Universidad
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Regeneración de la encina en ambientes fragmentados: una aproximación mecanicista

Holm oak regeneration in fragmented landscapes: a mechanistic approach

Teresa Morán López

Tesis doctoral

Madrid, 2015

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Que los trabajos de investigación desarrollados en la memoria de tesis doctoral: “Regeneración de la encina en ambientes fragmentados: una aproximación mecanicista; Holm oak regeneration in fragmented landscapes: a mechanistic approach”, han sido realizados bajo su supervisión y son aptos para ser presentados por la Lda. Teresa Morán López ante el tribunal que en su día se consigne, para aspirar al Grado de Doctor en Conservación de Recursos Naturales por la Universidad Rey Juan Carlos de Madrid.

VºBº Director de Tesis
Mario Díaz Esteban

VºBº Director de Tesis
Fernando Valladares Ros

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Teresa Morán López
Madrid, 29 octubre 2015
Proyecto de Tesis Doctoral presentado en el Departamento de Biología y Geología Física y Química Inorgánica.

Director:

Dr. Mario Díaz Esteban

Museo Nacional de Ciencias Naturales – CSIC

Co-director:

Dr. Fernando Valladares Ros

Museo Nacional de Ciencias Naturales – CSIC

Este trabajo ha sido realizado gracias a la financiación proporcionada por los proyectos RISKDISP (CGL2009-08430), *VULGLO* (CGL2010-22180-C0303) y VERONCA (CGL2014-42271-P) del Ministerio de Economía y Competitividad; REMEDINAL 2-CM (S2009 AMB 1783) y REMEDINAL 3-CM (S2013-MAE-2719) de la Comunidad de Madrid. Así como del programa de formación de personal investigador (FPI, BES-2011-048346) del Ministerio de Economía y Competitividad.

A mis padres, por su apoyo incondicional, por despertar mi curiosidad científica y enseñarme a respetar la Naturaleza.

A mis hermanas por ser mis compañeras de vida.

A Quini, por siempre creer en mis posibilidades.

A Santi, porque tu apuesta personal fue muy importante en este proyecto.

¿Qué tienes tú,

negra encina campesina,

con tus ramas sin color

en el campo sin verdor;

con tu tronco ceniciento

sin esbeltez ni altiveza,

con tu vigor sin tormento,

y tu humildad que es firmeza?

[…]

Brotas derecha o torcida

con esa humidad que cede

sólo a la ley de la vida

que es vivir como se puede.

Las encinas - Poema de
Antonio Machado

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ABSTRACT

Forest fragmentation is considered a major threat to biodiversity worldwide due to its extent and rate of change. It has become a major issue of ecological research promoting the documentation of its impacts on the structure and functioning of terrestrial ecosystems. However, we are increasingly aware of its multifactorial nature and the necessity of mechanistic approaches to build bridges between ecological research and conservation policies. In this context, studying fragmentation effects on key species is an efficient strategy when limited economic resources are available. The main goals of this thesis were (1) to detect which stages of holm oaks regeneration cycle (pollination, fructification and acorn dispersal) are more vulnerable to fragmentation effects and (2) determine which environmental changes trigger recruitment bottlenecks. We chose holm oaks (*Quercus ilex)* as a study system because it is widely spread in the western Mediterranean, the processes that modulate different stages of their life cycle are well known and management seems to hamper holm oak woodlands sustainability in the long term. Our results showed a positive effect of forest fragmentation on tree water-status and consequently on acorn production. Besides, we observed an extensive pollen flow in fragmented landscapes. However, the impoverishment of dispersal services seriously constrained recruitment and genetic diversity of new individuals. Therefore, the restoration of dispersal services needs to be a priority in any management policy. To this end, landscape structure and habitat quality needs to be analyzed from the dispersers' perspective. In the case of Eurasian jays (*Garrulus glandarius*) this implies the presence of forest habitats in the surroundings (<2 km) and the avoidance of extremely low stem densities. For wood mice

(*Apodemus sylvaticus)* the maintenance of antipredatory refuges within the habitat and high intraspecific competition for acorns will restore their role as local dispersers.

Key words: holm oak, *Quercus ilex,* fragmentation, regeneration, acorn production, acorn dispersal, Eurasian jay, *Garrulus glandariu*, wood mice, *Apodemus sylvaticus,* agent based models, pollination, functional connectivity, management guidelines.

ABSTRACT

RESUMEN

La fragmentación del hábitat es considerada una de las principales amenazas a la biodiversidad a escala global debido a su magnitud y velocidad de cambio. Esto lo ha situado en el punto de mira de la comunidad científica lo que ha impulsado grandes avances a la hora de documentar sus impactos sobre la estructura y funcionamiento de los ecosistemas. Sin embargo, cada vez somos más conscientes de la naturaleza multifactorial del problema y de la necesidad de enfoques mecanicistas para poder establecer puentes entre los avances científicos y las políticas de conservación. En este contexto, estudiar especies clave supone una estrategia eficaz cuando los recursos son limitados. Los principales objetivos de esta tesis doctoral fueron (1) detectar qué etapas del ciclo de regeneración de la encina (polinización, fructificación, dispersión de bellotas) son más vulnerables en ambientes fragmentados y (2) determinar qué cambios ambientales generan estos cuellos de botella. Escogimos la encina (*Quercus ilex)* como sistema de estudio porque domina la cobertura vegetal en áreas extensas en el Mediterráneo occidental, se conocen bien los procesos que modulan las distintas etapas de su ciclo vital y el manejo forestal parece amenazar su sostenibilidad a largo plazo. Nuestros resultados mostraron un efecto positivo de la fragmentación sobre el estado hídrico de las encinas y su producción de bellotas así como un flujo de polen extenso en ambientes fragmentados. Sin embargo, el empobrecimiento de los servicios de dispersión de bellotas comprometió seriamente tanto el reclutamiento como la diversidad genética de los nuevos individuos. Por tanto, la restauración de los servicios de dispersión debe ser prioritaria en cualquier política de manejo. Para ello, necesitamos tener en cuenta la estructura del paisaje y la calidad del hábitat desde el punto de vista del dispersante. En el caso de los arrendajos (*Garrulus glandarius*) esto se traduce en asegurar la presencia de bosques cercanos (< 2 km) y evitar densidades de arbolado demasiado bajas. En el caso del ratón de campo (*Apodemus sylvaticus),* es necesario mantener hábitats que les ofrezcan seguridad durante la movilización y que presenten una competencia intraespecífica por las bellotas alta.

Palabras clave: encina, *Quercus ilex,* fragmentación, regeneración, producción de bellotas, dispersión de bellotas, arrendajo, *Garrulus glandarius,* ratón de campo, *Apodemus sylvaticus*, modelos basados en agente, polinización, conectividad funcional, pautas de manejo.

RESUMEN

ANTECEDENTES

Se estima que entre un treinta y un cincuenta por ciento de la superficie terrestre ha sufrido algún tipo de transformación de origen antrópico (Vitousek et al. 1997). Los cambios en el uso de suelo han conllevado el reemplazamiento de extensas áreas boscosas por mosaicos de pequeños parches forestales embebidos en matrices agrícolas o urbanas (Riitters et al. 2000). En la actualidad la tasa de pérdida de área boscosa a escala global es de un 0,6 por ciento anual (Hansen et al. 2010). Debido a la extensión y a la velocidad de cambio, es considerado una de las principales amenazas de la biodiversidad a escala mundial (Sala et al. 2000, Fahrig 2003, Foley et al. 2005, Kettle and Koh 2014). Desde la década de los setenta los efectos de la fragmentación sobre los ecosistemas ha sido objeto de numerosos estudios. En un principio su enfoque se basó en la Teoría de la Biogeografía Insular (MacArthur and Wilson 1967) y la matriz de paisaje circundante era considerada como hábitat hostil. Sin embargo, durante los últimos quince años la dicotomía entre matriz y hábitat ha dado paso a otros conceptos más flexibles y realistas centrados en la heterogeneidad ambiental y los gradientes derivados de ella (McIntyre and Hobbs 1999, Haila 2002, Cadenasso et al. 2003, Harper et al. 2005). Se han hecho grandes avances a la hora de unificar conceptos y establecer una base teórica común sobre la que investigar los efectos de borde (Fernández et al. 2002, Ries and Sisk 2004, Harper et al. 2005) así como los relacionados con cambios en la configuración y estructura del paisaje (Fahrig 2003, Fischer and Lindenmayer 2007b). Sin embargo, cada vez somos más conscientes de la naturaleza multifactorial y compleja del problema y de la necesidad de enfoques mecanicistas para poder establecer puentes entre los avances científicos y las políticas de conservación (Murcia 1995, Young and Clarke 2000, Fischer and Lindenmayer 2007b, Ibanez et al. 2014).

La fragmentación del bosque (*sensu lato*) suele venir acompañada por la pérdida de vegetación nativa así como una intensificación del manejo en las áreas adyacentes (McIntyre and Hobbs 1999). Las poblaciones continuas quedan subdivididas en otras más pequeñas y con distinto grado de aislamiento y en las que las condiciones abióticas cambian (Lienert 2004). Los impactos de la fragmentación dependerán de la cantidad de hábitat disponible, la calidad el mismo, su configuración espacial y las características propias de la especie o proceso ecológico en cuestión (Saunders et al. 1991, Hobbs and Yates 2003, Fischer and Lindenmayer 2007b). Así por ejemplo, un paisaje fragmentado no es percibido de la misma manera por especies con distintos requerimientos de hábitat, capacidades motoras dispares o diferentes grados de especialización en el uso de recursos forestales (Greene and Johnson 1996, Fischer and Lindenmayer 2007b, Swift and Hannon 2010). Es más, la vulnerabilidad de una especie puede variar en sus distintas etapas ontogenéticas (Hobbs and Yates 2003, Berhane et al. 2013). Por ende, a la hora evaluar los efectos de la fragmentación sobre un determinado proceso ecológico es necesario identificar los eslabones más débiles de la cadena y traducir la fragmentación en cambios ambientales decisivos para que dicho proceso concluya con éxito.

La estructura y la composición de la vegetación dominan los ecosistemas terrestres, proporcionan hábitat a la fauna y reflejan físicamente gran cantidad de procesos ecológicos (Harper et al. 2005). Esto hace que la degradación de la cobertura vegetal debido al colapso de poblaciones de plantas dominantes pueda conllevar extinciones en cascada o la pérdida de servicios ecosistémicos (Fischer and Lindenmayer 2007b). La viabilidad de una población en un paisaje fragmentado depende del éxito reproductivo, la supervivencia y la dispersión de sus individuos (Selwood et al. 2015). En el caso de las plantas, necesitan ser capaces de responder a las nuevas condiciones ambientales impuestas por la desaparición de la cobertura vegetal circundante y dependen de los servicios de polinización y dispersión de semillas para el mantenimiento de su éxito reproductivo y la cohesión genética de las subpoblaciones (Wang and Smith 2002, Aguilar et al. 2006, Jordano 2010, Schupp et al. 2010). El fallo de cualquiera de estos procesos puede limitar la persistencia de una población (ej. Pulido and Díaz 2005). Por tanto, para evaluar de manera global los efectos de la fragmentación sobre la viabilidad de las poblaciones de plantas es necesario identificar posibles cuellos de botella en su ciclo de regeneración y detectar cuáles son los cambios ambientales que los generan (Fig. 1). De esta manera podremos entender los mecanismos biológicos que subyacen a la respuesta de las plantas frente a la fragmentación y establecer puentes con las políticas de manejo.

RESUMEN

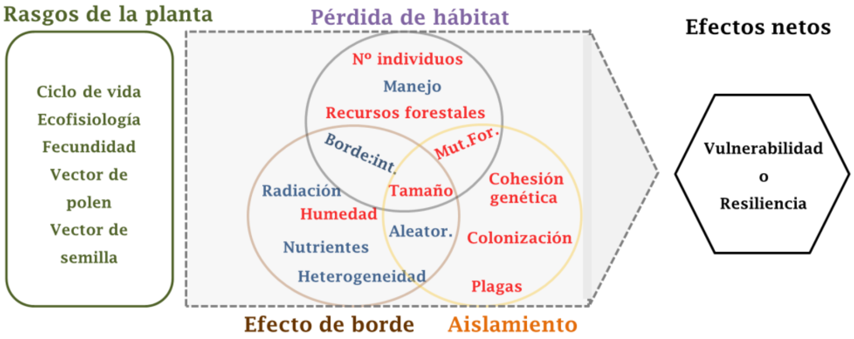

Fig. 1 Esquema conceptual de los principales motores de la respuesta de las plantas a la fragmentación del hábitat (*sensu lato).* Las letras en azul y rojo indican incremento y disminución, respectivamente. Abreviaciones: int. = interior, Aleator. = aletatoriedad, Mut.For. = mutualismos forestales

Motores de cambio en los sistemas fragmentados

Efectos de borde

Los conocidos como efectos de borde se derivan de los flujos de materia, energía y organismos entre las dos comunidades contiguas (bosque y matriz) (Cadenasso et al. 2003, Ries and Sisk 2004). El grado de penetración de dichos efectos en la masa forestal dependen de las diferencias entre la estructura y composición de ambas (Harper et al. 2005). En general, las áreas de borde se caracterizan por tasas de evapotranspiración más elevadas, mayor variación térmica, más exposición al viento y en algunos casos más concentración de nutrientes y compuestos contaminantes (Saunders et al. 1991, Weathers et al. 2001, Harper et al. 2005). No obstante, resulta difícil generalizar sobre los efectos netos de estos cambios ya que dependerán de la idiosincrasia climática de la región y las características propias de la especie (Hobbs and Yates 2003, Harper et al. 2005). Una mayor evapotranspiración en las áreas de borde no tendrá el mismo impacto en bosques mediterráneos, limitados por el agua, que en bosques de zonas templado-húmedas. Asimismo, una mayor exposición lumínica puede dificultar el desarrollo de especies de sotobosque pero supondrá una oportunidad para especies heliófilas. No obstante, podemos afirmar que las nuevas condiciones ambientales suelen conllevar cambios en el estado fisiológico de los individuos ya establecidos (ej. Ishino et al. 2012, Ramos et al. 2013) así como alteraciones en el éxito de establecimiento de las plántulas (ej. Benítez-Malvido and Martínez-Ramos 2003, Uriarte et al. 2010; revisado en Ibáñez et al. 2014).

A la hora de evaluar los efectos de borde sobre las poblaciones de plantas debemos plantearnos qué factores abióticos limitan el crecimiento y reproducción de la especie en cuestión y cómo son modulados a escala local por la desaparición de la cobertura vegetal adyacente. Además, necesitamos tener en cuenta qué fase del ciclo vital estamos analizando puesto que los requerimientos ecológicos pueden variar entre fases (Hobbs and Yates 2003; Fig. 2).

Polinización

En ambientes fragmentados, una diminución en la carga polínica o en la frecuencia de eventos de polinización cruzada suele conllevar una menor producción de frutos así como pérdida en la diversidad genética de los nuevos individuos (Aguilar et al. 2006, Eckert et al. 2010). La mayor parte de los estudios que han analizado los efectos de la fragmentación sobre la polinización de las plantas se han centrado en especies dependientes de relaciones mutualistas (ej. Aguilar et al. 2006, Aizen and Vázquez 2006, Steffan-Dewenter and Westphal 2008). Las especies anemófilas han sido consideradas más resilientes puesto que suelen presentar un flujo de polen extenso y las áreas de borde favorecen su movimiento debido a una mayor exposición al viento (Sork and Smouse 2006). Sin embargo, estudios recientes han demostrado que pueden ser igualmente vulnerables a la erosión genética en ambientes fragmentados (Vranckx et al. 2012) y que pueden ver limitada su producción de frutos cuando la fragmentación viene acompañada de una disminución drástica en la densidad de donadores de polen (Knapp et al. 2001). Además, a pesar de que los eventos de dispersión a larga distancia son relativamente frecuentes, en muchos casos un alto porcentaje de polen es depositado en áreas próximas al árbol focal (<200 m) (ej. Pakkad et al. 2008, Pluess et al. 2009, Marchelli et al. 2012). En ambientes fragmentados esto puede causar un descenso del número efectivo de donadores de polen y una mayor estructuración genética en las plántulas (revisado en Vakkari et al. 2006).

Los efectos de la fragmentación sobre el éxito de la polinización en especies que dependen de interacciones con animales son particularmente complejos (Aguilar et al. 2006, Eckert et al. 2010). En general la pérdida de hábitat supone una reducción en la densidad de plantas y polinizadores lo que conlleva una menor disponibilidad de polen así como una mayor competencia por el polinizador. Además, las relaciones mutualistas son contexto-dependientes, la presencia del vector no asegura una polinización eficaz (Magrach et al. 2014). Cambios en el comportamiento del animal asociados a una reducción en la extensión del área visitada o una menor probabilidad de visitas entre parches disminuirá la cohesión genética de las subpoblaciones de plantas e incluso las tasas de fertilización cruzada. Este tipo de situaciones son comunes cuando la matriz es percibida como hábitat hostil o el coste asociado a la alimentación en parches diferentes es alto. Además, si la fragmentación viene acompañada por cambios en la composición florística, puede haber alteraciones en la dieta de los polinizadores que disminuyan la pureza del polen depositado en el estigma (revisado en Hadley and Betts 2012).

Independientemente de la naturaleza del vector de polen, a la hora de analizar los efectos de la fragmentación sobre esta etapa del ciclo de regeneración necesitamos comprender qué factores ambientales modulan la disponibilidad de polen, sus distancias de deposición y la diversidad intra e inter-específica de la carga polínica para el sistema de estudio (Fig. 2).

Fructificación

En general, la limitación de polen en ambientes fragmentados produce una disminución en la producción de frutos. Esto puede ocurrir por una menor efectividad de los polinizadores (revisado en Aguilar et al. 2006), por desacoplamientos fenológicos entre subpoblaciones (revisado en Fuchs et al. 2003) o por sesgos en los sex ratios en especies monoicas (ej. Nuñez-Avila et al. 2013). Sin embargo, cuando el flujo de polen no es limitante, otros factores ambientales relacionados con el desarrollo de los frutos determinarán los efectos de la fragmentación (ej. Herrerías-Diego et al. 2006, Neal et al. 2010, Ayari and Khouja 2014). Conocemos poco sobre cómo los cambios ambientales en áreas de borde pueden producir alteraciones en el estado ecofisiológico de las plantas y por consiguiente en su fertilidad. Resulta paradójico pues sabemos que las condiciones climáticas determinan la producción de frutos de muchas especies (Ting et al. 2008, Pérez-Ramos et al. 2010) y que en las áreas de borde estas condiciones cambian (Saunders et al. 1991). Por tanto, los efectos de borde podrían causar cambios locales en la fecundidad de poblaciones de plantas fragmentadas con relativa frecuencia.

Una menor producción de frutos conlleva una menor tasa potencial de reclutamiento. Cuando evaluamos los efectos de la fragmentación sobre la fertilidad de las plantas debemos preguntarnos si la disponibilidad de polen puede ser limitante y qué factores ambientales determinan los patrones de floración y maduración de frutos. En este último caso, traducir los efectos borde en condiciones abióticas clave para la especie de estudio nos permitirá entender qué mecanismos fisiológicos regulan los impactos de la fragmentación (Fig. 2).

Dispersión de semillas

El reclutamiento real de una determinada población depende de la interacción entre la producción de semillas y la eficacia en la dispersión (Schupp et al. 2010). Por tanto, si las semillas no son transportadas a zonas favorables para su germinación y establecimiento las tasas de regeneración pueden ser prácticamente nulas incluso en situaciones de alta fecundidad (ej. Pulido and Díaz 2005, Blackham et al. 2014). Además, los patrones de dispersión determinan el área potencial de regeneración y los patrones espaciales en las que ésta se produce, condicionando importantes procesos post-dispersivos como la depredación, la competencia o la distribución de los nuevos genotipos (Nathan and Muller-Landau 2000). Finalmente, las tasas de migración entre subpoblaciones y la colonización de nuevos hábitats dependen de los patrones de movilización de semillas (Selwood et al. 2015).

Por tanto, en paisajes fragmentados la dispersión de las semillas es crucial para la dinámica y sostenibilidad de las poblaciones de plantas. Es por ello que los efectos de la fragmentación sobre los patrones de dispersión han sido estudiados en numerosas especies y sistemas (Bruna et al. 2009, McConkey et al. 2012). Aunque existe un mayor número de mecanismos de dispersión (van der Pijl 1982) aquí nos vamos a centrar en el viento y en los animales ya que ambos vectores son particularmente sensibles a cambios en la estructura de la vegetación. En especies anemócoras la dispersión depende de la velocidad del viento, la altura a la que es liberada la semilla y sus propiedades aerodinámicas (Greene and Johnson 1996, vanDorp et al. 1996, Nathan et al. 2001b). La vegetación altera la rugosidad de la capa límite haciendo un efecto mampara (ver Fig. 1 en Nathan et al. 2001a) lo que hace que en las áreas abiertas las distancias de dispersión de semillas sean potencialmente mayores y los eventos de dispersión a larga distancia más frecuentes (Nathan et al. 2001a). Por ello las especies anemócoras han sido consideradas resilientes a la fragmentación y los efectos de la estructura del paisaje sobre sus patrones de dispersión poco estudiados. No obstante, cuando se han evaluado los impactos de la fragmentación sobre el potencial de colonización y reclutamiento en estudios multiespecíficos se han obtenido resultados dispares (Hewitt and Kellman 2002, McEuen and Curran 2004) y estudios recientes han demostrado que los corredores y áreas de borde puede mejorar el potencial de recolonización en este tipo de especies (Damschen et al. 2014). Por tanto, si bien la remoción de la vegetación circundante suele favorecer la dispersión de este tipo de especies, la variabilidad intraespecífica del banco de semillas y la velocidad de colonización de nuevos hábitats dependen de la configuración espacial de los fragmentos forestales.

En el caso de la dispersión mediada por animales, la presencia del dispersante no asegura que los servicios de dispersión se mantengan, como ocurre con la polinización zoófila (Agrawal et al. 2007, Cortes and Uriarte 2013). Las distancias de dispersión dependen del movimiento del vector y del tiempo de retención del propágulo (Cousens et al. 2010). El desarrollo de la ecología del movimiento (Nathan et al. 2008a) ha supuesto un gran avance en el análisis de los patrones de dispersión de semillas desde un punto de vista mecanicista (Cortes and Uriarte 2013). Cómo se mueve un animal va a depender de su estado interno, de sus capacidades de navegación y desplazamiento y de factores ambientales externos (ver Fig. 2 en Nathan et al. 2008b). La estructura del paisaje determina la disponibilidad espacial de los recursos, el coste energético asociado al desplazamiento o el riesgo de depredación, por tanto, modula la motivación del dispersante para moverse durante un tiempo, dirección y velocidad determinada (Morales and Carlo 2006, Levey et al. 2008, Bialozyt et al. 2014). En un paisaje fragmentado, donde los recursos forestales están dispersos y existe una gran heterogeneidad ambiental, cabe esperar cambios en el comportamiento de los dispersantes y en los patrones de dispersión. En general, se observa un efecto negativo sobre las tasas de remoción de frutos y las distancias de dispersión debido a que el aislamiento incrementa los costes de desplazamiento y la matriz es percibida como hábitat adverso (revisado en McConkey et al. 2012).

Si bien el reclutamiento no puede ocurrir sin la llegada de semillas, ésta no garantiza su éxito (Nathan and Muller-Landau 2000). Una mayor efectividad en la dispersión depende de la cantidad de semillas que son movilizadas y de la probabilidad de que éstas finalmente produzcan nuevos individuos que se incorporen a la población (Schupp et al. 2010). Se sabe que las características del hábitat tienen un papel importante en la probabilidad de reclutamiento. Así por ejemplo, la llegada de semillas a zonas donde hay menos competencia (ej. huecos dejados por árboles caídos; Wenny and Levey 1998) o a microhábitats donde las condiciones climáticas son más suaves (ej. bajo plantas nodriza; Herrera et al. 1994), aumenta la probabilidad de germinación y establecimiento. De hecho el concepto "dispersión dirigida" hace referencia a la deposición de semillas en hábitats con condiciones ambientales óptimas (revisado en Wenny 2001). No obstante, la calidad del hábitat puede variar entre distintas etapas de reclutamiento (Schupp 2007). Por ello, para poder cuantificar la calidad de la dispersión en sentido estricto es necesario seguir la semilla dispersada desde su origen hasta el establecimiento de un individuo adulto (Schupp et al. 2010). Esta tarea resulta particularmente complicada para plantas de ciclo de vida largo debido a su madurez reproductiva tardía y a la alta tasa mortandad de las semillas dispersadas (Bacles and Jump 2011). Ahora bien, estudios que combinen modelos demográficos junto con patrones de dispersión pueden ayudarnos a evaluar el impacto de los cambios en la calidad de la dispersión en la dinámica de las poblaciones a escalas temporales más amplias (Robledo-Arnuncio et al. 2014).

En poblaciones fragmentadas, para poder identificar posibles cuellos de botella en la dispersión es necesario comprender qué factores ambientales producen cambios en el patrón espacial de remoción y deposición de las semillas (Nathan et al. 2001a, Cousens et al. 2010).

Esto nos permitirá predecir de manera dinámica cómo la estructura del paisaje condiciona la disposición de los nuevos individuos (Wang and Smith 2002). Qué o quién mueve la semilla, cuáles son las características del vector, y qué factores modulan su movimiento a través del paisaje son preguntas que nos sirven de guía a la hora de analizar los impactos de la fragmentación desde un punto de vista mecanicista (Nathan et al. 2008b, Cortes and Uriarte 2013). Finalmente, poder cuantificar los efectos netos de estos cambios sobre la demografía de las poblaciones de plantas debe ser uno de nuestros horizontes en el medio plazo si queremos valorar los efectos de la fragmentación en el medio-largo plazo (Wang and Smith 2002, Schupp et al. 2010, Robledo-Arnuncio et al. 2014; Fig. 2).

