed a Moran´s I autocorrelation test using the UTM of each tree as spatial coordinates, taking a maximum lag distance of 30 m. Significance was tested using 1000 permutations. After that, proportions were analyzed using a General Linear Mixed Model by the use of Restricted Maximum Likelihood (REML) method (Pinheiro et al. 2006). This model (M0) was then confronted to alternative models assuming different spatial (exponential, Gaussian, Linear, Rational quadratic and Spherical) correlation of the data using the UTM of each tree (Pinheiro and Bates 2000). Comparison between models were done using the Akaike and Bayesian information criterions (AIC, BIC) and the log Likelihood Ratio.

In the next season, I set a paired experiment in the Huenes valley considering 16 of the *Q. ilex* patches and the same 5 adults/patch as in the previous observations. Under these trees I set a selective enclosure composed of a metal wire cage of 1cm^2 mesh size of 0.5 m x 1.0 m x 0.1 m (wide x length x height dimensions). The net had two holes in the front in opposite directions to let rodents (but not wild boars) get into. Acorns were harvested, stored and painted as previously described. In fall 2005 forty acorns were set under each adult, 20 of them were set under the net (rodents treatment, R) while the other 20 acorns were set in the opposite direction in open space with free access to both rodents and boars (rodents + boars treatment, R+B). The fate of the acorns was recorded after 25, 30, 49 and 91 days after the experiment setting. The statistical analysis examine two components of seed predation: seed encounter (the probability of at least one seed being removed per plot) and seed exploitation (the proportion of seeds removed once encountered) (Hulme 1994). Considering seed encounter, differences among trees and treatments as well as the interaction between Tree x Treatment were analyzed using a Generalized Linear Model, using a binomial response with probit as link function, for each time interval (Quinn and Keough 2002). For seed exploitation the factor "Patch" and the interaction between Patch x Treatment were also added to the model. After that, the whole curve was analyzed comparing treatments, R *versus* R+B, using the Log-Rank and Wilcoxon survival tests (SAS 1997).

Seed predation at the entire landscape

In order to account the relative densities of rodents and wild boars, as well as its activities, for each landscape unit all the existing patches at each valley were used. For woodmice I used three random transects of 100 m^2 each one per patch. At each transect, I counted the number of woodmice burrows, eaten acorns, and feeders. These observations were repeated during 2004 and 2005, at summer and early fall. The same sampling design was used to measure wild boars faeces and rootings. In this case, each transect was 200 m$^{2.}$ Wild boars observations were all completed during summer 2004.

Rodent and boar density and activity were analyzed using Generalized Linear Mixed Models, and a hierarchical design using REML methods with Valley and Patch as random factors and landscape unit as a fixed factor. The estimated percent of variance explained was computed using the variance-covariance matrix for the random factors and equating mean squares to their expected values for the fixed factor (Quinn and Keough 2002).

Finally, in fall 2004 and 2005 I experimentally set a seed predation experiment at Huenes valley. In 2004, I established linear transects of 50 m in which 100 acorns were buried at 1-2 cm, mimicking biotic dispersal (Gómez 2003; Muñoz and Bonal 2007; Gómez et al. 2008). There was one transect per patch distributed among oak (8 patches) and pine (4 patches) woodlands and shrublands (4 patches), making a total of 1600 buried acorns. Acorns were marked with two dots of white painting and buried at each meter at both sides of the linear transect to facilitate future identification. So, each acorn was separated 1 meter at each direction from the nearest neighbour acorn. The microhabitat where the acorns were buried was noted. Emergence was recorded during fall 2006. Non- emerged acorns were considered as missing acorns.

In 2005, in the remaining patches of the Huenes valley, 50 experimental acorns were buried following a random 50 m linear transect (total number of acorns= 873). Acorns were buried following the line at each meter. Acorns were marked as previously described followed by a little coloured tag attached near the burial place to assure posterior recovering. The microhabitat where the acorns were buried was also recorded. During fall 2006, acorn fate in the original place was recorded in four categories (intact, germinated, emerged or missing). Missing acorns were considered as being predated. To check acorn viabilityin the field, acorn germination and emergence was also recorded using a subset of acorns of the same origin buried in a greenhouse. Emergence under these circumstances was on average (Puerta- Piñero et al. 2006) indicating good viability of the acorns. Data were analyzed using a Nominal Logistic Model containing the three spatial levels (Landscape unit, patch and microhabitat) as explanatory variables and percentage of emergence as the dependent variable. Data from 2004 and 2005 were joined together. Landscape Unit included 3 levels (oak woodland, shrubland and pine woodland); Microhabitat included the following levels: 1) Oak, 2) Pine, 3) Open areas, 4) Rock, 5) Broom, 6) Scrub, 7) Shrub, 8) Spiny scrub, 9) Spiny shrub and 10) Tussock (see Gómez et al. 2004 for a better description of each category of microhabitat). Finally, patch included a variable number of patches within each landscape unit, as described before (see also Fig. 3). In this model, final fate of the acorns was recorded as binomial response (Emerged vs. Missing).

Results

Post-dispersal seed predator activity

Woodmice on oak woodlands

The proportion of acorns consumed by *Apodemus sylvaticus* under *Q. ilex* trees differed between valleys and patches (Table 1). This proportion varied between Barranco Seco Valley, with the smallest proportion of acorns eaten by woodmouse (0.132 ± 0.062; mean ± SE), Huenes (0.243 ± 0.020) and Dornajo, with the larger value (0.263 ± 0.092).

Although the correlogram was globally not significant (p>0.05 after the sequential Bonferroni correction, Fig. 1), there were some distance classes marginally significant. Interestingly, those distances corresponded approximately to mean distances between trees (less than 10 m) and patches (20-25 m). However, of all the adjusted models, the non spatially-explicit model (M0) was the best in terms of AIC, BIC and logLik (see Appendix A).

Table 1. Acorn consumption by *Apodemus sylvaticus* under *Q. ilex* among valleys and oak woodlands patches

Source	F	P
Valley	6.426	0.004
Patch [Valley]	1.089	<0.05
R^2		0.217

Results from the general linear mixed model for Acorn consumption by *Apodemus sylvaticus* under *Q. ilex*. Data were ArcSin(Square root) transformed. Significance of the random factor (Patch) was computed comparing models with and without the random factor and via the confidence intervals of the variance-covariance matrix (in none of the cases the interval included 0).

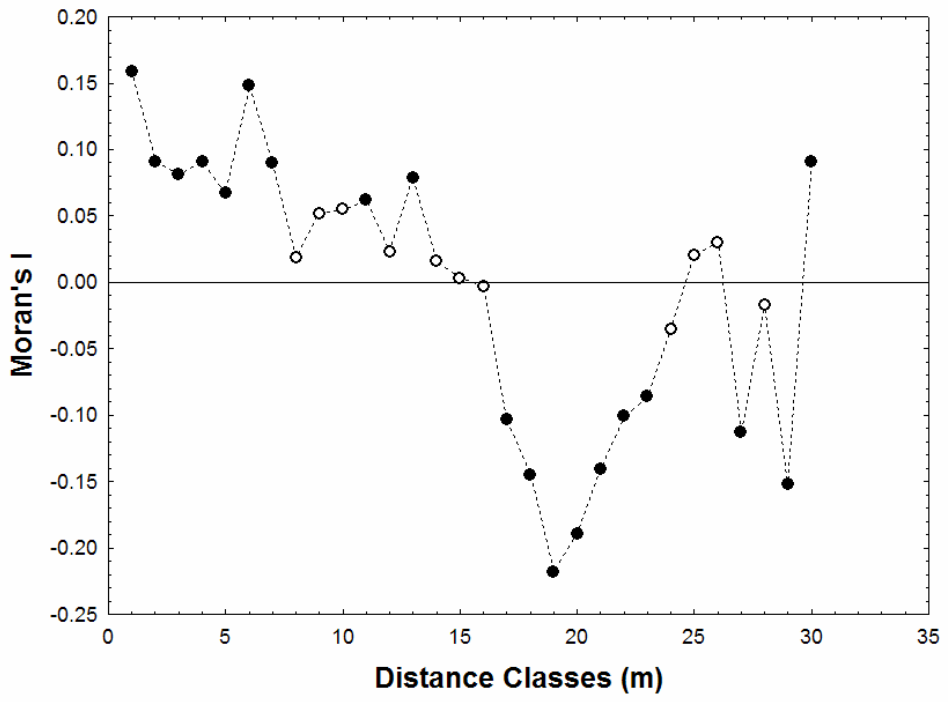


Figure 2. Moran´s I of the proportion of eaten/total acorns by A. Sylvaticus. The autocorrelogram was computed using the UTM of each tree as spatial coordinates and using a maximum lag distance of 30 m Significance was tested using 1000 permutations.

Table 2. Woodmice and Wild boars density and activity in the entire landscape

	Mice burrows		**Mice Feeders**		**Eaten Acorns**		**Boar faeces**		**Boar Rootings**	
	F	**p**	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**
Valley (V)	0.872	0.424	1.031	0.364	1.207	0.307	2.853	0.067	0.342	0.712
Landscape Unit (LU)	1.749	0.184	2.728	0.074	0.976	0.383	1.637	0.205	26.263	<0.0001
V*LU	0.286	0.886	0.095	0.984	0.209	0.932	0.952	0.442	1.347	0.266
Patch [LU,V]		<0.05		<0.05		<0.05		<0.05		<0.05

Results of the generalized mixed model for Apodemus sylvaticus and Sus scrofa density (burrows and faeces respectively) and activity (feeders, eaten acorns and rootings) among spatial levels. Significance of the p-value for the random effect (Patch) was computed using the confidence intervals, which did not include 0 values in any cases.

Woodmice in the entire landscape

There were between-patch differences for *Apodemus* burrows, feeders and number of eaten acorns (Table 2). Furthermore, there were partially significant differences for *Apodemus* feeders between landscape units (Table 2). Patch explained most of the variance in woodmouse burrows and feeders, over 30% and 20% respectively (Fig 2). Similarly, transect explained most of the variance in number of acorns eaten by woodmice, almost 100% (Fig. 2). Oak woodlands had the highest mean values either for estimates of *Apodemus* presence (mean number of burrows 0.05±0.02, Mean±SE) or activity (mean numbers of feeders 0.17±0.04 or eaten acorns 5.04±2.21, Table 3). There were no woodmouse burrows either in pine woodlands or in shrublands. In this latter landscape unit there were a few feeders (0.05±0.08) and eaten acorns (0.21±4.45). Then again, pine woodlands did not contain any single feeder or eaten acorn.

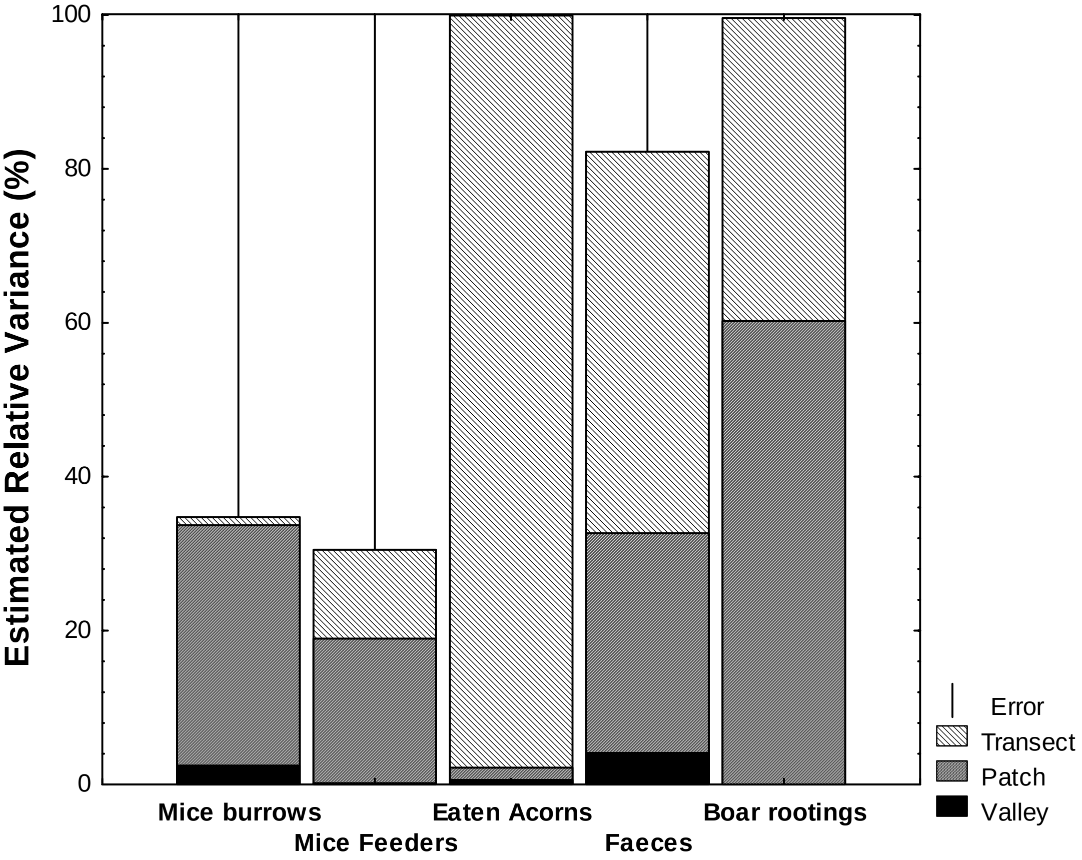


Figure 3. Variance components of the random factors using the restricted Maximum Likelihood (REML) method. Note: Columns denote cumulative sums of components that were computed.

Wild boars in the entire landscape

The patch level was again significant for boar presence (number of faeces) and activity (number of rootings) (Table 2). There were also differences among landscape units in the amount of boar rootings, and more than 80% of the estimated variance for the fixed factor (Landscape Unit)

(Table 2, Table 3). Most of boars´ visits were to pine woodlands (0.72± 0.49 mean ± SE of faeces), which was also the landscape unit where they mostly root (38.64 ± 4.44, mean ± SE of rootings) (Table 3). Oak woodlands received higher number of faeces (1.32 ± 0.29) and intermediate amount of rootings (7.88 ± 2.65). Finally, shrublands contained the smaller values of faeces (0.33± 0.49) and rootings (4.53± 4.85).

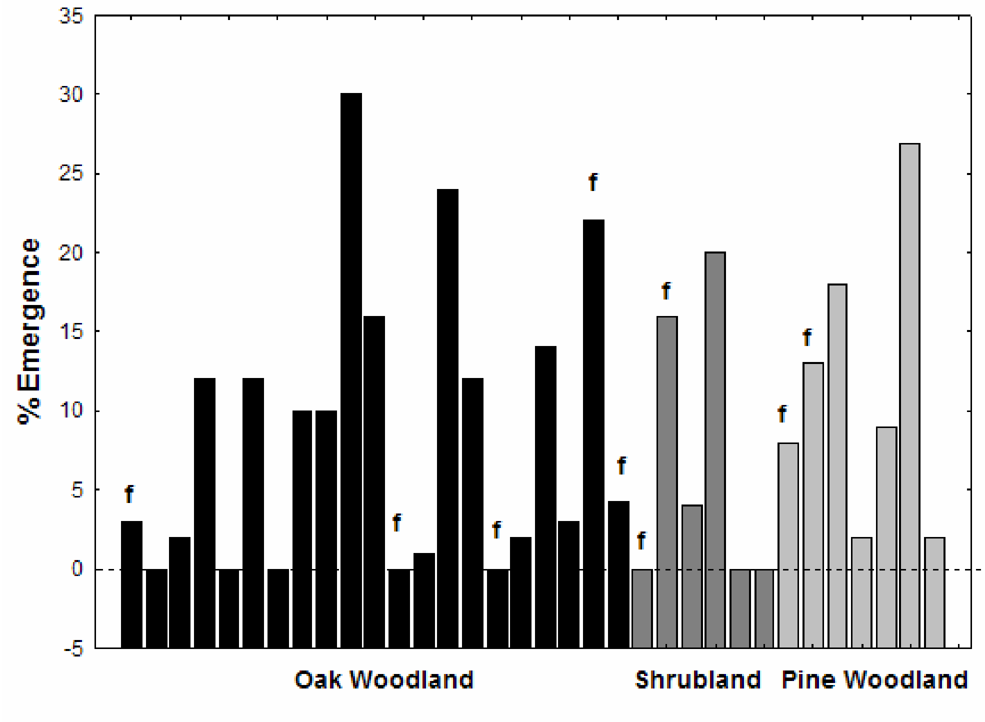


Figure 4. Percentage of emergence per patch. Columns followed by "f" indicate patches inside a selective ungulates enclosure (mainly wild boars). Note down that the dashed line indicate the value of 0 emergence so values below have no biological meaning.

Most of the variance in wild boar faeces and rooting was explained by the factor Patch (30% and 60% of the explained variance, respectively, Fig. 3). In contrast, most of the variance in wild boar rooting was explained by the factor Landscape Unit, which explained more that 80% of the total variance for that variable (Table 3).

Table 3. Estimated Variance for Landscape Unit (fixed factor)

	Mice burrows	**Mice Feeders**	**Eaten Acorns**	**Boar Faeces**	**Boar Rootings**
Landscape Unit	**Mean ± SE**	**Mean ± SE**	**Mean ± SE**	**Mean ±SE**	**Mean ± SE**
Oak Woodland	0.05± 0.02	0.17±0.04	5.04±2.21	1.32±0.29	7.88±2.65
Shrubland	0.00± 0.04	0.05±0.08	0.21±4.45	0.33±0.49	4.53±4.85
Pine Woodland	0.00±0.04	0.00±0.08	0.02±4.41	0.72±0.49	38.64±4.44
Estimated Variance (% of total)	0.00	5.18	4.59	5.29	84.13

Estimated Variance and Mean ± Standard Error for the fixed effect (landscape unit) of the whole nested model. Variance was computed equating mean squares to their expected values (Quinn and Keough 2002).

Predator identity

Acorn encounter varied among trees and treatments (Table 5). After 25 days, survival probability to encounter in the Rodents (R) treatment was 0.22 ± 0.04 (Mean ± SE) and 0.14 ± 0.03 in Rodents + Boars (R + B) treatment. Following 30 days, the differences vanished with mean values of 0.11 ± 0.03 in the R treatment versus 0.08 ± 0.03 in the R+B treatment. Finally, after 49 days the R + B treatment gained 100% of acorn encounter, with a survival probability in the R treatment of 0.06 ± 0.02. In the last census (after 91 days) all the supply points in both treatments where found.