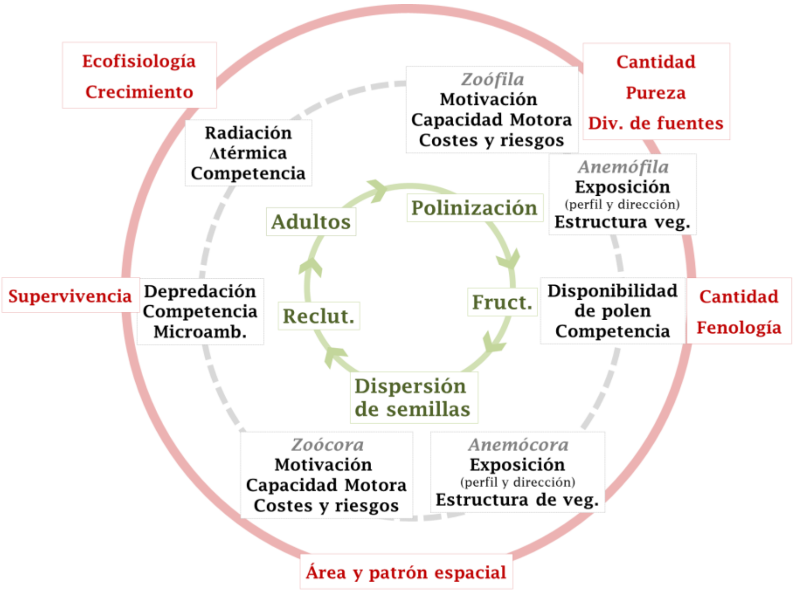

Fig. 2 Esquema conceptual de la relación entre los etapas clave del ciclo de regeneración de las plantas (verde) y los efectos de la fragmentación (rojo) (modificado de Wang and Smith 2002). En el círculo gris se señalan los factores moduladores de la respuesta final. Abreviaciones: Reclut. = reclutamiento, Fruct. = fructificación, Microamb. = condiciones microambientales, Veg. = vegetación, Div. = diversidad.

La importancia de las especies clave en el enfoque mecanicista

Para poder comprender los efectos de la fragmentación desde un punto de vista mecanicista en la mayoría de los casos se necesita un enfoque centrado en la especie (Cortes and Uriarte 2013). Sin embargo, resulta inviable estudiar con ese grado de detalle todas las especies de un determinado sistema. Es necesario encontrar una estrategia intermedia entre las investigaciones basadas en correlaciones entre patrones del paisaje y composición de las comunidades y aquellos que analizan unas pocas especies en profundidad (Fischer and Lindenmayer 2007b).

En este contexto evaluar los efectos de la fragmentación sobre especies clave resulta de gran utilidad. En sentido estricto una especie clave es aquella cuyo efecto sobre el ecosistema es desproporcionadamente mayor a su abundancia (Paine 1969, Power et al. 1996). Sin embargo, este término puede ser ampliado a aquellas especies cuya desaparición puede amenazar el equilibrio y sostenibilidad del ecosistema (Fischer and Lindenmayer 2007a). En general, esto puede ocurrir cuando son especies estructuradoras del hábitat, como ocurre con la vegetación dominante (Andren 1994, Tews et al. 2004) o cuando son especies nodo dentro de las redes de interacción (Soule et al. 2005). Estudiar los efectos de la fragmentación sobre la viabilidad de las poblaciones de especies clave supone una estrategia eficaz para la conservación cuando los recursos son limitados.

Nuestro sistema de estudio: el encinar en ambientes fragmentados

La encina (*Quercus ilex)* se encuentra ampliamente distribuida en el Mediterráneo occidental (Barbero et al. 1992). En la península ibérica, una gran parte de los encinares han sido manejados, principalmente en forma de adehesamiento, extracción de leñas en monte bajo o fragmentación (Romane and Terradas 1992, Campos et al. 2013, Santos and Tellería 1998). Durante mucho tiempo estos sistemas agro-forestales fueron considerados sostenibles a largo plazo debido al ciclo de vida largo de las encinas, su resistencia a la sequía, su capacidad de rebrote y su polinización anemófila (ej. Tognetti et al. 1998, Campos et al. 2013). Sin embargo, cada vez parece más claro que el manejo de los encinares puede comprometer ciertas etapas del ciclo de regeneración. Así por ejemplo, a pesar de que las distancias de polinización pueden alcanzar cientos de metros (Ortego et al. 2014), se ha observado una menor diversidad genética en las plántulas de ambientes fragmentados (Ortego et al. 2010). El aumento de la competencia intraespecífica en estructuras de monte bajo limita la producción de frutos (Sánchez-Humanes y Espelta 2011). Con respecto a la dispersión de las bellotas, en pequeños fragmentos forestales desaparece el arrendajo (principal dispersante a larga distancia) (Andren 1994, Brotons et al. 2004) y la depredación de las bellotas por los roedores puede agotar la producción (Santos and Telleria 1997). Finalmente, en las dehesas la falta de dispersión hacia microhábitats óptimos limita el reclutamiento de plántulas lo que conlleva estructuras demográficas envejecidas (Pulido et al. 2001, Plieninger et al. 2004, Pulido and Díaz 2005).

La encina es una especie muy atractiva a la hora de evaluar los efectos de la fragmentación desde un enfoque mecanicista. Domina la cobertura vegetal en áreas extensas, se conocen bien los procesos que modulan las distintas etapas de su ciclo vital y el manejo forestal parece amenazar su sostenibilidad a largo plazo. Si somos capaces de identificar qué etapas del ciclo de regeneración de la encina se ven comprometidas y de determinar cuáles son los cambios ambientales que modulan dicha respuesta podremos evaluar de manera más realista su vulnerabilidad frente al cambio global y guiar políticas de conservación más adecuadas.

OBJETIVOS Y ESTRUCTURA DE LA TESIS

Nuestros objetivos principales de esta tesis fueron: (1) detectar qué etapas del ciclo de regeneración de la encina son más vulnerables frente a la fragmentación y (2) determinar qué cambios ambientales generan estos cuellos de botella.

Para detectar qué etapas del ciclo podrían estar comprometidas cuantificamos los efectos de la fragmentación sobre la producción de bellotas, su dispersión y la conectividad genética entre subpoblaciones. En cada una de estas etapas evaluamos la respuesta frente a la fragmentación a través de cambios en factores ambientales clave. Para ello hemos abordado los siguientes objetivos específicos:

1. Cuantificar los efectos de la fragmentación sobre la producción de bellotas y analizar si dichos efectos están mediados por cambios en la competencia intraespecífica por el agua (Capítulo 1).
2. Comparar los servicios de dispersión de bellotas que ofrecen los arrendajos (*Garrulus glandarius*) en bosques y dehesas adyacentes, determinando si los cambios en el comportamiento del dispersante dependen de la estructura del paisaje o de alteraciones en la calidad de la cosecha de los árboles (Capítulo 2).
3. Medir los efectos de la fragmentación sobre la dispersión de bellotas por el ratón de campo (*Apodemus sylvaticus),* analizando si los patrones observados responden a cambios en la competencia intraespecífica por las bellotas y la presencia de

zonas de refugio frente a depredadores durante la movilización (Capítulo 3).

4. Construir un modelo basado en agente (ABM) para demostrar que los efectos del manejo en el mutualismo roedor-encina pueden ser predichos a través enfoques mecanicistas que integren cambios en la toma de decisiones por parte del dispersante debido a alteraciones en las condiciones ambientales (Capítulo 4).
5. Cuantificar la conectividad funcional de encinares fragmentados utilizando la teoría de redes, teniendo en cuenta los patrones de producción de bellotas, la dispersión del polen y el comportamiento del dispersante. Determinar qué etapas de la regeneración limitan el flujo génico entre parches y detectar qué características del paisaje modulan las dinámicas fuente-sumidero (Capítulo 5).

6. Ilustrar cómo los enfoques mecanicistas pueden ayudar a predecir los impactos del manejo sobre distintas etapas del ciclo de regeneración y a diseñar políticas de conservación más adecuadas (Capítulos 5 y 6).

7. Discutir qué etapas del ciclo de regeneración de la encina limitan su sostenibilidad en ambientes fragmentados, qué factores ambientales las modulan y proponer ciertas pautas de manejo.

Resumen

A continuación se presenta un esquema gráfico donde quedan recogidos cómo los objetivos de cada uno de los capítulos se integran en el ciclo de regeneración de las encinas.

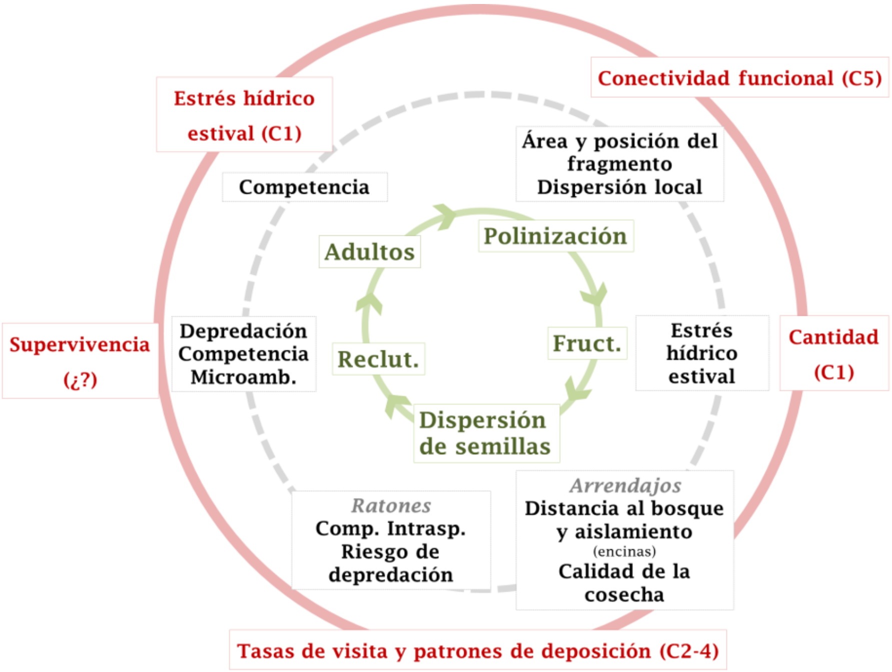

Fig. 3 Esquema conceptual de la tesis doctoral en el que se indican qué fases del ciclo de regeneración de las encinas han sido abordadas en cada capítulo. En negro y rojo se indican los factores ambientales moduladores y las respuestas evaluadas, respectivamente. C1-C5 indican los capítulos. ¿? Indica preguntas abiertas, no abordadas durante el desarrollo de la tesis.

METODOLOGÍA

Zonas de estudio

El estudio de los efectos de la fragmentación sobre la producción y dispersión de bellotas por roedores (Capítulo1, Capítulo 3) fueron llevados a cabo en las localidades de Lerma (submeseta norte; 42°5'N, 3°45'W) y Quintanar de la Orden (submeseta sur; 39° 35’ N, 3°02’W). En esta última, además, se estimó la conectividad funcional del paisaje en términos de flujo génico (Capítulo 5). El estudio de los servicios de dispersión de los arrendajos se llevó a cabo en el Parque Nacional de Cabañeros (39°39′N, 4°28′W) (Capítulo 2). Datos pertenecientes a las tres localidades fueron usados en la parametrización y validación del modelo de dispersión de bellotas por ratones (Capítulo 4).

Lerma y Quintanar de la Orden se encuentran en las submesetas norte y sur, respectivamente (Fig. 4), donde el cultivo de cereal ha reducido la cobertura de bosque hasta un ≈8% del área original. Los bosques inicialmente continuos están reducidos a fragmentos cuya extensión oscila entre 0,1 y 2000 ha. Estas dos localidades fueron escogidas porque sus encinares son representativos de lo que encontramos en la meseta central (Santos and Tellería 1998) y porque son climáticamente contrastadas, sobre todo en verano (Fig. 5).

Los encinares de Quintanar de la Orden se caracterizan por una baja densidad de árboles por hectárea (121 en promedio) y la mayoría de los árboles tienen una estructura de troncos múltiples. El sotobosque está poco desarrollado representando sólo un 14% de la cobertura total. Está compuesto por coscojas (*Quercus coccifera)* y especies de arbustos típicas del mesomediterráneo xérico (*Rhamnus lycioides, R. alaternus, Cistus ladanifer, Asparagus acutifolius*) (Fig. 6B). La precipitación anual es de 421 mm y las temperaturas medias de 14ºC. En promedio, se caracteriza por una sequía estival aguda con un déficit hídrico acumulado entre abril y agosto es de -690.92 mm (Fig.5).

En Lerma, las encinas también suelen tener una estructura de troncos múltiples pero los encinares se caracterizan por una mayor densidad de tocones por hectárea (404 en promedio) y un sotobosque bien desarrollado que representa un 25% de la cobertura total. Junto con la encina aparecen de manera esporádica quejigos (*Q. faginea)* y sabinas (*Juniperus thuriphera).* Las especies del sotobosque son típicas de zonas supramediterráneas (e.g. *Cistus laurifolius, Genista scorpius, Thymus zygis*) (Fig.6A). La precipitación anual es de 567 mm y las temperaturas medias son 11 ºC. La sequía estival es relativamente suave con un déficit de agua acumulado (Abril-Agosto) de -393 mm.

El parque Nacional de Cabañeros (39º 34’ N , 4º40’ W) se localiza en la submeseta sur (Fig. 4). En él podemos encontrar dos tipos de hábitats- bosque y dehesas (Fig. 6E). Los bosques se encuentran en los piedemontes de sierras bajas de dirección E-O. Presentan una densidad media de 97 encinas por hectárea con zonas donde se mezclan con pinos (*Pinus pinea*). El sotobosque está bien desarrollado con más de un 60% de cobertura de arbustos. Las dehesas se localizan en las llanuras intercaladas entre las sierras, y presentan una estructura sabanoide (12 árboles por hectárea, en promedio). En ellas la cobertura de sotobosque es prácticamente nula (<1%). La precipitación media anual en cabañeros es de 636 mm y las temperaturas medias 15ºC (Fig. 5). Esta zona de estudio se escogió por cuestiones prácticas. Para poder realizar estudios sobre comederos es necesario habituar a los pájaros a su presencia y mantener estas estructuras al menos un año antes de comenzar ninguna medida. Además, necesitábamos medir de manera fina los patrones de producción de bellotas, sus tamaños y tasas de infestación predispersiva para testar hipótesis sobre el comportamiento de los arrendajos por lo que fue necesario instalar trampas de semillas en las encinas. Este tipo de despliegue en el medio-largo plazo hubiera sido difícil de mantener en zonas sujetas a un alto grado de manejo. Además, creemos que las hipótesis testadas en el capítulo 2 pueden ser extrapolables a ambientes fragmentados.

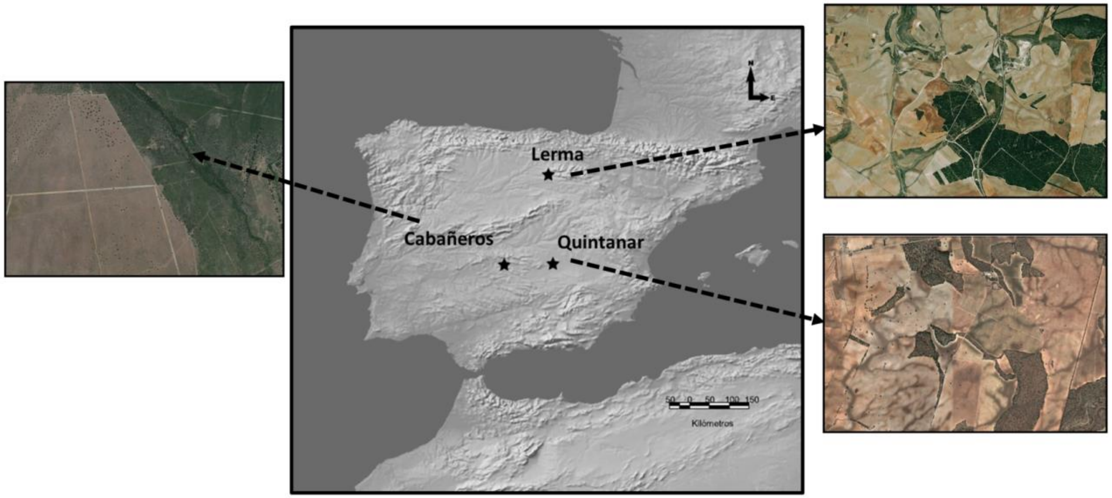

Fig. 4. Localización de las áreas de estudio en la península Ibérica y fotografías aéreas a escala 1:12000 de cada una de ellas.

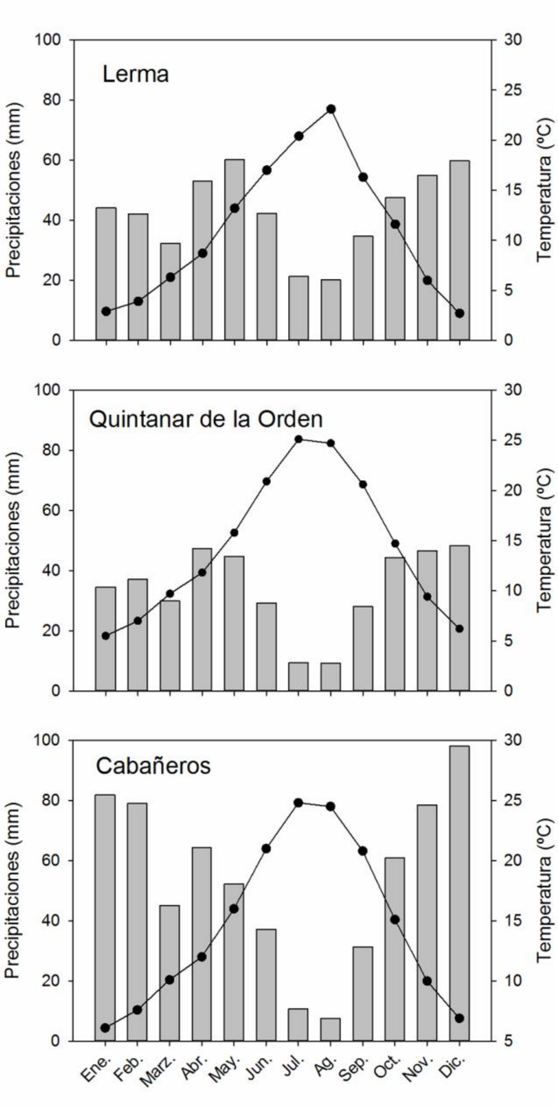

Fig. 5. Diagrama ombrotérmico de las zonas de estudio. Las barras representan la precipitación acumulada mensual (mm, eje izquierdo) y las líneas la temperatura promedio (ºC, eje derecho). Datos tomados de (Ninyerola et al. 2005).

RESUMEN

Diseño experimental

En Lerma y Quintanar de la Orden el muestreo de campo siguió un diseño factorial. Se escogieron tres fragmentos grandes (>100 ha) y se dividió su área en zonas de borde (<60 m al cultivo más próximo, García et al. 1998) y zonas de interior. Además se eligieron 10 y 11 fragmentos forestales pequeños (0.04 ha en promedio) embebidos en la matriz agrícola con al menos tres encinas. Las áreas de borde se escogieron a lo largo de líneas rectas para evitar efectos geométricos (Fernández et al. 2002). En todos los casos los fragmentos forestales pequeños estaban embebidos en matriz agrícola de cultivo de cereales. En cada uno de estos niveles de fragmentación escogimos al azar 15 o 30 encinas focales (dependiendo del experimento). Así pues, nuestro diseño experimental tiene dos factores- localidad (norte y sur) y fragmentación (interior, borde, fragmentos pequeños) (Fig. 6).

En Cabañeros 20 árboles focales se encuentran en el bosque y 26 en la dehesa. Éstos fueron escogidos previo al desarrollo de esta tesis doctoral en función de características de los árboles tanto de su configuración espacial como de su cosecha que pueden afectar el comportamiento de los arrendajos (producción de bellotas, tamaño, tasas de infestación, aislamiento y distancia a hábitats forestales). Para facilitar el uso de los árboles por individuos distintos los árboles focales fueron escogidos lo más espaciados posible cubriendo un área de 780 ha. Entre estos árboles, en el año 2012 se seleccionaron 16 para llevar evaluar los patrones de deposición de semillas. Nuestro diseño experimental tiene el factor hábitat (bosque *vs* dehesa) y dentro de estos factores un gradiente ambiental en las características de los árboles focales.

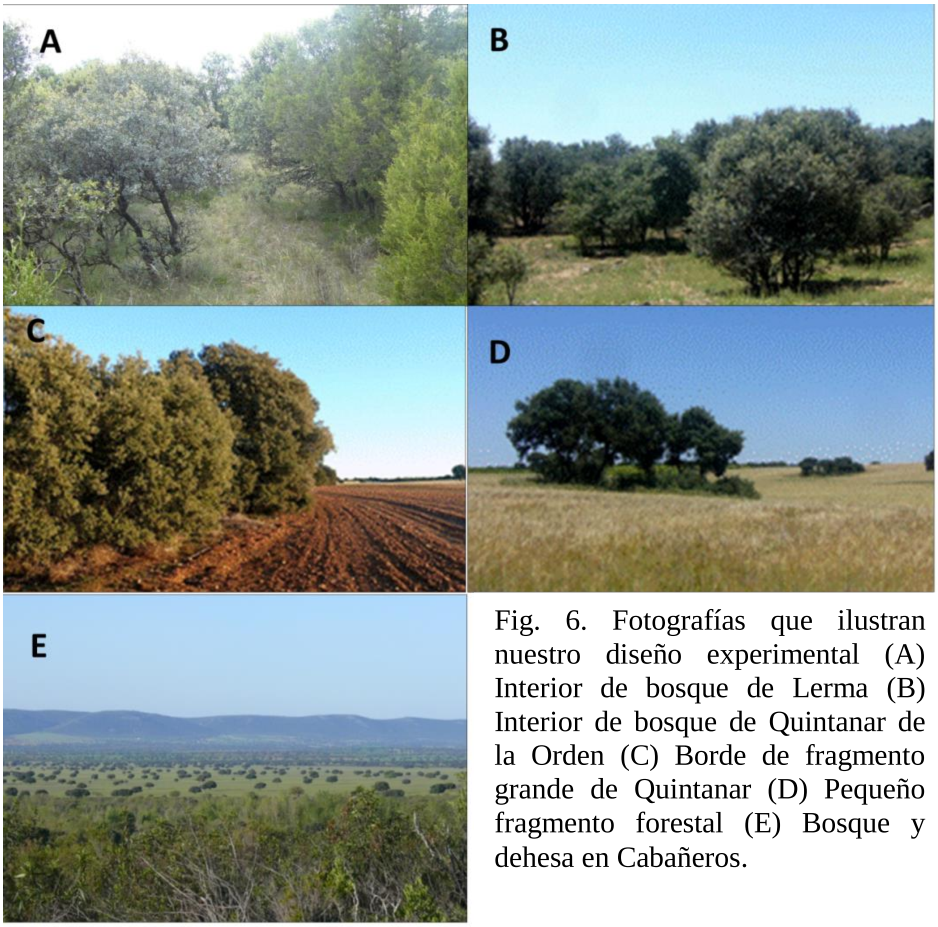

Fig. 6. Fotografías que ilustran nuestro diseño experimental (A) Interior de bosque de Lerma (B) Interior de bosque de Quintanar de la Orden (C) Borde de fragmento grande de Quintanar (D) Pequeño fragmento forestal (E) Bosque y dehesa en Cabañeros.

RESUMEN

Ecofisiología de las encinas y producción de bellotas

Entre los años 2012 y 2014 se siguió la producción de semillas en 180 encinas en Lerma y Quintanar de la Orden (30 por nivel de fragmentación y localidad). El tamaño de la cosecha se estimó visualmente con una medida semi-cuantitativa que va desde 0 (no hay producción) hasta 4 (90% de la copa está cubierta por bellotas (Díaz 2011). En Agosto de 2012 y 2013 se midió en estos árboles el potencial hídrico antes del amanecer (Ψ_{pd}) como un indicador de estrés. Para ello se usó una cámara de Scholander (Scholand.Pf et al. 1965). Además, en cada uno de los árboles focales se midió el tamaño de la copa, el número de troncos por individuo y su competencia en un buffer de 20 m. Para cuantificar los efectos de la fragmentación sobre la producción de bellotas así como para testar si estos efectos estaban mediados por una menor competencia intraespecífica por el agua se usaron modelos mixtos lineales, logísticos y acumulativos.

Dispersión de bellotas por los arrendajos

En Cabañeros, entre el año 2005 y 2012 se seleccionaron 46 encinas en los que se monitoreó las tasas de visita de los arrendajos durante el invierno. Asimismo, durante esos años se hizo un seguimiento de las característica de la cosecha mediante trampas de semilla. Se midió- la producción de bellotas, su tamaño y las tasas de infestación predispersivas. Además se calculó anualmente la producción de bellotas por hectárea en bosque y en dehesa. Las características espaciales de los árboles (aislamiento y distancia al bosque) fueron calculados con ortofomapas. Para evaluar si existían diferencias entre hábitats en las tasas de visitas y en los patrones de producción de bellotas se usaron modelos mixtos lineales y logísticos. Posteriormente, para comprender qué factores ambientales podían causar las diferencias entre hábitats analizamos qué características de los árboles (cosecha *vs* configuración espacial) explicaban los patrones de selección de los arrendajos. Para ello usamos sistemas de ecuaciones estructurales (SEM) (Shipley 2002).