Table 4. Acorn removal through the landscape

Explanatory variables	df	SS	F	p
Landscape Unit	2	1468.101	2.292	0.105
Patch[LU]	31	30736.511	3.096	<0.0001
Microhabitat[LU]	26	9727.323	1.168	0.277
R^2	0.271			

Results of the nominal logistic hierarchical model containing the three spatial levels as explanatory variables and percentage of emergence as dependent variable. Landscape Unit includes 3 levels: oak woodland, shrubland and pine woodland. Microhabitat includes 10 levels, see methods. Patch includes a variable number of patches within each landscape unit, see Fig. 3. In this model, final fate of the acorns was recorded as binomial response (Emerged vs. Missing). Data from years 2004 and 2005 were joined together.

Additionally, there were differences among patches, trees and treatments in acorn exploitation between Rodents (R) and Rodents + Boars (R+B) treatments. The interaction term between treatment and patches and treatment and trees were also significant, suggesting different species-specific behavior through the landscape. However, those differences disappeared through time (Table 6). While differences were significant at the beginning of the experiment (until 49 days there were differences among patches, trees, treatment, and their interactions), at the end, all the acorns were missing. So, after 91 days only the effect of patch and treatment remained significant (Table 6).

The results of the survival analysis indicated that, as a whole, there were differences between treatments (Log-Rank and Wilcoxon tests <0.0001). Thus, acorns exposed both to rodents and wild boars disappeared faster than those exposed only to rodents (Fig. 5). After 25 days, in the rodent treatment 73.4% of the acorns disappeared; in contrast of the 85.5% of missing acorns in the rodents + boars treatment. After 30 days the difference was 86.6% versus 91.3% of missing acorns for R and R+B treatments, respectively. Later than 49 days R + B treatment gained 100% of acorns removed while the R treatment got a hold of more than 90% of missing acorns.

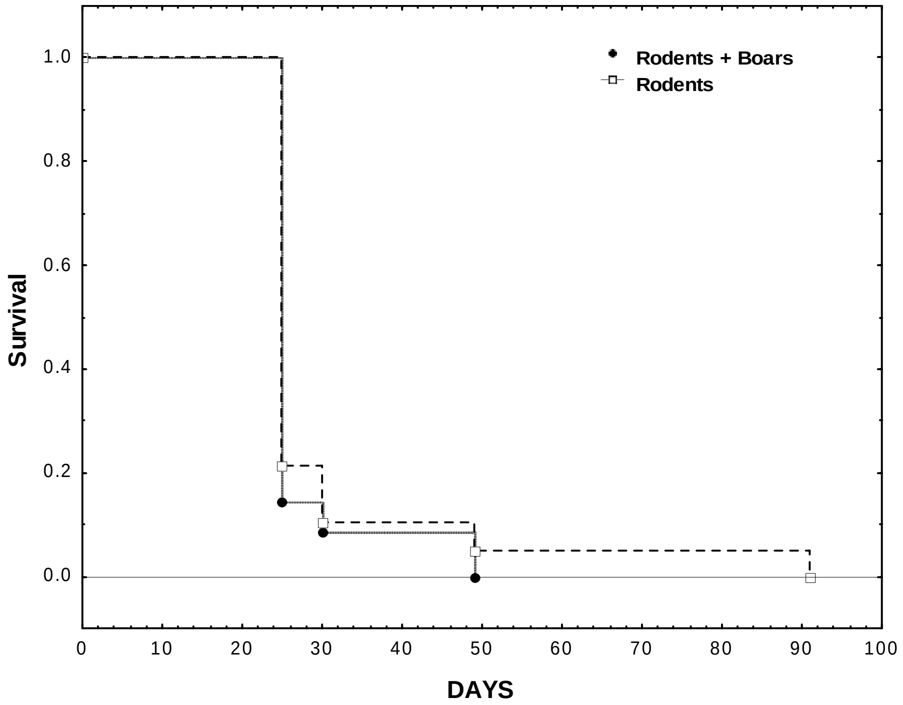


Figure 5. Survival curve comparing rodents (R) and Rodents + Boars treatment (R + B) during the experimental period (91 days).

Table 5. Seed encounter

		25 days		30 days		49 days	
	df	**LogLik**	**χ^2**	**LogLik**	**χ^2**	**LogLik**	**χ^2**
Tree	82	-11.09	107.69*	-2.77	80.61	-2.77	16.11
Treatment	1	-9.00	4.19*	-2.77	0.00	-0.00	5.54*

Results of the generalized linear model using Binomial response and probit as link function for seed encounter. The explanatory variables were Tree and Treatment (R *vs.* R+B treatments, see methods) at different periods since the experiment setting. *: p-value <0.05.
Note: After 91 days of the experiment setting there was no variance between treatments (total of supply points found) so, χ^2 and Log likelihood tests are not shown for this time period.

Spatial pattern of postdispersal acorn removal

Acorn removal on oak woodlands among valleys

At the end of the experiment, 100% of the acorns disappeared (see methods). So, there were no differences among valleys or patches in the final fate (whether stay in the original place or not) of the acorns at the end of the dispersal period.

Acorn removal and seedling emergence through the landscape

According to the results of the nominal logistic model, patch was the only spatial level significantly affecting emergence (Table 4, Fig. 3). In contrast, the type of microhabitat or landscape unit did not have any effect on emergence. However, there were minor differences in percentage of emergence in oak woodlands (10.3 ± 1.79, mean ± SE) that was higher than pine woodlands (9.14 ± 4.47) and this, higher than in shrublands (8.39 ± 3.31) (See Appendix B).

Different microhabitats also had different percentage of emergence, ranging from the higher values of shrubs (50.00 ± 18.00, mean ± SE) and pines (17.32 ± 8.73) to the smaller values in brooms (0.00 ± 0.00), rock (2.78 ± 2.78) with intermediate values in Scrub or Open microhabitats with 5.66± 2.01 and 7.86 ± 2.49 % of emergence respectively.

Table 6. Seed exploitation

		25 days		**30 days**		**49 days**		**91 days†**	
	df	**LogLik**	χ^2	**LogLik**	χ^2	**LogLik**	χ^2	**LogLik**	χ^2
Patch	14	-88.20	1171.715****	-287.65	1440.303****	-287.65	1440.303****	-53.277	82.321****
Tree	63	-315.24	1143.919****	-114.98	345.334****	-114.98	345.334****	-26.462	53.629
Treatment	1	-245.09	140.313****	-96.67	36.611****	-96.67	36.611****	-11.247	30.431****
P x Treat	15	-189.34	11.495****	-66.77	59.811****	-66.77	59.811****	-11.247	
Tree x Treat	63	-118.26	142.157****	-24.34	84.864*	-24.34	84.864*	-11.247	

Results of the generalized linear model with a Binomial response and probit as link function for seed exploitation. The explanatory variables were Patch, Tree and Treatment (R *vs.* R+B treatments, see methods) and the interaction between P x Treatment, and Tree x Treatment. The same model was compute for different periods since the experiment setting. *: p-value <0.05; ****: p-values<0.0001. †Note. For 91 days after the setting of the experiment, the model was unstable and iterations were mostly biased. Thus, χ^2 and p-values are not shown for this time period for these interactions.

On the other hand, considering the 2005 data with final fate of acorns as a multinomial variable (Emerged, Missing, Germinated or Untouched), there were also small differences between final fates and landscape units (see Appendix C). Percentage of missing acorns was 72.15 ± 3.46 % (Mean ± SE) on oak woodlands, 66.81±15.31 on pine woodlands and 59.56±10.22 % on shrublands (See Appendix B). Percentage of emergence was 17.31 ± 2.88 % for oak woodlands; 22.04 ± 8.24 % in shrublands and 30.52 ± 15.31 % in pine woodlands. However, the only significant difference (p= 0.001) was between germination on shrublands (1.22 ± 0.57 %; mean ± SE) and oak woodlands (mean 6.43 ± 1.42%). Then again, different microhabitats entailed differences in percentage of emergence that array from higher values in Shrubs (61.11 ± 20.03 %), intermediate in Spiny scrubs (20.32 ± 7.62 %), Spiny shrubs (23.33 ± 10.00 %), Pines (24.05 ± 9.78) or Tussock (27.78 ± 12.86 %) and the smaller values in Scrubs (8.57± 2.89 %) and Brooms (0.00 ± 0.00 %).

Discussion

Different spatial levels showed differences in pre and post-dispersal acorn removal. The patch level consistently appears to be a key explanatory variable. This finding suggests that the landscape behaves as a dynamic mosaic of different quality patches (Watt 1947), where valuable patches for plant recruitment (patches with low seed predation) are intermingled with bad quality patches where the arrived-seeds more often disappear and thus, the recruitment fail

(Wiens 2000). The tree and valley levels also were important in some cases. Thus, rodents fed differently in the three valleys and so the rate of acorn removal differed among trees. In contrast to previous studies (Herrera et al. 1994; Pulido and Díaz 2005; García-Castaño et al. 2006; see also Gómez 2004 and Puerta- Piñero et al. 2007 for complementary results in the same area), the current results suggest that the microhabitat or the landscape unit do not have substantial importance in terms of seed removal (Castro et al. 1999; Obeso and Fernandez-Calvo 2003; Fleury and Galetti 2006; Rey and Alcántara 2000) and/or seedling emergence after dispersal (Rey et al. 2002). This implies that the initial seed shadow created by seed dispersers was probably not reshaped at the smaller and broader spatial scales (Castro et al. 1999; Alcantara et al. 2000; Rey and Alcantara 2000; Arrieta and Suarez 2005). However, in most cases these contrasting results did not apply to different spatial levels at the same time, instead they often focus on a single spatial level and this probably is one of the main causes of discrepancy. If we consider all the existing spatial levels as a whole within the same landscape the outcome is very different (Schupp 1992). In fact, recent studies have shown that seed predation can be mostly affected at intermediate spatial scales (Balcomb and Chapman 2003; García and Chacoff 2007). Nathan and Casagrandi (2004) even proposed a model that predicted that the total number of seeds surviving predation is lowest at intermediate distances (such as the case here for the patch level) suggesting that distance-dependent predation promotes either short or long dispersal distances or both (dimorphism); as is also the observed scenario of this study site, with dispersal agents (jays and rodents) operating at contrasting spatial scales. The present study supports these latest empirical and theoretical contributions, and also encourages the necessity of taking into account different spatial levels at a time (Schupp 1992).

The present study states that the presence and activity of the main acorn predators (rodents and boars) vary within the landscape. They vary between valleys, landscape units and, especially, patches. Wild boar rooting activity was mainly focused on pine woodlands while rodents feeding activity was mainly centered on oak woodlands. On the other hand, there were some oak woodland patches where the removal is faster and where wild boars and rodents center their activity. The most important animal species interacting with *Q. ilex* in the study area include a range from a few meters in the case of small rodents (mainly *Apodemus sylvaticus*) (Gómez et al. 2008), to several kilometers or hectares in the case of jays (Gómez 2003) or wild boars (Meriggi and Sacchi 2000). So, it is logical to assume that they also differ in the grain as well as the extent of their home ranges and activities (Wiens 2000). There are several seminal studies indicating that different species play different roles through the landscape (Rey et al. 2002; Orrock et al. 2003) or even that the same species acts differently in different parts of the same landscape (Gómez 2003). The consequences of this species-specific perception of the landscape are of special importance since they affect landscape connectivity. This also implies that the role of seed dispersers and predators and how they perceive the landscape is crucial for understanding plant recruitment.

Moreover, post-dispersal seed removal at different spatial levels translates into different quality sites for future plant recruitment. The post-dispersal seed removal and emergence varied spatially. Moreover, the patch level appears as the most important for recruitment. Dispersal to other habitats or landscape units appears to have no effect on subsequent acorn survival, germination or emergence. This suggests that both the escape and colonization hypothesis in the Janzen-Connell hypothesis should be revisited (Schupp 1992). On the other hand, in this system with acorns predators operating at wide and different spatial scales it would be expected to find other patterns such as the Hubbell´s or McCanny´s (Nathan and Casagrandi 2004). In the case of rodents, when dispersal and predation distances are of equivalent magnitude, the Hubbell pattern would be more plausible, while, in the case of seed predation by rodents and wild boars simultaneously the McCanny patterns would be more plausible because it emerges when seed predators are attracted to adult trees but also tend to forage farther away (Nathan and Casagrandi 2004). Within the same landscape unit, different microhabitats did not show significant results in posterior germination or emergence. However, there were slight negative differences of the oak microhabitat compare to other microhabitats within oak woodland patches. This could indicate that escaping from the mother tree could provide to some extent benefit for further recruitment.

In summary, I have found in this study significant differences in seed predator presence and activity, mainly found at the intermediate patch level. Second, I have also found that postdispersal seed removal also depends on the patch, and this is also true if we consider acorn germination and emergence. These results suggest that seed predators influence the spatial distribution of *Q. ilex* populations by reshaping the seed distribution along the landscape, especially by variations among patches. I have also presented some evidences of different predator behavior throughout different spatial levels of the landscape. So, this study emphasizes that considering heterogeneity explicitly in the design and analysis of these interactions become crucial to understand the entire picture. After that, it would also be interesting to disentangle the possible causes of the leading patch importance. For instance, there are some structural (such as area or shape) and functional (as the connectivity with other patches) characteristics of the patches that could further explain the results presented here.

Acknowledgements

José María Gómez Reyes gently supervised all the intellectual processes of this manuscript. Manuel Martínez helped doing all the enclosures in the lab. Gustavo P. Bornemann, Seila López, Carla Steffler and Alba Puerta Piñero gave precious assistance during the field work. The headquarters of the Sierra Nevada National Park and especially of the Jardín Botánico de la Cortijuela always offered support and facilities for working. This study was support ed by the Spanish Ministry of Science and Education via the FPU fellowship AP2003-344, and financial project REN2003-07048.

References

Arrieta S, Suarez F. 2005. Spatial dynamics of Ilex aquifolium populations seed dispersal and seed bank: understanding the first steps of regeneration. Plant Ecology: 177: 237-248.

Balcomb SR, Chapman CA. 2003. Bridging the gap: Influence of seed deposition on seedling recruitment in a primate-tree interaction. Ecological Monographs 73: 525-642.

Castro J, Gómez JM, García D, Zamora R, Hódar JA. 1999. Seed predation and dispersal in relict Scots pine forests in southern Spain. Plant Ecology 145: 115-123.

Clark JS, Macklin E, Wood L. 1998. Stages and spatial scales of recruitment limitation in Souther Appalachian forests. Ecological Monographs 68: 213-235.

Den Ouden J, Jansen PA, Smit R. 2005. Jays, Mice and Oaks: Predation and Dispersal of *Quercus robur* and *Q. petraea* in North-western Europe. In: P.-M. Forget, J. E. Lambert, P. E. Hulme & S. B. Vander Wall (eds.) *Seed Fate*, pp.223-239. CAB International, Oxfordshire, UK.

Espelta JM, Riba M, Retana J. 1995. Patterns of seedling recruitment in west Mediterranean coppiced holm-oak (*Quercus ilex* L.) forests as influenced by canopy development. Journal of Vegetation Science 6: 465-472.

Focardi S, Capizzi D, Monetti D. 2000. Competition for acorns among wild boar (*Sus scrofa*) and small mammals in a Mediterranean woodland. J. Zool. 250: 329-334.

García D, Chacoff NP. 2007. Scale-dependent effects of habitat fragmentation on hawthorn pollination, frugivory, and seed predation. Conservation Biology 21: 400-411.

García-Castaño JL, Kollmann J, Jordano P. 2006. Spatial variation of post-dispersal seed removal by rodents in highland microhabitats of Spain and Switzerland. Seed Science Research 16: 213-222.

Gómez JM, García D, Zamora R. 2003. Impact of vertebrate acorn- and seedling-predators on a Mediterranean *Quercus pyrenaica* forest. Forest Ecology and Management 180: 125-134.

Gómez JM. 2003. Spatial patterns in long-distance dispersal of *Quercus ilex* acorns by jays in a heterogeneous landscape. Ecography 26: 573–584.

Gómez JM. 2004. Importance of microhabitat and acorn burial on *Quercus ilex* early recruitment: non-additive effects on multiple demographic processes. Plant Ecol 192: 287-297.

Herrera CM, Pellmyr O. 2001. Plant-Animal Interactions. Blackwell Science, Oxford, UK.

Howe HF, Smallwood J. 1982. Ecology of seed dispersal. Ann. Rev. Ecol. Syst 13: 201-228.

Howe HF, Westley LC. 1990. Ecological relationships of plants and animals. Oxford University Press. New York. USA.

Hulme PE. 2002. Seed-eaters: seed dispersal, destruction and demography. In: Levey DJ, Silva WR, Galetti M. (eds) Seed Dispersal and Frugivory: Ecology,Evolution and Conservation. CAB International, Wallingford, UK, pp 257-273

Kunstler G, Thuiller W, Curt T Bouchaud M, Jouvie R, Deruette F, Lepart J. 2007. *Fagus sylvatica* L. recruitment across a fragmented Mediterranean Landscape, importance of long distance effective dispersal, abiotic conditions and biotic interactions. Diversity and Distributions 13: 799-807.

Levey DJ, Silva WR, Galetti M. 2002. Seed Dispersal and Frugivory: Ecology,Evolution and Conservation. CAB International, Wallingford, UK.

López-Barrera F, Newton A, Manson R. 2005. Edge effects in a tropical montane forest mosaic: experimental tests of post-dispersal acorn removal. Ecol. Res. 20: 31-40.

Meriggi A, Sacchi O. 2000. Habitat requirements of wild boars in the northern Appennines (N Italy): a multi-level approach. Ital. J. Zool 68: 47-55.

Montgomery DC. 1997. Design and analysis of experiments. John Wiley & Sons. New York. USA.

Nathan R, Neeman G. 2004. Spatiotemporal dynamics of recruitment in Aleppo pine (*Pinus halepensis* Miller). Plant Ecology 171: 123-137.

Nathan R, Muller-Landau H. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. Trends in Ecology and Evolution 15: 278- 285.

Orrock JL, Danielson MJ, Burns MJ, Levey DJ. 2003. Spatial ecology of predator-prey interactions: corridors and patch shape influence seed predation. Ecology 84: 2589-2599.

Pinheiro J, Bates D, DebRoy S., Sarkar D. 2006. nlme: Linear and nonlinear mixed effects models. R package version 3.1-79.

Pinheiro JC, Bates D.M. 2000. Mixed-Effects Models in S and S-PLUS, Springer.

Pulido FJ. 1999. Herbivorismo y regeneración de la encina (*Quercus ilex* L.) en bosques y dehesas. PhD thesis. University of Extremadura, Spain.

Pulido FJ, Díaz M. 2005. Regeneration of a Mediterranean oak: A whole-cycle approach. Ecoscience 12: 92-102.

Quinn GP, Keough MJ. 2002. Experimental Design and data analysis for biologists. Cambridge University Press.