En el invierno 2012 se escogieron 16 árboles focales en los que se ofertaron bellotas radiomarcaradas a los arrendajos y en los que se grabó su comportamiento (Pons and Pausas 2007a, Pons and Pausas 2007b). Los patrones de dispersión fueron analizados en términos de distancias de movilización y selección de microhábitat para el almacenamiento. En cada hábitat se calculó la distancia, media y máxima, los percentiles 25 y 75 así como el porcentaje de bellotas que habían sido movilizadas más de allá de 100 m. Además, se computó el parámetro de selección de Manly para cada uno de los microhábitats de deposición (bajo arbusto, bajo copa, en macollas de hierba, en áreas abierta; Manly et al. 2002). Con respecto al comportamiento de los arrendajos se analizó la selección de las bellotas ofertadas (pequeña, grande, transporte múltiple) a través de modelos multinomiales. Además, se evaluó si había diferencias entre hábitats en el tiempo total de la visita en el comedero y el tiempo invertido en actividades de vigilancia, selección y manipulación. Para ello se usaron modelos lineales y logísticos, respectivamente.

Dispersión de bellotas por el ratón de campo

En el otoño de 2012 se seleccionaron 90 madres en Lerma y Quintanar de la Orden (15 por categoría de fragmentación y localidad). En noviembre y marzo, se estimó la abundancia local de *Apodemus sylvaticus* así como la disponibilidad de bellotas combinando un índice semi-cuantitativo de cantidad de bellotas en árbol (0-4; (Díaz 2011) con otro que estimaba el tamaño (1-6). La estructura de la vegetación se caracterizó mediante transectos en los que se midió la proporción de proyección de áreas abiertas (suelo desnudo, hierbas y arbustos < 25 cm de altura), arbustos y copas de árboles. En diciembre, enero y febrero se ofertaron nueve bellotas (tres grandes, medianas y pequeñas) en cada uno de los árboles focales. Tras una y tres noches de exposición se anotó el estado de la bellota (movilizada, almacenada, depredada, no manipulada, roída), la distancia de movilización y su dirección. Las bellotas almacenadas fueron seguidas a lo largo del invierno.

Los patrones de dispersión fueron caracterizados en términos de distancias de movilización, proporción de bellotas almacenadas (*vs* depredadas) y supervivencia de los almacenes a corto plazo. El efecto global de la fragmentación sobre la toma de decisiones de los roedores (almacenar, roer, depredar etc.) fue analizado mediante modelos mixtos multinomiales y logísticos. Por cada localidad y nivel de fragmentación aproximamos la kernel de dispersión ajustando distintas funciones de probabilidad (normal, log-normal, weibull y gamma) a los datos de distancias de movilización y escogimos aquella función que tuviera menor AIC global (Greene et al. 2004). Con el fin de testar si había diferencias en las kernel de dispersión entre localidades para un mismo nivel de fragmentación y entre niveles de fragmentación por localidad usamos test de Kolmogorov-smirnov y Anderson-Darling. Además, calculamos la distancia máxima y media, los percentiles 25 y 75 y el porcentaje de bellotas movilizadas más allá de 20 m. Las preferencias en los microhábitats de deposición de las bellotas fueron evaluadas mediante tests de Manly (2002).

Para determinar si los efectos de la fragmentación podían ser explicados por cambios en factores ambientales clave, en cada zona de muestreo (entre 3 y 5 por cada nivel de fragmentación y localidad) se calculó- la competencia intraespecífica (como el ratio entre la abundancia de ratones y disponibilidad de bellotas), la proporción de cobertura de microhábitats abiertos, la proporción de bellotas almacenadas y los parámetros de forma y escala de la kernel de dispersión. Usamos modelos lineales para evaluar si las distancias de movilización dependían de la proporción de microhábitats abiertos, la competencia y su interacción. Además, analizamos si las tasas de almacenamiento estaban condicionadas por las distancias de movilización mediante modelos logísticos. Finalmente usamos modelos logísticos para evaluar si la distancia de movilización y el microhábitat de deposición determinaban la probabilidad de surpervivencia de los almacenes en el corto plazo.

Construcción de un modelo de dispersión de bellotas por ratones

Se desarrolló un modelo que combinaba los efectos del manejo (fragmentación, adehesamiento y remoción de arbustos) sobre factores ambientales clave para los roedores (competencia intraespecífica por las bellotas y presencia de zonas de refugio); con un modelo basado en agente (ABM; Grimm and Railsback 2005). Nuestro modelo asume que la producción de las bellotas está mediada por la competencia intraespecífica por el agua (Capítulo 1). La abundancia local de roedores depende de la cantidad de hábitat forestal (Ylonen et al. 1991, García et al. 1998), de la presencia de árboles y arbustos (Muñoz et al. 2009, Díaz 2014) y del solapamiento máximo de sus áreas de campeo (Tattersall et al. 2001). Además, asume que los microhábitats abiertos son percibidos por los roedores como zonas de alto riesgo de depredación (Tew y Macdonald 1993). En función de estas reglas, las características ambientales a escala local varían de manera dinámica con el manejo. Las decisiones de los roedores persiguen tres objetivos específicos (1) movilizar las semillas lejos de competidores potenciales, (2) evitar arriesgarse demasiado durante la movilización y (3) guardar las semillas en áreas donde la probabilidad de robo por conespecíficos es baja. De la interacción entre las motivaciones del dispersante y las características del paisaje emergen los patrones de dispersión de semillas medidos en términos de distancias de movilización y tasas de almacenamiento.

Una vez el modelo fue construido se parametrizó usando un aproximación bayesiana orientada en patrones observados (Hartig et al. 2011). Para ello usamos datos de las zonas de borde de Lerma. Posteriormente se validó el modelo con cinco paisajes independientes que incluían, las zonas de interior de fragmento grande de Lerma, zonas de borde e interior de Quintanar, fragmentos forestales pequeños y la dehesa de Cabañeros. Tras su validación se realizaron pruebas de sensibilidad del modelo a cambios en los patrones del paisaje (cantidad de hábitat forestal, número de árboles por hectárea y cobertura de arbustos) así como a cambios en la toma de decisiones de los roedores (riesgo aceptado de depredación y de robo de almacenes). Para ello usamos test de correlaciones parciales (Pujol et al. 2014). Finalmente para ilustrar el potencial de este tipo de enfoques como herramientas de gestión se simuló el proceso de matorralización de una dehesa y evaluamos los cambios en la calidad de la dispersión en términos de distancias de movilización y de tasas de almacenamiento.

Construcción de redes de conectividad funcional

Se cuantificó la conectividad funcional (en términos de flujo génico) a escala de paisaje utilizando datos obtenidos en campo de dispersión de polen, producción de bellotas (Capítulo 1) y tasas de almacenamiento de las semillas por los ratones (Capítulo 2). Nuestra localidad de estudio fue Quintanar de la Orden. Los arrendajos fueron excluidos de este análisis porque estaciones de escucha a lo largo de transectos dieron resultados negativos, algo posteriormente confirmado por los guardas de las fincas.

En el otoño 2012 se muestrearon 28 árboles madre repartidos entre los tres niveles de fragmentación y con distancias que oscilaban entre 4 y 5477 m. Se genotiparon tanto las encinas madre como 12 hijos (aprox.) usando10 microsatélites (siguiendo el protocolo de extracción y análisis de Ortego et al. 2014). Con estos datos se utilizó el modelo KINDIST (Robledo-Arnuncio et al. 2006, Robledo-Arnuncio et al. 2007) para estimar la función de probabilidad de deposición del polen con la distancia (kernel). La construcción de la red se realizó mediante los siguientes pasos: (1) se calcularon las tasas de migración de polen entre fragmentos a una resolución de píxeles de 20 x 20 m ; (2) se simuló el *pool* de conectividad funcional en las bellotas no dispersadas teniendo en cuenta las tasas de migración de polen y los efectos borde positivos sobre la producción de bellotas (Capítulo 1); (3) se simuló el *pool* de conectividad funcional de las bellotas almacenadas por los roedores teniendo en cuenta el efecto borde negativo sobre la dispersión (Capítulo 2). Así construimos dos redes, una previa al almacenamiento de las bellotas y otra posterior.

RESUMEN

Para determinar si el flujo génico estaba espacialmente estructurado realizamos un análisis de modularidad siguiendo el algoritmo de Newman (2006). Para evaluar el impacto de la actividad de los roedores sobre la conectividad funcional del paisaje se analizaron las diferencias entre las dos redes en la modularidad relativa (Fortuna et al. 2008), número de módulos, tamaño mínimo, máximo y medio de los módulos y en las tasas de migración. Para ello usamos modelos logísticos y pruebas de rangos de Wilcoxon. Además evaluamos qué características del fragmento (área, centralidad, aislamiento) determinaban su papel dentro de la red (tasas de migración y grado del nodo) mediante modelos generalizados (distribución quasipoisson y quasibinomial). Finalmente, construimos paisajes teóricos en los que cambiamos la configuración espacial y el área de los fragmentos forestales grandes (>10 ha) para valorar si las conclusiones que se desprenden de análisis a nivel de fragmento pueden ser extrapolados a políticas de manejo a nivel de paisaje. Asimismo simulamos redes en las que no existía un efecto borde negativo sobre las tasas de almacenamiento de los roedores para comparar la efectividad de políticas de manejo a gran escala (cambios en el paisaje) con otras a escala local (cambios en el comportamiento de los ratones

CONCLUSIONES GENERALES

Integrando los resultados de los cinco capítulos de esta tesis doctoral, se han extraído las siguientes conclusiones

1. Los efectos netos de la fragmentación pueden traducirse en cambios ambientales clave para las distintas etapas del ciclo de regeneración.
2. El sentido de dichos efectos puede cambiar entre etapas por lo que para valorar la viabilidad de las poblaciones en paisajes fragmentados necesitamos un enfoque integrado.
3. La fragmentación tuvo un efecto positivo sobre la producción de bellotas mediado por una disminución de la competencia intraespecífica por el agua durante el verano.
4. En zonas fragmentadas los servicios de dispersión tanto del arrendajo (*Garrulus glandarius*) como del ratón de campo (*Apodemus sylvaticus)* se ven empobrecidos.
5. El uso de zonas adehesadas por los arrendajos es esporádico y de menor calidad que en los bosques. Si queremos recuperar el papel de estas aves como dispersantes es necesario tener en cuenta la estructura del paisaje asegurando la presencia de parches forestales cercanos y evitando densidades de arbolado extremadamente bajas.
6. Las tasas de depredación de las bellotas por los roedores se disparan en los pequeños fragmentos forestales debido al aumento de la cobertura de microhábitats abiertos junto con una disminución importante de la competencia intraespecífica. Si

mejoramos la permeabilidad de la matriz a los movimientos de los roedores esta situación puede revertirse.

7. Los efectos negativos de la fragmentación sobre las tasas de almacenamiento de bellotas en las zonas de borde pueden comprometer la diversidad genética de las plántulas a pesar de la existencia de un flujo de polen extenso a través del paisaje.
8. De todas las etapas del ciclo, la dispersión de las semillas es el cuello de botella en la regeneración de la encina y en la cohesión genética de las subpoblaciones. Mejorar los servicios de dispersión debe ser un objetivo prioritario en las políticas de manejo.

GENERAL CONCLUSIONS

Integrating the results of the five chapters developed along this thesis, we have drawn the following conclusions:

1. The net effects of forest fragmentation can be translated into key environmental changes for different stages of holm oak regeneration cycle.
2. The sign of these effects can change along different stages, and hence, to assess the viability of holm oak populations in fragmented landscapes an integrated approach is needed.
3. Fragmentation positively affected acorn production through a reduction of intraspecific competition for water sources.
4. Acorn dispersal services provided by Eurasian jays (*Garrulus glandarius*) and wood mice (*Apodemus sylvaticus*) decreased in fragmented landscapes.
5. Dehesa habitats were exploited by jays sporadically and late in autumn-winter. Management practices designed to restore their dispersal services should take into account landscape structure ensuring the presence of forest habitats in the surroundings and avoiding extremely low stem densities.
6. Acorn predation by wood mice shot up at small forest fragments due to an increment of unsafe microhabitats for rodents together with an acute decrement of intraspecific competition for acorns. However, when the surrounding matrix became more permeable, mice acted as local acorn dispersers.

7. Negative effects of forest fragmentation on acorn caching rates can hamper the genetic diversity of seedlings in spite of an extensive pollen flow across the landscape.

8. Of all stages, acorn dispersal proved to be the most vulnerable to fragmentation effects acting as a bottleneck for regeneration and limiting the genetic cohesiveness of holm oak subpopulations. Improving dispersal services in fragmented landscapes should be a priority in holm oak conservation policies

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CAPÍTULOS

CHAPTER 1

Forest fragmentation alleviates water stress and increases holm oak acorn crops

Morán-López T.[1], Forner A.[1], Flores-Rentería D.[1], Diaz M[1] and Valladares F.[1]

(1) Department of Biogeography and Global Change (BCG-MNCN). National Museum of Natural Sicence CSIC. c/Serrano 115 bis, E-28006 Madrid, Spain.

ABSTRACT

In water-limited systems, such as the Mediterranean, forest management effects on acorn yields will be mediated by its effects on physiological status of trees during seed development. In fragmented landscapes, the creation of forests edges reduces tree-to-tree competition for sources, which will temper water shortage of oaks during summer and, as a result, enhance acorn production. To test this hypothesis we monitored acorn production (2012-2014) in two holm oaks (*Quercus ilex)* forest archipelagos of the Iberian Peninsula at three fragmentation levels- forest interiors, edges and small woodlots. We then evaluated if changes in intraspecific competition due to fragmentation were related to tree water status, and if this translated into differences in acorn crops.

Acorn production and fragmentation effects did not differ between localities despite of showing contrasting climatic conditions. In general, forest interiors showed a higher proportion of non-producing trees than that expected by random while trees at small forest fragments showed enhanced acorn productivity. As expected, lower intraspecific competition in small forest fragments alleviated summer water stress of trees, which entailed increased acorn production. Overall, our results show a positive effect of forest fragmentation on acorn production mediated by changes in tree water status. Besides, they indicate that local management effects on water availability can override those of climate.

Key words: *Quercus ilex,* holm oak, acorn production, fragmentation, competition, water stress

CHAPTER 1

INTRODUCTION

Habitat loss, resource overexploitation and poor management are the main drivers of forest degradation in the Mediterranean Basin, and their impacts are expected to be intensified by climate change (Sala et al. 2000, Valladares et al. 2014). On one hand, summer water availability is one of the main limiting factors for plant growth in Mediterranean ecosystems (Flexas et al. 2014) and future scenarios of climate change predict an increase in drought intensity in the coming decades (IPCC 2013). On the other hand, despite of having been exploited for centuries (Blondel 2010), forest management can have pervasive effects on forest regeneration potential driven by a complex interplay between habitat availability, isolation and edge effects (Valladares et al. 2014).

Holm oaks (*Quercus ilex)* are widely distributed in the Western Mediterranean playing a key socio-economic role over large areas (Barbero et al. 1992, Campos et al. 2013). They have been considered as tolerant to severe water stress due to their deep root system (Moreno et al. 2005), their ability to rapidly recover from damage by summer drought and their resprouting capability (Tognetti et al. 1998). However, when compared to other Mediterranean species they are quite vulnerable to xylem cavitation and in summer months they function close to the point of hydraulic failure (Martinez-Vilalta et al. 2002, Quero et al. 2011). Furthermore, high defoliation rates and dieback episodes have been registered in holm oak forest stands after extreme drought events (Penuelas et al. 2000).

Regarding fruit production, despite of high inter-annual variability, there is mounting evidence that acorn yields depend on water availability during spring and summer months. In general, moister springs involve higher investment on female flowers, which entail enhanced acorn production. Nonetheless, if summer drought is too severe, acute water shortage can lead to high abortion rates and constrain final acorn yield (Ogaya and Penuelas 2007, Espelta et al. 2008, Perez-Ramos et al. 2010, Misson et al. 2011, Rodriguez-Calcerrada et al. 2011, Sanchez-Humanes and Espelta 2011, Fernandez-Martinez et al. 2012, Garcia-Mozo et al. 2012). This suggests that spring weather conditions set the template of annual acorn production, which is then modified by summer drought effects on seed development. Thus, under a climate change scenario, increased aridity may hamper oaks regeneration potential. In fact, rainfall exclusion experiments have shown that reductions in summer rainfall similar to those expected by the end of the century in the Mediterranean basin (between 15 and 30 percent), can constrain oaks reproduction (Perez-Ramos et al. 2010, Rodriguez-Calcerrada et al. 2011, Sanchez-Humanes and Espelta 2011, IPCC 2013).

In parallel to climatic conditions, forest management can modify water availability of individual trees. Most of holm oak woodlands are subjected either to tree coppicing, clearance or fragmentation (Terradas 1999, Campos et al. 2013, Santos and Tellería 1998). In dense multi-stemmed stumps, increased competition for sources limits oaks growth and sexual reproduction (Rodriguez-Calcerrada et al. 2011, Sanchez-Humanes and Espelta 2011). Selective thinning of weaker stems has been proposed as a management strategy for natural restocking of holm oak woodlands since it stimulates tree growth (e.g. Retana et al. 1992, Mayor and Roda 1993). However, its impacts on acorn production seem minor (Rodriguez-Calcerrada et al. 2011, Sanchez-Humanes and Espelta 2011).

Another way of buffering the negative effects of summer drought on holm oak water status is tree clearance (Moreno and Cubera 2008). For instance, trees in savanna-like woodlands (dehesas and montados) show acorn crops an order of magnitude higher than those found in forest habitats (Pulido and Diaz 2005). Therefore, management effects on holm oaks acorn production seem to be driven by local changes in intraspecific competition, which in turn modulates the negative effects of summer drought.

In the Iberian Peninsula, agricultural intensification has led to the replacement of large continuous holm oak forests by archipelagos of isolated fragments embedded in croplands (Santos and Tellería 1998). Despite that forest fragmentation has well-known negative effects on acorn dispersal and seedling recruitment (Santos and Telleria 1997, Morán-López et al. 2015), the creation of forest edges may entail lower intraspecific competition, and thus temper oaks water stress during summer. If this was the case, a positive effect of forest fragmentation on acorn production is expected (Carevic et al. 2010). To test this hypothesis we (1) monitored acorn yield in two forest archipelagos of the Iberian Peninsula (2012-2014) and (2) evaluated if fragmentation effects depended on competition impacts on tree water status.

METHODS

Study area

The two holm oak archipelagos studied are located in the Northern and Southern plateau of the Iberian Peninsula —an extensive treeless agricultural region where cereal cultivation has reduced the original forests cover to about an eight per cent of the land area (Santos and Tellería 1998). Fieldwork in the southern plateau was carried out in the vicinity of Quintanar de la Orden (39º 35’ N, 3º02’W, 870 m a.s.l.) within an area of 3,850 ha. The dominant tree is the holm oak *Quercus ilex* with the understory composed by shrubby Kermes oak *Q. coccifera* and shrub species typical from xeric Mesomediterranean localities (e.g. *Rhamnus lycioides*, *R. alaternus*, *Cistus ladanifer*, *Asparagus acutifolius*). Annual precipitation and mean temperature are 421 mm and 14 ºC, respectively. Fieldwork in the northern plateau was undertaken in an area of 66,500 hectares around Lerma (42°5'N, 3°45'W, 930 m a.s.l.). The dominant tree is also holm oak, with isolated Lusitanian oak *Q. faginea* and Spanish juniper *Juniperus thurifera* and understory shrubs typical from wetter and cooler Supramediterranean localities (e.g. *Cistus laurifolius, Genista scorpius, Thymus zygis*). Annual precipitation is 567 mm and annual mean temperatures are 11 ºC.

Climatic data

Climatic data for the studied years were obtained from the closest weather station belonging to the Spanish Meteorological Agency (AEMET); Ocaña (at 57 km from Quintanar de la Orden; 733 m a.s.l.) and Villamayor de los montes (13 km from Lerma; 882 m a.s.l.).

Incomplete monthly data in the weather station of the Southern locality prevented us from using more accurate climatic information. However, monthly precipitation and mean temperatures for the available data indicated a good agreement between Ocaña and Quintanar de la Orden (0.96 and 0.78 Pearson correlation coefficient for temperatures and precipitation respectively). In order to characterize site-specific climatic conditions we used longer time series from nearby meteorological stations (1982-2014). Toledo weather station was used for Quintanar (89 km away; 515 m a.s.l.) and Villafría for Lerma (39 km away; 891 m a.s.l.). In both cases, significant correlations were found between long-time series and those of the studied years (0.99 and 0.80; 0.99 and 0.87 Pearson correlation coefficients for temperatures and precipitation in Lerma and Quintanar, respectively).

From the available climatic data we estimated potential evapotranspiration and accumulated precipitation. Two drought indexes were calculated: (1) the ratio between precipitation and potential evapotranspiration on a monthly basis (P/PET; UNEP 1992) and (2) a drought index (Di), estimated as the difference between accumulated precipitation and potential evapotranspiration from April to August (Rigling et al. 2013). In all cases, PET was estimated following Hargreaves method (Hargreaves et al. 1982).

Experimental design and acorn production estimation

In each locality we selected three large (> 100 ha) forest fragments in which we defined forest interiors and edges depending on the distance to the cultivated border (60 m threshold; García et al. 1998). Edge plots were selected along long straight borders to avoid influences of border geometry on edge effects (Fernández et al. 2002). Besides, 10-11 small woodlots (0.047±0.031 ha in the South, 0.031±0.024 ha in the North, mean±SE) were also selected. This way three fragmentation levels were defined —forest interior, forest edge and small fragments— in each locality —northern and southern plateaus.

In a pilot study carried out in 2011 we observed that site-specific variability on acorn production stabilized at sample sizes of about 75 (25 trees per fragmentation level). Therefore, we established a sampling effort of 30 randomly selected trees per fragmentation level and locality (total sample size = 180). During 2012-2013-2014 crop size of focal trees was visually estimated using a semi-quantitative scale ("acorn score") ranging from 0 (no acorns) to 4 (more than 90% of the canopy covered with acorns) (Díaz et al. 2011). Our large sample sizes made it advisable to use visual surveys. They are less time-consuming than seed traps and are highly correlated with quantitative measures (Koenig et al. 1994a, Carevic et al. 2014b). Large differences in stand structure between localities and fragmentation levels deterred us from using other estimates like acorn counts per second. Changes in canopy closure, and hence, visibility made it advisable to use acorn scores estimates instead.

Predawn water potential and environmental factors measurements

During the first fortnight of August 2012 and 2013 we measured predawn water potential (Ψ_{pd}) of focal trees. On average, each day 15 trees were measured following a randomized factorial design. Measurements were conducted on two twigs per tree. Excised twigs were collected into sealable plastic bags, with saturated humidity and CO_2, and kept refrigerated and in dark (Perez-Harguindeguy et al. 2013). All measurements were performed by means of a Scholander chamber (Scholand.Pf et al. 1965). In each focal tree we also measured canopy radius (average of four measures per tree), number of stems per focal tree and estimated intraspecific competition. Competition was estimated as the proportion of area within a radius of 20 m from focal trees covered by other canopies (4 transects per tree - N, S, E, W directions).

Data analysis

To evaluate if drought stress during the studied years were within the normal ranges of both localities, percentiles (5 and 95%) for monthly P/PET and yearly Di were obtained for the long-term climatic data. These values were compared to those observed during 2012, 2013 and 2014.

We assessed fragmentation effects on acorn production by means of cumulative link mixed models using the R package ordinal (Christensen 2015). Firstly, we evaluated if acorn productivity differed between localities taking into account inter-annual variability and forest fragmentation. Our response variable was acorn score (0, 1, 2, 3, 4). Our fixed effects were locality (North, South) fragmentation level (interior, edge, small fragment), year (2012, 2013, 2014) and their interaction. Subsequently, we evaluated fragmentation effects on acorn production in each locality separately. Our response variable was acorn score, our fixed effects were fragmentation level, year and their interaction. In both analyses mother tree was introduced as a random factor. We did not introduce spatial correlation effects due to convergence problems. However, no significant associations among residuals were detected in spatial autocorrelograms (ncf package; Ottar 2013).

We used generalized linear mixed regression models to evaluate if intraspecific competition, tree size and number of stem per focal tree differed between fragmentation levels in each locality. Binomial, gaussian and poisson models were used respectively. Since habitat quality may be tightly related to fragment management history and agricultural exploitation in the surroundings we introduced cluster as a random effect. Trees located within the same interior and edge areas were assigned to the same cluster, as well as trees located in groups of nearby fragments (within areas of 35 hectares). A total of 18 clusters were obtained (3 clusters per fragmentation level and locality). Lme4 R package was used (Bates et al. 2013).

To test if fragmentation effects in holm oak water-status during summer were related to changes in local environmental variables we used linear mixed models (nlme package, Bates et al. 2013). Our response variable was predawn water potential in August (Ψ_{pd}). In the South, fixed effects were intraspecific competition, year (2012, 2013) and their interaction. In the North, number of stems per focal tree was also included since higher number of stems per stump was found in forest interiors (Table 1.1). In both cases mother tree was included as a random factor. Besides we calculated the percentage of trees showing predawn water potentials below -3 or -3.5 MPa and beyond -1.5 MPa. The former values are considered thresholds of loss of hydraulic conductivity and acorn production (Martinez-Vilalta et al. 2002, Alejano et al. 2008, Carevic et al. 2010, Carevic et al. 2014a). The latter is an intermediate value between those reported to trigger acorn production (-2.5 MPa; Carevic et al. 2010) and those typically found in highly productive dehesa trees (-0.5, -1 MPa; Moreno et al. 2007). Finally, we evaluated if fragmentation effects on acorn production were mediated by summer water stress through cumulative link mixed models. Our response variable was acorn score (0, 1, 2, 3, 4). Our fixed effects were predawn water potential in August (Ψ_{pd}), year (2012, 2013) and their interaction. Mother tree was introduced as a random effect.