R Development Core Team. 2006. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Retana J, Espelta JM, Gracia M, Riba M. 1999. Seedling recruitment. *Ecology of Mediterranean Evergreen Oak Forests* (eds. Rodá, F. Retana, J. Gracia C. A., & Bellot J.), pp. 89-103, Springer-Verlag, Berlin.

Rey PJ, Alcantara JM. 2000. Recruitment dynamics of a fleshy-fruited plant (*Olea europaea*): connecting patterns of seed dispersal to seedling establishment. Journal of Ecology 88: 622-633.

Rey PJ, Alcantara JM, Sánchez-Lafuente AM, Valera F. 2000. Early effects of rodent post-dispersal seed predation on the outcome of the plant-seed disperser interaction. Oikos 88: 362-370.

Rey PJ, Garrido JL, Alcantara JM, Ramirez JM, Aguilera A, García L, Manzaneda AJ, Fernández R. 2002. Spatial variation in ant and rodent post-dispersal predation of vertebrate-dispersed seeds. Functional Ecology 16: 773-781.

Sokal RR, Rohlf FJ. 1995. Biometry: principles and practice of statistics in biological research. Freeman WH and Company. New York.

Sone K, Hiroi S, Nagahama D, Ohkubo C, Nakano E, Murao SI, Hata K. 2002. Hoarding of acorns by granivorous mice and its role in the population processes of *Pasania edulis* (Makino) Makino. Ecological Research 17: 553-564.

Schupp EW. 1992. The Janzen-Connell model for tropical tree diversity: population implications and the importance of spatial scale. The american naturalist 140: 526-530.

Tomita M, Hirabuki Y, Seiwa K. 2002. Post-dispersal changes in the spatial distribution of *Fagus crenata* seeds. Ecology 83: 1560-1565.

Vander Wall SB, Kuhn KM, Beck MJ. 2005. Seed removal, seed predation, and secondary dispersal. Ecology 86: 801-806.

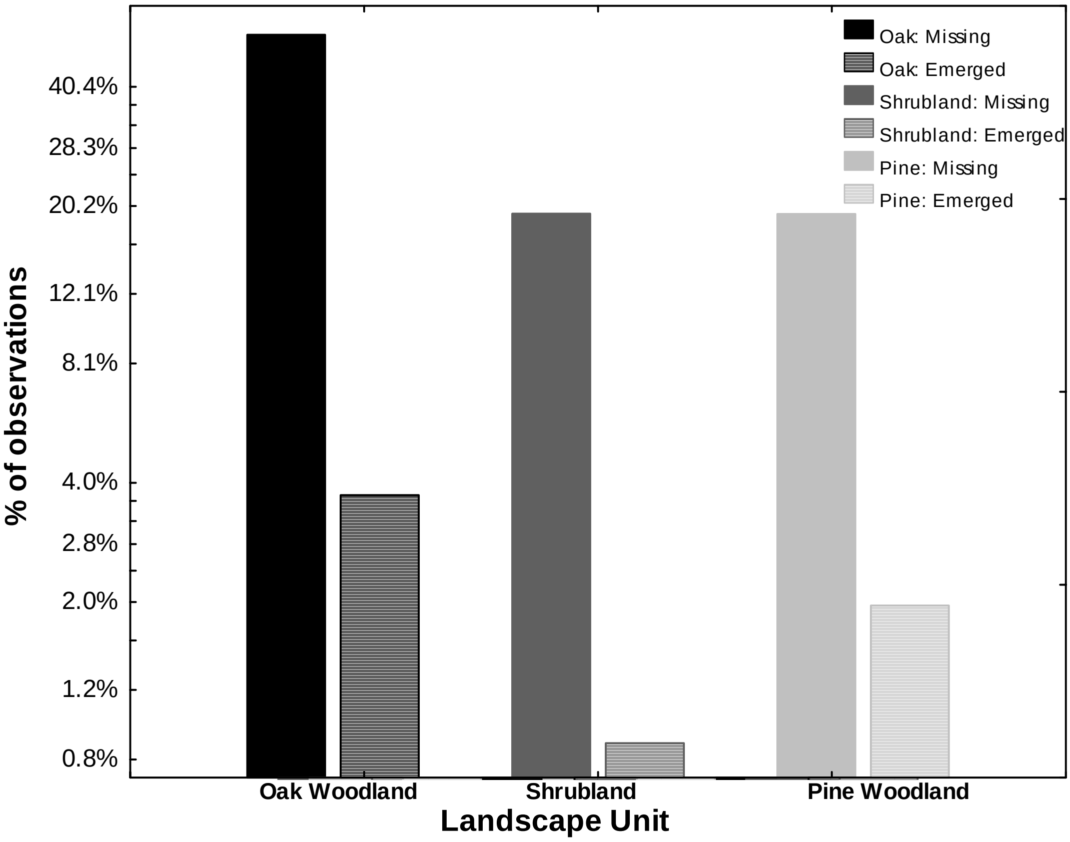
Vander Wall SB. 1990. Food Hoarding in Animals. University of Chicago Press. Chicago. USA.

Wiens JA. 2000. Ecological heterogeneity: an ontogeny of concepts and approaches. In: The Ecological consequences of environmental heterogeneity. M.J. Hutchings, E.A. John, A.J.A. Steward (eds). Blackwell Science Ltd.

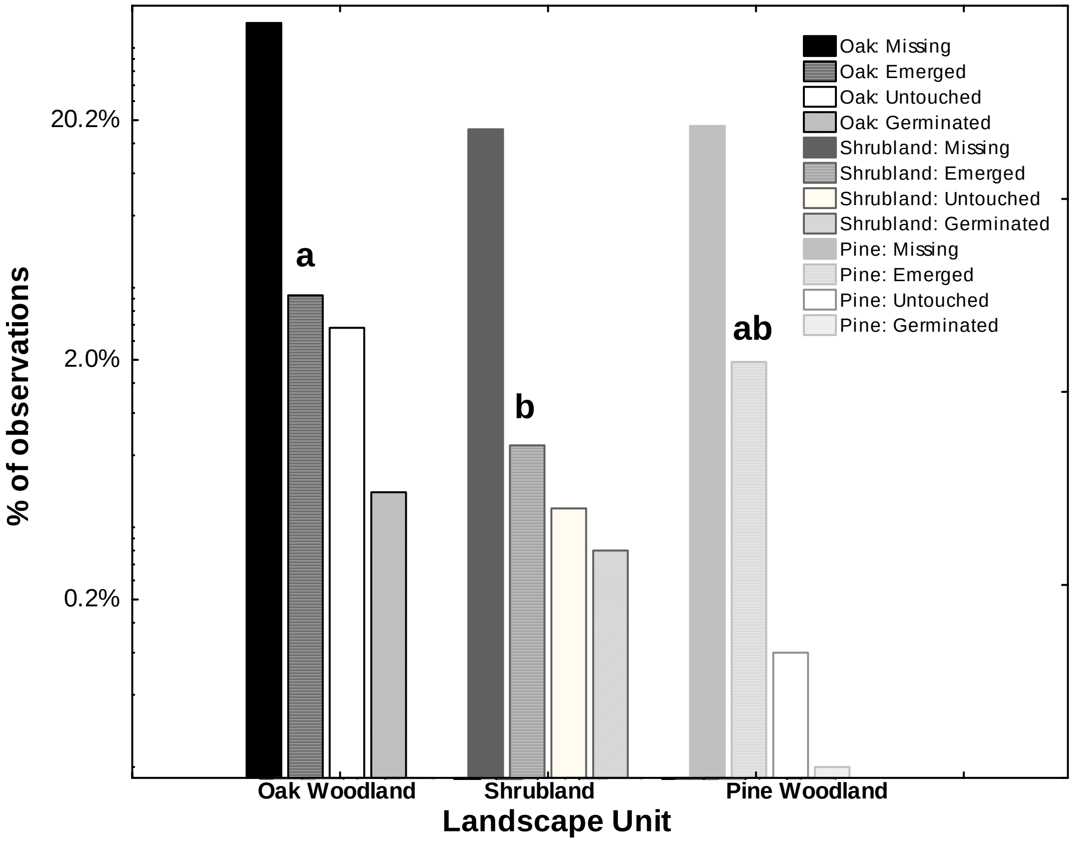
Williams NSG, Morgan JW, McCarthy MA, McDonnell MJ. 2006. Local extinction of grassland plants: the landscape matrix is more important than patch attributes. Ecology 87: 3000-3006.

Model	AIC	BIC	logLik
M0	**392.1592**	**409.9240**	**-191.0796**
MRatio	394.1592	415.4769	-191.0796
MSpher	394.1590	415.4767	-191.0795
MGauss	394.1592	415.4769	-191.0796
MExp	394.1591	415.4769	-191.0796
MLin	394.1589	415.4767	-191.0795

Appendix A. Results of the models contrasting different spatial correlation structure (corresponding to Rational quadratic, Spherical, Gaussian, Exponential and Linear correlation respectively) *versus* the non spatially-splicit model (M0). Subsequent columns indicate the Akaike Information Criterion (AIC), Bayesian Information Criterion (BIC) and log Likelihood Ratio (logLik).



Appendix B. Appendix B. Differences in seed fates among landscape units using a binomial response (emerged vs. missing). Note that y axis has log-range values.



Appendix C. Seed fates using a multinomial response (Missing, Emerged, Untouched, Germined). Note that y axis has log-range values.

CHAPTER 4

Stage-dependent effects of biotic interactions on *Quercus* establishment within a heterogeneous landscape

Make everything as simple as possible, but not simpler

A. Einstein

Puerta-Piñero C, Gómez JM, Pino J. ***In preparation.***

Abstract. An emerging view is that the consequences of plant-animal interactions should be examined in conjunction with other biotic and abiotic components of the environment. Understanding patterns in terms of the processes that produce them is the essence of plant ecology. However, formal links between processes and patterns have been seldom formulated. Landscape characteristics have been widely reported to influence population dynamics. Dynamic patch-centered approaches offer a way to consider environmental heterogeneity or patchiness in spatially explicit terms. Our theoretical framework considers the density of *Q. ilex*, at different life cycle stages, as a function of the activity of interactor animals. We used structural equation modeling to address: 1) whether landscape characteristics affect *Q. ilex* recruitment directly or via the activity of interactor animals; 2) which is the actual contribution of these interactions to recruitment, and 3) whether there are differences among *Q. ilex* life cycle stages. We found evidences that landscape characteristics and biotic interactions influenced *Quercus ilex* demography having different stage-dependent effects. Furthermore, abiotic characteristics of the landscape seem to have clear effects on the activity of animals. The effects of irradiance always have negative effects on the density of seedlings and saplings. The elevation and slope of each patch highly influenced positively the activity of wild boars and negatively the number of jays arriving per patch. Afterward, wild boars and jays had a negative and positive effect respectively on seedling density. The positive effects of acorn dispersal by jays remained at the two-year seedlings stage. Abiotic landscape characteristics also affected the acorn production per patch. Our results suggest that correlation between acorn production and recruitment is mainly via the indirect effects of plant-animal interactions. In the first stage, acorn crop was affected by the topography and irradiance. One-year seedling were directly constrained because wild boars predation and high irradiance and indirectly by topography. Two-year seedlings establishment depended on the number of jay-flights arriving at each patch and low irradiance conditions. Finally, it seems that herbivory pressure as well as high irradiance conditions limited the establishment of the saplings. Our results suggest that including simultaneously the action of abiotic factors as well as biotic interactions should be enforced on further landscape demographic studies and sustains the idea of different stage-dependence requirements on plant life-cycles.

Keywords: Irradiance, GIS, herbivory, Holm oak, Mediterranean Region, recruitment, seed dispersal, seed predation, Structural Equation Modeling.

Introduction

How animal interactions influence the natural regeneration of plant species is a crucial objective of many studies of plant-animal interactions. Plants and animals interact in many ways ranging from antagonisms (such as predation *sensu lato*) to mutualisms (such as pollination or seed dispersal). In most of the cases, however the studies have been focus on only one single interaction at the same time (references in Rey and Manzaneda 2007). An emerging view is that the consequences of an interaction with animals on the ecology of the plant should be examined in conjunction with other biotic and abiotic components of the environment (Rey and Manzaneda 2007). Few studies on seed dispersal by animals however have adopted this view (Jordano 1995; Alcántara et al. 2000; Rey and Manzaneda 2007). Many studies have independently reported important abiotic and biotic constraints on different demographic stages. In those studies, it is often that different factors simultaneously modulate population dynamics at a local scale (Gómez-Aparicio et al. 2004). However, the most of the time these abiotic and biotic factors, that clearly influence natural regeneration, have been only studied at small population-level spatial scales. On the one hand, each species observes the environment on its own unique suite of scales of space and time (Levin 1992). On the other hand, individual-level mechanisms operating in a heterogeneous mosaic produce ecological patterns that are spatially dependent (Wiens et al. 1993). And thus, different species operating in the same ecological context can operate at a wide variety of spatial scales, so including higher spatial dimensions is becoming crucial for full understanding of these processes operating at the same time.

The world is composed of landscapes, be they natural or altered by human activities. Landscape ecology deals with the effects of the spatial configuration of mosaics on a wide variety of ecological phenomena (Wiens et al. 1993). Such spatial mosaics are the focus of the emerging discipline of landscape ecology. The main focus of these studies has been on spatially explicit patterns of landscape mosaics and interactions among their elements (references in Turner 2001). Landscape characteristics have been widely reported to influence population dynamics. However, formal links between processes and patterns have been seldom formulated (Nathan and Muller-Landau 2000). Landscape mosaics are not static, but have temporal dynamics produced by disturbances and by the regeneration time lags characteristic of particular patch types (Shugart 1984; Turner et al. 1989). This dynamic patch-centered approach offers a way to consider environmental heterogeneity or patchiness in spatially explicit terms (Wiens 1993). Moreover, most of the “patch dynamics” studies have considered spatial heterogeneity in terms of simple, internally homogeneous, shapeless patches, embedded in a featureless and ecologically neutral matrix (Orrock et al. 2003). This fact has made difficult to unravel the mechanisms underlying landscape dynamics (Turner 2001). Implementing this mechanistic framework requires not only quantification of critical features of mosaics and movements, but the interplay of theoretical and empirical approaches as well (Clark et al. 1998).

Understanding patterns in terms of the processes that produce them is the essence of science in general and landscape ecology in particular (Levin 1992). So, mechanistic approaches to landscape ecology are essential to deriving generalizations about how spatial heterogeneity influences ecological systems (Wiens et al. 1993). However, experimental tests are difficult to conduct at the broad landscape scales. Nevertheless, it is not necessary to study every species in every situation to understand the important linkages between explicit spatial patterns and processes at broader spatial scales (Levin 1992; Wiens 1993). The essence of modeling is, in fact, to facilitate the acquisition of understanding, by abstracting and the incorporation of just enough detail to produce the observed patterns (Levin 1992). One may practice descriptive approaches judiciously as well as select for investigation focal species or situations that occupy key positions on gradients in life history strategies, spatial heterogeneity, etc. (Wiens 1993). Thus, the next stage will be to search for such patterns in natural systems, and to use models to explore the causes (Levin 1992).

Structural equation models (SEM) have a wide range of applications for ecological and evolutionary studies, including both experimental and descriptive data (Grace 2003). SEM represent translations of a series of hypothesized cause-effect relationships between variables into a composite hypothesis concerning patterns of statistical dependencies (Shipley 2000). The relationships are described by parameters that indicate the magnitude of the effect (direct or indirect) that independent variables have on dependent variables (Hershberger et al. 2003). On the other hand, they can provide a flexible and powerful method for analyzing multivariate relationships (Grace 2003). In general, there will be many conceivable mechanisms that could give rise to any set of patterns (Levin 1992). Thus, SEM represent a useful tool for landscape ecologists, especially in the case of simultaneous biotic and abiotic factors operating at the same time. Our theoretical framework considers the density of *Q. ilex*, at different life cycle stages, as a function of the activity of interactor animals. We used structural equation modeling to address the following major questions: 1) whether landscape characteristics affect *Q. ilex* recruitment directly or via the activity of interactor animals; 2) which is the actual contribution of these animal-plant interactions to plant recruitment, and 3) whether there are differences among these animal contributions between different stages of *Q. ilex* life cycle.

Material and Methods

Landscape description

The study site is located within the Sierra Nevada protected area, Southeastern Spain (see Figure 1). The landscape is a highly fragmented area, where oak woodlands appear in a mosaic landscape intermingled with pine woodlands and shrublands as well as other minor landscape units (Figure 1). This mosaic landscape is composed of patches (areas with the same predominant vegetation type separated from others at least 30m) which differ in some important characters such as area, shape, altitude, orientation, etc. Those patches are also internally heterogeneous with different contiguous species of shrubs and misdstory cover intermingled between the trees. For this study, we selected three high mountain upper river valleys (named Huenes, Barranco Seco and Dornajo, see Figure 1 for specific locations), range between 1500-2000 m a. s. l. Climate in the area is continental Mediterranean. The Mediterranean climate is characterized by hot and dry summer periods and low winter temperatures and episodic frosts in altitudinal and continental districts and little precipitation mainly during spring and fall (Larcher 2000). This Mediterranean climatic constraints lead temperature, summer drought and excessive irradiance become the main abiotic stresses (Larcher 2000), which are in fact considered a major cause of high seedling mortality rates of many plant species (Herrera et al 1994; Rey and Alcántara 2000; Ramírez et al. 2006), including *Q. ilex* (Gómez-Aparicio et al. 2004, 2005; Puerta-Piñero et al. 2007).

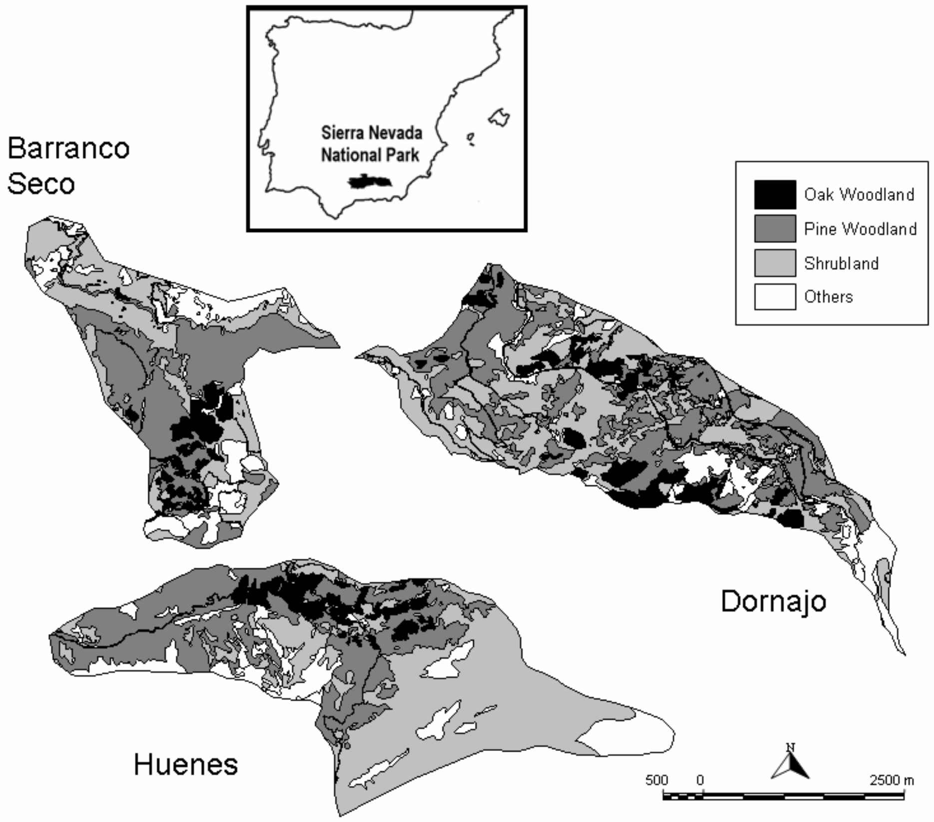


Figure 1. Map showing landscape structure and geographical position of the study sites. Black patches belong to oak woodland patches, dark grey to pine woodland patches and light grey to shrublands. White areas correspond to other landscape units mainly open or urbane areas.

Study species

Quercus ilex L. is a sclerophyllous evergreen tree very abundant in the Mediterranean region. Acorns are dispersed during fall abiotically and biotically mainly by jays and rodents, (Pulido 1999; Gómez 2003; Muñoz and Bonal 2007; Pons and Pausas 2007). Biotically dispersed acorns are usually transported far from adult oaks, and buried 1-2 cm under shrubs or trees (Gómez 2003; Muñoz and Bonal 2007). Postdispersal seed predation is mainly due to rodents and wild boars in the study site (Gómez 2004; Chapter 3). Rodents are basically represented in the area by the woodmouse *Apodemus sylvaticus* and the red squirrel, *Sciurus vulgaris*. Natural *Q. ilex* seedlings appear mostly under shrubs and pines (Gómez et al. 2004); sites that also have the highest emergence and survival (Espelta et al. 1995; Retana et al. 1999; Gómez 2004; Muñoz and Bonal 2007; Puerta- Piñero et al. 2007).

Experimental design

The data collection followed a hierarchical design using three valleys (Huenes, Barranco Seco and Dornajo), three landscape units within each valley (*Quercus ilex* woodlands, *Pinus spp.* woodlands, and shrublands) and a variable number of patches per landscape unit and valley. This implies a total of 21 patches of *Q. ilex* woodlands, seven patches of *Pinus* woodlands and six shrubland patches in the Huenes Valley; A total of 12 patches of *Q. ilex* woodlands, two patches of *Pinus* woodlands and two patches of shrublands in Barranco Seco and, finally, six patches of *Q. ilex* woodlands, three patches of *Pinus* woodlands and three patches of shrublands in Dornajo Valley (See Figure 2 for individual patch position).

These patches were selected because they included high-quality representations of each landscape unit with different landscape characters (such as area, elevation, slope, etc.) as well as having fine accessibility to data collection. Within each of these patches (experimental units) we collected several field data variables that were subsequent included in the previously generated GIS.

Patch variables

Forest patches were digitized by on-screen GIS photo interpretation of 1:10,000 digital ortho-photomaps (consejería de medio ambiente Junta de Andalucía, 2003). After that, some of the patches were selected for taking field variables that will be described below. Landscape structure was inferred from two basic metrics (Forman 2005) measured in those previously GIS-generated patches: (1) *Patch Area* (in ha), a basic mesure of patch size, and (2) *Normalized Patch Perimeter*, the actual perimeter of patch divided with that of a circle with the same area, as an indicative of patch shape. Data were log transformed to better further comparison with other variables; (3) *X*; and (4) *Y* coordinates, as the UTM of the centroid of each patch.

We obtained the mean values of elevation (m), and slope (degrees) for each patch using a Digital Elevation Model (DEM) with 10 of pixel size (Junta de Andalucía, Consejería de Medio Ambiente). Subsequently, after having the patches including the information of elevation and aspect, we created the limit angles responsible of the shading models, taking into account latitude, Sun position, incidence angles, projected shades and the distance from Earth to Sun. Then we calculated the total solar radiation for a typical day per patch, and then multiplied for the number of days per month. Finally obtained the total radiation per patch (in KJ/(m^2·micrometer)(2 bytes/pixel)) by the addition of the radiation of all the pixels at each patch. For further analysis we used total summer radiation, including the sum of data from June, July and August. We selected this period because is responsible of summer drought, main cause of seedling mortality at first year (Herrera et al 1994; Rey and Alcántara 2000; Gómez 2004; Ramírez et al. 2006; Puerta-Piñero et al. 2007). As a rule, irradiance is highly correlated with temperature and water content in the soil (Clark et al. 2003), as is also the case of similar Mediterranean areas (Larcher 2000; Ramirez et al. 2006) and the study system (Gómez-Aparicio et al. 2005). All GIS processes were performed using MiraMon, a GIS software developed at CREAF (Pons 2000).

We obtained the *elevation* and *slope* of each plot from the abovementioned DEM. The rest of patch variables were obtained in the field as follows:

Acorn Production

Acorn production was recorded during fall 2004 and 2005 in five holm oak trees per patch. Trees were haphazardly selected within each patch. We used a semi-quantitative scale, ranging from 0 (no acorns) to 4 (all the branches in the canopy full with acorns). This estimate has been used in a variety of systems offering accurate quick approximations to the total crop when quantitative methods are not affordable (see references in Nilsson 1985; Jordano 1991; Ostfeld et al. 1996 and Herrera et al. 1998). After that, we computed the mean value for each patch and multiplied by the number of trees presented per patch to estimate the acorn production at each patch. Seed crop have been reported to influence different biotic interactions, especially in the case of seed dispersal and seed predation (see references in Nilsson 1985; Herrera et al. 1998 and Chapter 2) as well as subsequent plant demography (Herrera et al. 1998; Nathan and Muller-Landau 2000 and references therein).

Jays

The movement pattern of acorns dispersed by jays was estimated during two years (2004–2005) by observing jays moving acorns during the natural dispersal period (October–December). Observations were carried out from sunrise to sunset from five positions, recording: time, weather, and number of jays arriving on the observed patch (see Gómez 2003 for similar methods). The location of these positions allowed tracking the flight paths of the jays after feeding on acorns as well as scanning the whole study area including all the patches in the Huenes valley. When a jay left an oak patch, it was followed until it landed, noting the patch of destination. At the end, we obtained a total of 491 destination flights from 34 patches (of the 62 total patches). For further analysis we considered the sum of destination flights per patch.

Rodents

For woodmice we used three randomly selected transects of 100 m^2 for each patch in where we counted the number of 1) woodmice burrows, 2) eaten acorns and 3) feeders. Those measurements offer easy and quick measurements of rodent’s abundance and activities at a landscape level (Brown 1969; Halle 1993; Sutherland 2006) for relative comparisons among patches. Woodmice burrows were identified by small holes on ground surface (Wolf 1996). As far as we know no other species have burrows alike in the study area. Acorns eaten by woodmice were easily identifiable by clear clean gnaws compared to other rodents (Perkins 1976; Authors´ personal observations). Woodmice feeders were counted when at least two eaten acorns were found in the same place (See chapter 3 for further detailed methods explanations).

Wild Boars

The same sampling design was used to search for wild boars density and activity. At each patch we randomly selected three transects of 200 m^2. At each transect we searched and count number of faeces and rootings. Wild boar faeces were easily recognize and certainly identified by visual inspection with no other similar faeces for other animals in the area (Perkins 1976; Author´s personal observations). Wild boar rootings were only considered when clear evidences of wild boar activity and conservatively counted only when apparent separate traces were found (Meriggi and Sachi 2000; Author´s personal observations). This measure represents a cumulative estimate of wild boar activity, since it is the number of rootings present in the patch until the date of the data collection.

Herbivory

To estimate the potential herbivory pressure per patch we measured the percent of damage by ungulates (mainly *Capra pyrenaica hyspanic*a and livestock) on the saplings. Damage intensity was quantified as the proportion of apical shoots consumed by ungulates. This measurement was done by visual inspection, counting the total number of shoots as well as the number of shoots with visible ungulate damage (Zamora et al. 2001). This estimate represents a cumulative estimate of herbivory intensity, since it is the number of shoots removed by ungulates over time.

Light

As we mentioned before, irradiance is usually highly correlated with temperature and water content (Clark et al. 2003), as is also the case of Mediterranean areas (Larcher 2000; Ramirez et al. 2006; Gómez-Aparicio et al. 2005). So, we used irradiance as a surrogate of these important stressing factors (see Puerta-Piñero et al. 2007 for a similar approach). Thus, for recording irradiance at the microsite scale, we took hemispherical photographs for a subset of seedlings at each microhabitat (Rich, 1990; Chen et al., 1991; Roxburgh and Kelly, 1995). Each photograph was taken above each seedling, at a height of 0.25 m above the ground using a horizontally-levelled digital camera (CoolPix 995 digital camera, Nikon, Tokyo, Japan) and aimed at the zenith, using a fish-eye lens of 180^{o} field of view (FCE8, Nikon). All photographs were taken, either before dawn, after sunset, or at other times of the day when the sun was blocked by clouds, so an homogeneous illumination of the overstorey canopy and a correct contrast between the canopy and the sky was ensured. Photographs were analyzed using Hemiview canopy analysis software version 2.1 (1999, Delta-T Devices Ltd, Cambridge, UK). We then computed the Global site factor (GSF) for each seedling. GSF is generally used to assess light availability at small scales and is inversely related to canopy plant cover (Ramirez et al. 2006 and references therein). GSF is a fraction of radiation that reaches the soil surface relative to the amount of radiation above the canopy (Ramírez et al. 2006). It combines direct radiation (DSF), by calculating the annual solar track, and diffuse radiation (ISF), based on a uniform overcast sky model (Clark et al., 2003) and represents the proportion of full sunlight penetrating the forest canopy.

Finally, for each patch we multiplied the total irradiance per patch (calculated from the GIS) by the average irradiance per landscape unit (oak woodland, pine woodland or shrubland) to obtain mean summer radiance per patch (L_{patch}) and then multiplied by the mean irradiance, in GSF, of the microhabitats of the seedlings found at each patch (L_{microh}).

Seedling and sapling density

For demographic density at each stage we used three randomly selected transects of 100 m^2 for each patch. At each transect we searched for naturally emerged seedlings and saplings by carefully inspection. We searched and counted the number of one-year and two-year seedlings during last summer and early fall of 2004 and 2005, so a total area of $600m^2$ was covered. All the saplings densities were estimated during 2004, including an area of $300m^2$. *Quercus ilex* seedlings are easy to find since they have big size and bright green colour when alive and brown dark colour when dead (Puerta-Piñero et al. 2007). At the time we searched for natural seedlings we could also recorded the number of seedlings surviving (still with bright green colour) to summer drougth, and thus considered them as *two-year seedlings*. Saplings were considered when no evidences of remaining cotyledon marks (seedling stage acording to Gómez 2004 and

Puerta-Piñero et al. 2007) and when no reproductive traces (neither flowers nor acorns) were found (adult stage).

Data analysis

We explored causal relations between different traits on subsequent demographic stages using structural equations modeling (hereafter SEM; Bollen 1989; Shipley 2000, Pugesek 2003b; see Myers & Cadigan 1993 for a related ecological approach). SEM evaluates complex hypotheses of multivariate relationships through the analysis of correlations (or covariances), and specifies a multivariate dependence model that can be statistically compared to data (Grace 2006). Among other advantadges, SEM provides an efficient, simultaneous solution to a set of regression relationships (Grace 2006) and offers the possibility to evaluate simultaneously direct and indirect cause and correlation effects on the target variable. On the other hand, this method allows considering the action of different variables as a single, inclusive, and multidimensional factor (latent construct) (Adams and Rosenberg 1998). Latent variables are conceptual variables that the researcher does not measure directly but attempts to estimate with measurement-level indicator variables (Pugesek 2003b). We defined five latent variables, as follows: 1) *Light*, compiling the information of irradiance per patch (L_{Patch}) and microhabitat (L_{Microh}); 2) *Topography*, including the Elevation and Slope data; 3) *Patch Structure*, that accumulates the Area, Normalized Perimeter and X and Y coordinates of each patch. We included the X and Y coordinates within Patch Structure, because it has been generally recommended to use multiple indicators for each latent variable (Hershberger et al. 2003). On the other hand, we did not considered them separately because prior inspection indicated no spatial correlation of the variables; 4) *Wild Boars*, using the densities of faeces and rootings found at each patch, and finally 5) *Rodents*, using the densities of woodmice burrows, eaten acorns and feeders at each patch. See Appendix A for mean values of the GIS-generated patch variables and Appendix B for mean values of field data values per patch of each variable considered. SEM models are usually presented graphically as path diagrams, with variables connected to one another by arrows (Grace 2006).

In our saturated model (graphically shown in Figure 3) we show a path diagram that will assume animal behavior and acorn production to be affected by light and patch structure and topography. This model was built based on the natural history of the species, supported by bibliographic references and/or personal observations. That is, here we test the plausible hypothesis that landscape characteristics as well as the total radiation per patch directly or indirectly (via animal effects) can modulate the demographic density of *Q. ilex* at different stages. Additionally, acorn production per patch may modulate the behavior of seed predators and disperser animal species, thus they normally search for acorns, and this could also directly or indirectly affect the density of seedlings/saplings (see references in Herrera et al. 1998).

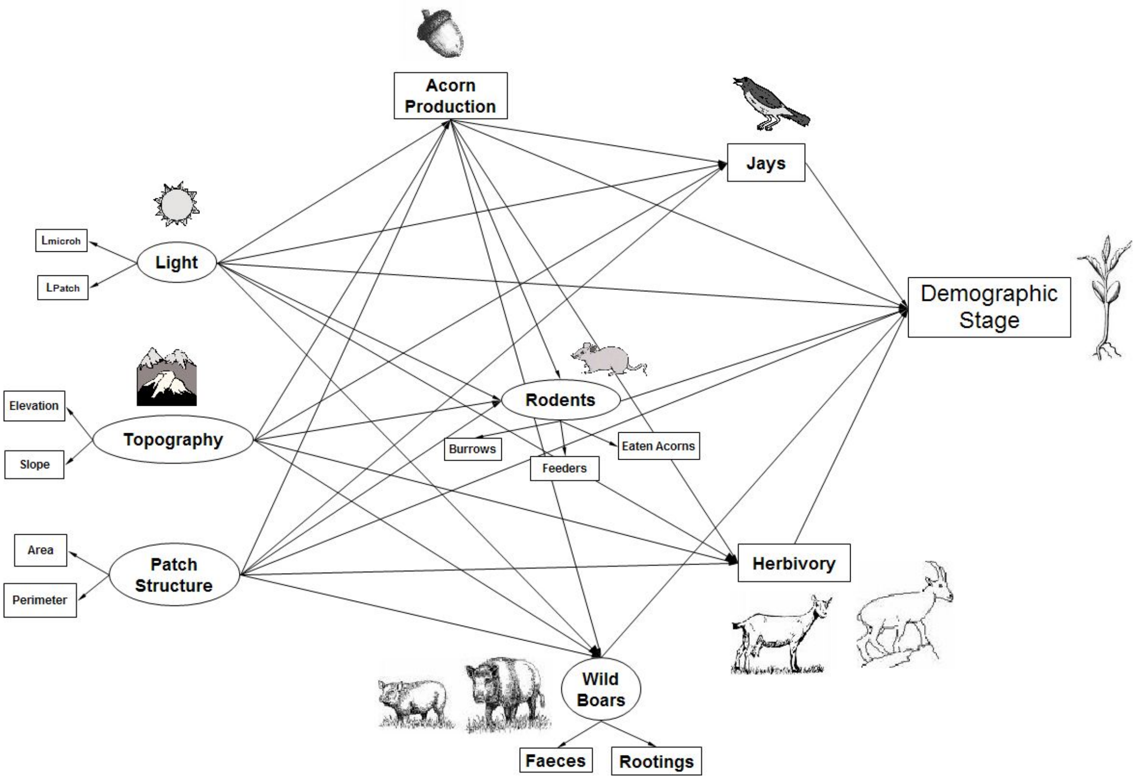


Figure 3. Path diagram showing our saturated hypothetical model considering different causal effects of the traits on different *Q.ilex* demographic stages. Lines indicate causal effects on plant demography (response variable). Latent construct variables indicated on ellipses and manifest variables on squares.

Finally, the output of our hypothetical models will be the density of 1) seedlings, 2) two year seedlings, defined as seedlings surviving to the first summer drought, and 3) saplings. So, the number of recruits per $600m^2$ of area for one-year and two-year seedlings or $300m^2$ for saplings.

To select the best fitting model(s), we performed an information-theoretic approach (Burnham and Anderson 2002). We used Maximum-Likelihood Estimation (MLE) on the variance-covariance matrix to test the goodness of fit of each model and to calculate the Akaike and Bayesian Information Criterion (AIC, BIC). While running the models we decided to maintain the latent variables as a whole, without taking out any of their inclusive measured variables (Grace 2006). We first selected those models obtaining an appropriate goodness of fit (p>0.05, Grace, 2006). From this set of candidate models, we calculated the Akaike Information Criterion (AIC), the second-order AIC (AICc= AIC+[(2k(k+1))/n-k-1]), the AIC_C increment (AIC_{INC}), the likelihood of each model, given data (_ (gi|x)= e-0.5 AIC_{INC}) and the Akaike weights of each model i of the R candidate models as:

$$w_i = \frac{e^{-0.5\Delta AICc_i}}{\sum_{r=1}^{R} e^{-0.5\Delta AICc_i}}$$ w_i is considered as the weight of the evidence in favour of a given model i from a set of R candidate models, taking into account that $\sum_{i=1}^{r} w_i = 1$. All models having w_i >0.7 were considered appropriated representation of the raw data (Burnham and Anderson 2002).All the SEM were computed using the SEPATH module in Statistica 7.0 (StatSoft, Inc. 2002).

Results

Seedlings

Results indicated that there were four possible models that describe adequately the causal relationships by the hypothesized saturated model (models 9-12 in Table 1), as they were non significant models. From these models, one of them was the more plausible (model 12 in table 1, graphically shown in Figure 4) completing all the requirements, having the highest Weighted AIC, and the smaller AIC, Second –order AIC, Akaike differences and BIC (Table 1).