Table 1.1. Environmental variables with respect to fragmentation and locality. Intraspecific competition was calculated as the proportion of area in a buffer of 20 m covered by other oak canopies. Size is given as canopy radio in m. N Stems is the number of stems per stump. Letters depict significant differences between fragmentation levels per locality (P<0.05) * Marginal significant differences

Locality	**Fragmentation**	**Competition**	**Group (comp.)**	**Size**	**Group(size)**	**N Stems**	**Group(stems)**
Lerma	*Interior*	0.65±0.02	A	1.95±0.09	A	9.85±1.40	A
	Edge	0.52±0.02	B	2.26±0.10	A	10.41±2.05	B
	Small	0.31±0.08	C	2.6±0.15	A	7.70±1.28	B
Quintanar	*Interior*	0.46±0.04	a	3.73±0.42	A	10.36±2.14	A
	Edge	0.36±0.03	ab	2.14±0.15	A*	3.58±0.44	A
	Small	0.27±0.14	b	3.31±0.21	A	5.57±1.26	A

RESULTS

Climatic variables

The Southern locality showed much drier conditions (Fig. 1.1). Accumulated water deficit from April to August (Di) was a 43% higher on average in the South. (-393.2±11.93 mm; -690.92 ±16.88 mm; North and South, respectively). Besides, although in both localities summer months were characterized by drought conditions (P/PET < 1); water shortage in the South was an order of magnitude more severe (0.18 and 0.21 vs 0.03 and 0.04 average P/PET in July and August, North and South, respectively).

In both localities studied years were within the site-specific normal range. However, differences with the long term mean and between years were more pronounced in the North. There, 2013 was the wettest year with an accumulated water deficit (April-August) a 19% lower than the average, while 2012 (the driest year) showed an accumulated water deficit a 10% higher (Fig. 1.1). In the South, although 2012 was drier, summer-spring water shortage only differed a 3.74 % from the long-term mean, and in 2013 it was a 1.36% higher. Only 2014 showed quite drier climatic conditions with an 11.88% of accumulated water deficit above the long-term average.

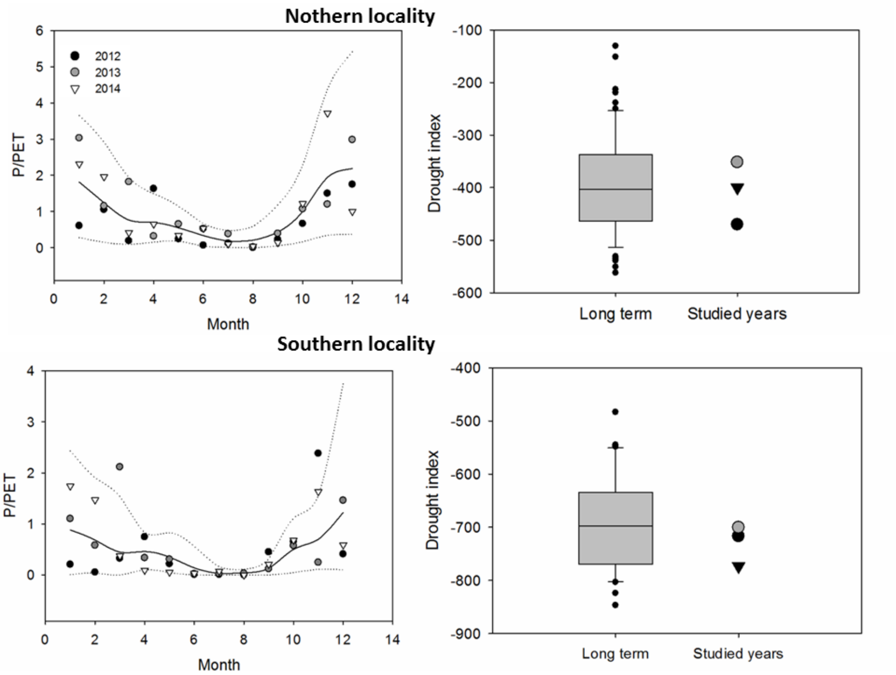

Fig.1.1 (Left panels) Mean long term monthly drought index (P/PET) (solid line) and confidence intervals (95%; dashed line). Mean values of studied years are also plotted. (Right pannels) Riglings' drought index ($\sum_{April}^{August} P - \sum_{Ap.}^{Aug.} PET\,; mm$). In both cases lower values indicate higher drought. Upper and lower panels correspond to the Northern and Southern locality, respectively. Note that y-axis of upper and lower panels have different scale for Riglings' index.

General patterns of fragmentation effects on acorn production

Acorn productivity did not differ between localities (likelihood-ratio test = 0.47; df = 1; P=0.54) and fragmentation effects were consistent among sites (likelihood-ratio test = 1.60; df=2; P=0.44). Besides, in both cases, 2014 showed the highest acorn production (2.11±0.12, 1.64±0.11 mean acorn score ± se; North and South respectively) while 2013 showed the poorest crops (0.68±0.07; 0.93±0.09, mean acorn score ± se; North and South respectively).

Forest fragmentation enhanced acorn production in both sites (Table 1.2, Fig.1.2).In general, forest interiors showed a significantly higher frequency of non-producing trees than expected by random while small forest fragments showed a significantly higher frequency of trees with intermediate and high acorn crops (Fig.1.2). Forest edges showed intermediate responses albeit more similar to forest interiors (Table 1.2).

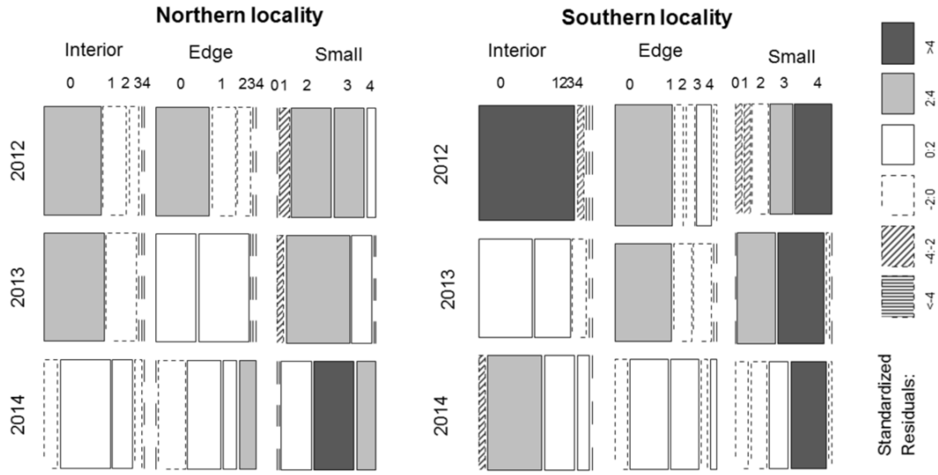

Fig.1.2. Mosaic plot of the observed frequency of holm oak trees with different crop sizes (0-4) in different years and fragmentation levels . The area of each rectangle is proportional to the cell frequency of the corresponding contingency table. Solid and broken lines indicate positive and negative deviation from the expected frequencies under the null model. The shading of each triangle is proportional to standardized residuals from the fitted model (values indicated in the legend). Grey and black rectangles indicate significant positive deviations from the expected frequencies. Striped rectangles show significant negative deviations from the expected frequencies ($p<0.05$)

Table 1.2 Results of cumulative mixed model with crop size (0,1,2,3,4) as a function of year (2012, 2013, 2014), fragmentation (interior, edge, small) and their interaction. LRT = likelihood ratio test, df= degrees of freedom, P = p-value, R^2 = McFadden's pseudoR^2. Letters depict groups ($p<0.05$).

Locality	Effect	LRT	df	P	R^2	Year	Interior	Edge	Small
North	Year	103.06	2	<0.01	0.29	2012	A	A	B
	Fragmentation	71.72	2	<0.01		2013	A	A	B
	Year*Frag	31.42	4	<0.01		2014	A	B	C
South	Year	31.71	2	<0.01	0.20	2012	a	b	c
	Fragmentation	60.36	2	<0.01		2013	a	a	b
	Year*Frag	56.58	4	<0.01		2014	a	a	b

Differences in environmental variables among fragmentation levels

Out of the selected environmental variables only intraspecific competition showed clear patterns with fragmentation (Table 1.1). However, fragmentation effects on competition varied between localities. In the North, high stand densities in forest interiors (404 stems per ha on average) resulted in significant differences in intraspecific competition among all fragmentation levels. It was a 20% and a 52% lower in forest edges and small forest fragments with respect to forest interiors. In the South, low stand density (121 stems per ha on average) lead to much lower intraspecific competition in forest interiors (29 % lower than in the North) and more subtle differences among fragmentation levels. Finally, despite of differences in the stand structure of forests, trees located in small fragments from both localities showed similar competition values. Regarding tree traits, only number of stems per stump was significantly higher in northern forests.

Competition effects on tree water status

Intraspecific competition for water sources had a great impact on predawn water potential in both localities. Besides, predawn water potentials were higher and competition effects lower in 2013 (Table 1.3, Fig. 1.3). In the North, predawn water potentials were within -0.83 and -4.4 MPa in 2012 and within -0.5 and -2.97 MPa in 2013 (Fig. 1.3). In 2012, 48.1% of measured trees showed predawn water potentials below -3MPa. These represented a 56% and a 59% of measured trees in forest interiors and edges. In 2013, 27% of trees showed predawn water potentials beyond -1.5 MPa. Most of them were located at small forest fragments (48%) with little representation in forest interiors (4%).

In the South, predawn water potential ranged between -1.68 and -5.90 MPa in 2012 and between -0.64 and -3.46 in 2013 (Fig. 1.3). In 2012, 89% of trees located in forest interiors showed predawn water potentials below -3.5 MPa while in small forest fragments only a 11% reached these values. In 2013, 19% of trees showed predawn water potentials beyond -1.5 MPa. In small forest fragments they represented a 35% while in forest interiors they only accounted for a 7%.

Table 1.3. Results of linear mixed model with predawn water potential (MPa) as a function of intraspecific competition, year (2012, 2013) and their interaction. LRT = likelihood ratio test, df= degrees of freedom, P = p-value, R_m= marginal pseudoR^2

Locality	**Effect**	**LRT**	**df**	**P**	**Estimate**	**R^2_m**
North	Competition	29.46	1	<0.01	-1.94±0.32	0.62
	Year(2013)	332.65	1	<0.01	0.70±0.19	
	Competition*Year(2013)	8.46	1	<0.01	1.05±0.36	
South	Competition	23.20	1	0.03	-1.34±0.44	0.56
	Year(2013)	492.74	1	<0.01	1.11±0.16	
	Competition*Year(2013)	15.58	1	<0.01	1.49±0.40	

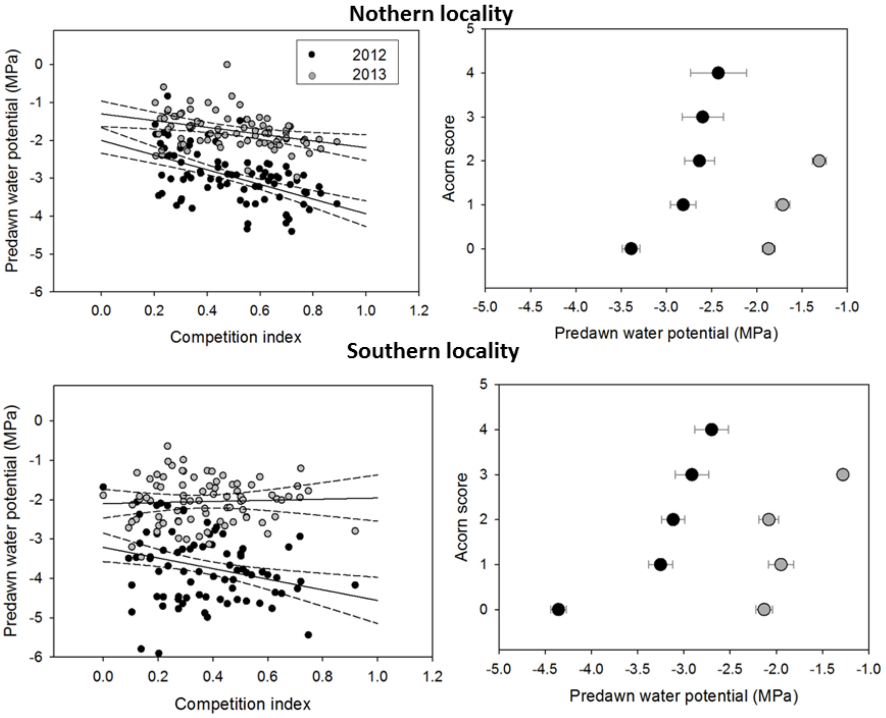

Fig.1.3. (Left panels) Intraspecific competition effects on holm oaks predawn water potential in August. Solid lines correspond to model predictions per year and dashed lines to 95% confident intervals (Right panels) Predawn water potential effects on acorn production. Bars represent 95% confident intervals. Upper and lower panels correspond to the Northern and Southern locality, respectively-

Water status effects on acorn production

In both localities predawn water potential affected acorn production of trees (Table 1.4, Fig 1.3). However, patterns differed between years. In 2012, a threshold-like response was observed in both localities. Main differences occurred between producing and non-producing trees. In the North, predawn water potentials below – 3MPa constrained acorn production while in the South this threshold dropped to -4 MPa (Fig. 1.3). On the contrary, in 2013 trees with the highest crops made the difference (Fig 1.3). In this case, trees with predawn water potentials higher than -1.5 MPa showed the highest productivity in both localities (Fig 1.3).

Table 1.4. Results of cumulative mixed model with crop size (0,1,2,3,4) as a function of predawn water potential (Ψ, MPa), year (2012,2013), stems per stump and their interaction. Only significant effects are shown. LRT = likelihood ratio test, df= degrees of freedom, P = p-value, R_m= marginal pseudoR^2

Locality	**Effect**	**LRT**	**df**	**P**	**Estimate**	**R^2_m**
North	Ψ	27.08	1	<0.01	1.87±0.39	0.10
	Year	37.69	1	<0.01	-3.40±0.65	
South	Ψ	44.14	1	<0.01	3.99±0.56	0.22
	Year(2013)	52.01	1	<0.01	-13.89±2.06	
	Ψ* Year(2013)	44.71	1	<0.01	-3.76±0.07	

DISCUSSION

Negative effects of forest fragmentation on plant reproduction success have been largely observed, especially in animal-pollinated plants (reviewed in Aguilar et al. 2006). In most of these cases the impairment of plant-animal mutualistic relationships due to habitat loss or edge effects causes hampered fruit production. However, in wind-pollinated plants, as is the case of holm oaks, extensive pollen flow may prevent from pollen limitation in fragmented populations (Ortego et al. 2014). Instead, fragmentation effects will depend on other environmental factors related to plant phenology and seed development.

Overall, our results show a positive effect of forest fragmentation on acorn production mediated by summer water stress mitigation. Despite that the Southern locality is characterized by more severe summer drought, we did not find significant differences in acorn productivity between localities and the impacts of forest fragmentation were consistent among sites. In both cases, forest interiors showed a high proportion of non-producing trees while trees located at small forest fragments exhibited enhanced acorn productivity in all studied years. These results support the idea that poor acorn yields in holm oak woodlands may be relatively frequent since high density stands are widely spread (Espelta et al. 2008). Besides, they show that management impacts on acorn production can override climatic effects.

As expected, fragmentation effects were driven by tree-to-tree competition, which exerted a strong impact on tree water-status during summer (see Moreno and Cubera 2008, for similar results in stand density gradients). Although the studied years did not represent extreme drought events in any of the localities, water shortage was more pronounced in 2012. In that year, almost half of trees in forest interiors of the North and more than eighty percent in the South, showed predawn water potentials below –3 and -3.5 MPa, respectively. This resulted in a high proportion of non-producing trees, which is consistent with predawn water potential thresholds previously reported (Alejano, 2008, Carevic 2010, Misson2011)(). When water potential falls below -3.5 MPa stomatal closure and an important loss of hydraulic conductivity (e.g. Martinez-Vilalta, 2002; Tognetti, Carevic 2010) hinders water supply to acorns triggering increased abortion rates (Carevic, 2014). Interestingly, these thresholds were site-specific. In the North, trees experiencing predawn water potentials below -3 MPa during summer 2012 failed to produce acorns while this occurred at values of -4 MPa in the South. This explains the lack of differences between localities in seed crops despite trees experiencing more severe water shortage in the South. Besides, these results suggest that southern populations of holm oaks are more resistant to summer drought.

In 2013, when climatic conditions were milder, predawn water potentials did not fall below -3.5 MPa in any of the localities. Besides, main differences in summer water status were found in trees with the highest crops. Trees in forest fragments showed water potentials comparable to those of dehesa trees, which are characterized by extremely high acorn production (>-1.5 MPa; Pulido and Diaz 2005, Moreno et al. 2007). Overall these results suggest that, depending on drought severity, fragmentation effects can reflect either an overrun of hydraulic security limits or improved water conditions of individual trees.

Strikingly, despite of the improved water status of trees in 2013, acorn production was not greater than in 2012 and forest interiors continued to show high proportions of non-producing trees. Endogenous cycles of acorn production could explain this pattern (Siscart D 1999). However, we did not find significant correlations between current and prior year crops (data not shown) and long-term studies have shown that regular patterns in acorn yields actually reflect temporal regularity of drought events (Perez-Ramos et al. 2010). Xylem anatomy adjustments boosted by climatic conditions could explain the observed inter-annual variability in water potential thresholds. In holm oaks, moister conditions along the growing season can result in wider and less compacted xylem vessels resulting in improved hydraulic conductivity but lower resistance to cavitation (Corcuera et al. 2004, Abrantes et al. 2013). Thus, wetter summer-spring in 2013 could have led to higher susceptibility to water shortage during acorn ripening. Since Mediterranean climate is characterized by a high inter-annual variability (Bolle 2003), future studies combining physiological monitoring with tree-ring anatomy measures will help to draw a full picture of long-term fragmentation effects on holm oaks acorn production.

Though we used a broad-brush approach to estimate crops, we could detect a significant effect of tree water-status on acorn production. Moreover, threshold-like responses here observed are consistent with previous work (Alejano et al. 2008, Carevic et al. 2010). However, the variability explained by our crop-water status models was relatively low. Probably, quantitative estimations would have resulted in more clear patterns since they would have differentiated between intermediate acorn scores. However, other factors related to differences in habitat quality beyond changes in tree-to-tree competition cannot be ruled out. For instance, in the study area soils in small forest fragments are characterized by higher nutrient availability (Flores-Renteria et al. 2015) and fertilization stimulates acorn productivity in dense holm oak stands (Siscart D 1999). Changes in habitat quality in small forest fragments may act concomitantly with competition effects.

Contrary to the preconceived idea of negative effects of forest fragmentation on plant populations, our results show that the softening of tree-to-tree competition in small forest fragments enhances acorn production. In 2012, trees in forest interiors experienced predawn water potentials close to the point of hydraulic failure, while nearby ones located at small forest fragments only suffered moderate water stress (according to Carevic et al. 2010), which resulted in much higher acorn productivity. These results highlight the importance of local environmental conditions in modulating summer water scarcity and illustrate how management impacts can override those of climate. However, it is necessary to be cautious when interpreting forest fragmentation effects on holm oaks regeneration potential. Net positive effects will only occur if there is a higher probability of seedling recruitment in small fragments (Schupp et al. 2010) and forest fragmentation constrains acorn dispersal. Eurasian jays (*Garrulus glandarius)* - main acorn disperser in Europe- are absent in small forest fragments (Andren 1992) and dispersal services provided by wood mice (*Apodemus sylvaticus)* are much poorer (Santos and Telleria 1997, Morán-López et al. 2015). Besides, seedling dry out in open land microhabitats (Smit et al. 2008) can act as an important post-dispersal recruitment bottleneck in surrounding croplands. Therefore, to assess fragmentation effects on holm oaks regeneration potential in a realistic way, all stages of the regeneration cycle need to be integrated (see Pulido and Diaz 2005 for a similar approach in dehesas). Thanks to the wealth of the studies on key processes of oaks regeneration cycle, we now have the pieces in place to develop such a global approach.

CONCLUSIONS

In summary, our study shows a positive effect of forests fragmentation on acorn production mediated by changes in tree-to-tree competition. Reduced competition for sources in small forest fragments alleviated summer water stress of trees, which resulted in enhanced acorn productivity. Under a climate change scenario with more frequent and acute drought events, forest fragmentation may buffer large-scale climatic effects. However, other key processes like acorn dispersal or seedling survival need to be integrated before drawing conclusions on the impacts of forest fragmentation on holm oaks regeneration potential.

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CHAPTER 2

Landscape effects on jay foraging behavior decrease acorn dispersal services in dehesas

Morán-López T.[1], Alonso C.L.[1], Díaz M.[1]

(1) Department of Biogeography and Global Change (BCG-MNCN). National Museum of Natural Sicence CSIC. c/Serrano 115 bis, E-28006 Madrid, Spain.

Chapter published in Acta Oecologica (2015) 69:52-64

ABSTRACT

Dehesas are savanna-like, oak woodlands with a high conservation value that are threatened by chronic regeneration failure. Acorn dispersal by Eurasian jays (*Garrulus glandarius*) is vital for oak recruitment although jay preference for continuous forests may condition this mutualism in dehesas. In this study, we evaluated whether the acorn dispersal services provided by jays to oaks differed between both habitats and assessed factors that could potentially drive such differences. We (1) monitored acorn removal rates at feeders located close to focal trees in a holm oak (*Quercus ilex*) forest and in a nearby dehesa over a 6-year period; (2) measured the spatial traits of focal trees and their acorn production; and (3) monitored dispersal distances and microhabitat selection for acorn caching during 2012.

Our results indicated that jays were able to exploit dehesas located close to forest habitats, but did so infrequently and as a secondary food source (acorn removal rates were six times lower in dehesa than in nearby forests). This likely occurred because dehesas did not offer new or more abundant food sources on a landscape scale. In forests, tree choice was driven by crop traits while in dehesas it was driven by spatial location. Jays preferentially foraged at dehesa trees near forest patches and aggregated to other trees, regardless of crop traits. Acorns were mobilized four times closer in dehesas, and seeds were preferentially cached in unsuitable microhabitats for seedling establishment. Our results suggest that (i) distance to forest habitats and tree isolation effects on jay foraging behavior reduces their dispersal services in dehesas as compared to nearby forests, and (ii) practices designed to enhance acorn dispersal by jays in this habitat should focus on the maintenance or creation of forest patches interspersed within dehesa areas.

Keywords Quercus ilex, Garrulus glandarius, forest management, dehesa, acorn dispersal

INTRODUCTION

Seed dispersal is a key factor in the maintenance of most plant populations (Farwig and Berens 2012 and references therein), especially for large-seeded, dominant forest trees that depend on keystone animal-plant mutualisms (Herrera and Pellmyr 2009, Schupp et al. 2010). Many studies have highlighted the importance of seed dispersers for buffering the effects of environmental changes on plant regeneration potential (e.g. Higgins and Richardson 1999, Hampe 2011). However, mutualistic relationships are context-dependent and global change drivers may shift the outcomes of plant-animal interactions (Agrawal et al. 2007, McConkey et al. 2012). In particular, changes in land use may alter key environmental factors such as the food and habitat available for dispersers, local competition for sources, matrix permeability to their movement, or the perceived risk of predation. Under such new conditions, dispersers may modify their foraging behavior altering seed dispersal patterns, which set the template on which recruitment occurs (as reviewed by McConkey et al. 2012). Landscapes are changing in the world. Thus, detecting environmental factors that impact seed-dispersers foraging decisions and seed deposition patterns in anthropogenic habitats provides highly valuable information for the assessment of plant vulnerability to land use change, as well as the development of adequate conservation policies.

Natural-human systems with contrasting landscape configurations are largely distributed within the Mediterranean Basin (Blondel 2010). Among them, savanna-like holm oak (*Q. ilex*) woodlands (dehesas and montados) are of particular interest due to the wide areas they cover, the high biological diversity they host, and the great cultural heritage they hold (Diaz et al. 1997, Campos et al. 2013). Although holm oaks are often considered as resistant to global change due to their drought tolerance as adults (Tognetti et al. 1998, David et al. 2007), recent research indicates recruitment limitations in dehesas as a result of low seed dispersal to safe sites for seedling establishment (Pulido and Diaz 2005, Smit et al. 2008, Pulido et al. 2010). The oak (*Quercus* spp.) - Eurasian jay (*Garrulus glandarius*) relationship is a typical example of a seed dispersal mutualism that may buffer management effects on oak regeneration potential (Bossema 1979, Purves et al. 2007). Jays provide high-quality seed dispersal to oaks in forest habitats, where they nest and forage (Santos et al. 2002, Brotons et al. 2004), by mobilizing acorns to safe sites for oak recruitment, and have the potential to connect habitat mosaics (Gomez 2003). Therefore, efficient dehesas exploitation by jays would result in the enhancement of seedling recruitment in these habitats and/or their connection with nearby forests.

The goals of this study were: (1) to determine if the dispersal services provided by jays in dehesas differed from those found in forest habitats, and (2) to assess which factors could drive such differences. In general, forest-dwelling animals are more prone to exploit non-forested areas if they offer different or more abundant food sources (e.g. DaSilva et al. 1996). However, the food source in dehesas and forests during autumn is the same (acorns). Therefore, the attractiveness of this habitat to jays may depend on higher acorn production at the landscape scale or on the higher crop quality of dehesa trees. In dehesas, tree thinning and pruning results in higher acorn production. However, low stand density (10-30 stems/ha) may counteract this effect, leading to similar acorn production at the landscape scale in both types of habitats, discouraging jays from exploiting dehesas. For such a case, low visitation rates would hamper acorn dispersal by jays in this habitat.