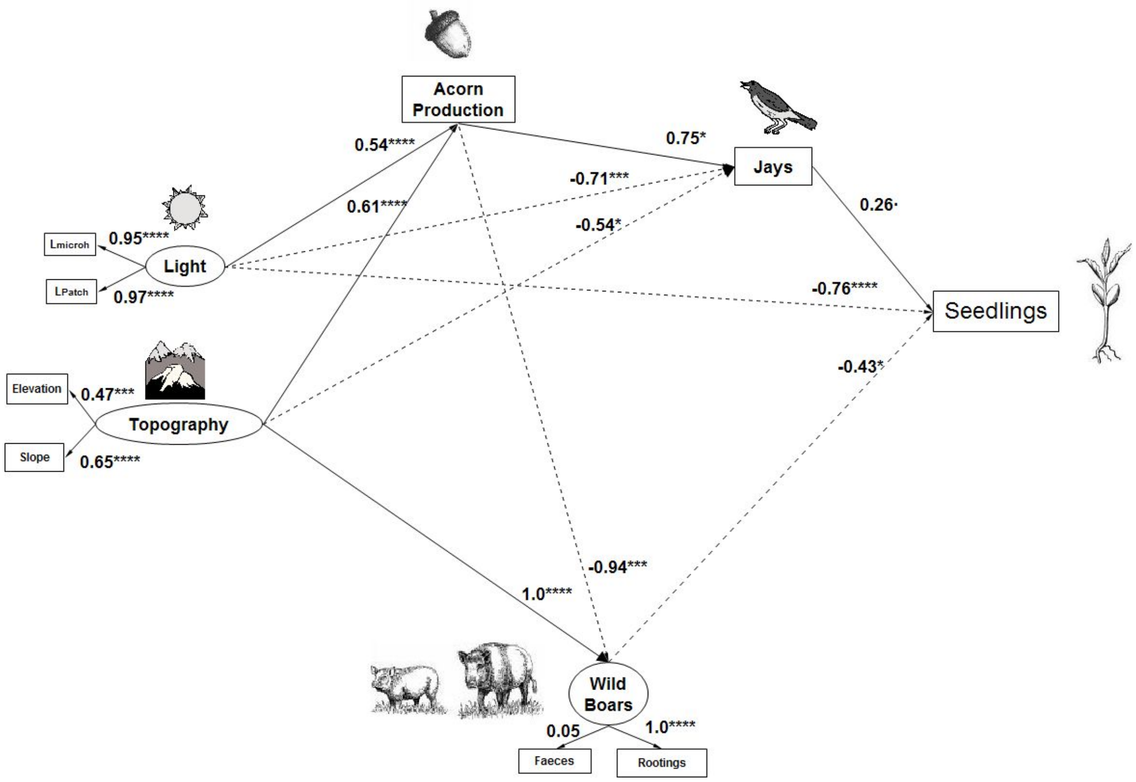


Figure 4. Path diagram showing the best model for seedling density. Diagram shows the influence of direct effects of Jays, Wild boars and light availability on seedling density. Latent construct variables indicated on ellipses and manifest variables on squares. Negative effects appear as dashed lines, positive effects as solid lines. · P<0.1, *P<0.05; **P<0.01, ***P<0.001, ****P<0.0001.

In this model seedling density was positively affected directly by the number of arrival jay flights and indirectly by acorn production (Fig 4). Thus, the more acorn production and jays arrivals more seedlings would be found. As light positively affected acorn production and number of jays flights, indirectly affected positively the density of seedling, although the direct effect of light on seedlings was strong ($P<0.0001$ and correlation 0.76) and negative (Fig. 4). Thus, high light patches would have less arrival flight by jays and seedlings, but more acorns and so, positive indirect effects via acorn production.

The negative relation between the wild boars and seedling density indicated that, as hypothesized, the action of wild boars affected negatively the density of the seedlings. The presence and activity of wild boars was highly positively ($p< 0.0001$, correlation = 1.0, Fig 4) influenced by the topography i.e. the more elevation and slope the more presence and activity of wild boars; and negatively influenced by acorn production, so in high crop patches it is expected to find less wild boars than in low crop patches.

Finally, the topography of the patch slightly affected negatively ($p< 0.05$, correlation = 0.54) the number of jays arrivals and positively affected acorn production per patch. Thus, patches with higher slope and elevation would have more acorns but receive fewer arrivals of jay flights.

Joining all the results of this model, it appears that the action on wild boars is mainly negative for recruitment. On the other hand, the action of jays seems to have a net positive effect (and thus, act as effective acorn dispersers). Light availability seems to have a strong negative effect on seedling density.

Two-year old seedlings

Results indicated that there were two possible models adjusting adequately the causal relationships by the hypothesized model (models 13 and 14 in Table 2, both shown in Figure 5) for two-year old seedlings density. Both models were almost equivalents (Table 2, Fig. 5), so no possible distinction between them was possible. Model 13, having the highest p-value and smallest AIC while model 14 had smallest Weighted AIC, Second –order AIC, Akaike differences and BIC (Table 1).

In the first model (model 13 in Table 2, at the top of Figure 5) seedling density appears to be positively affected by the number of jays flights per patch on the one hand, and directly ($p<0.0001$, correlation = 0.59) and indirectly (via the action of jays) negatively by light on the other. Thus according to these results, high irradiance patches will have less seedlings surviving to summer drought, as well as less jays arriving to these patches.

In the second model (model 14 in Table 2, at the bottom of Figure 5), it appears that the number of arrivals by jays increased the two-year-old seedling densities. On the other hand, as expected, low light conditions positively affected the survival of the seedlings to summer drought.

Table 1. Seedling Density.

Model	K	AIC	AIC_C	AIC_{INC}	AIC_W	BIC	χ^2	p-value	Paths
0	58	24.315	245.089	220.039	0.000	26.825	461.246	<0.0001	PStr→H
1	57	37.170	243.795	218.744	0.000	39.885	748.921	<0.0001	PStr→Seedlings
2	56	31.607	225.062	200.011	0.000	34.271	622.970	<0.0001	L→R
3	55	31.703	212.880	187.829	0.000	34.315	627.167	<0.0001	PStr→R
4	54	34.669	204.383	179.333	0.000	37.179	699.388	<0.0001	H→Seedlings T→H PStr→H L→H
5	50	27.998	158.767	133.717	0.000	30.169	667.953	<0.0001	PStr→WB
6	49	14.825	137.325	112.274	0.000	16.946	314.268	<0.0001	PStr→AP
7	48	28.318	143.050	117.999	0.000	30.439	678.579	<0.0001	PStr→Jays
8	39	14.482	76.882	51.831	0.000	16.307	317.010	<0.0001	T→Seedlings
9	38	4.153	62.271	37.220	0.000	5.929	40.125	0.554	AP→Seedlings
10	37	4.017	58.094	33.043	0.000	5.744	38.451	0.669	L→WB
11	36	3.970	54.234	29.183	0.000	5.648	39.189	0.678	R→Seedlings T→R AP→R
12	**26**	**2.765**	**25.051**	**0.000**	**1.000**	**3.998**	**24.647**	**0.215**	Jays→Seedling T→Jays AP→Jays L→Jays
13	21	3.556	†	†	†	4.378	116.478	<0.0001	

Results of the Structural Equation Modeling for seedling density. The best model considering all the information criterion is shown in bold (and Figure 4). The last column (Paths) indicates paths that were excluded for the subsequent step, from the previous-step model, starting by the saturated model (Figure 3). Abreviations: AIC: Akaike Information Criterion; AIC_C: Second order AIC; AIC_{INC} : AIC increment ; AIC_W: Weighted AIC; BIC: Bayesian Information Criterion; H: Herbivory; T: Topography; PStr: Patch Structure; AP: Acorn production per Patch; R: Rodents; WB: Wild Boars; L: Light.

Note: † Not calculated because the model was significative.

Table 2. Two-year seedlings.

Model	Parameters	AIC	AIC$_{C}$	AIC$_{INC}$	AIC$_{W}$	BIC	χ^2	p-value	Paths
0	58	65.914	286.688	284.257	0.000	68.674	948.631	<0.0001	PStr→H
1	57	59.671	266.296	263.865	0.000	62.379	850.737	<0.0001	PStr→SxS
2	56	62.266	255.720	253.290	0.000	64.974	892.259	<0.0001	R→SxS
									T→R
									PStr→R
									L→R
									AP→R
3	44	33.288	121.288	118.857	0.000	35.371	452.604	<0.0001	AP→WB
4	43	23.074	105.335	102.900	0.000	25.105	291.177	<0.0001	PStr→AP
5	42	31.447	108.298	105.867	0.000	33.478	425.145	<0.0001	PStr→WB
6	41	20.430	92.180	89.749	0.000	22.305	254.888	<0.0001	PStr→Jays
7	32	11.092	48.145	45.7138	0.000	12.654	117.464	<0.0001	AP→SxS
8	31	12.388	46.595	44.164	0.000	13.950	138.204	<0.0001	T→SxS
9	30	7.755	39.280	36.850	0.000	9.265	66.083	<0.0001	WB→SxS
									T→WB
									L→WB
10	22	4.356	19.460	17.030	0.000	5.501	25.689	0.028	T→Jays
11	21	4.246	17.834	15.403	0.000	5.340	25.939	0.039	AP→Jays
									T→AP
									L→AP
12	17	3.312	11.812	9.381	0.005	4.198	18.997	0.061	H→SxS
									T→H
									L→H
13	**9**	**1.047**	**3.300**	**0.866**	**0.391**	**1.519**	**1.896**	**0.169**	L→Jays
14	**7**	**1.065**	**2.431**	**0.000**	**0.603**	**1.484**	**0.121**	**0.121**	

Results of the Structural Equation Modeling for two-year seedling density. The best models considering all the information criterion is shown in bold (and Figure 5). The last column (Paths) indicates paths that were excluded for the subsequent step, from the previous-step model, starting by the saturated Model 0 (shown in Figure 3). Abreviations: K: number of parameters of the model; AIC: Akaike Information Criterion; AIC$_{C}$: Second order AIC; AIC$_{INC}$: AIC increment ; AIC$_{W}$: Weighted AIC; BIC: Bayesian Information Criterion; H: Herbivory; T: Topography; PStr: Patch Structure; AP: Acorn production per Patch; R: Rodents; WB: Wild Boars; L: Light.

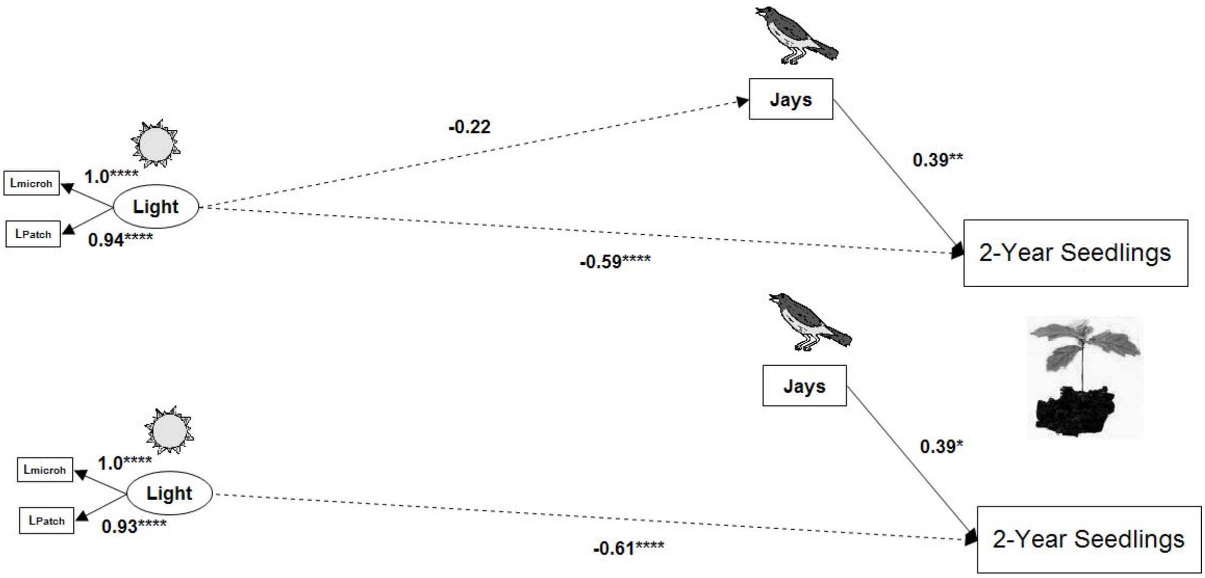


Figure 5. Path diagrams showing the two best models for two-year seedling density. Diagram shows the influence of jays and light availability on two-years seedling density. Latent construct variables indicated on ellipses and manifest variables on squares. Negative effects appear as dashed lines, positive effects as solid lines. *P<0.05; **P<0.01, ****P<0.0001.

Saplings

From all the candidates models, only one was non significant for the density of the *Q. ilex* saplings (model 12 in Table 3, shown in Figure 6). It had the lowest AIC and BIC (0.426 and 0.772 respectively, Table 3), and also had very small values of AIC increments and high values of weighted AIC (Table 3).

This model showed that either high levels of light (correlation = 0.51) or herbivory (correlation = 0.34) negatively affected the density of *Q. ilex* saplings (with p< 0.0001 and p<0.01 respectively). So, apparently those patches with high herbivory pressure and more light will have fewer saplings than those under lower light conditions and less herbivores damage. These results remark an antagonist interaction between the Spanish ibex and livestock on *Q. ilex* saplings.

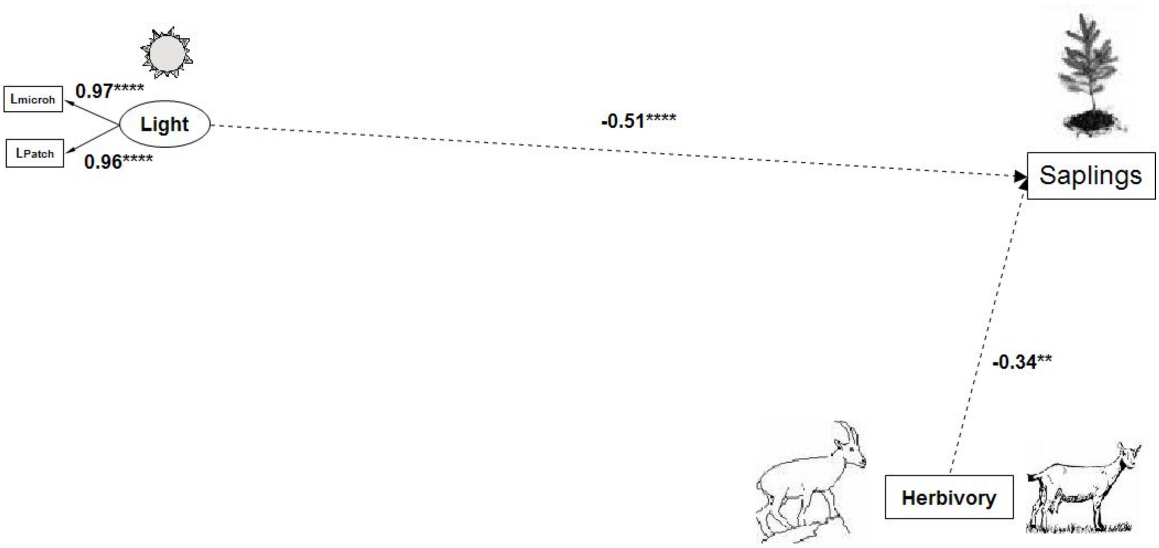


Figure 6. Path diagram showing the best model for sapling density. Diagram shows the influence of herbivores damage and light availability on sapling density. Latent construct variables indicated on ellipses and manifest variables on squares. Negative effects appear as dashed lines. **P<0.01, ****P<0.0001.

Discussion

We found evidences that landscape characteristics as well as biotic interactions influenced *Quercus ilex* demography on different life cycle stages. Furthermore, abiotic characteristics of the landscape seem to have clear effects on the activity of animals. Of those abiotic factors light and topography appears to be the most important. The effects of irradiance always have negative effects on the density of seedlings and saplings. Then, the elevation and slope of each patch highly influenced positively the activity of wild boars and negatively the number of jays arriving per patch. Afterward, wild boars and jays had a negative and positive effect respectively on seedling density. The positive effects of acorn dispersal by jays remained at the two-year seedlings stage. Abiotic landscape characteristics also affected the acorn production per patch. Thus, the higher the elevation and slope, and the higher the irradiance, the more acorns were produced in the patch. More interestingly, this acorn production then affected negatively the action of wild boars and positively the activity of acorn deposition by jays. This agrees with other authors suggesting that seed crop affect seed disperser behavior (Clotfelter et al. 2007) and plant recruitment (see references in Herrera et al. 1998). However, our results suggest that this correlation between acorn production and recruitment is mainly via the indirect effects of plant-animal interactions. Elevations have been also described to influence the probability of emergence in Mediterranean climate (Ramirez et. al 2006). On the other hand, the action of herbivores affected negatively the density of saplings. Herbivory has been reported to affect plant demography at different stages (reviewed in Baraza et al. 2007). On the seedlings and two-year seedlings no effect was found, maybe because young seedlings are not apparent to

Table 3. Sapling density.

Model	Parameters	AIC	AIC$_{C}$	AIC$_{INC}$	AIC$_{W}$	BIC	χ^2	p-value	Paths
0	58	38.598	259.372	257.580	0.000	41.108	789.764	<0.0001	PStr→H
1	57	43.818	250.443	248.651	0.000	46.635	897.811	<0.0001	Jays→Juveniles L→Jays T→Jays PStr→Jays AP→Jays
2	51	30.447	170.026	168.234	0.000	32.439	1095.448	<0.0001	R→Juveniles T→R PStr→R L→R AP→R
3	40	30.519	97.458	95.666	0.000	32.035	1120.241	<0.0001	PStr→Juveniles
4	39	22.376	84.776	82.984	0.000	23.849	804.678	<0.0001	T→Juveniles
5	38	22.574	80.692	78.900	0.000	24.046	812.371	<0.0001	AP→Juveniles
6	37	5.260	59.337	57.545	0.000	6.689	139.156	<0.0001	L→H
7	36	4.667	54.931	53.139	0.000	6.053	118.027	<0.0001	PStr→AP
8	35	8.265	54.932	53.140	0.000	9.607	260.336	<0.0001	PStr→WB
9	26	2.572	24.858	23.066	0.000	3.568	54.324	<0.0001	AP→WB L→AP T→AP
10	21	4.856	18.444	16.652	0.000	5.722	149.395	<0.0001	WB→Juveniles
11	14	1.266	6.866	5.074	0.073	1.829	23.357	0.003	T→ H
12	**7**	**0.426**	**1.792**	**0.000**	**0.926**	**0.772**	**0.601**	**0.741**	

Results of the Structural Equation Modeling for sapling density. The best model considering all the information criterion is shown in bold (and Figure 6). The last column (Paths) indicates paths that were excluded for the subsequent step, from the previous-step model, starting by the saturated model (Figure 3). Abreviations: AIC: Akaike Information Criterion; AIC$_{C}$: Second order AIC; AIC$_{INC}$: AIC increment ; AIC$_{W}$: Weighted AIC; BIC: Bayesian Information Criterion; H: Herbivory; T: Topography; PStr: Patch Structure; AP: Acorn production per Patch; R: Rodents; WB: Wild Boars; L: Light.

herbivores perception. So, our results suggest that the action of ungulates browsing *Q. ilex* start affecting at the sapling stage (see similar results in Gómez et al. 2003; Gómez 2004).

Thus, if we consider the net effects of plant-animal interactions in this study system, we can say that ungulates have a negative effect and jays had a big positive effect on *Q. ilex* demography. This is the case of wild boars acting as pre- and post-dispersal acorn and seedling predators and Spanish ibex and livestock browsing the saplings. They do not offer any positive aspect for *Q. ilex* so they definitively act as antagonistic species as have been widely described in a variety of cases (Meriggi and Sacchi 2000; Zamora et al. 2001). On the other hand, the interaction with jays seems to be highly positive, being beneficial for recruitment ranging from the one-year seedling to the two-year seedling stage. This result is in accordance to Gómez et al. (2004) showing that the total variance of structural heterogeneity in terms of irradiance had significant differences with the functional irradiance heterogeneity after dispersal by jays. In this study, jays are described to filter the total available irradiance dispersing the acorns to habitats with lower irradiance, and thus more humidity and less temperature, that increase the probabilities of emergence and seedling survival (Gómez 2004; Ramirez et al. 2006; Puerta-Piñero et al. 2007), our results support these ideas.

Plant-animal interactions had an effect on the establishment of Holm oaks having different stage-dependent effects (Schupp and Fuentes 1995). Different life stages showed differences in causal relationships between landscape and biotic traits and *Q. ilex* demography (Schupp 1992). In the first stage, acorn crop appears to be affected by the topography and irradiance. Thus, the higher the elevation and slope and more irradiance per patch, the higher the acorn production was. After that, at the one-year seedling stage it appears that *Q. ilex* recruitment is directly constrained because of the predation activity of wild boars and high irradiance and indirectly by topography. Whereas recruitment of one-year seedlings was enhance indirectly by larger acorn crops and directly by the arrival of jays. On the other hand, the establishment of the two-year seedlings depended on the number of jay-flights arriving at each patch and low irradiance conditions. Finally, it seems that herbivory pressure as well as high irradiance conditions limited the establishment of the saplings (Zamora et al. 2001). This results support the idea that different species interacting within the same landscape can results in very different consequences (Wiens 2000).

Only the factor light had the similar negative influences at all the stages. Light has been widely reported to influence plant recruitment at different stages in a variety of systems. In tropical systems the norm is usually the more the light the better recruitment and establishment while in Mediterranean ones the rule is usually the opposite (Espelta et al. 1995; Gómez et al. 2004; Gómez-Aparicio et al. 2005; Puerta-Piñero et al. 2007). Either the case, environmental conditions seem to determine the probability of recruitment (see Gómez-Aparicio et al. 2004 and Ramirez et al. 2006 for similar results). As expected in this study, summer conditions imposed severe restrictions on seedling survival (Espelta et al. 1995; Ramirez et. al 2006). Thus, the mortality of one-year seedlings seems to be highly and negative affected by total irradiance, and thus because high correlations, by summer drought. On the other hand, the activity of jays dispersing the acorns had positive effects for both the seedling and the two-year seedling stages. As previously discussed, this suggest that jays dispersing the acorns is highly beneficial for *Q. ilex* recruitment and establishment (Gómez et al. 2004; Pons and Pausas 2007), suggesting somehow that jays act as directed seed dispersers in this, and probably other systems as well. As different *Q. ilex* stages showed different cause- correlation traits, our results encourage that including together the action of different key agents should be obligatory in studies of landscapes patterns and processes.

In sum, few studies of landscape ecology have really challenged mechanistic approaches to the study of the observed patterns. Our results suggest that including simultaneously the action of abiotic factors as well as biotic interactions should be enforced on further landscape demographic studies (Rey and Manzaneda 2007). On the other hand, this study sustains the idea of different stage-dependence requirements on plants life-cycles (Schupp 1992; Schupp and Fuentes 1995). Without considering different parts of the life cycle and all the key factors affecting the observed pattern our knowledge will be far from completed.

Acknowledgements

We deeply thank Fernando Valladares for doing the hemispherical photographs and computing and sharing the irradiance estimates; Migue Calero for helping in the field and Lluís Pesquer and Xavier Pons for precious technical assistance during the GIS procedure. The headquarters of the Sierra Nevada National Park and especially of the Jardín Botánico de la Cortijuela offered support for working in the study site. This study was possible thanks to the Spanish Ministry of Science and Education by a FPU fellowship AP2003-3444, and short stay grant to CPP and financial support via projects REN2003-07048. The Spanish network GLOBIMED (www.globimed.net) facilitated the collaborative work.

References

Adams DC, Rosenberg MS. 1998. Partial warps, phylogeny, and ontogeny: a comment of Fink and Zeldiths. Systematic biology 47: 168-173.

Agrawal AA, Ackerly DD, Adler F, Arnold AE, Cáceres C, Doak DF, Post E, Hudson PJ, Maron J, Mooney KA, Power M, Schemske D, Stachowicz J, Strauss S, Turner MG, Werner E. 2007. Filling key gaps in population and community ecology. Front Ecol Environ 5: 145-152.

Alcántara JM, Rey PJ, Sánchez-Lafuente AM, Valera F. 2000. Early effects of rodent post-dispersal seed predation on the outcome of the plant-seed disperser interaction. Oikos 88: 362-370.

Baraza E, Zamora R, Hódar JA, Gómez JM. 2007. Plant-herbivore interaction: beyond a binary vision. In: Pugnaire, F.I. y Valladares, F. (eds.). Handbook of functional plant ecology, 2nd ed. Marcel Dekker Inc., New York.

Bollen KA. 1989. Structural equations with latent variables. John Wiley and Sons, New York.

Brown LE. 1969. Field experiments on the movements of Apodemus sylvaticus L. using trapping and tracking techniques. Oecologia 2: 198-222.

Burnham KP, Anderson DR. 2002. Model Selection and Multimodel Inference: A Practical-Theoretic Approach, 2nd ed. Springer-Verlag.

Chen JM, Black TA, Adams RS. 1991. Evaluation of hemispherical photography for determining plant area index and geometry of a forest stand. Agricultural and Forest Meteorology 56: 129-143.

Clark JS, Mohan J, Dietze M, Ibañez I. 2003. Coexistence: how to identify trophic trade-offs. Ecology 84: 17-31.

Clotfelter ED, Pedersen AB, Cranford JA, Ram N, Snajdr EA, Nolan V, Ketterson ED. 2007. Acorn mast drives long-term dynamics of rodent and songbird populations. Oecologia 154: 493-503.

Espelta JM, Riba M, Retana J. 1995. Patterns of seedling recruitment in west Mediterranean coppiced holm-oak (*Quercus ilex* L.) forests as influenced by canopy development. Journal of Vegetation Science 6: 465-472.

Gómez JM. 2003. Spatial patterns in long-distance dispersal of *Quercus ilex* acorns by jays in a heterogeneous landscape. Ecography 26: 573–584.

Gómez JM. 2004. Importance of microhabitat and acorn burial on *Quercus ilex* early recruitment: non-additive effects on multiple demographic processes. Plant Ecol 192: 287-297.

Gómez JM, García D, Zamora R. 2003. Impact of vertebrate acorn- and seedling-predators on a Mediterranean *Quercus pyrenaica* forest. Forest Ecology and Management 180: 125-134

Gómez JM, Valladares F, Puerta-Piñero C. 2004. Differences between structural and functional environmental heterogeneity caused by seed dispersal. Functional Ecology 18: 787-792.

Gómez-Aparicio L, Valladares F, Zamora R, Quero JL. 2005. Response of tree seedlings to the abiotic heterogeneity generated by nurse shrubs: an experimental approach at different scales. Ecography 28: 757–768.

Gómez-Aparicio L, Zamora R, Gómez JM, Hódar JA, Castro J, Baraza E. 2004. Applying plant facilitation to forest restoration: a meta-analysis of the use of shrubs as nurse plants. Ecological Applications 14:1128- 1138.

Gough L, Grace JB. 1999. Effects of environmental change on plant species density: comparing predictions with experiments. Ecology 80: 882-890.

Grace JB. 2003. Examining the relationship between environmental variables and ordination axes using latent variables and structural equation modeling. Pp 171- 193. In Pugesek, BH, Tomer A and von Eye A, eds. Structural equation modeling, applications in ecological and evolutionary biology. Cambridge University Press, Cambridge, UK.

Grace JB. 2006. Structural equation modeling and natural systems. Cambridge University Press, Cambridge, UK.

Herrera CM, Jordano P, Guitián J, Traveset A. 1998. Annual variability in seed production by woody plants and the masting concept: reassessment of principles and relationships to pollination and seed dispersal. The American Naturalist 152: 576-594.

Herrera CM, Jordano P, López-Soria L, Amat JA. 1994. Recruitment of a mast-fruiting, bird-dispersed tree: bridging frugivore activity and seedling establishment. Ecological monograph 64: 315-344.

Hershberger SL, Marcoulides GA, Parramore MM. 2003. Structural equation modeling: an introduction. Pp 3-41. In: Pugesek, B.H., Tomer A and von Eye A, eds. Structural equation modeling, applications in ecological and evolutionary biology. Cambridge University Press, Cambridge, UK.

Johnson JB, Omland KS. 2004. Model selection in ecology and evolution. Trends in ecology and evolution 19: 101-108.

Jordano P. 1995. Frugivore-mediated selection on fruit and seed size: birds and St. Lucie´s Cherry *Prunus mahaleb*. Ecology 76: 2627-2639.

Kubota Y, Murata H, Kikuzawa K. 2004. Effects of topographic heterogeneity on tree species rechness and stand dyamics in a subtropical forest in Okinawa Island, southern Japan. Journal of Ecology 92: 230-240.

Larcher W. 2000. Temperature stress and survival ability of Mediterranean sclerophyllous plants. *Plant Biosystems* 134:279-295.

Levin SA. 1992. The problem of pattern and scale in ecology. Ecology 73: 1943-1967.

Meriggi A., Sacchi O. 2000. Habitat requirements of wild boars in the northern Appennines (N Italy): a multi-level approach. Ital. J. Zool. 68: 47-55.

Mitjà A, Batalla E. 1982. Manual de radiación solar. UPC-Instituto de Ciencias Energéticas-ETSIIB. Prensa XXI, Barcelona.

Muñoz A, Bonal R. 2007. Rodents change acorn dispersal behaviour in response to ungulate presence. Oikos 116: 1631-1638.

Myers RA, Cadigan NG. 1993. Density-dependent juvenile mortality in marine demersal fish. Can J. Fish. Aquat. Sci. 50: 1576-1590.

Nathan R, Muller-Landau H. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. Trends in Ecology and Evolution 15: 278- 285.

Nilsson SG. 1985. Ecological and evolutionary interactions between reproduction of beech *Fagus silvatica* and seed eating animals. Oikos 44: 157-164.

Orrock JL, Danielson MJ, Burns MJ, Levey DJ. 2003. Spatial ecology of predator-prey interactions: corridors and patch shape influence seed predation. Ecology 84: 2589-2599.

Perkins RM.1976. Guide to animal tracks. Stackpole books.

Pons J, Pausas JG. 2007a. Rodent acorn selection in a Mediterranean oak landscape. Ecological research 22: 1440-1703.

Pons J, Pausas JG. 2007b. Acorn dispersal estimated by radio-tracking. Oecologia 153: 1432-1939. DOI 10.1007/s00442-007-0788-x

Pons, X. 1996. "Estimación de la radiación solar a partir de modelos digitales de elevaciones. Propuesta metodológica" in Juaristi, J & I. Moro "Modelos y Sistemas de Información en Geografía" (458 p) p. 87-97 ISBN: 84-605-5896-7.

Pons, X. 2002. MiraMon. Sistema d'Informació Geogràfica i software de Teledetecció, Centre de Recerca Ecològica i Aplicacions Forestals, CREAF, Bellaterra.

Posada D, Buckley TR. 2004. Model selection and model averaging in phylogenetics: advantages of Akaike information criterion and Bayesian approaches over likelihood ration tests. Syst. Biol. 53: 793-808.

Puerta-Piñero C, Gómez JM, Valladares F. 2007. Irradiance and oak seedling survival and growth in a heterogeneous environment. Forest Ecology and Management 242: 462-469.

Pugesek BH, Tomer A, von Eye A. 2003. Structural equation modeling, applications in ecological and evolutionary biology. Cambridge University Press, Cambridge, UK.

Pugesek BH. 2003a. Concepts of structural equation modeling in biological research. Pages 42-59 *in* Pugesek, B.H., Tomer A. and von Eye, A. eds. Structural equation modeling, applications in ecological and evolutionary biology. Cambridge University Press, Cambridge, UK.

Pugesek BH. 2003b. Modeling means in latent variable models of natural selection. Pages 297-311 *in* Pugesek, B.H., A. Tomer and A. von Eye, eds. Structural equation modeling, applications in ecological and evolutionary biology. Cambridge University Press, Cambridge, UK.

Pulido FJ, Díaz M. 2005. Regeneration of a Mediterranean oak: A whole-cycle approach. Ecoscience 12: 92-102.

Pulido FJ. 1999. Herbivorismo y regeneración de la encina (*Quercus ilex* L.) en bosques y dehesas. PhD thesis. University of Extremadura, Spain.

Retana J, Espelta JM, Gracia M, Riba M. 1999. Seedling recruitment. Ecology of Mediterranean Evergreen Oak Forests (eds. Rodá, F. Retana, J. Gracia C. A., & Bellot J.), pp. 89-103, Springer-Verlag, Berlin.

Rey P, Alcántara JM. 2000. Recruitment dynamics of a fleshy-fruited plant (Olea europaea): connecting patterns of seed dispersal to seedling establishment. Journal of Ecology 88: 622-633.

Rey P, Manzaneda AJ. 2007. Geographical variation in the determinants of seed dispersal success of a myrmecochorous herb. Journal of Ecology 95: 1381-1393.

Rich PM. 1990. Characterizing plant canopies with hemispherical photographs. Remote Sensing Reviews 5: 13-29.

Roxburgh JR, Kelly D. 1995. Uses and limitations of hemispherical photography for estimating forest light environments. New Zealand Journal of Ecology 19: 213- 217.

Shipley B. 2000. Cause and correlation in biology. Cambridge University Press, Cambridge, UK.

Shugart HH. 1984. A theory of forest dynamics. Springer. New York.

Sutherland WJ. 2006 Ecological Census Techniques: A handbook. Cambridge University Press. UK.

Turner MG, Gardner RH, Dale VH, O`Neill RV. 1989. Predicting the spread of disturbance across heterogeneous landscapes. Oikos 55: 121-129.

Turner MG, Gardner RH, O´Neill RV. 2001. Landscape ecology in theory and practice: Pattern and Process. Springer.

Verheyen K, Guntenspergen GR, Biesbrouck B, Hermy M. 2003. An integrated analysis of the effects of past land use on forest herb colonization at the landscape scale. Journal of Ecology 91: 731-742.

Wiens JA, Stanseth NC, Van Horne B, Ims RA. 1993. Ecological mechanisms and landscape ecology. Oikos 66: 369-380.

Wiens JA. 1995. Landscape mosaics and ecological theory. Pp 1-30. In Mosaic landscapes and ecological processes. Hansson L., Fahrig L., Merriam G. (eds). Chapman & Hall.

Wiens JA. 2000. Ecological heterogeneity: an ontogeny of concepts and approaches. In: The Ecological consequences of environmental heterogeneity. M.J. Hutchings, E.A. John, A.J.A. Steward (eds). Blackwell Science Ltd.

Zamora R, Gómez JM, Hódar JA, Castro J, García D. 2001. Effect of browsing by ungulates on sapling growth of Scots pine in a Mediterranean environment: consequences for forest regeneration. Forest Ecology and Management 144: 33-42.

Appendix A. Mean values of GIS-generated Patch variables.