Between-habitat differences in visitation rates may be related to differences in the key environmental factors driving tree-choice by jays. Reaching trees in dehesas may imply a high cost for jays whose nesting territories are centered in forest patches (Pons and Pausas 2008). For such conditions, we expected that the spatial location of trees (distance to forest habitats and isolation) would override crop trait effects on tree choice (see Luck and Daily 2003, Pizo and dos Santos 2011) for frugivorous forest-dependent birds). On the contrary, in forest habitats we expected jays to select trees based on crop traits that enhance foraging benefits (Sallabanks 1993, Blendinger et al. 2008). In such case, practices designed to enhance the seed dispersal services of jays in dehesas should focus on managing landscape structure rather than enhancing crop quantity or quality of individual trees.

Jays may deposit acorns differently in forests and dehesas, as seed dispersal distances and their habitat selection for acorn caching largely depends on landscape composition and structure (Gomez 2003, Pons and Pausas 2007a). Since jays cache acorns for later consumption, their hoarding strategies facilitate seed retrieval and hamper cache pilferage by other granivores. In terms of mobilization distances, we hypothesized that jays would mobilize acorns collected in dehesas towards forest habitats (nesting sites) (Yahner 2012). Such a practice would entail higher dispersal distances in dehesas and the maintenance of landscape connectivity between both habitats. Regarding microhabitat selection, we expected a strong negative selection by jays for tree canopies and shrubs in forests in order to avoid cache pilferage by rodents or wild boars (Gomez 2003, Pons and Pausas 2007a). However, lower mouse and wild boar abundances in dehesas (Díaz 2014) would relax microhabitat selection for acorn caching. Since microhabitat-related, post-dispersal acorn predation and seedling dry-out are the main bottlenecks for oak early recruitment stages in Mediterranean areas, differences in microhabitat selection by jays could have important effects on final seed fate (Gomez 2004, Smit et al. 2008, Pulido et al. 2010).

In summary, at the outset of the experiment, we expected a low use of dehesas by jays leading to limits for seed dispersal. We hypothesized that low dispersal services provided by jays in dehesas would be related to similar acorn production than forests at the landscape scale together with the increased costs associated with reaching dehesa trees. Therefore, we expected that jay foraging preferences in dehesas would be driven by the spatial location of trees rather than by crop quality, opposite to our expectations in forests. Finally, we expected that acorns collected in dehesas would be mobilized towards forests, entailing increased dispersal distances and promoting spatial connectivity between habitats.

METHODS

The overall goals of determining whether and why dispersal services provided by jays in dehesas differ from those found in forests were divided into the following related aims.

(1) To determine how and why jays use the dehesas as a food source during the fall, we monitored acorn removal rates at feeders located close to focal trees in a forest and in nearby dehesa plots over a period of 6-years. We also simultaneously measured acorn production in both habitats in order to assess whether between-habitat differences in visitation rates were related to acorn production at the landscape scale or to differences in the crop quality of focal trees.

(2) To determine if key factors driving tree-choice by jays differed between the forest and dehesa, we tested the effects of crop quality and the spatial location of trees on acorn removal rates in each habitat.

(3) To test between-habitat differences on seed deposition patterns we monitored dispersal distances and microhabitat selection for seed caching during the winter of 2012 in both habitats. Specific expectations, methods, and sample sizes for each related analysis are provided in Table 2.1.

Study area and experimental design

We studied holm oaks and the behaviour of Eurasian jays (*Garrulus glandarius*) in the National Park of Cabañeros (Ciudad Real province, central Spain, 30S 385450, UTM 4353479, see Díaz 2011)for details and map). The climate is Mediterranean with hot dry summers and mild wet winters, has a characteristic period of summer drought, and strong among-year variability in temperature and rainfall. Mean annual rainfall was 636 mm for the period from 1985-2009 (range 291-920 mm) and the mean annual temperature was 15.0 ºC (range 14.0-16.7 ºC).

Two spatial configurations of oak woodlands are found in the park: forests and dehesas. Forests occupy hills and lower slopes. The tree density is 97 trees ha^{-1}, on average, and understory cover is well developed (>60% of shrub cover). Dehesas occupy plain lowlands and are savannah-like woodlands (12 trees ha^{-1}, on average). Scattered trees grow in an open grassland matrix with almost no shrub cover (<1%). To monitor acorn removal rates by jays, we selected 46 holm oak trees in 2005 (20 in two forest sites and 26 in two dehesa sites). We selected focal trees so that they spanned the range of spatial locations and tree characteristics that potentially influence jay foraging decisions (crop size, acorn size, infestation rates, isolation from nearby trees, and distance to forest habitats; (Bossema 1979, Dixon et al. 1997, Pons and Pausas 2007b, Perea et al. 2011), Table 2). To facilitate use by different individual birds, we also selected focal trees as spaced as possible (within an area of 780 ha). In February 2012, we selected 16 trees from our original pool in order to video-record birds and radio-track acorns (eight trees per habitat). During this period, we divided the study area into two blocks. Trees within areas of 150 ha encompassing four video-monitored trees located in forests and four video-monitored trees located in the dehesa were assigned to the same block.

Quantifying focal tree traits (crop and location)

To quantify acorn production, infestation rates, and acorn size, we placed seed traps, covering 1.5-2% of the canopy area, below trees. After collecting seed trap contents at the end of winter, we sorted the acorns collected as aborted, infested by pre-dispersal seed predators, or sound.

We estimated the acorn crop as the number of full-sized acorns (sound plus infested) per square meter, and the infestation rate as the proportion of full-sized acorns infested by insects. We estimated acorn size, to the nearest 0.01 g, based on the length and maximum width measured with digital (Díaz 2011). Regarding spatial configuration of trees, focal tree size, tree isolation, and distance to forest habitats (in the dehesa) were measured. We estimated focal tree size as its canopy projection using diameter measurements. Using ArcGIS software, we calculated tree isolation, defined as the proportion of area within a buffer with a 50 m radius from each focal tree not covered by other tree canopies. In the dehesa, we also calculated the shortest distance to forest habitats.

Quantifying tree visitation rates by jays

The density of jays in the study area was 0.1-0.7 birds/10 ha and most records were collected in forests (Díaz 2011). Simultaneous observations indicated that focal trees were regularly exploited by 6-8 individuals. From 2005-2012, we monitored tree visitation rates by jays using feeders that consisted of 30 cm x 30 cm x 3 cm open trays made of 0.5 cm steel wire net placed at the top of 1.70 m poles erected close to (<1 m), but not under the canopy edge of each focal tree. During autumn-winter, we supplied the feeders with 5-10 medium-sized sound acorns (representing 2.8 ± 0.4 % of the total acorn availability of trees) and replaced acorns removed at each weekly visit. The accessibility and detectability of feeders from the tree canopy needed to be standardized because tree pruning in dehesas highly modifies canopy structure. To avoid a feeder pull effect, feeder rewards were standardized and remained low as compared to the acorn production of trees. As a result, the difference in feeder used reflected differences in the tree visitation rate by jays

(Carrascal and Alonso 2006). As ascertained by ~6,000 h of direct observations and video recordings, feeders were almost exclusively used by jays.

The computed variables were as follows: (1) mean yearly removal rates, defined as the proportion of offered acorns that were removed; (2) the latency period of the feeder, defined as the proportion of time elapsed between the first day of seed-offering and the first recorded removal; and (3) removal rates subsequent to the first visit (removal rates after). Variables two and three enabled measurement of the temporal patterns of feeder use, allowing us to: (a) assess whether differences in removal rates between habitats were consistent during the season; and (b) whether these differences, or lack thereof, were related to tree detectability (higher latency periods) or to acorn depletion in trees exploited early in the season (increased removal rates after the first visits). Data from the first year were not included in the analyses, since this period was used to habituate birds to the feeders' presence and the fixed locations.

Foraging behaviour at feeders and seed deposition patterns

We analysed the foraging behaviour of jays at feeders and seed deposition patterns at the end of winter 2011-2012 in 16 focal trees (eight per habitat). We provided feeders with two radio-tagged acorns, one small and one large (5.5 ± 0.07 and 7.5 ± 0.08 g fresh mass respectively, N = 70, $P<0.05$). We also installed a video-recording device on feeders that allowed continuous recording over three days (Appendix 2.A and 2.C). We viewed these recordings using Windows Movie Maker software (Microsoft Corporation). Regarding jay activity, we measured the total time spent at trays (in seconds) and the proportion of this time allocated to vigilance (bill tip above eye level), choice (bill tip below eye level, looking at acorns), and manipulation (seizing and/or swallowing movements) (Carrascal and Alonso 2006). To assess if acorn selection by jays differed between habitats, we also noted whether jays took the small or large acorn first, or if they took both acorns in the same foraging bout (Bossema 1979, Pons and Pausas 2007b). We repeated this procedure 1-3 times in each feeder (depending on the number of visits by jays, see below).

To determine seed fate, acorns were provided with radio-transmitters (Appendix 2A;Pons and Pausas 2007a). Trays were checked at midday on the three days following placement. If both acorns had been removed, we began to search for the radio-tagged seeds. Remaining acorns were not manipulated. Although we initially attempted to repeat this procedure three times so that we could offer 96 tagged acorns to jays by recycling the 40 transmitters available, the low use of feeders in the dehesa (a 6.33 ± 0.39 day delay between acorn offering and feeder use), a limited life-span for radio-transmitters (2 months), and transmitter losses prevented us from increasing our sample size within a reasonable time window (before breeding; Pons and Pausas 2007a). We finally offered 70 tagged acorns to jays. The acorn offering procedure was repeated two times in 13 feeders and three times in the remaining three. To detect acorn movements beyond radio-transmitter detection distances (200 m), we systematically searched mobilized acorns by walking the circumference of a 700 m radius circle and 13 radial transects regularly spaced so that all points within the circle were 100 m (half of detection distance) from the transects or closer. We also scanned habitats suitable for acorn hoarding (i.e. pine-plantations, unpaved roads; see Appendix 2A for additional details). We marked cache locations, as well as the locations of feeders, using a sub-metric GPS. Lineal dispersal distances were obtained from GPS data and we determined whether (or not) acorns taken from dehesa feeders were dispersed towards the forest. Mobilized acorns that were pilfered by mice were excluded from subsequent analyses.

We registered the microhabitat in which acorns were cached: under shrub, under tree canopy, within herb turfs, or in open grasslands. Microhabitat availabilities were estimated as their lineal covers over four 50 m line transects, 0.5 m wide, that were randomly established from the eight feeders; and from eight cached acorns randomly selected at each habitat (3,200 m of transect per habitat).

Table 2.1. Summary table of our aims, hypotheses, and specific data analysis.

Dispersal component	**Specific aim**	**Hypothesis**	**Scale**	**Response variable**	**Effect**	**Analysis**	**Sample size**
Tree visitation rates	Are the tree visitation rates different between habitats? Why?	Open woodlands are scarecely used by forest-dwelling birds.	Landscape	Annual removal rates (latency period + removal rates after first use)	Habitat	Mixed models	83 forest 100 dehesa
		Acorn production in dehesas “per ha” are similar to forests in spite of the higher production of dehesa trees.		Acorns/ha Crop production per tree Acorn size per tree Infestation rates per tree	Habitat	Linear model (corAR1) Mixed models	83 forest 104 dehesa 6 years
	Are the factors determining tree choices by jays similar in both habitats?	Forest:driven by crop traits Dehesa: driven by the spatial location of trees	Tree	Annual removal rates (latency period + removal rates after first use)	Crop traits Location traits	Structural Ecuation Models	83 forest 100 dehesa
Seed deposition patterns	Are jay foraging strategies similar between habitats? Does this translate into differences in seed deposition patterns?	Foraging bout and cache retrieval optimization in both habitats.	Landscape	Acorn choice Time spent at feeder Vigilance (%) Choice (%) Manipulation (%)	Habitat Block	Mutinomial model Anova Binomial model Binomial model Binomial model	27 choice events 16 dehesa 11 forest
		Lower microhabitat selection in dehesas.		Dispersal distances	Habitat	Distances descriptors	22 forest 24 dehesa
				Microhabitat selection	Usage vs. availability	Manly test	

Data analysis

Between-habitat differences in tree visitation rates and acorn production patterns

To assess between-habitat differences in tree visitation rates, we analyzed the overall use of feeders with the use of binomial mixed models (logit link). Response variables were the proportion of acorns removed during the entire autumn-winter season (total removal rates), the proportion of time it took jays to begin using a feeder (latency period), and the proportion of acorns removed after the first use (remove after). Fixed effects were habitat type, year, and their interaction. Tree was included as a random factor.

We also evaluated if differences in habitat exploitation by jays were related to between-habitat differences in acorn availability at a landscape scale, or to the crop quality of individual trees. To test for between-habitat differences in acorn production at the landscape scale, we calculated acorn production "per hectare" by multiplying acorns produced per tree by stem density for each year (2006-2011). The response variable was acorns produced per hectare (log-transformed data) and the fixed effects were habitat type (forest vs. dehesa), year, and their interaction. To take into account temporal autocorrelations in acorn production, a corAR1 structure was introduced into the model. The crop quality of individual trees was estimated by the response variables acorns produced per tree, acorn size, and infestation rates (logit link). Fixed effects were habitat type, year, and their interaction; tree was included as a random factor. Packages nlme and lme4 of R software were used (Bates et al., 2014; Pinheiro et al., 2011). In mixed models, pseudo-R^2

was calculated following Nakagawa and Schielzeth (2013) using the MuMIn package of the R software (Barton, 2015).

Between-habitat differences in factors driving tree choice by jays

The foraging preferences of jays at a tree scale were evaluated by testing a *a priori* causal hypothesis based on expectations from models of foraging optimization (Stephens and Krebs 1986). We used structural equation modeling (SEM), an extension of multiple regression and path analysis (Shipley 2002), because jay foraging behavior could result from indirect complex relationships between study variables. Since our experimental design included repeated measurements, we evaluated whether measurements over time in the same trees could be considered independent replicates by checking for the temporal correlation of response variables by means of autocorrelograms, with tree as a random factor using the nlme package (Pinheiro and Team 2011). No significant autocorrelations ($\alpha > 0.05$) were found. As a result, structural models were built by considering the samples as independent. Once the SEMs were developed, we further tested for tree effects on model residuals. Spatial autocorrelation was also assessed through autocorrelograms using the ncf package of the R software (Bjornstad 2013). No significant effect was obtained for any habitat. Sample sizes were 83 for forests and 100 for dehesas. Focal trees with acorn production below 1 acorn/m^2 (all in forests) were discarded since jays could have been attracted by feeders rather than by crop traits. Trees not used over the entire season (all in dehesa) were also excluded. We opted for this conservative strategy because we could not unmistakably attribute this lack of use to jay preferences or to a lack of detection.

Path diagrams were designed on the basis of current knowledge regarding the foraging preferences of jays for acorns, and on alternative foraging strategies that forest-dwelling birds may follow when exploiting continuous and scattered forest habitats. The final response variable of our path models was mean yearly acorn removal rates, which depended on the latency period of feeders and removal rates following the first visit. Both the latency period and removal rates depended on tree crop traits (crop size, acorn size, infestation rates) related to the benefits of exploiting such trees, as well as tree location (isolation, distance to forest) related to foraging costs. Causal relationships amongst explanatory variables in the path diagrams arose from recent reviews of acorn production on natural and man-made holm oak woodlands (e.g. Koenig 2013, Díaz 2014). For SEM specifications see Appendix 2B.

Path models were developed separately for each habitat because (a) the causal relationships among several explanatory variables are expected to differ among habitats and (b) the distance to the forest was an explanatory variable only in the dehesa models. Two alternative theoretical models were tested for each habitat, one including all traits measured at individual trees (*full models*, hereafter), and an alternative model containing only spatial traits in dehesas and crop traits in forests (*simplified models*, hereafter; Appendix 2B). Both, the full and simplified models were compared by means of the Akaike information criterion corrected for small sample sizes (Burnham and Anderson 1998). The significance of the path coefficients were evaluated by bootstrapped generalized least squares. The degree of fit between the observed and expected covariance structures was assessed using a χ^2 goodness of fit. A significant χ^2 indicates that the model does not fit the data. However, a non-significant χ^2 (model acceptance) can also result from inadequate statistical power (Bentler 1989). Therefore, we also evaluated model fit by means of the goodness of fit index (GFI) and the normed fit index (NFI). Values range between 0 and 1, with values >0.9 indicating good model fit.

Explanatory variables were divided by the maximum value observed in each habitat and year. Transformed variables ranged from 0 to 1, being 1 the maximum value observed. In this way, the foraging decisions of jays were evaluated in relation to the resources available each year. This procedure was particularly important for crop characteristics because holm oaks displayed a high inter-annual variability for acorn production (Koenig 2013). If not standardized by the maximum of the year, the model can reflect differences in acorn removal rates related to inter-annual variability in acorn availability or crop quality rather than to tree selection by jays on the basis of the crop traits of focal trees.

To test if patterns of tree-choice differed between years of high and low acorn production, we used Multigroup SEM analysis (Shipley 2002; see Appendix2 B for further details). We considered 2008 and 2011 as years of high acorn availability (91.7 ± 11.1 acorns/m^2 of tree canopy) and 2009 and 2010 as years of low acorn availability (53.4 ± 6.2 acorn/m^2 of tree canopy). All SEM analyses were performed using AMOS 20.0 (Arbuckle 2011). For additional details see Appendix 2B and Table 2B1.

Between-habitat differences in foraging behaviour at feeders and seed deposition patterns

Differences between habitats in the selection of tagged acorns by jays were analysed by means of multinomial models using the nnet package of the R software (Venables and Ripley 2002). The response variable was acorn choice – big first, small first, or both. Explanatory variables were habitat type (forest and dehesa), block (A and B), and their interaction. In this manner we assessed whether habitat effects on foraging behaviour were spatially consistent among different individual birds (presumably) using each block. Regarding the foraging behaviour of jays when using feeders, the between-habitat differences in time spent at feeders (in seconds) were tested using an ANOVA, and proportional allocations to different activities (vigilance, choice, and manipulation) through generalized quasibinomial models. Our fixed effects were habitat, block, and their interaction. The package stats of R software was used (R_Core_Team 2013). For logistic regressions, McFaddens' pseudoR^2 was calculated (McFadden 1974).

Between-habitat differences in seed deposition patterns were analysed in terms of seed mobilization distances and microhabitat selection for seed caching. Mean and maximum dispersal distances, distances for percentiles 25 and 75 and the proportion of acorns mobilized beyond 100 m were calculated for each habitat. Low sample sizes (22 and 24 acorns mobilized and retrieved in forests and dehesas, respectively; see below) precluded us from performing more complex analyses such as dispersal kernels fit. Microhabitat selection for acorn caching was measured using the Savage selectivity index ($W_i = U_i/A_i$), where U_i is the proportion of times that microhabitat i is used and A_i is its proportional availability. The statistical significance of W_i values were established by comparing the statistics $(W_i - 1)^2/\mathrm{se}(W_i)$ with the corresponding χ^2 value for one degree of freedom, being $\mathrm{se}(W_i) = \sqrt{(1 - Ai)/((\sum Ui) * Ai)}$ (Manly et al., 2002).

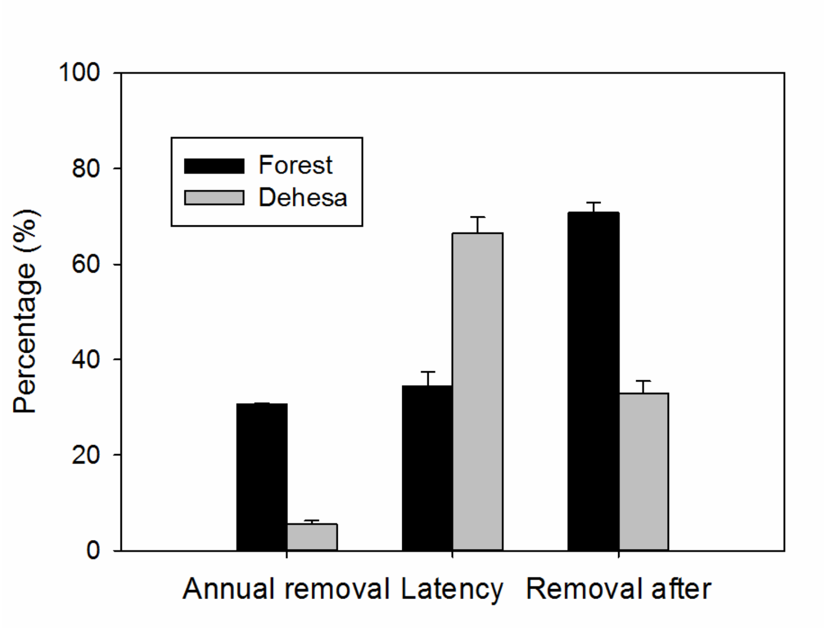
Table 2.2. Summary statistics for focal tree traits. Canopy: canopy projection (m^2); Isolation: percentage of area within a buffer of a 50 m radius from each focal tree not covered by other tree canopies (%); Pinewoods: linear distance to the nearest pinewood (m); Forest: linear distance to the nearest forest (m); Crop size: density of full-sized acorns (acorns/m^2 of tree canopy projection); Acorn size: acorn fresh mass (g); Infestation rate: percentage of full-sized acorns infested by seed-boring insects (%).

Habitat	Parameter	Canopy	Isolation	Pinewoods	Forest	Crop size	Acorn size	Infestation
Forest (*n* = 20)	Mean±SE	17.94±8.74	10.73±1.58	757.00±640.89	--	44.54±70.22	2.71±1.29	28.64±2.94
	Maximum	45.49	29.07	1460.00	--	516.67	6.96	100
	Minimum	9.07	2.71	60.00	--	0.76	0.43	0
Dehesa (*n* = 26)	Mean±SE	46.30±17.33	49.36±8.74	1768.85±444.64	1341.67±321.78	70.00±84.35	3.32±1.35	27.35±27.67
	Maximum	83.28	164.32	2620.00	1790.00	545.45	7.92	92.73
	Minimum	9.10	3.36	1280.00	783.33	1	0.65	0

RESULTS

Between-habitat differences in tree visitation rates and acorn production patterns

The overall use of feeders was smaller in the dehesa than in forests (Fig. 2.1). Dehesa trees displayed annual removal rates that were six times lower than forest trees (Fig.2.1-annual removal, habitat effects $P < 0.01$, $R^2_m= 0.42$ $R^2_c= 0.45$; $N = 183$). Use for dehesa trees began later than for forest trees (26 days later on average; Fig 2.1- latency; habitat effects $P<0.01$,, $R^2_m = 0.37$; $R^2_c = 0.44$; $N = 183$). Moreover, removal rates remained lower for dehesa trees subsequent to the first visit (Fig. 2.1-removal after; habitat effects $P < 0.001$, $R^2_m = 0.32$; $R^2_c = 0.34$, $N = 183$). Crop sizes were more than three times larger in dehesa trees (3,480 ± 402 *vs.* 1,037 ± 1,652 acorns/tree in the forest, habitat effects $P <0.01$, $R^2_m = 0.17$, $R^2_c = 0.23$, $N = 183$). However, lower stand densities in the dehesa (12 *vs.* 98 stems/ha) resulted in lower acorn production at a landscape level (91875 ± 25718 *vs.* 40566 ± 7222 acorns/ha for forest and dehesa, respectively; habitat effects $P = 0.02$, pseudo$R^2 = 0.56$; $N = 18$, 6 years * 2 habitats). Seed size and infestation rates did not differ between forests and dehesas (Table 2.2, $P = 0.16$, $P = 0.7$, habitat effects respectively; $N = 183$ in both cases).



Fig, 2.1. Between-habitat differences in feeder use for the period 2006-2012. Response variables were annual removal (percentage of acorns removed *vs*. offered), latency period (percentage of time it took jays to begin tree visitations), and removal subsequent to first use (percentage of acorns removed after first use). Values are expressed as mean ± SE.

Between-habitat differences in factors driving tree-choice by jays

All fitted SEM models were congruent with observed data (P>0.05 in all comparisons). GFI values were close or above 0.90, indicating a good fit (Fig. 2.2, Fig. 2.3). In forest, annual removal rates were primarily affected by the latency of feeder use and secondarily by removal rates subsequent to first use (Fig. 2.2). As expected, tree selection depended on crop traits rather than on the spatial location of trees. Acorn size determined jay preference for focal trees. Trees with larger acorns were visited later and received fewer visits once they began to be used, resulting in lower total removal rates (the standardized indirect effect of acorn size on total removal rates = -0.30; Fig. 2.2). There was no significant crop size-acorn size effects potentially affecting this result (mixed ANCOVA with tree as a random factor; P = 0.69 for the effect of seed size on crop size and P = 0.55 for the habitat x acorn size interaction; additional analysis performed with the nlme package of the R software). The simplified model parsimoniously yielded similar results (Fig. 2.2B, ($\Delta|R^2|$ between full and simplified models 0.01). Multigroup analysis indicated that model fit improved when the paths from the latency period to total acorn removal and the path between acorn size and infestation rates were released. In years of high acorn availability, the effects of latency period on total acorn removal rates were stronger than in low acorn availability years (-0.81 *vs.* -0.61 high and low acorn production years, respectively, see Table 2B1). However, in both cases they were negative and their strength comparable.