Valley	Landscape Unit	Patch	X	Y	Elevation	Slope	Area	N Perimeter	L_{Patch}	L_{Microh}
Huenes	**Oak Woodland**	**E1**	457979.38	4104737.00	1659.75	20.64	16450.38	454.67	134752.75	68126.11
Huenes	**Oak Woodland**	**E10**	457951.54	4104806.25	1684.14	28.80	7910.50	315.29	131167.19	58048.85
Huenes	**Oak Woodland**	**E11**	458089.71	4104882.00	1729.99	29.40	19634.34	496.72	130063.51	NA
Huenes	**Oak Woodland**	**E12**	457927.23	4104967.75	1730.80	21.07	21841.14	523.89	134609.61	NA
Huenes	**Oak Woodland**	**E13**	457619.66	4105194.19	1764.74	23.13	48654.17	781.92	135031.05	NA
Huenes	**Oak Woodland**	**E14**	457415.75	4105068.50	1678.61	26.87	56352.38	841.51	133088.51	58156.16
Huenes	**Oak Woodland**	**E15**	457150.42	4105141.75	1653.65	26.08	42554.04	731.27	131706.08	34053.65
Huenes	**Oak Woodland**	**E16**	458036.38	4105163.50	1820.67	21.34	9823.56	351.35	133637.02	75448.38
Huenes	**Oak Woodland**	**E17**	458291.33	4105022.25	1818.28	13.45	16852.01	460.18	136322.68	76964.64
Huenes	**Oak Woodland**	**E18**	458240.57	4104855.25	1774.55	17.30	10413.38	361.74	135698.70	60691.62
Huenes	**Oak Woodland**	**E19**	458407.27	4104754.25	1774.59	22.74	7892.13	314.92	133525.41	75385.37
Huenes	**Oak Woodland**	**E2**	458424.70	4104442.94	1696.08	14.48	8697.48	330.60	135312.77	65504.81
Huenes	**Oak Woodland**	**E20**	459022.97	4104713.50	1889.50	18.83	10633.20	365.54	133151.25	42679.70
Huenes	**Oak Woodland**	**E21**	458985.63	4104949.00	1885.63	25.97	28428.03	597.69	132156.50	74612.51
Huenes	**Oak Woodland**	**E22**	458644.51	4104833.50	1850.11	29.54	45109.99	752.91	129217.70	67646.08
Huenes	**Oak Woodland**	**E23**	458228.66	4104454.21	1653.59	18.78	8163.82	320.30	132907.61	65887.13
Huenes	**Oak Woodland**	**E3**	457416.57	4105248.75	1758.80	20.08	10909.55	370.26	133900.10	71216.52
Huenes	**Oak Woodland**	**E4**	457720.64	4104900.25	1674.53	17.39	24810.05	558.37	136221.46	71315.38
Huenes	**Oak Woodland**	**E5**	458868.39	4104648.00	1814.70	16.83	53145.00	817.21	134349.64	67155.96
Huenes	**Oak Woodland**	**E6**	458046.76	4104535.50	1625.87	13.24	5273.59	257.43	137287.73	55781.14
Huenes	**Oak Woodland**	**E7**	458130.00	4104449.25	1625.97	14.50	1718.59	146.96	136041.11	34870.41
Huenes	**Shrubland**	**M1**	457940.67	4104580.13	1613.11	16.45	7848.04	314.04	151844.12	63808.82
Huenes	**Shrubland**	**M2**	458097.43	4104606.50	1643.75	13.24	4603.25	240.51	152692.91	NA
Huenes	**Shrubland**	**M3**	458266.95	4104595.42	1672.80	15.77	13751.94	415.71	151880.27	85748.10
Huenes	**Shrubland**	**M4**	458269.58	4104747.75	1756.56	24.01	77235.02	985.17	146210.49	NA
Huenes	**Shrubland**	**M5**	458626.18	4104920.25	1867.43	22.51	24382.86	553.54	136823.25	NA
Huenes	**Shrubland**	**M6**	457644.21	4105358.25	1785.27	23.10	69175.34	932.35	135965.52	76762.99
Huenes	**Pine Woodland**	**P1**	458060.84	4104482.25	1619.49	14.68	7116.83	299.05	66458.25	13192.94
Huenes	**Pine Woodland**	**P2**	458320.16	4104460.51	1676.61	15.07	7173.39	300.24	65612.99	13025.14

Valley	**Landscape Unit**	**Patch**	**X**	**Y**	**Elevation**	**Slope**	**Area**	**N Perimeter**	$\mathbf{L_{Patch}}$	$\mathbf{L_{Microh}}$
Huenes	**Pine Woodland**	**P3**	459303.37	4105032.75	1899.43	12.37	84720.76	1031.81	65740.71	NA
Huenes	**Pine Woodland**	**P4**	458768.71	4105045.79	1850.60	16.71	130466.93	1280.43	63798.62	12664.96
Huenes	**Pine Woodland**	**P5**	457991.53	4105078.00	1783.16	24.51	103942.74	1142.88	64333.01	18131.78
Huenes	**Pine Woodland**	**P6**	457915.21	4104883.25	1687.72	23.61	4941.77	249.20	63335.42	17520.99
Huenes	**Pine Woodland**	**P7**	457389.20	4105358.56	1752.35	12.88	6995.16	296.49	64637.84	36493.03
B. Seco	**Oak Woodland**	**E24**	456594.61	4107355.25	1738.23	23.53	44542.25	748.15	129138.56	NA
B. Seco	**Oak Woodland**	**E25**	456220.00	4107289.00	1611.43	32.04	188075.21	1537.34	120603.08	68514.53
B. Seco	**Oak Woodland**	**E27**	456026.75	4107096.00	1589.18	25.74	51571.57	805.03	116067.50	57151.80
B. Seco	**Oak Woodland**	**E28**	456393.67	4106842.75	1634.00	25.79	15351.13	439.21	128271.30	70330.41
B. Seco	**Oak Woodland**	**E29**	456283.51	4106654.25	1656.06	22.24	12929.75	403.09	130241.90	NA
B. Seco	**Oak Woodland**	**E30**	456199.81	4106511.25	1682.93	15.58	3900.17	221.38	135324.97	61011.56
B. Seco	**Oak Woodland**	**E31**	456116.90	4106164.50	1744.14	14.38	19907.81	500.17	134213.03	NA
B. Seco	**Oak Woodland**	**E32**	455895.22	4106137.00	1805.90	17.56	18769.29	485.66	131675.20	74959.20
B. Seco	**Oak Woodland**	**E33**	456048.70	4106273.81	1741.82	19.22	43453.03	738.95	127322.06	71883.10
B. Seco	**Oak Woodland**	**E34**	455852.77	4106488.25	1776.90	19.24	17973.79	475.25	126204.42	59702.44
B. Seco	**Oak Woodland**	**E35**	456026.44	4106628.58	1722.58	15.56	23457.74	542.94	132131.10	61937.28
B. Seco	**Shrubland**	**M7**	456406.90	4106450.50	1682.16	13.17	23664.20	545.32	147688.85	NA
B.Seco	**Shrubland**	**M8**	455700.09	4106338.00	1816.10	16.82	71686.74	949.13	144135.25	63787.95
B. Seco	**Pine Woodland**	**P8**	456134.27	4106699.75	1661.21	19.52	66466.76	913.92	60677.91	16924.36
B. Seco	**Pine Woodland**	**P9**	456013.58	4106473.50	1732.23	16.56	123444.01	1245.49	62391.95	17633.66
Dornajo	**Oak Woodland**	**E36**	461770.32	4107804.75	1992.21	17.47	63332.85	892.11	136268.82	NA
Dornajo	**Oak Woodland**	**E39**	461301.96	4107834.25	1952.11	20.65	76938.21	983.28	135457.09	77021.25
Dornajo	**Oak Woodland**	**E43**	460976.50	4108006.25	1942.73	19.97	20285.38	504.89	135595.32	76553.99
Dornajo	**Oak Woodland**	**E44**	460326.14	4107843.25	1911.46	30.09	32501.00	639.08	130365.36	58297.20
Dornajo	**Oak Woodland**	**E45**	460572.66	4107966.66	1953.93	24.95	36656.79	678.71	132827.67	59398.30
Dornajo	**Oak Woodland**	**E46**	461051.30	4108174.32	2003.60	23.65	32312.84	637.22	132945.32	66616.11
Dornajo	**Shrubland**	**M10**	461663.83	4108117.55	2077.70	20.11	223223.89	1674.85	148710.44	NA
Dornajo	**Shrubland**	**M11**	461300.97	4108239.92	2005.00	18.58	60331.24	870.72	148290.19	NA
Dornajo	**Shrubland**	**M9**	461327.52	4107727.00	1927.74	14.48	18869.74	486.95	152925.38	86338.14
Dornajo	**Pine Woodland**	**P10**	461561.86	4107836.00	1985.85	16.91	26532.50	577.42	66147.66	NA
Dornajo	**Pine Woodland**	**P11**	461278.86	4108089.75	1989.24	16.95	30179.68	615.83	64644.95	12832.97

Valley	**Landscape Unit**	**Patch**	**X**	**Y**	**Elevation**	**Slope**	**Area**	**N Perimeter**	**L_{Patch}**	**L_{Microh}**
Dornajo	**Pine Woodland**	**P12**	460879.13	4108011.00	1911.11	27.31	21394.16	518.50	64136.80	NA

Mean values of the GIS-generated patch variables. Abbreviations: L: Light. L_{Patch}: Total summer (June, July and August) irradiance per landscape unit and patch; L_{Microh} irradiance per patch multiplied by Global Site Factor of the natural seedlings existing at each patch; N Perimeter: the actual perimeter of patch divided with that of a circle with the same area. See methods for further definitions of each variable. NA cells indicate not available data.

Appendix B. Mean values of field data per patch.

Valley	Landscape Unit	Patch	Seedlings	2-Y Seedlings	Saplings	R Burrows	R Feeders	Eaten Acorns	WB Faeces	WB Rootings	Herbivory damage	Jays	Acorn Patch
Huenes	**Oak Woodland**	**E1**	0.33	0.28	17.67	0.00	0.00	0.00	0.00	0.00	NA	107.00	75.56
Huenes	**Oak Woodland**	**E10**	0.50	0.25	3.33	0.00	0.17	0.83	2.33	36.67	5.00	19.00	212.00
Huenes	**Oak Woodland**	**E11**	0.00	0.00	2.67	0.00	0.17	0.50	0.33	7.00	7.14	22.00	12.40
Huenes	**Oak Woodland**	**E12**	0.00	0.00	3.33	0.00	0.00	0.17	4.00	21.00	4.00	4.00	46.00
Huenes	**Oak Woodland**	**E13**	0.00	0.00	3.00	0.00	0.50	22.83	1.33	1.67	5.00	10.00	30.60
Huenes	**Oak Woodland**	**E14**	0.50	0.50	6.67	0.00	0.00	0.00	0.67	5.00	16.47	12.00	123.00
Huenes	**Oak Woodland**	**E15**	1.50	0.30	2.00	0.00	0.33	6.17	1.00	6.00	5.00	0.00	49.50
Huenes	**Oak Woodland**	**E16**	0.33	NA	2.67	0.00	0.00	0.00	0.00	16.00	57.50	0.00	12.40
Huenes	**Oak Woodland**	**E17**	0.50	NA	1.00	0.00	0.17	25.00	2.67	5.67	8.33	2.00	26.31
Huenes	**Oak Woodland**	**E18**	0.50	NA	1.33	0.00	0.17	0.33	1.33	5.33	5.00	10.00	31.80
Huenes	**Oak Woodland**	**E19**	0.83	0.00	3.33	0.33	0.00	0.00	6.00	6.67	9.20	4.00	12.00
Huenes	**Oak Woodland**	**E2**	1.00	0.53	9.33	0.17	0.83	3.33	0.00	0.00	0.00	17.00	26.34
Huenes	**Oak Woodland**	**E20**	0.50	NA	7.00	0.17	0.00	0.00	3.00	7.33	17.86	1.00	37.91
Huenes	**Oak Woodland**	**E21**	0.17	0.17	2.67	0.00	0.00	0.17	1.00	14.67	28.75	1.00	116.51
Huenes	**Oak Woodland**	**E22**	1.00	1.00	2.67	0.17	0.17	1.83	1.00	13.00	31.25	16.00	72.20
Huenes	**Oak Woodland**	**E23**	1.17	1.17	12.33	0.67	0.17	1.17	0.00	0.00	0.00	5.00	22.16
Huenes	**Oak Woodland**	**E3**	0.67	0.33	2.33	0.00	0.00	0.17	5.00	8.67	15.71	9.00	57.18
Huenes	**Oak Woodland**	**E4**	0.83	0.50	1.67	0.17	0.00	0.00	6.67	11.33	10.00	10.00	48.06
Huenes	**Oak Woodland**	**E5**	1.17	0.88	9.33	0.00	0.00	0.00	2.00	4.33	NA	11.00	89.43
Huenes	**Oak Woodland**	**E6**	2.00	2.00	26.00	0.00	0.00	0.00	0.00	0.00	0.00	18.00	6.40
Huenes	**Oak Woodland**	**E7**	2.50	2.50	12.00	0.00	0.50	15.00	0.00	0.00	0.00	5.00	3.60
Huenes	**Shrubland**	**M1**	0.67	0.67	0.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Huenes	**Shrubland**	**M2**	0.33	NA	0.00	0.00	0.00	0.00	0.00	0.00	NA	4.00	0.00
Huenes	**Shrubland**	**M3**	0.17	NA	0.33	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00
Huenes	**Shrubland**	**M4**	0.00	0.00	0.33	0.00	0.00	0.00	0.33	4.33	40.00	0.00	0.00
Huenes	**Shrubland**	**M5**	0.00	0.00	0.00	0.00	0.00	0.11	0.00	12.67	NA	0.00	0.00
Huenes	**Shrubland**	**M6**	1.00	NA	1.33	0.00	0.33	2.00	0.67	6.33	2.50	0.00	0.00
Huenes	**Pine Woodland**	**P1**	8.17	8.17	76.00	0.00	0.00	0.00	0.00	0.00	NA	88.00	0.00
Huenes	**Pine Woodland**	**P2**	5.17	5.17	23.67	0.00	0.00	0.17	0.00	0.00	0.00	42.00	0.00

Valley	Landscape Unit	Patch	Seedlings	2-Y Seedlings	Saplings	R Burrows	R Feeders	Eaten Acorns	WB Faeces	WB Rootings	Herbivory damage	Jays	Acorn Patch
Huenes	**Pine Woodland**	**P3**	0.00	0.00	0.67	0.00	0.00	0.00	0.67	47.67	25.00	44.00	0.00
Huenes	**Pine Woodland**	**P4**	1.00	1.00	8.67	0.00	0.00	0.00	2.00	52.00	0.00	2.00	0.00
Huenes	**Pine Woodland**	**P5**	2.17	2.17	12.00	0.00	0.00	0.00	0.00	75.67	0.57	20.00	0.00
Huenes	**Pine Woodland**	**P6**	1.00	1.00	12.67	0.00	0.00	0.00	0.33	40.00	3.68	3.00	0.00
Huenes	**Pine Woodland**	**P7**	0.17	NA	8.00	0.00	0.00	0.00	2.67	18.33	1.74	4.00	0.00
B.Seco	**Oak Woodland**	**E24**	0.00	0.00	5.00	0.00	0.00	0.00	0.33	4.00	31.25	NA	0.00
B.Seco	**Oak Woodland**	**E25**	0.67	0.67	4.67	0.00	0.00	0.00	1.00	19.00	21.82	NA	0.00
B. Seco	**Oak Woodland**	**E27**	0.50	0.50	3.67	0.00	0.17	4.33	0.67	8.67	8.00	NA	40.50
B.Seco	**Oak Woodland**	**E28**	0.33	0.33	7.33	0.17	0.33	1.00	0.67	14.33	8.70	NA	38.40
B. Seco	**Oak Woodland**	**E29**	0.00	0.00	NA	0.00	0.00	0.00	NA	NA	NA	NA	0.00
B. Seco	**Oak Woodland**	**E30**	2.00	NA	4.00	0.00	1.00	79.00	2.67	7.33	16.67	NA	14.40
B. Seco	**Oak Woodland**	**E31**	0.00	0.00	6.00	0.00	0.00	0.00	0.00	11.33	17.78	NA	0.00
B. Seco	**Oak Woodland**	**E32**	0.50	0.50	2.33	0.00	0.17	1.00	0.00	21.33	25.71	NA	16.20
B. Seco	**Oak Woodland**	**E33**	0.17	0.00	3.67	0.17	0.67	19.00	3.67	7.67	18.44	NA	108.60
B. Seco	**Oak Woodland**	**E34**	1.33	1.33	7.67	0.00	0.00	0.33	0.33	10.00	12.27	NA	18.40
B. Seco	**Oak Woodland**	**E35**	1.50	1.50	5.33	0.00	0.00	0.00	0.00	1.00	16.25	NA	0.00
B. Seco	**Shrubland**	**M7**	0.00	0.00	0.67	0.00	0.33	0.67	2.67	14.00	40.00	NA	0.00
B.Seco	**Shrubland**	**M8**	0.50	NA	0.33	0.00	0.00	0.17	0.00	8.00	40.00	NA	0.00
B. Seco	**Pine Woodland**	**P8**	2.17	2.17	5.00	0.00	0.00	0.00	1.67	60.33	10.00	NA	0.00
B. Seco	**Pine Woodland**	**P9**	3.00	2.67	16.33	0.00	0.00	0.00	0.33	14.00	15.10	NA	0.00
Dornajo	**Oak Woodland**	**E36**	0.00	0.00	0.67	0.00	0.17	1.17	0.00	0.00	65.00	NA	186.00
Dornajo	**Oak Woodland**	**E39**	0.83	0.83	1.67	0.00	0.17	1.67	0.00	0.00	8.00	NA	220.00
Dornajo	**Oak Woodland**	**E43**	0.83	0.83	3.00	0.00	0.00	0.17	0.00	3.33	11.43	NA	75.00
Dornajo	**Oak Woodland**	**E44**	0.33	0.33	NA	0.00	0.00	0.00	NA	NA	NA	NA	36.00
Dornajo	**Oak Woodland**	**E45**	0.33	NA	2.33	0.00	0.33	1.17	0.00	0.00	4.44	NA	116.40
Dornajo	**Oak Woodland**	**E46**	1.00	1.00	1.33	0.00	0.00	0.17	0.00	5.33	20.00	NA	77.20
Dornajo	**Shrubland**	**M10**	0.33	0.33	0.00	0.00	0.00	0.00	0.00	0.00	NA	NA	0.00
Dornajo	**Shrubland**	**M11**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	NA	NA	0.00
Dornajo	**Shrubland**	**M9**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	NA	NA	0.00
Dornajo	**Pine Woodland**	**P10**	0.00	0.00	0.00	0.00	0.00	0.00	1.00	76.33	NA	NA	0.00
Dornajo	**Pine Woodland**	**P11**	1.00	1.00	0.33	0.00	0.00	0.00	0.00	42.33	50.00	NA	0.00

Valley	Landscape Unit	Patch	Seedlings	2-Y Seedlings	Saplings	R Burrows	R Feeders	Eaten Acorns	WB Faeces	WB Rootings	Herbivory damage	Jays	Acorn Patch
Dornajo	**Pine Woodland**	**P12**	0.00	0.00	1.33	0.00	0.00	0.00	0.00	37.00	15.00	NA	0.00

Mean values of data collected in the field per patch of each variable considered. Abbreviations: R: Rodents; WB: Wild Boars; Herbivory damage: number of shoots with visible ungulate damage divided by the total number of shoots; Jays: the sum of destination jays flights per patch; Acorn Patch: Acorn production per patch, estimated with a semi-quantitative scale and multiplied by the number of trees presented per patch. See methods for further definitions of each variable. NA cells indicate not available data.

DISCUSIÓN GENERAL

La teoría es asesinada tarde o temprano por la experiencia

A. Einstein

En todos los capítulos de la presente tesis se percibe una importancia clave de las interacciones planta-animal para el reclutamiento de la encina *Quercus ilex*. Diferentes dispersores de bellotas parecen tener una actividad diferente a lo largo del paisaje, así en los capítulos 1 y 2 encontramos que los roedores pueden alterar la configuración espacial del arbolado a escala fina de microhábitats. Esto, unido a que los roedores parecen actuar principalmente como depredadores de bellotas y su papel como dispersores es limitado a corto plazo (Muñoz y Bonal 2007; Capítulo 1), haría pensar que el papel de los roedores es el de incrementar a muy largo plazo, poblaciones preexistentes de encinar. Los roedores parecen utilizar determinados microhábitats con preferencia sobre otros (Muñoz y Bonal 2007; Capítulo 1). Esto podría conllevar a una reestructuración en la distribución espacial de la encina a escala local de medio a largo plazo temporal. El efecto facilitador de los matorrales sobre el reclutamiento ha sido corroborado en varios sistemas (Callaway 1995; Ramírez et al. 2006; Gómez-Aparicio et al. 2005a), incluido el sistemas de estudio que aquí se presenta (Gómez-Aparicio et al. 2004, 2005b; Puerta-Piñero et al. 2006, 2007). No obstante, con frecuencia existen efectos especie-específicos en estas interacciones planta-planta (Callaway 1998; Puerta-Piñero et al. 2006) por lo que determinar si los roedores están ejerciendo una dispersión efectiva a microhábitats favorables para el establecimiento de la encina o si por el contrario desarrollan una preferencia a microhábitats perjudiciales para el desarrollo de plántulas y brinzales sería crucial para comprender cuál es el balance final de la interacción roedores-encina.

Cabe destacar sin embargo que los roedores parecen tener un componente cualitativo fuerte en cuanto a que dispersan más efectivamente las bellotas de mayor peso y aquellas que van a ser guardadas para la estación invernal, y por tanto susceptibles de germinar y emerger en primavera (Capítulos 1 y 2). A la vez que, en presencia de ungulados, posibles competidores de bellotas bajo la copa de la encina, presentan un comportamiento más eficiente como dispersores, dispersando las bellotas de una manera más esparcida que en ausencia de grandes ungulados (Muñoz y Bonal 2007; Capítulo 2). Aunque se ha comprobado en varios sistemas que diferentes factores denso-dependientes afectan claramente al reclutamiento y establecimiento en muchas especies vegetales (Augspurger and Kelly 1984; Howe 1989; Inderjit 1999; Harms et al. 2000; Schupp et al. 2002; Callaway and Howard 2006), habría que estudiar más profundamente nuestro caso de estudio para saber a ciencia cierta si efectivamente éste componente cualitativo en la dispersión por parte de los roedores ejerce un papel importante en la regeneración natural de la encina.

En el capítulo 4 vemos como los arrendajos parecen afectar el reclutamiento de la encina de una manera muy positiva. Así, tal y como encontraron otros autores (Gómez 2003; Pons & Pausas 2007) parece que su actividad se centra en determinadas unidades de paisaje, siendo los rodales de encinar fuentes de bellotas y con frecuencia otras unidades paisajísticas los sumideros de deposición de éstas (Gómez 2003; Pons & Pausas 2007). Por otro lado, los resultados obtenidos en el capítulo 4 apoyan previos trabajos en los que se remarca el carácter beneficioso neto del arrendajo realizando una dispersión dirigida hacia unidades de paisaje y microhábitats beneficiosos para el reclutamiento y establecimiento de la encina (Gómez 2003; Gómez et al. 2004). Por tanto los arrendajos podrían actuar como dispersores efectivos de bellotas de encina, por un lado como agentes de potencial colonización de nuevas áreas por parte de la encina, y por otro facilitando el establecimiento de plántulas y brinzales mediante una dispersión dirigida a hábitats y microhábitats beneficiosas para el reclutamiento, y por tanto regeneración natural de la encina a través del paisaje.

Si bien en el capítulo 3 vemos que la depredación postdispersiva de semillas por parte de roedores y ungulados (principalmente jabalís) no parece variar entre diferentes microhábitats o unidades de paisaje; se dejan patentes grandes diferencias en depredación entre rodales o parches de vegetación. Esto podría conllevar que el paisaje se constituyera como un mosaico dinámico de regeneración (Watt 1947) a través de los efectos negativos de la depredación. Existiendo algunos rodales buenos para el posterior reclutamiento (con baja depredación pre- y post-dispersiva de bellotas) entremezclados con otros rodales en los que la depredación de bellotas puede actuar como un cuello de botella para el reclutamiento (rodales con alta depredación).

El papel de los grandes ungulados ya sea como depredadores de bellotas en el caso de los jabalís o de tejido vegetativo en el caso de la cabra montés o el ganado doméstico, tal y como se ha supuesto en éste (Capítulos 3 y 4) y otros muchos trabajos (véanse por ejemplo Meriggi y Sacchi 2000; Zamora et al. 2001; Baraza et al. 2007) se remarca como negativo para el reclutamiento de la encina en esta tesis. Sin embargo, caben destacar dos puntos novedosos encontrados que hasta ahora no habían sido examinados. Primeramente, el herbivorismo se pone de manifiesto a partir de la etapa de brinzal, no afectando aparentemente a la densidad y supervivencia de las plántulas naturales (Capítulo 4). Segundo, a pesar del gran efecto negativo de los jabalís como depredadores pre y post dispersivos de bellotas (Capítulo 3), capaces de mermar rápidamente la disponibilidad de bellotas bajo la copa, su efecto global teniendo en cuenta el conjunto de interacciones tanto bióticas como abióticas parece tener un efecto menor, afectando únicamente a la densidad de plántulas encontradas por rodal, aunque no a la supervivencia de plántulas ni a la densidad de juveniles (Capítulo 4).

En el presente trabajo se ha puesto de manifiesto la necesidad de incluir diferentes escalas espaciales dentro de un mismo entorno (Levin 1992). En el capítulo 1 observamos que los roedores realizan movimientos no aleatorios de dispersión y depredación utilizando unos microhábitats más de lo disponible al azar y otros menos de lo disponible al azar. Resultados similares han sido obtenidos en varias ocasiones (Jordano y Schupp 2000; Muñoz y Bonal 2007). En el capítulo 2 hemos considerado diferencias a escala espacial fina en el patrón de dispersión por parte de los roedores. En el capítulo 3, hemos encontrado que el efecto del rodal aparece como el más importante mientras que el efecto de los microhábitats y la unidad de paisaje queda enmascarado si consideramos más de una escala o nivel espacial al mismo tiempo. Se hace necesario por tanto incorporar información a varias escalas espaciales a la vez para comprender íntegramente los procesos y mecanismos que gobiernan el funcionamiento de los ecosistemas (Levin 1992). Muchos son los autores que han destacado que los mecanismos generadores de patrones en las poblaciones o ecosistemas deberían de estudiarse al menos en una escala inferior y una escala superior a la que ocurre el fenómeno de estudio (ver referencias en Perry et al. 2002). El trabajo aquí presentado suma evidencias empíricas y observacionales a esta recomendación.

Muchos son los estudios que han sugerido la importancia crucial de los microhábitats o unidades de paisaje para la regeneración natural de diferentes especies leñosas (Ramírez et al. 2006), incluidos incluso algunos dentro de la misma área de estudio (véase por ejemplo Castro et al. 1999; Gómez 2004; Gómez-Aparicio et al. 2005; Quero et al. 2007; Gómez et al. 2008). Los resultados obtenidos en los capítulos 3 y 4 de la presente tesis, a pesar de no negar la existencia de esos efectos individuales, indican que al incorporar varias escalas espaciales o diferentes tipos de interacciones los resultados en cuanto al éxito en la regeneración pueden cambiar considerablemente. Ya sea debido a algún artefacto estadístico o de diseño experimental o evidencia empírica directa, el caso es que a efectos prácticos, el manejo y tratamiento de la regeneración de especies leñosas parece ser algo más complejo que simples diferencias entre microhábitats o hábitats. Cabe por tanto reflexionar pausadamente antes de aplicar resultados parciales a pequeña o gran escala a programas de manejo de uno u otro tipo en este tipo de ecosistemas.

Muy raros son los casos en los que las interacciones planta-animal ocurren de manera aislada como fenómenos exclusivos de una o unas pocas especies, si no que frecuentemente aparecen sin embargo junto a un conjunto de interacciones bióticas y abióticas dentro de un mismo entorno. Esto conlleva a que en los últimos años se hayan incrementado exponencialmente el número de trabajos que consideran más de una interacción a la vez o los efectos simultáneos de factores bióticos y abióticos sobre el reclutamiento y la regeneración natural de varias especies (Jordano 1995; Alcántara et al. 2000; Rey and Manzaneda 2007). Por otro lado, muchos son los autores que en los últimos años dedican sus esfuerzos a esclarecer cómo los modelos y análisis espacialmente explícitos dan información cuantitativa y muchas veces incluso cualitativa que antes quedaba enmascarada en los estudios de patrones ecológicos observados tanto a escala fina como a unas escalas mucho más extensas (Véanse referencias en Turner 2001; Perry et al. 2002).

Estudios previos en éste (Puerta-Piñero et al. 2006b) y otros sistemas han destacado que, de no incorporarse ambos tipo de información, los resultados, a pesar de ser valiosos *per se*, están lejos de aproximarse a la realidad conjunta de los mecanismos globales que operan dentro de poblaciones o comunidades naturales. La distinción entre reduccionismo y generalismo u holismo en ecología es muchas veces sin embargo espúrea (Wiens 1993). En el capítulo 4 hemos visto cómo al unir varios factores dentro de un paisaje común los efectos destacables estudiados por separado (Capítulos 1, 2 y 3) parecen cambiar de rumbo, modificando así el balance global de las interacciones planta-animal y planta-ambiente abiótico sobre el reclutamiento. Idealmente, la investigación empírica necesitaría estar focalizada en sistemas modelo cuidadosamente seleccionados que ocupen posiciones clave en las matrices ecológicas o ambientales (Wiens 1993). De éste modo, ya sean las especies de interés económico relevante o actuar como especies modelo, el estudio de los procesos en conjunto, utilizando varias aproximaciones ya sean observacionales u experimentales, se podremos discernir quizás sobre la existencia de propiedades emergentes de los ecosistemas que hasta ahora han quedado enmascaradas en estudios reduccionistas o centrados en uno o pocos tipos de especies.

Referencias

Alcántara JM, Rey PJ, Sánchez-Lafuente AM, Valera F. 2000. Early effects of rodent post-dispersal seed predation on the outcome of the plant-seed disperser interaction. Oikos 88: 362-370.

Augspurger CK, Kelly CK. 1984. Pathogen mortality of tropical tree seedlings: experimental studies of the effects of dispersal distance, seedling density, and light conditions. Oecologia 61: 211-217.

Baraza E, Zamora R, Hódar JA, Gómez JM. 2007. Plant-herbivore interaction: beyond a binary vision. In: Pugnaire, F.I. y Valladares, F. (eds.). Handbook of functional plant ecology, 2nd ed. Marcel Dekker Inc., New York.

Callaway, R.M., 1995. Positive interactions among plants. Bot. Rev. 61, 306–349.

Callaway, R.M., 1998. Are positive interactions species-specific? Oikos 82, 202–207.

Callaway RM, Howard TG. 2006 Competitive networks, indirect interactions, and allelopathy: a microbial viewpoint on plant communities. Progress in Botany 68: 315-335.

Castro J, Gómez JM, García D, Zamora R, Hódar JA. 1999. Seed predation and dispersal in relict Scots pine forests in southern Spain. Plant Ecology 145: 115-123.

García D, Chacoff NP. 2007. Scale-dependent effects of habitat fragmentation on hawthorn pollination, frugivory, and seed predation. Conservation Biology 21: 400-411.

Gómez JM, García D, Zamora R. 2003. Impact of vertebrate acorn- and seedling-predators on a Mediterranean *Quercus pyrenaica* forest. Forest Ecology and Management 180: 125-134.

Gómez JM. 2003. Spatial patterns in long-distance dispersal of *Quercus ilex* acorns by jays in a heterogeneous landscape. Ecography 26: 573–584.

Gómez JM. 2004. Importance of microhabitat and acorn burial on *Quercus ilex* early recruitment: non-additive effects on multiple demographic processes. Plant Ecol 192: 287-297.

Gómez JM, Puerta-Piñero C, Schupp EW. 2008. Effectiveness of rodents as local seed dispersers of an oak with a stratified dispersal system. Oecologia, In press.

Gómez JM, Valladares F, Puerta-Piñero C. 2004. Differences between structural and functional environmental heterogeneity caused by seed dispersal. Functional Ecology 18: 787-792.

Gómez-Aparicio L, Valladares F, Zamora R, Quero JL. 2005. Response of tree seedlings to the abiotic heterogeneity generated by nurse shrubs: an experimental approach at different scales. Ecography 28: 757–768.

Gómez-Aparicio L, Zamora R, Gómez JM, Hódar JA, Castro J, Baraza E. 2004. Applying plant facilitation to forest restoration: a meta-analysis of the use of shrubs as nurse plants. Ecological Applications 14:1128- 1138.

Harms WR, Whitesell CD, DeBell DS. 2000. Growth and development of loblolly pine in a spacing trial planted in Hawaii. Forest Ecology and Management 126: 13-24.

Howe HF. 1989. Scatter and clum-dispersal and seedling demography: hypothesis and implications. Oecologia 79: 417-426.

Inderjit, Dakshini, K.M.M., Foy, C.L., 1999. Principles and Practices in Plant Ecology Allelochemical Interactions. CRC Press, Boca Raton, FL, USA.

Jordano P. 1995. Frugivore-mediated selection on fruit and seed size: birds and St. Lucie´s Cherry *Prunus mahaleb*. Ecology 76: 2627-2639.

Jordano P, Schupp EW. 2000. Seed disperser effectiveness: the quantity component and patterns of seed rain for *Prunus mahaleb*. Ecological Monographs 70: 591-617.

Levin SA. 1992. The problem of pattern and scale in ecology: the Robert H. MacArthur award lecture. Ecology 73: 1943-1967.

Meriggi A, Sacchi O. 2000. Habitat requirements of wild boars in the northern Appennines (N Italy): a multi-level approach. Ital. J. Zool 68: 47-55.

Muñoz A, Bonal R. 2007. Rodents change acorn dispersal behaviour in response to ungulate presence. Oikos 44: 157-164.

Nathan R, Muller-Landau H. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. Trends in Ecology and Evolution 15: 278- 285.

Perry JN, Liebhold AM, Rosenberg MS, Dungan J, Mirita M, Jakomulska A, Citron-Pousty S. 2002. Illustrations and guidelines for selecting statistical methods for quantifying spatial pattern in ecological data. Ecography 25: 576-600.

Pons J, Pausas JG. 2007b. Acorn dispersal estimated by radio-tracking. Oecologia 153: 1432-1939. DOI 10.1007/s00442-007-0788-x

Puerta-Piñero C, Gómez JM, Zamora R. 2006. Species-specific effects on topsoil development affect *Quercus ilex* seedling performance. Acta Oecologica 29:65-71.

Puerta-Piñero C, Gómez JM, Iniesta C. 2006. “Poniendo los pies en la tierra: Estructura espacial de patrones demográficos en la encina *Quercus ilex*”. Actas del VIII Congreso de la AEET (Ed AEET). Lisboa, Portugal.

Puerta-Piñero C, Gómez JM, Valladares F. 2007. Irradiance and oak seedling survival and growth in a heterogeneous environment. Forest Ecology and Management 242: 462-469.

Pulido FJ, Díaz M. 2005. Regeneration of a Mediterranean oak: A whole-cycle approach. Ecoscience 12: 92-102.

Quero JL, Gómez-Aparicio L, Zamora R, Maestre FT. 2007. Shifts in the regeneration niche o fan endangered tree (Hacer opalus ssp. Granatense) during ontogeny: Using an ecological concept for application. Basic and applied ecology.

Ramírez JM, Rey PJ, Alcántara JM, Sánchez-Lafuente AM. 2006. Altitude and woody cover control recruitment of Helleborus foetidus in a Mediterranean mountain area. Ecography 29: 375-384.

Rey P, Manzaneda AJ. 2007. Geographical variation in the determinants of seed dispersal success of a myrmecochorous herb. Journal of Ecology 95: 1381-1393.

Schupp EW, T. Milleron, and S.E. Russo. 2002. Dissemination limitation and the origin and maintenance of species–rich tropical forests. *In*: D.J. Levey, W.R. Silva, and M. Galetti, eds. Seed dispersal and frugivory: Ecology, evolution and conservation. CABI Publishing, Wallingford, Oxfordshire, UK.

Schupp EW. 1993. Quantity, quality and the effectiveness of seed dispersal by animals. Vegetatio 107/108: 15-29.

Watt, AS. 1947. Pattern and process in the plant community. Journal of Ecology 35: 1-22.

Wiens JA, Stanseth NC, Van Horne B, Ims RA. 1993. Ecological mechanisms and landscape ecology. Oikos 66: 369-380.

Zamora R, Gómez JM, Hódar JA, Castro J, García D. 2001. Effect of browsing by ungulates on sapling growth of Scots pine in a Mediterranean environment: consequences for forest regeneration. Forest Ecology and Management 144: 33-42.

CONCLUSIONES GENERALES

La más necesaria de todas las ciencias
es la de olvidar el mal que una vez se aprendió
Aristóteles

Conclusiones Generales

1. Los arrendajos parecen actuar como dispersores efectivos de bellotas de encina, actuando como agentes de colonización potencial de nuevas áreas y facilitando el establecimiento de plántulas y brinzales mediante una dispersión dirigida a hábitats y microhábitats beneficiosas para el reclutamiento.

2. El papel de los roedores podría ser el de incrementar a muy largo plazo poblaciones preexistentes de encinar. Presentan a su vez un componente cualitativo fuerte en cuanto a que dispersan más efectivamente las bellotas de mayor peso y aquellas que van a ser guardadas para la estación invernal, y por tanto susceptibles de germinar y emerger en primavera. Asimismo, en presencia de ungulados, presentan un comportamiento más eficiente como dispersores, dispersando las bellotas de una manera más esparcida que su ausencia.

3. El papel de los grandes ungulados ya sea como depredadores de bellotas en el caso de los jabalís o de tejido vegetativo en el caso de la cabra montés o el ganado doméstico, se remarca como negativo para el reclutamiento de la encina, tanto por la disminución de la densidad de reclutas como por el debilitamiento de brinzales ya establecidos.

4. Se hace ineludible Incluir información espacialmente explícita a los modelos clásicos de mecanismos poblacionales mediados por interacciones planta-animal. Aportando información cuantitativa y/o cualitativa clarificando procesos que quedaban enmascarados siguiendo aproximaciones clásicas tanto a escala fina de microhábitat como a unas escalas más extensas de paisaje.

5. Asimismo, se percibe la necesidad de incorporar información a varias escalas espaciales simultáneamente para comprender íntegramente los procesos y mecanismos que gobiernan el funcionamiento de los ecosistemas.

6. Se impera por último, considerar las diversas interacciones clave existentes en el ecosistema, ya sean planta-animal o planta- ambiente abiótico en su conjunto para ver cómo afectan individualmente o su efecto colectivo sobre el reclutamiento y la regeneración natural de varias especies.

Si no pudieras despertar de ese sueño,
¿cómo sabrías que estás soñando?
The Matrix