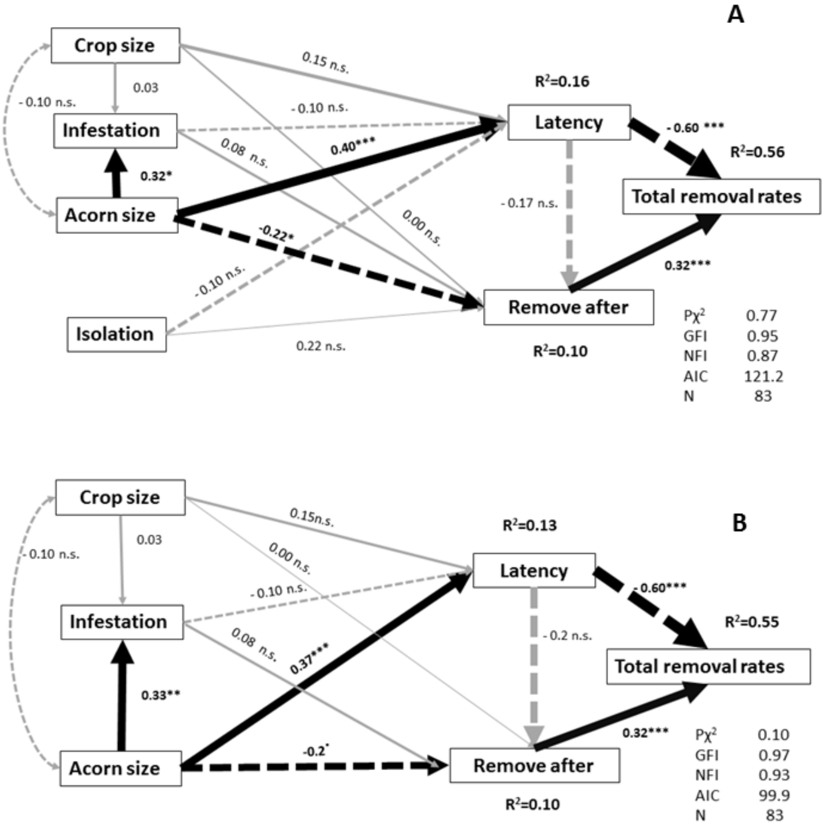


FIG. 2.2. (A) Full structural equation model for the causal relationships determining jay foraging behavior in the forest (crop and spatial characteristics were taken into account) (B) A simplified model in which only crop traits were included. One-headed arrows depict causal relationships, whereas two-headed arrows depict correlations. Dashed and solid lines indicate negative and positive relationships, respectively. Arrow width is proportional to path coefficients. Numbers near the paths indicate standarized path coefficients. Black lines correspond to paths that are significantly different from 0 (* $P < 0.05$, **$P<0.01$, ***$P<0.001$). Gray lines correspond to paths not significantly different from 0 (n.s.). Pχ2 corresponds to the probability associated with the χ2 statistic, GFI to the goodness of fit index, NFI to the normalized fit index, AIC to the akaike information criterion corrected for small sample sizes, and N to the sample size.

The initial selection of feeders was essentially random in relation to measured variables in dehesas (9% and 1% of the variance was explained by the full and simplified models, respectively; Fig. 2.3). In contrast, 20% of the observed variance of removal rates following first use could be explained by spatial characteristics. Unlike forest habitats, tree selection by jays was driven by the spatial location of trees, not by their crop traits. Removal rates were lower in dehesa trees located further from woodlands and, secondarily, more isolated. No crop size-seed size relationship was found and the simplified model parsimoniously yielded similar results as compared to the full model (Fig. 2.3B, $\Delta|R^2|$ between the full and simplified models 0.04). In low crop years, tree isolation had stronger effects on acorn removal rates but the effect vanished when the annual crop was high (0.06 and -0.40 for high and low acorn production years, respectively; Table 2B1). Additionally, the effects of removal rates subsequent to first use on annual removal rates were stronger during low crop years (0.60 and 0.86 for high and low acorn production years, respectively). However, for this result the effect was positive and significant for both groups.

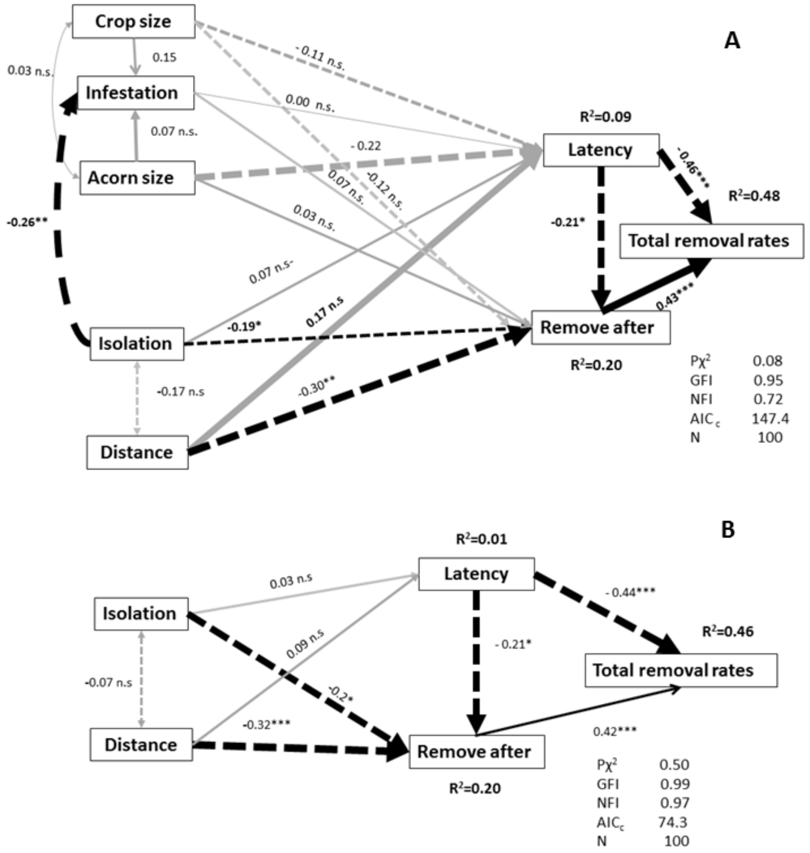


FIG.2. 3. (A) Full structural equation model for the causal relationships of jay foraging behavior in dehesas (crop and spatial characteristics were taken into account) (B) A simplified model in which only spatial configuration traits were included. One-headed arrows depict causal relationships, whereas two-headed arrows depict correlations. Dashed and solid lines indicate negative and positive relationships, respectively. Arrow width is proportional to path coefficients. Numbers near the paths indicate the standarized path coefficients. Black lines correspond to paths that are significantly different from 0 (* $P < 0.05$, **$P < 0.01$, ***$P < 0.001$). Gray lines correspond to paths not significantly different from 0 (n.s.). Pχ2 corresponds to the probability associated with the χ2 statistic, GFI to the goodness of fit index, NFI to the normalized fit index, AICc to the akaike information criterion corrected for small sample sizes, and N to the sample size.

Between-habitat differences in foraging behaviour at feeders and seed deposition patterns

We obtained 38 recordings of jays taking acorns from feeders documenting 27 choice events. Time spent at the feeders did not differ between habitats or blocks, and the habitat x block interaction was not significant (F = 1.36, P = 0.27, differences between the full model and the null model, N = 38). Most of the time spent at the feeders was devoted to vigilance, but relative allocation to this task did not differ between habitats or blocks (F = 1.26, P = 0.31, N = 38). Time devoted to acorn choice also did not differ between habitats (F = 2.3, P = 0.10, N = 38), whereas time devoted to manipulation was marginally significantly longer in the forest (F = 1.99, P = 0.06, N = 38, pseudoR^2 = 0.12).

Jays showed clear-cut, between-habitat differences in acorn choice (Fig. 2.4A; χ^2_1 = 11.99, P = 0.002, pseudoR^2 = 0.32; habitat effect in a multinomial model, N = 27) that did not differ amongst blocks (P = 0.101 and P = 0.858 for the block and habitat x block effects, N = 27). In dehesas, jays took acorns at random according to size (Fig. 2.4A; χ^2_1 = 0.31, P = 0.858, N = 27), whereas in the forest, in most cases, they first chose big acorns. Multiple-acorn transports, taking the large acorn in the beak after swallowing the small one, only occurred in forests (Fig. 2.4A).

Out of the 57 acorns mobilized by jays, 46 were recovered within 700 m circles surrounding feeders (22 in the forest and 24 in the dehesa). Eleven acorns fell beyond the 700 m search area (eight in the forest and three in the dehesa) and were not recovered. In forests, all acorns mobilized in double-acorn transports belonged to this category. Thirteen acorns were not used by jays during the entire experiment.

Acorn mobilization distances largely differed between habitats despite the low sample size in this part of the experiment (Fig. 2.4B). For forests, the mean dispersal distance was 85.70 m and ranged from 2 to 621.3 m (the 25 and 75 percentiles were 7.4 and 72.5, respectively, N = 22). Twenty-five percent of retrieved acorns were deposited 100 m beyond the source tree. In contrast, acorns were deposited much closer in dehesas. The mean dispersal distance was 21.13 m and ranged from 2.82 to 50 m (the 25 and 75 percentiles were 9.13 and 29.63, respectively, N = 24) and no acorns were retrieved beyond 100 m.

Habitat selection for acorn caching by jays differed between habitats (Fig. 2.4C). In forests, most acorns were cached under shrubs and the selection of this microhabitat was positive even after accounting for its high availability. Locations under tree canopies were selected and open habitats were avoided in the dehesa. Herb turfs were selected in both habitats.

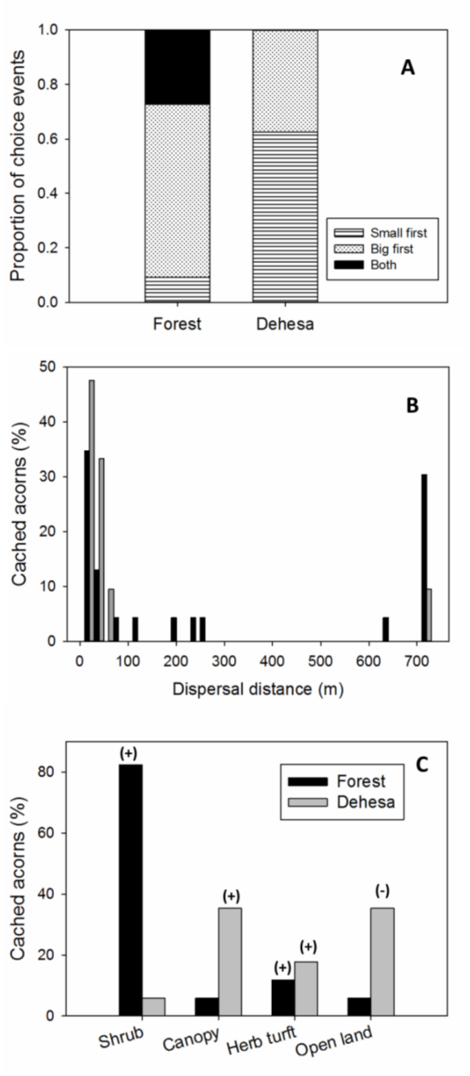


FIG. 2.4. The main results for our assessment of jay foraging behavior at feeders, as well as acorn deposition patterns. (A) Acorn choice patterns according to habitat type (N = 11 for forests and N = 16 for dehesa); (B) Histogram of acorn mobilization distances for forests and dehesa habitats (N = 22 for forests, N = 24 for dehesa). Distances below 700 m show acorns recovered, whereas larger distances correspond to acorns not recovered after an exhaustive search in 700 m circles surrounding feeders (see the text for details); (C) The percentage of acorns cached according to microhabitat in the two habitat types. Cached acorns pilfered by mice are also shown. Jay preference for (+) or the avoidance of (-) microhabitats according to Manly tests are also provided. In figure B and C black and grey bars correspond to forest and dehesa respectively.

DISCUSSION

Jays exploited both habitats although dehesa trees were used later and sporadically, indicating that they represent a secondary food source. Previous studies have indicated that jays are able to exploit non-nesting habitats in Mediterranean mosaics in order to acquire food sources more abundant or different from those found in forests (Rolando 1998). The fact that dehesas offered the same food (acorns) as forests at similar or lower abundances on a per-hectare basis may have decreased dehesa attractiveness to jays in spite of higher acorn crops for individual trees.

Key factors driving tree choices by jays differed between habitats. In general, inter-annual variability in acorn production did not modify qualitative patterns, just modulated the strength of causal relationships. Jay preference was determined by the crop traits of trees in forests, while in dehesas preference depended on their spatial location. Contrary to our expectations for forests, crop size was not linked to jay tree selection. Fruit production in the vicinity, rather than individual trees crop size, may have determined the foraging behavior of jays (see Sargent 1990, Saracco et al. 2005, Carlo and Morales 2008 for local seed production effects on the foraging behaviour of seed dispersers). Unfortunately, these neighborhood effects could not be tested based on our data on focal trees only. No effects of infestation rates on tree selection by jays were detected, although jays are known to negatively select insect-infested acorns (Pons and Pausas 2007b, Perea et al. 2011). As indicated by the lack of effects of time of latency and removal rates following first use on tree selection, the depletion of crops did not impact this result. The mismatch between our results and previous work is likely due to a matter of scale. In the past, studies on jay sensitivity to acorn traits have been performed at the scale of individual acorns, while our study addressed jay preferences at the tree scale. Jays may select non-infested acorns when foraging within a canopy, but high infestation rates of acorn crops may not deter them from exploiting a specific tree unless infestation is almost widespread.

Acorn size had a strong impact on removal rates. Medium- and small-seeded trees were used first and received more visits than large-seeded ones (see Bartlow et al. 2011, for similar results for blue jays). The ability of jays to swallow large acorns is limited (Pons and Pausas 2007b), but multiple-acorn transports are the most frequent behavior (Bossema 1979, Gomez 2003). In fact, acorns in multiple transports are smaller than those transported in single-acorn flights (Pons and Pausas 2007b). Therefore, although jays may positively select larger acorns within the canopy, the selection of medium and small-seeded trees during fall-winter would lead to an increase in foraging benefits by allowing birds to transport more than one acorn per visit. Taken together, our results suggest a foraging strategy in forests aimed at maximizing the number of acorns taken per foraging bout, favoring small-seeded trees independent of their location or crop size. However, whether this phenotypic selection translates into higher overall fitness for small-seeded trees depends on the effects of other selective pressures on acorn size acting at different stages of the regeneration cycle (Gomez et al. 2008).

Tree preferences in dehesas occurred once feeders began to be used, but the order of tree use was not related to any tree trait considered. Random encounters with trees were consistent, with occasional rather than usual visits to dehesas from bird territories in forests. However, once trees began to be used, jays showed a strong selection for specific traits. As expected, tree-choice by jays in dehesa was driven by the spatial location of trees. As is the case for other forest-dwelling species, the distance to forest edges negatively impacted tree visitation rates by jays (i.e. DaSilva et al. 1996, Luck and Daily 2003, Pizo and dos Santos 2011). In fact, trees located more than 2 km away from the forest displayed extremely low removal rates (<4%). In addition to distance effects, tree isolation also negatively affected visitation rates, although to a lesser extent. The isolation of trees embebedded in pastures or savanna-like woodlands can increase the species richness of bird assemblages and global visitation rates by seed dispersers (Sheldon and Nadkarni 2013). For this reason, special attention has been paid to the potential role of isolated pasture trees as potential nuclei for succession, especially in tropical areas (Manning et al. 2006). However, forest-dependent birds usually forage in clustered trees when exploiting open areas (Pizo and dos Santos 2011, Lasky and Keitt 2012). Therefore, if keystone tree species rely on forest-dependent seed dispersers, tree isolation may preclude woodland regeneration instead of catalyzing it.

Jay avoidance of isolated trees far from nesting territories may be due to the energy or predation risk costs associated with reaching trees. Jay foraging behavior at dehesa feeders points to risk rather than to energy costs. Energy-based costs would have produced a higher duration of visits and larger loads per visit as a means of compensation (Waite and Ydenberg 1996, Luck and Daily 2003). In contrast, when foraging in dehesa feeders, jays tended to spend less time manipulating seeds, acorn choice was random, and no double-acorn transports were detected, suggesting that increased predation risks in savanna-like woodlands may have precluded jays from the efficient exploitation of dehesa trees. The fact that tree selection by jays was solely driven by spatial location has important implications from a management perspective. Strategies aimed at enhancing oak recruitment in dehesas should focus on mitigating the limitations imposed by landscape structure, especially by considering the creation of forest patches in the surroundings (< 2 km) of dehesa plots. Otherwise, low or null dispersal services by jays are to be expected, irrespective of the stem density of dehesas or the crop quality of their trees.

Regarding seed deposition patterns, we found remarkable differences between habitats in spite of the low sample sizes obtained. Contrary to our expectations, most acorns taken in dehesas were cached within tens of meters from the feeder, while in forests they were transported up to hundreds of meters. The fact that acorn dispersal distances observed in forests were consistent with those found in previous studies with larger sample sizes (72 m mean dispersal distances; Gomez 2003; from 2.8 to 545 m; Pons and Pausas 2007a) suggests that the dispersal patterns found in this habitat reflect the general patterns of jay foraging behavior, and that behavior in dehesas was due to changes in jay foraging and hoarding strategies. We could not identify acorn movements between habitats, suggesting low landscape connectivity. However, this result may have been due to low sample size.

Acorn destinations also differed between dehesas and nearby forests. Jays are known to move acorns non-randomly towards microhabitats that favor acorn recovery and that reduce pilferage risk (Gomez 2003, Pons and Pausas 2007a). Contrary to our expectations, most acorns were cached beneath shrubs in forests and this microhabitat was positively selected in spite of its large availability. In dehesa, caches were more evenly distributed amongst the microhabitats available, although canopies and herb turfs were positively selected. Analyzing the final seed fate of cached acorns by replacing tagged seeds by sound ones would have helped to determine if such a fate differed between habitats. Even though our study lacked the data to test this possibility, previous work in the study area (Smit et al. 2008) and in a similar dehesa-forest system (Pulido and Diaz 2005) has indicated a net facilitative effect of shrubs in oak recruitment in both habitats. Despite being unsafe microhabitats at acorn stages (due to increased post-dispersal predation; Gomez 2004) they mitigate the negative effects of summer drought leading to positive net effects on seedling recruitment (Pulido and Diaz 2005, Smit et al. 2008). Therefore, our results suggest that acorns dispersed in forests were more likely to recruit than those dispersed in dehesas. In dehesas, effective recruitment of jay-dispersed acorns would have, in fact, been nearly zero because they were directed to unsuitable microsites for seed and seedling survival (Pulido and Diaz 2005, Smit et al. 2008).

The scarce use of dehesas by jays imposed important limitations, especially in our ability to obtain large sample sizes for estimations of seed deposition patterns using a balanced design. However, within its limitations, our study is relevant. To our knowledge, it is the first to address the potential causes of changes in Eurasian jay foraging behavior when exploiting highly managed habitats, as well as their consequences for seed dispersal services. In particular, the role of jays as acorn dispersers in dehesas has not been previously addressed, despite holm oak recruitment limitations in this habitat (Pulido and Diaz 2005). Rotation strategies at the farm or landscape scale and artificial oak plantations have been proposed as potential strategies for promoting oak regeneration in dehesas (e.g. Ramirez and Diaz 2008, Pulido et al. 2010, Leiva et al. 2013). Special attention has also been paid to the role of shrubs as nurse plants (Leiva et al. 2013, Rolo et al. 2013) and to acorn losses due to post-dispersal predation (Pulido and Diaz 2005, Pulido et al. 2010). Nevertheless, the role of the spatial structure of oak forests has been overlooked. Restoring dispersal services provided by jays would enhance the effectiveness of any of the above-mentioned strategies by promoting the natural regeneration of trees. Our results indicate that in order to achieve this goal we need to preserve nearby forest habitats, as well as to intersperse them within dehesa areas. The rotation of plots left to shrub and tree encroachment within dehesas, supplemented with some shrub or tree plantation, if necessary, seems to be the best option for creating these interspersed forest plots (Ramirez and Diaz 2008, Díaz 2014).

CONCLUSIONS

Our results indicate that despite jays being able to exploit dehesas, they use them infrequently and as a secondary food source. In addition to low visitation rates, dispersal distances were shorter and acorns were cached in unsuitable microhabitats for seedling recruitment. Overall, our results suggest that acorn dispersal by jays is limited in dehesas. Restoration of the role of jays for oak regeneration in this habitat should first focus on ensuring the presence of suitable forest patches for jays interspersed within dehesa landscapes and second on promoting higher aggregation for isolated trees.

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APPENDICES

Appendix 2.A. Jay behaviour at feeders and acorn radio-tracking

Jay behaviour at feeders was video-monitored at the end of winter to ensure the usage of tagged acorns by jays, but before breeding in order to avoid seasonal differences in dispersal distances (Pons and Pausas, 2007). The video-recording device was composed by a mini video-camera OmniVision CMOS 380 LTV (3.6 mm lens) targeted at the feeder by means of an 80 cm x 50 cm right-angle steel arm attached on top of the pole. The arm was balanced by a rope nailed to the ground. Video-cameras were provided with ELRO dvr32 card-based recorders, and the whole video-recording set was powered by car batteries (70 Ah, acid-lead) attached to solar panels (ono-silicon erial P_20; 20 w). The system was fully autonomous for continuous recording during three days by setting the recording quality at 5 frames s^{-1} and using 16 GB recording cards.

Experimental acorns put on feeders were opened and partially emptied to fit into them a transmitter (TW-4 twin-button celled tag; Biotrack, Wareham, Dorset, UK; weight: 3.9 g; mean life span: 3 months; detection distance: 200 m) with the antenna rolled up inside. Acorns were then closed and sealed (superglue 3; Loctite, Warrington, Pa ; Pons and Pausas, 2007). Tags used were slightly heavier than those used by Pons and Pausas (2007) to allow for larger detection distances (200 m). Therefore, tagged final weight was 1 g heavier on average that the initial fresh mass (5.5±0.07 and 7.5 ± 0.08 g fresh mass for small and big acorns respectively).

Tagged acorns were located with a Sika receiver (8 MHz) provided with a Yagi antenna for approaching acorns and a stick antenna for fine-scale location. Systematic searches were made by walking the circumference of a 700-m radius circle and 13 radial transects regularly spaced so that all points within the circle were 100 m (half of detection distances) from transects or closer. Searches around focal trees were made well before the end of the mean life span of transmitters to ensure that detection distances did not change during searches. Approximate locations provided by triangulation with Yagi antennas were afterwards refined with stick antennas until cached acorns were located. Since not all acorns could be found within the search circle, we extensively searched in habitats suitable for acorn hoarding –pine plantations and riparian woodlands along paths and unpaved roads (Gomez, 2003; Pons and Pausas, 2007).

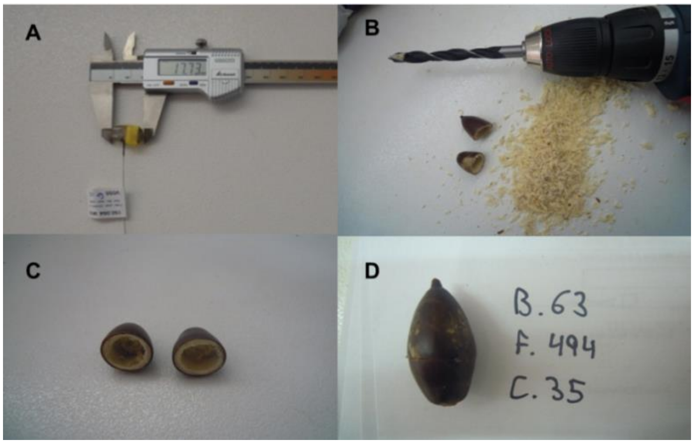

Fig. 2A1. Photographs of the assembly of radiotagged acorns. (A) Radio-transmitters used during the experiment; (B-C) sound acorns emptying; (D) radio-tagged acorn assembled.

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Appendix 2B. SEM specifications

The quantitative component of acorn dispersal effectiveness by jays in oak woodlands was estimated as the overall acorn removal rate at feeders located close to focal trees. We modeled two components of this overall removal rate (Fig. B1, B2): latency period of the feeder (defined as the proportion of time elapsed between the first day of seed-offering and the first recorded removal) and removal rates subsequent to the first visit (removal rates hereafter). Modeled this way, we could determine if a) differences in removal rates among habitats were consistent during the season and b) whether these differences, or lack thereof, were related to tree detectability (higher latency periods) or to acorn depletion in trees exploited early in the season (increased removal rates subsequent to the first visit).

Crop quantity and quality is expected to determine seed removal rates under scenarios of maximization of foraging benefits. Trees with higher seed production will be used preferentially (Blendinger et al., 2008; Martinez et al., 2014; Sallabanks, 1993). Higher crop sizes may imply higher rewards per visit, particularly in multiple seed loaders like jays. Trees with medium and small acorn sizes would show higher removal rates due to gape-size limitations for multiple acorn transports (see

Bartlow et al., 2011 for blue jays). Finally, higher infestation rates would deter jays from visiting trees (Bossema, 1979; Perea et al., 2011).

The spatial location of trees will determine the cost of reaching them for foraging for acorns. Reaching more isolated trees may imply higher energy costs (Graham, 2001) and higher predations risks, as they offer lower antipredatory cover. Similarly trees located further from forest are expected to be used less frequently due to both energy (Luck and Daily, 2003) and predation risk costs.

Crop traits and tree scattering may also interact causally (reviews in Díaz, 2014; Koenig, 2013). Size-number trade-offs have been proposed as universal for plants, although there is mixed evidence in the case of Holm oaks (Koenig, 2013).We opted for a conservative strategy including an expected size-number correlation. Crop size is known to vary widely among years both in forests and dehesas, but spatial variation within-years in relation to isolation and distance to forest is less clear-cut (reviewed in Koenig, 2013). Therefore, we did not include a causal relationship between tree isolation and crop size. Acorn size, crop size and tree isolation are expected to influence acorn infestation rates due to complex interactions among size-related larval survival, satiation at the seed and crop scales, and dispersal ability of pre-dispersal seed predators (Bonal et al., 2007; Perez-Izquierdo and Pulido, 2013). We hypothesized that in forests where tree isolation is low, trees with larger acorns would show higher infestation rates either because of enhanced larval survival or positive selection of larger seeds. In dehesas, where trees are highly scattered, tree isolation rather than acorn size will drive infestation rates by precluding selection, colonization or re-colonization of trees. The fact that infestation rates were not measured independently from crop size but estimated as the number of infested acorns divided by the number of acorns produced made it advisable to include this path as a fixed value (standardized partial regression coefficients). Finally, a correlation between tree isolation and distance to forest was included in dehesas as areas farther from forests could have been more intensively managed.

Multigroup SEM consisted in fitting the same hypothetical model for years with high and low acorn crops separately and assessing the model fit. Once a good model fit for both groups was confirmed, we assessed differences between configural (unconstrained), metric (factor loadings constrained) and scalar (factor loadings and intercepts constrained) models. If differences between configural and metric or scalar models were observed we analyzed individual paths and intercept differences among groups. For this purpose, equally constraints were removed one at a time to identify which one would improve the model (Shipley, 2002). Differences in the χ^2 statistics were used to test differences in parameter values among groups.

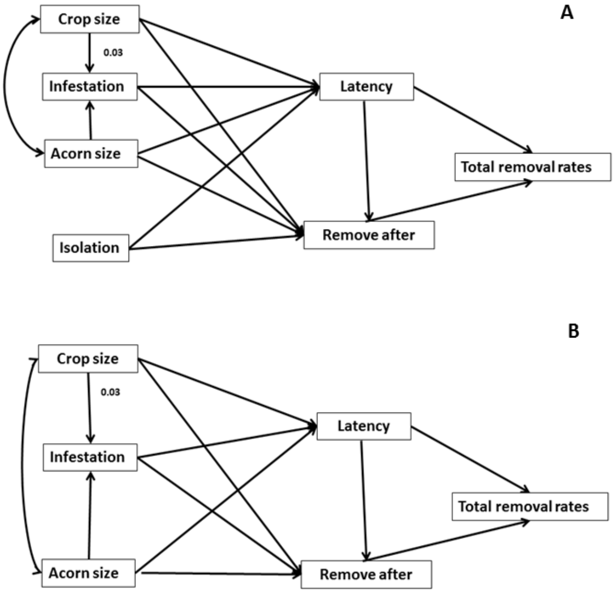

Fig. 2B1. (A) Hypothetical full structural equation modeling for the causal relationships of jays' foraging behavior in forests (crop and spatial characteristics taken into account) (B) Simplified model for forest habitats (only crop traits included). One-headed arrows depict causal realtionships whereas two-headed arrows depict correlations.

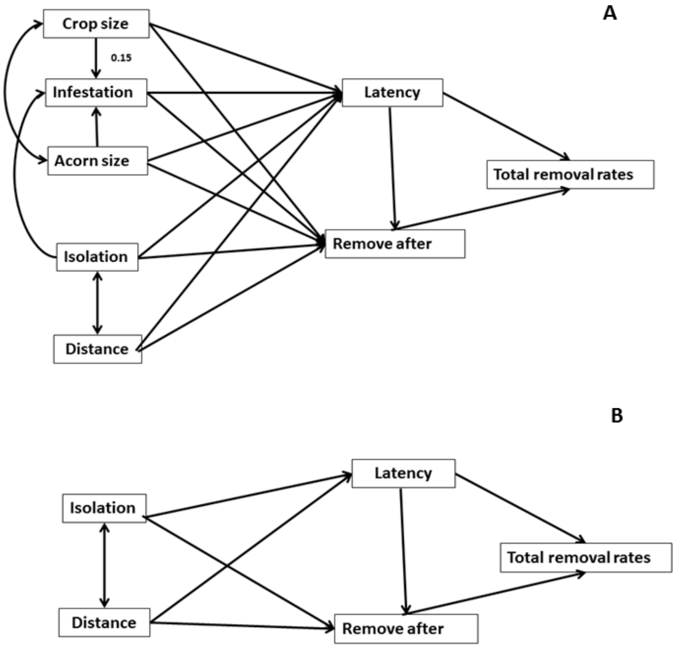

Fig. 2B2. (A) Hypothetical full structural equation modeling for the causal relationships of jays' foraging behavior in dehsas (crop and spatial traits included) (B) Simplified model for dehesas, only spatial traits taken into account. One-headed arrows depict causal realtionships whereas two-headed arrows depict correlations.

Table 2B1. Multigroup comparison of SEM models between high crop and low crop years. Only paths that differed significantly between groups are shown. Std. weights (standardized regression weights). P: p-value associated to $\Delta\chi2$ between fully constrained and unconstrained model (for the specific path). N=36 for high and low crop years in the forest; N=34 and 25 for low and high crop years respectively in the dehesa.

Habitat	**Paths**	**Crop years**	**Std. weights**	**Sig.**	**P**
Forest	Delay → Total removal	High	-0.81	<0.001	0.03
		Low	-0.61	<0.001	
	Acorn size → Infestation rates	High	0.45	<0.01	0.02
		Low	0.05	n.s.	
Dehesa	Remove after → Total removal	High	0.60	<0.01	0.05
		Low	0.86	<0.001	
	Isolation→ Remove after	High	0.06	n.s.	0.02
		Low	-0.40	<0.01	

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CHAPTER 3

Effects of forest fragmentation on the oak-rodent mutualism

Morán-López T.[1], Fernández M.[1], Alonso C.L.[1],

Flores-Rentería D.[1], Valladares F.[1] and Díaz M.[1]

(1) Department of Biogeography and Global Change (BCG-MNCN). National Museum of Natural Sicence CSIC. c/Serrano 115 bis, E-28006 Madrid, Spain.

Chapter published in Oikos (2015) 124:1482-1491

ABSTRACT

Land-use changes are expected to affect plant-disperser conditional mutualisms through changes in animal behavior. We analyzed the oak-rodent conditional mutualism in Mediterranean fragmented forests at two climatically different locations. We quantified fragmentation effects on seed dispersal effectiveness and assessed if such effects were due to changes in habitat structure and intraspecific competition for acorns in fragmented areas. Fragmentation decreased cover from predators within mouse territories as well as intraspecific competition for acorns. This resulted in lower dispersal effectiveness in small forest fragments. Globally, habitat structure was the main driver in mouse foraging decisions. In small fragments, low shelter availability precluded mouse movements, leading to short mobilization distances and low caching rates. However, as the proportion of cover from predators increased, mice were able to modulate their foraging decisions depending on intraspecific competition for acorns, resulting in higher dispersal quality. In addition to fragmentation effects, delayed breeding in the southern locality caused lower number of rodents during the dispersal season, which reduced acorn mobilization rates. Our study shows that seed dispersal patterns in managed systems can be analyzed as the result of management effects on key environmental factors in dispersers' foraging decisions.

Key words: Apodemus sylvaticus, *Quercus ilex*, forest fragmentation, acorn dispersal, foraging behavior.

CHAPTER 3

IINTRODUCTION

Seed dispersers provide key services for the maintenance of many plant populations (Farwig and Berens, 2012). This is particularly true for large-seeded dominant forest trees that depend on keystone plant-animal mutualisms to efficiently disperse their seeds (Herrera and Pellmyr 2002). However, these mutualistic relationships are not always unconditional, as seed dispersal effectiveness (*sensu* Schupp et al. 2010) depends heavily on dispersers' foraging decisions. Such decisions are governed by environmental factors that shape the cost-benefit balance of seed dispersal from the dispersers' point of view and will ultimately determine plants' regeneration potential.

There is general consensus about the key role of seed dispersal in mediating the responses of plants to past and present environmental changes (i.e. Hampe 2011). Besides, main global change drivers (land use change, resource overexploitation, biological invasions and climate change) can have strong effects on seed dispersal patterns (McConkey et al. 2012).Therefore, plants' vulnerability to global change
will depend to a large extent on how environmental changes affect seed dispersal effectiveness. In particular, recruitment failure in fragmented forests has been extensively related to the loss or decrease of potential seed dispersers (i.e. Moran et al. 2004, Cramer et al. 2007).The presence of dispersers does not, however, ensure seed dispersal success. Forest fragmentation may also entail changes in environmental factors that modulate dispersers' foraging decisions (i.e. food availability, predation risks) and consequently dispersal patterns. Therefore, analyzing seed dispersal effectiveness from a behavioral perspective will help to unveil

which are the key environmental factors that modulate fragmentation effects on plants' regeneration potential. This approach shall provide highly valuable information for the assessment of plants' vulnerability to global change and the development of effective mitigation and conservation policies (Cousens et al. 2010, Valladares et al. 2014).

Forest fragmentation, resource overexploitation and poor management are the main drivers of forest degradation in the Mediterranean basin (FAO 2011, Doblas-Miranda et al. 2015), and these effects are most likely enhanced by climate change (Valladares et al. 2014). Among Mediterranean forests, Holm oak (*Quercus ilex*) woodlands play a pivotal ecological and socioeconomic role over large areas (Campos et al. 2013). Holm oak dispersal in fragmented areas depends largely on rodents' hoarding activity since the main oak dispersers in Europe (Bossema 1979)—Eurasian jays— depend on extensive woody areas for nesting and foraging (Andren 1992, Santos et al. 2002, Brotons et al. 2004). On the contrary, wood mice are able to occupy even the smallest forest fragments thanks to their generalist habitat requirements (Fitzgibbon 1997, García et al. 1998, Díaz et al. 1999, Macdonald et al. 2000, Tew et al. 2000, Díaz and Alonso 2003).

Previous studies have suggested that acorn predation by mice could be responsible for oak regeneration failure in small forest fragments (Santos and Telleria 1997). However, seed fate was not assessed, and therefore potentially dispersed seeds were dismissed. Subsequent studies have shown that wood mice can act as moderately effective seed dispersers (Gómez et al. 2008) affecting early stages of oak recruitment (Puerta-Piñero et al. 2012). Therefore, when assessing oak regeneration potential in fragmented forests, the mouse-oak relationship needs to be analyzed as a conditional mutualism in which acorn dispersal takes part. This conditional mutualism depends on a fine balance in which environmental conditions shape rodents' hoarding activity (Den Ouden et al. 2005, Theimer 2005). Key environmental factors that condition the outcome of the mouse-oak relationship by driving mouse behavior are (1) intraspecific competition for acorns (defined as the ratio between local mouse abundance and acorn crop),which is related to the net benefits between *in situ* seed consumption *vs* hoarding, post-dispersal acorn retrieval and the likelihood of cache pilferage by conspecifics (Theimer 2005 , Vander Wall 2010) and (2) the presence of shelter, which conditions mouse perception of predation risks while mobilizing seeds (Perea et al. 2011a, Perea et al. 2011b). Forest fragmentation may have major effects on these factors. Regarding intraspecific competition for acorns, small oak woodlots house denser wood mouse populations than continuous forest (i.e. García et al. 1998, Díaz and Alonso 2003). Besides, acorn production is expected to be larger in small oak woodlots due to relaxed intraspecific competition among trees at forest edges since acorn production is strongly dependent on local tree density (Koenig et al. 2013b). Therefore, forest fragmentation effects on intraspecific competition for acorns will depend on its net effects on the mouse abundance-acorn availability ratio. Finally, cultivation and agricultural practices near forest fragments have obvious effects on vegetation structure, precluding mouse movements outside fragments due to increased predation risks (Zhang and Usher 1991, Díaz 1992, Tew and Macdonald 1993, Fitzgibbon 1997).

In the Mediterranean basin, geographic location and its associated climate is also expected to affect the mouse-oak mutualistic relationship in addition to fragmentation effects mainly due to its influence on the intensity of summer drought. Summer drought has been found to affect mouse breeding activity (Moreno and Kufner 1988, Rosario and Mathias 2004, Díaz et al. 2010), acorn production (see Koenig et al. 2013a and references therein) and vegetation structure (Santos and Tellería 1998). Therefore, we have assessed the effects of forest fragmentation and the underlying behavioural mechanisms in two forest archipelagos located at two climatically contrasting geographic locations to increase the potential generality of our findings. We hypothesized that (1) forest fragmentation would decrease acorn dispersal effectiveness by mice, and (2) such decrease would be driven by fragmentation effects on intraspecific competition for acorns and habitat structure. In particular, we expected that the lack of cover from predators in fragmented forests would be the main limiting factor of acorn dispersal beyond changes in intraspecific competition for acorns.

METHODS

Study area

The two Holm oak archipelagos studied were located in the plateau of central Spain —an extensive treeless agricultural region where cereal cultivation has reduced the original forests to smaller woodland patches ranging in size between 0.1 and 2,000 ha. Overall forest cover is 7-8% (Santos and Tellería 1998). Fieldwork in the southern plateau was carried out in the vicinity of Quintanar de la Orden (39º 35' N, 3º02'W, 870 m a.s.l.) within an area of 3,850 ha. The dominant tree is the Holm oak *Quercus ilex* with the understory composed by shrubby Kermes oak *Q. coccifera* and shrub species typical from xeric Mesomediterranean localities (e.g. *Rhamnus lycioides*, *R. alaternus*, *Cistus ladanifer*, *Asparagus acutifolius*). Annual precipitation and mean temperature are 421 mm and 14 ºC, respectively. Fieldwork in the northern plateau was undertaken in an area of 66,500 hectares around Lerma (42°5'N, 3°45'W, 930 m a.s.l.). The dominant tree is also Holm oak, with isolated Lusitanian oak *Q. faginea* and Spanish juniper *Juniperus thurifera* and understory shrubs typical from wetter and cooler Supramediterranean localities (e.g. *Cistus laurifolius*, *Genista scorpius*, *Thymus zygis*). Annual precipitation is 567 mm and annual mean temperatures are 11 ºC (see Díaz et al. 1999, Díaz and Alonso 2003 for further details).

Experimental design

We selected three large (> 100 ha) forest fragments in which we defined forest interior and forests edge depending on distance to the cultivated border in each locality (60 m threshold; García et al. 1998). Edge plots were selected along long straight borders to avoid influences of border geometry on edge effects (Fernández et al. 2002). Moreover, 10-11 small woodlots (0.047±0.031 ha in the South, 0.031±0.024 ha in the North, mean±SE) were also selected in each locality. This way three fragmentation levels were defined —forest interior, forest edge and small fragments— in each locality —northern and southern plateaus.

We selected 180 trees at random (30 for each fragmentation level x locality combination) at the beginning of autumn 2012. Focal trees were supplied with an open Petri dish with 30 g of Canary grass *Phalaris canariensis* seeds (Díaz 1992, Díaz and Alonso 2003) within wire cages to avoid seed consumption by birds or rabbits. Dishes were checked after three days and after one week. Canary grass consumption after one week was used as a surrogate of mouse activity. Finally, the 90 trees (15 for each fragmentation level x locality combination) with the highest mouse activity were selected as focal trees for the seed dispersal experiment. Selected trees and their surroundings were used to estimate acorn crop sizes, mouse abundance, vegetation structure and acorn dispersal behavior during the winter 2012-2013. The surroundings of each tree differed in size depending on the estimated variable (see below).

Quantifying crop size, mouse abundance and vegetation structure

Crop size was measured using a semi-quantitative scale ranging from 0 (no. acorns) to 4 (more than 90% of the canopy covered with acorns; Koenig et al. 2013). Acorn size was visually estimated using a 1-6 scale (increasing size). Both indices were multiplied to obtain a composite estimate ranging from 0 to 24. Crop size was measured for each focal tree and its four nearest mature trees in random directions whenever possible.

Mice were live-trapped within three days of the new moon of November 2012 and March 2013 (to control for moonlight effects on rodent activity; Díaz 1992, Perea et al. 2011a) by means of standard Sherman live traps. Interior and edge areas were sampled by means of grids of 6 x 5 traps spaced 10 m, thus covering ca. 0.3 ha, and small fragments by means of 1-6 pairs of traps (depending on fragment size, measured on 1:5,000 aerial photographs) distributed over the entire woodlot to ensure all individuals living in each fragment during the trapping sessions were trapped (i.e. Díaz and Alonso 2003). Traps were operated following the standard guidelines of baiting and comfort (Díaz et al. 2010) during three consecutive nights and checked daily early in the mornings. Trapped mice were identified to species, marked by cutting a small portion of the tail tip (for recapture control and genetic and parasitological analyses), weighed, sexed and inspected for reproductive status. Complete trapping was corroborated by plotting the number of new captures per night against the number of nights of exposure.

Finally, vegetation structure was estimated as the lineal covers of three main microhabitats, open land (covered by bare ground, herbs or low shrubs), shrubs taller than 25 cm and tree canopies. Covers were measured over two 20-m line, 0.5 m wide transects randomly established from each focal tree.

Seed dispersal

Experimental acorns were collected in November. They were individually marked, weighed to the nearest 0.1 g, and the maximum width and length measured with digital calipers to the nearest 0.01 mm. Each tree was supplied with three small (1.2±0.3 g SE; n=819), three medium-sized (2.5±0.3 g, n=819) and three large acorns (4.9±0.8 g, n=819) with similar length-width ratio (2.21±0.01, n=819). A metal wire (0.6 mm ø) with a numbered plastic tag was attached to each acorn (Xiao et al. 2006). All acorns were manipulated with gloves in order to avoid effects of human scent (Duncan et al. 2002).

Marked acorns were placed beneath the canopies of focal trees and were protected with 35 cm x 35 cm x 15 cm wire cages with a 6 cm mesh that only allowed the entrance of rodents. Each tree was supplied with 9 acorns during the new moon of December, January and February (27 acorns in total per tree, 2,430 acorns overall). The first measure was made in December, a month after trapping, to avoid behavioral changes due to mouse trapping and manipulation. Supply points were checked one night and three nights after offering acorns. Mobilized seeds (in December and January) were tracked after one and two months to assess consumption of cached acorns throughout the winter and final seed fate.

Data analysis

Mouse abundance and population dynamics

Differences in abundance, sex- and age-ratios and reproductive activity among localities and fragmentation levels, as well as its changes during winter, were analysed by means of the fit of log-linear models to the six-way contingency table generated by the following factors: locality (northern or southern), season (November or March), fragmentation (small fragments, edge or forest interior), sex/age (adult male, adult female or juvenile), reproductive activity (active or not) and presence/absence of capture, taking into account the structural zeros resulting from the impossibility to find sexually active juveniles (Table 3.A1; see Díaz et al. 1999 for a similar approach).

Fragmentation effects on mouse foraging decisions

The global effect of forest fragmentation on mouse handling decisions was assessed through multinomial mixed models using the SPSS 20.0 and lme4 package in R (Bates et al. 2011). Acorns were assigned to five state categories in their first use: predated, gnawed (partially eaten), cached (buried and intact), intact-mobilized (mobilized, unburied and intact), and unhandled (not mobilized, unburied and intact). We did not remove unhandled acorns from this analysis because a high proportion of source points showed both handled and unhandled acorns. Therefore we cannot unequivocally dismiss the possibility that not manipulating a specific acorn was not a decision. In a first analysis (multinomial model), our response variable was acorn state (N= 27 per tree) and our fixed explanatory variables were fragmentation level, locality and their interaction. Subsequently, the effect of habitat fragmentation on each acorn-state category was analyzed separately in each locality by means of binomial mixed models. Our response variable was the proportion of acorns predated, gnawed, cached, intact-mobilized and unhandled (N=3 per tree). Our fixed effect was fragmentation level. In all cases, spatial correlation effects were accounted for by introducing trees nested within a new variable, cluster, as a random effect. Trees located within the same interior and edge areas were assigned to the same cluster, as well as trees located in groups of nearby fragments (within areas of 35 hectares). A total of 18 clusters were obtained (3 clusters per fragmentation level and locality).

Preliminary analysis revealed that month of exposure did not have significant effects (P>0.05, month and month*fragmentation) either on mouse hoarding activity (caching rates) or on mobilization distances (rate parameter of gamma distributions; see below). Hence, all data were pooled together for further analysis. Besides, unhandled acorns (not mobilized and intact) were removed from subsequent analysis since we were interested in mouse foraging decisions after first use. Microhabitat selection by mice to mobilize acorns was tested by means of the Savage selectivity index. The statistical significance of habitat selection was tested by means of Wi values of Manly's test (Manly et al. 1993). Wi = Ui/Ai, were Ui is the proportion of times that microhabitat i is used and Ai is its proportional availability. Analyses were performed separately for each locality and fragmentation level.

Seed mobilization kernels were evaluated using the fitdistrplus package in R (Delignette-Muller et al. 2010). Frequency distributions of mobilization distances were fitted to gamma, Weibull, log-normal and normal distributions using maximum likelihood approximation and the Akaike information criterion to select best fits. Differences in mobilization kernels among localities within fragmentation levels and among fragmentation levels within localities were tested by means of Kolmogorov-Smirnov tests and Anderson-Darling tests, which take into account extreme values. Distribution tails (long-distance movements) were measured as the percentage of acorns mobilized beyond 20 m. Fragmentation effects on such tails were tested by means of zero-inflated Poisson models using the glmmADMB package in R (Fournier et al. 2012; Table 3.A1)

Effects of environmental factors on mouse foraging decisions

Mouse abundance and the variables derived from it could only be measured at fragment/trapping grid scale. Hence clusters rather than trees were the experimental units of these analysis (N=18 global analysis, N=9 within locality analysis).

We tested if intraspecific competition for acorns and the timing of mouse breeding could explain differences between localities in acorn mobilization rates. The response variable was the proportion of offered acorns handled during the first three nights. Fixed effects were mouse fluctuation throughout the winter, mouse-acorn ratio and their interaction. Mouse fluctuation was defined as the difference between $\log_{10}$-transformed mouse abundance in March and November. Stable populations will show values close to zero whereas positive values indicate that mouse abundance peaked in late winter, after acorn fall. Mouse-acorn ratio was estimated as the ratio between mean mouse abundance (between November and March) and average crop size. Higher values imply greater intraspecific competition for acorns (see Theimer 2005 , Xiao et al. 2013). Explanatory variables were not significantly correlated (P = 0.13, coefficient= -0.09). Quasibinomial models were used.

Dispersal quality was analyzed in terms of caching rates (proportion of handled acorns that were cached) and mobilization distances. Distances were summarized as the rate parameters of the gamma distributions fitted to data, which measure the frequency of mid- and long-distance mobilization events. Higher rate parameters indicate lower frequencies of long-distance events. The effects of intraspecific competition for acorns and habitat structure on dispersal distances were assessed by means of linear regression models. Our response variable was the rate parameter of dispersal kernels. Our explanatory variables were the proportion of open land cover, mouse-acorn ratio and their interaction. Regarding caching rates, we first evaluated if higher mobilization distances enhanced caching (as found by Gómez et al. 2008) by means of binomial regression models. The response variable was the proportion of handled seeds that were cached and the fixed effect was the rate parameter of dispersal kernels. If caching rates were not related to distance, we assessed the effects of open land cover, mouse-acorn ratio and their interaction. Data from both localities were first pooled together to assess global patterns in mouse foraging decisions. Then, data from both localities were analyzed separately to evaluate whether environmental factors driving mouse foraging decisions were consistent among localities (Table 3.A1). In all cases, alternative models were compared through the Akaike information criterion corrected for small sample sizes (Burnham and Anderson 2004, Burnham and Anderson 2010).

Effects of microhabitat of destination and mobilization distances on cache survival

Effects of microhabitat of destination and mobilization distances on short-term seed survival were evaluated through binomial mixed models. Our response variable was acorn survival over the first three nights (binomial, 1/0, N = 7-27 per tree). Preliminary analysis revealed that the effects of microhabitat of destination and mobilization distances on seed survival were consistent among localities and fragmentation levels (χ^2=1.84, P= 0.76, Locality*Fragmentation*Habitat χ^2=3.02, P=0.22, Locality*Fragmentation*distance). Therefore, data from both localities and fragmentation levels were pooled together for further analysis. In our final models fixed effects were microhabitat of destination (canopy, shrub and open land), mobilization distance, and their interaction. Cluster was included as random effect. Regarding final seed fate, low sample sizes (18 clusters) and high percentages of zeros (due to acorn recovery by mice) precluded us from performing any meaningful statistical analysis (Table 3.A1).

RESULTS

General patterns of forest fragmentation effects

The highest crop sizes were found in trees located in forest fragments (Table 3.1). Forest edges and small fragments showed similar values of habitat structure variables among localities, with much higher open land cover around trees in fragments. Besides, canopy and understory cover were much lower in forest interior areas of the southern than in the northern locality. Consequently open microhabitats only covered 27% of land around trees in northern forest interiors but up to a 53% in the southern ones (Table 3.1).

We caught 136 rodents, most of them (98%) wood mice *Apodemus sylvaticus*. Small forest fragments showed higher mouse abundances in both localities (Table 3.1, Table 3.A2), that also increased throughout the winter (Fig. 3.1, Table 3.A2). However, mouse reproductive status differed among localities throughout the winter (Fig. 3.1, locality*season*sex/age interaction in Table 3.A2). In the northern locality, reproduction peaked in November and was already declining in March, while the opposite pattern was observed in the South (Fig. 3.1). Consequently, northern populations were more stable throughout the winter than southern ones (Table 3.1, locality*season interaction in Table 3.A2).

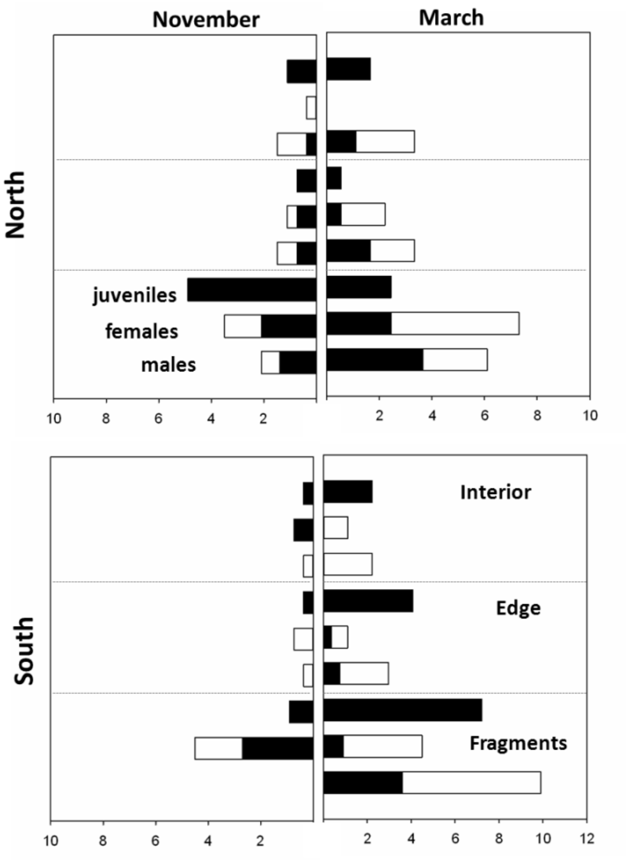

Fig. 3.1. Rodent abundance, sex-ratio (number of male and female adults) and reproductive activity (number of juveniles and proportion of sexually inactive –filled bars- and active –open bars- adults) according to locality (northern or southern), season (November or March) and forest fragmentation (forest interior, edge, small fragments).

Table 3.1. Summary statistics (mean ± SE) for habitat structure variables (expressed as proportions along 20 m transects), crop size (semi-quantitative variable 0-24), mouse abundance (mean number of mice/100 traps night between November and March) and mouse fluctuation ($\log(\text{mouseabundance} + 1)_{\text{March}} - \log(\text{mouseabundance} + 1)_{\text{Nov}}$).

	North			**South**		
	Interior	**Edge**	**Small**	**Interior**	**Edge**	**Small**
Shrub	0.12±0.03	0.07±0.02	0.04±0.01	0.09±0.02	0.07±0.02	0.07±0.03
Open land	0.27 ± 0.03	0.50±0.01	0.59±0.05	0.53±0.03	0.53±0.05	0.61±0.04
Canopy	0.60 ± 0.06	0.51 ± 0.05	0.37 ±0.04	0.37±0.03	0.39 ± 0.05	0.32±0.03
Crop size	0.6 ± 0.24	1.96 ± 0.92	6.78 ± 1.59	0.22±0.20	2.52±1.06	12.81±2.62
Mouseabundance	3.15 ± 0.81	3.70 ± 1.34	10.56 ± 2.46	3.51±1.30	4.81±1.031	14.42±3.22
Mouse fluctuation	0.06 ± 0.06	-0.06± 0.22	0.21 ± 0.19	0.43± 0.06	0.55±0.11	0.76±0.21

Mouse activity was significantly higher in the North, where only 6.29% of offered acorns were unhandled within the first three days as opposed to 36.63% in the southern locality (Fig. 3.2). Our results showed a significant effect of mouse fluctuation dynamics on acorn mobilization rates (B= - 2.19± 1.06, P= 0.05, pseudoR^2 = 0.12) while no significant effect of mouse-acorn ratio. Fragmentation and locality had significant effects on mouse foraging decisions, but their interaction was not significant (multinomial model, fragmentation P<0.01; locality P<0.01, fragmentation*locality P=0.6, correct assignment=0.7, Δ|AIC| =39.22). Main differences occurred in caching activity, which differed among localities and fragmentation levels. Caching rates were two-fold larger in the forest interior areas of the northern locality than in southern interiors (Fig. 2, mean ±SE, 16.83±0.41%, 8.22±0.14%, north and south respectively). Besides, caching rates were significantly higher in forest interiors in the North while they did not significantly differ from forest edges in the South (Fig. 3.2).

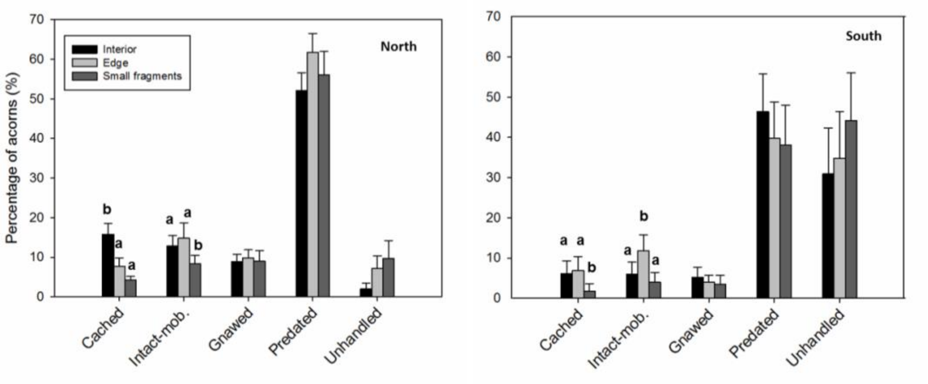

Fig. 3.2.Wood mouse foraging decisions expressed in percentage of acorns cached (intact and buried), intact-mobilized (intact, unburied and mobilized), gnawed (partially predated), predated or unhandled (intact and not mobilized) during the first three nights of exposure. Bars represent standard errors. Letters express groups in binomial mixed models (α= 0.05).

Acorns were mobilized differently among localities and fragmentation levels. Overall, small forest fragments showed the shortest mobilization distances in both localities. Besides, no significant differences between localities were found in acorn mobilization patterns at forest edges and small fragments (Fig. 3.3; mean, Q25-75, Table 2, Table 3, among-locality test). Further, long-distance mobilization events did not occur in small forest fragments in any of the localities (Table 3.2, >20 m). However, fragmentation effects on seed mobilization distances differed among sites. In the North, seed mobilization kernels were different among all fragmentation levels (within-locality test in Table 3.3) and the proportion of long-distance mobilization events was significantly higher in forest interiors than in forest edges ($P<0.05$, pseudoR^2=0.36, zero-inflated Poisson models; Table 3.2 >20 m). In the South, forest edges and small fragments showed similar mobilization distances (within-locality test in Table 3.3) and long-distance mobilization events did not differ between forest interior and edges (P=0.83, zero-inflated Poisson models; Table 3.2 >20 m).

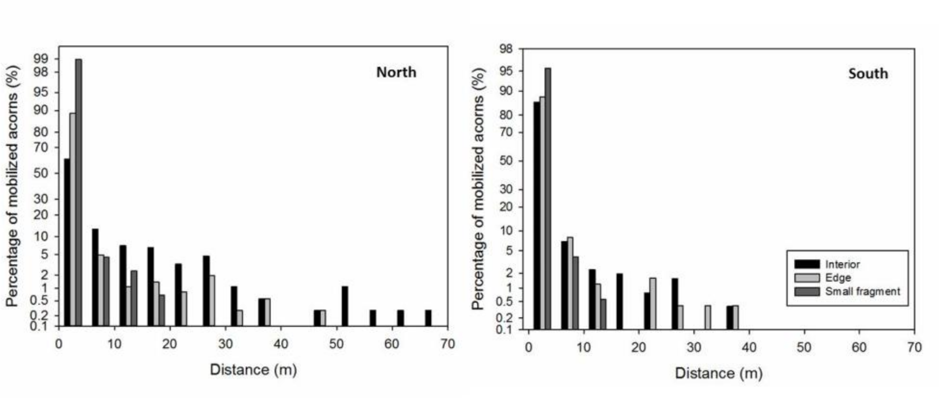

Fig. 3.3. Acorn dispersal kernels generated by *Apodemus sylvaticus* at (A) northern (B) southern localities along the three of forest fragmentation (forest interior, edge, small fragments). Note that y-axis scale is in probability scale.

Table 3.2. Summary statistics of acorn dispersal distances (m) along forest fragmentation levels and among sites. N_{seeds} = number of seeds, Q_{50}= median Q_{25-75}= range of distances between first and third quantile, >20m (%) = percentage of movements beyond 20 m, considered long distance dispersal events. Fragment. = fragmentation level

Locality	Fragment.	N_{seeds}	Max.	Q_{50}	Mean	Q_{25-75}	>20m (%)
North	**Interior**	363	69.19	2.18	7.40	0.32-10.3	11.98
	Edge	363	47.97	0.46	2.64	0.28-1.98	3.80
	Small	310	17.60	0.82	1.89	0.30-2.60	0
South	**Interior**	257	37.45	0.37	2.52	0.25-1.41	2.72
	Edge	251	35.61	0.46	2.24	0.30-1.93	2.83
	Small	187	10.04	0.66	1.52	0.31-2.15	0

Table 3.3. Results of gamma distribution fit on acorn mobilization distances. Gamma distribution fit- AIC, Akaike information criterion, fitted gamma distribution parameters shape and rate. Within-locality differences in acorn mobilization patterns along fragmentation levels- letters define groups (Ks-tests; α= 0.05). Among-locality differences in acorn mobilization patterns within the same fragmentation level, p-values of Ks-test (Anderson-Darling test showed similar results, not shown). Fragent.= fragmentation level.

Lo.y	Fragmennt.	AIC	Rate	Shape	Within-locality	Among-locality	
North	**Interior**	1827.5	0.01±0.00	0.38±0.02	A	Interior	**<0.011**
	Edge	954.84	0.13±0.01	0.34±0.02	B		
	Small	843.03	0.24±0.03	0.45±0.03	C	Edge	0.45
South	**Interior**	615.23	0.13±0.01	0.32±0.02	a		
	Edge	722.60	0.19±0.02	0.42±0.03	b	Small	0.51
	Small	491.09	0.38±0.05	0.58±0.05	b		

Effects of environmental factors on mouse hoarding activity

Globally habitat structure drove mouse foraging decisions (Table 3.4, Global). The proportion of open land had significant negative effects on acorn mobilization distances and consequently on caching rates (Table 3.4, Global, Fig. 3.4). However, the relative importance of each key factor differed among localities. In the North, mobilization distances had a clear positive effect on caching rates. At the same time, open land cover and mouse-acorn ratio significantly affected mobilization distances. Areas with higher open land cover and lower mouse-acorn ratio showed higher rate parameters in dispersal kernels (shorter tails) and consequently lower caching rates (Table 3.4, North). In the southern locality, mobilization distances did not explain caching rates (P=0.25). However, caching rates decreased as open land cover increased (Table

3.4, South). Regarding mobilization distances, no clear patterns were found.

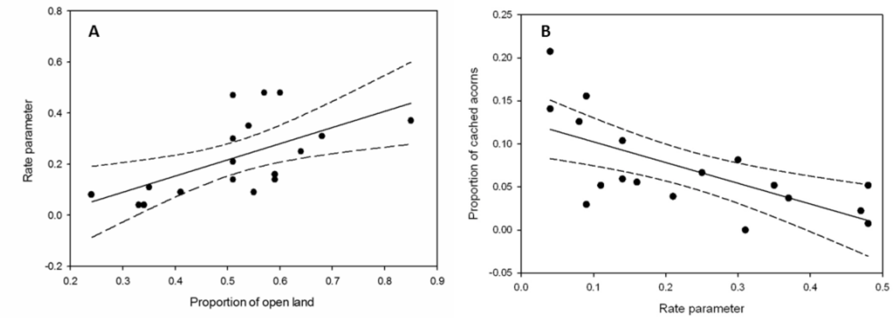

Fig. 3.4 (A) Effects of proportion of open land (along 20 m transects) on rate parameter ($rate = \sqrt{(shape/\sigma)}$) of fitted gamma distribution (higher values imply shorter kernel tails) (B) effects of rate parameter on caching rates. Each point represents a cluster. See, Table 3.4.

Table 3.4. Results from multiple regression models assessing the effects of open land cover (proportion), mouse-acorn ratio (higher values imply higher intraspecific competition for acorns) and their interaction on rate parameters of dispersal kernels (note that higher values imply shorter kernel tails) and results from binomial models assessing the effect of rate parameter on caching rates (proportion). When no clear effect of the rate parameter was detected the effects of open land cover, mouse-acorn ratio and their interaction were assessed. N= sample size, df= degrees of freedom, ∑weights = sum of weights of multimodel inference results, P = p-value, Δ|AICc| with respect to null model (only intercept included). Significant effects are in bold.(1) Multi-model inference results (2) Only p-values for differences between null model and full model are shown when Δ|AICc| < 2. M-A:Mouse-acorn

Locality	**Response**	**Effects**	**Estimate**	**N**	**df**	**∑weights**	**P**	**Δ|AICc|**	**R^2**
Global	**Caching**	Intercept	**-1.70±0.13**	18	17	--	<0.01	51.8	0.51
		Rate	**-4.55±0.69**			--	<0.01		
	Rate	Intercept	-0.11 ± 0.11	18	17	--	0.39	6.09	0.32
		Open land	**0.64±0.21**			--	<0.01		
North	**Caching**	Intercept	**-1.40±0.14**	10	6	--	<0.01	53.00	0.77
		Rate	**-6.63±1.20**				<0.01		
	Rate(1)	Open land	**0.22±0.14**	--	--	0.44	--	--	0.18
		Mouse-acorn	**-0.01±0.14**	--	--	0.69	--	--	0.32
South	**Caching**	Intercept	0.28±1.36	8	6	--	0.84	3.64	0.18
		Open land	**-5.51±2.4**			--	0.02		
	Rate(2)	Open land	--	--	--	--	0.20	--	--
		Mouse-acorn	--	--	--	--		--	--
		Open*M-A	--	--	--	--		--	--

Effects of microhabitat of destination on mouse hoarding activity and seed fate

In both localities and at all fragmentation levels, mice preferentially foraged under canopies and avoided open land microhabitats (Manly tests, P <0.01; Savage indices>1 for under-canopy movements in both localities, and Savage indices<1 for open land movements, respectively). Shrubs were used in proportions equivalent to local availability (Manly tests, P>0.05). Microhabitat of destination, distance from supply points and their interaction had significant effects on short-term survival of individual acorns (Table 3.5). Caches in open land showed significantly larger survival rates than caches under shrub or tree canopies (17.5, 14.3, 37.5% for shrub, tree canopy and open-land caches, respectively, Table 3.5). Besides, acorns mobilized further showed higher short-term survival rates, and such effects were stronger when acorns were mobilized towards shrubs (Table 3.5). Whole winter cache survival rates were much lower in northern than in southern interior areas (11% *vs* 20%, respectively). However, low number of sites (clusters) with at least one cache surviving until the end of winter precluded a comprehensive test of the effects of habitat structure and mouse phenology on overall cache survival.

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Table 3.5. Effects of microhabitat of destination, mobilization distance and their interaction on the probability of acorn survival within the first three days. P = p-value, n = sample size, Δ|AICc| with respect to null model (only intercept). Assig. = correct assignment of the model. Significant effects are highlighted in bold. Int. = Intercept- Canopy

Response variable	**Locality**	**Effects**	**Estimate**	**N**	**P**	**Δ|AICc|**	**Assig.**
Probability of surviving the first three days	**Global**	(Intercept-Canopy)	-1.97±0.25	1,035	<0.01	19.90	0.84
		Shrub	-1.20±0.73		0.10		
		Open land	**1.13±0.36**		**<0.01**		
		Distance	**0.02±0.01**		**0.07**		
		Shrub:distance	**0.13±0.05**		**<0.01**		
		Openland:distance	-0.01±0.02		0.54		

DISCUSSION

Negative effects of forest fragmentation on seed dispersal effectiveness have been previously reported in temperate and tropical ecosystems (McConkey et al. 2012). In general, negative impacts of forest fragmentation on seed dispersal have been linked to the loss of effective dispersers in the impoverished communities inhabiting fragments (Kirika et al. 2008, Cordeiro et al. 2009, Lehouck et al. 2009). Therefore, plant species with higher redundancy in their potential dispersers or being dispersed by generalist species are expected to be more resilient to forest fragmentation (Aizen and Feinsinger 1994). However, not only the presence of potential dispersers matters, fragmentation effects on dispersers' behavior can also have strong negative effects on seed dispersal quality and plants' regeneration potential (Serio-Silva and Rico-Gray 2002). This might be particularly true for conditional mutualisms, like the mouse-oak interaction, in which environmental factors modulate the outcome of the plant-animal interaction.

As we hypothesized, forest fragmentation resulted in lower dispersal quality due to its net effects on key environmental factors in mouse foraging decisions. Forest fragmentation modified habitat structure and intraspecific competition for acorns, and these factors determined mouse foraging behavior and consequently seed dispersal effectiveness. In forest edges and small fragments, open land microhabitats accounted for up to 50% of total cover resulting in low availability of safe microhabitats for rodents. Besides, trees located in these areas showed higher acorn production. Acorn crop monitoring in the study area between 2011 and 2014 showed a consistent pattern among years and preliminary results suggest that increased acorn production is related to the improvement of water status of trees from these fragments (Teresa Morán López, Alicia Forner Sales and Dulce Flores Rentería unpublished results). In accordance to previous studies, small forest fragments hosted denser mouse populations (García et al. 1998, Díaz et al. 1999). On average, increments in acorn production in small forest fragments (compared to forest interiors) were 8.6 times higher than increments in mouse abundance. As a result, intraspecific competition for acorns was lower in fragmented areas.

In both localities, mouse abundance increased throughout the winter, which is typical of Mediterranean rodent populations (Moreno and Kufner 1988, Rosario and Mathias 2004). However, the time at which the reproductive peak occurred differed among localities. In the North, the highest reproductive activity occurred in early autumn, while in the South it was delayed until late winter, a fact that entailed higher fluctuations in mouse abundance throughout the winter and lower acorn mobilization rates. These results suggest that delayed breeding in the South involved a phenological decoupling between mouse reproductive activity and acorn production. As summer drought limits mouse reproductive activity in Mediterranean areas (Moreno and Kufner 1988, Rosario and Mathias 2004, Díaz et al. 2010), increased aridity in the southern locality may be the cause for the delayed breeding observed. However, multi-year studies are needed to assess whether such decoupling is drought-driven or repeated every year (see Gordo and Sanz 2005).

When data from both localities were analyzed together habitat structure was the key driver of mouse foraging decisions. Globally mice avoided open microhabitats leading to lower mobilization distances and caching rates in areas with high proportions of open land. Wood mice are known to avoid open habitats due to increased predation risks (i.e. (Díaz 1992, Tew and Macdonald 1993, Muñoz et al. 2009). However, the role of habitat structure on mouse activity can differ among croplands and forests due to the existence of vaster areas of open land in the former. For instance, in forest habitats, open land microhabitats can enhance dispersal quality in terms of mobilization distances and seed survival (i.e. Perea et al. 2011b, Steele et al. 2014 for grey squirrels). In contrast, in arable land, the massive removal of cover that occurs after harvest precludes mouse movements outside forest fragments (i.e. Díaz 1992, Todd et al. 2000, Tattersall et al. 2001).Our results suggest that the lack of cover from predators in fragmented areas limited mouse movements leading to shorter acorn mobilization distances. As a result, seeds were deposited closer to tree canopies, where seed predation is usually higher (Gómez 2004, Smit et al. 2008).

Interestingly, key environmental factors driving mouse foraging decisions differed among localities. In the North, where proportion of open land was much lower, the presence of shelter and higher intraspecific competition for acorns enhanced mobilization distances and consequently caching rates. Likewise, in forest habitats, where understory cover offers antipredatory refuges for rodents, mice tend to mobilize more valuable acorns further (Den Ouden et al. 2005, Gómez et al. 2008, Puerta-Piñero et al. 2010, Perea et al. 2011b) probably to avoid seed pilfering under canopies (Gómez 2004). By contrast, the effects of intraspecific competition for acorns on mouse foraging decisions vanished in the southern locality. Only habitat structure seemed to drive mouse hoarding activity by precluding seed caching in areas with high proportions of open land. Our results show that when shelter is scarce, predation risks drive mouse foraging decisions constraining effective seed dispersal. However, as risk perception decreases, mice are able to adopt different foraging strategies in order to ensure food supply during winter resulting in higher dispersal quality. This change in the relative importance of open land cover in mouse foraging decisions might imply threshold-like responses of acorn dispersal effectiveness to habitat loss.

Cache survival is another key issue when accounting for seed dispersal effectiveness by rodents since dispersal success only occurs when seed caches are not recovered or pilfered (Den Ouden et al. 2005). In accordance with previous studies (Gómez et al. 2008), our results showed that higher dispersal distances enhanced the likelihood of short-term seed survival. Besides, seeds mobilized towards open microhabitats were more prone to escape post-dispersal predation probably due to lower mouse activity in these areas (Smit et al. 2008, Perea et al. 2011b).Hence, even though high proportions of open land limited effective seed dispersal by precluding mouse movements, the existence of open microhabitats within structurally complex areas enhanced seed survival in agreement with Perea et al (2011a) and Steele et al (2014). Finally, our results suggest that post-dispersal predation throughout winter is higher in more stable mouse populations although mouse population dynamics effects on final cache survival could not be tested. Analyzing oak recruitment patterns would have helped to evaluate fragmentation effects on the long-term seed fate.

Despite the limited time duration of our study (one year), we still argue that our results are indicative of how the system functions. Firstly, summer-autumn precipitation and temperatures —both main factors determining acorn production (Koenig et al. 2013b) and mouse breeding activity (Moreno and Kufner 1988) in the Mediterranean— were comparable to the long-term mean in both localities. Secondly, increased acorn productivity in small forest fragments and edges has been observed in multiple years (Teresa Morán López, Alicia Forner Sales and Dulce Flores Rentería unpublished results) and fragmentation effects on mouse abundance were consistent to those found in extensive previous studies (García et al. 1998, Díaz et al. 1999). Finally, fragmentation effects on seed dispersal patterns as well as mouse responses to key environmental factors were comparable between the two climatically different localities. However, our results cannot be generalized to masting years and we were unable to analyze fragmentation effects on long-term seed fate and seedling establishment. Future studies developed in fragmented areas surrounded by abandoned croplands will help assessing to what extent differences in seed dispersal patterns found here are reflected into changes in the demographic structure of oak populations.

CONCLUSIONS

Within its limitations, our study is still significant in demonstrating that large scale process like forest fragmentation may affect seed dispersal effectiveness through local environmental changes that modulate dispersers' behavior. In particular, our results showed that the mouse-oak interaction in fragmented landscapes was conditioned by habitat structure and, to a lesser extent, intraspecific competition for acorns. Therefore, wood mice may potentially contribute to the recovery of holm oak woodlands if the surrounding matrix becomes more permeable to mouse movements (i.e. by shrub encroachment). Interestingly, acorn dispersal quality was lower in small forest fragments despite the higher acorn production of trees. These results highlight the importance of taking into account plant-animal mutualistic relationships when assessing plants' vulnerability to global change, since the proper functioning of both terms of the interaction will ultimately determine plants' regeneration potential. Overall, our study points out the need of analyzing seed dispersal patterns in managed woodlands as a result of management effects on key environmental factors in dispersers' foraging decisions (Levey et al. 2005, Herrera et al. 2011, Uriarte et al. 2011). Such analysis should unveil key behavioral mechanisms that underlie changes in dispersal effectiveness, detect possible causes of dispersal failures and improve management practices to enhance forest resilience to global change.

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Chapter 3

APPENDIX

Table 3.A1. Summary table of data analysis. Loc. = locality, Frag. = fragmentation level, Mouse-acorn = mouse-acorn ratio, AIC = Akaike information criterion, KS-test = Kolmogorov-smirnov test, AD-test = Anderson-Darling test, Zero-inflated = zero-inflated Poisson models. In multinomial or logistic mixed models the experimental individual acorns were the experimental units and cluster was included as random factor. In linear or logistic regression models cluster was the experimental unit.

Specific aim	Activity	Response	Effects	Analysis
Fragmentation effects	Mouse population dynamics throughout winter	Abundance Sex & age ratios Reproductive activity	Frag.*Loc.*Season	Contingency
	Mobilization distances	Frequency distribution fit	Fragmentation within locality	Maximum likelihood, AIC
		Distribution comparisons	Frag.*Locality	KS-test AD-test Zero-inflated
	Hoarding activity	Acorn state	Frag.*Locality	Multinomial & binomial mixed models
		Microhabitat selected	Frag.*Locality	Savage Manly test
Environmental factors effects	Acorn mobilization rates	Mobilized acorns (%)	Mouse population dynamics *Mouse-acorn	Logistic regression models
	Mobilization distances	Rate parameter Gamma distribution	Mouse-acorn* Open land	Multiple linear regression models
	Hoarding activity	Cached acorns (%)	Rate parameter or Mouse-acorn *Openland	Logistic regression models
	Short-term seed fate	Survived first days (1/0)	Microhabitat*Distance	Logistic mixed regression models

Table 3.A2. Results of the fit of log-linear models to the six-way contingency table generated by the factors locality (northern or southern), season (November or March), fragmentation (small fragments, edge or forest interior areas), sex/age (adult male, adult female or juvenile), reproductive activity (active or not) and presence/absence of capture, taking into account the structural zeros resulting from the impossibility of finding sexually active juveniles (Everitt 1977, Díaz et al. 1999). Values are shown in Fig. 1. Significant effects (P<0.05) are in bold.

Source	**df**	**G^2**	**P**
Locality	1	0.06	0.813
Season	1	24.81	**0.000**
Fragmentation	2	44.68	**0.000**
Sex/age	2	2.23	0.328
Rep. activity	1	2.31	0.128
Locality x season	1	4.21	**0.040**
Locality x fragmentation	2	0.21	0.902
Locality x sex/age	2	1.21	0.545
Locality x activity	1	0.30	0.582
Season x fragmentation	2	0.29	0.864
Season x sex/age	2	4.44	0.108
Season x activity	1	1.12	0.289
Fragmentation x activity	4	3.38	0.497
Fragmentation x sex/age	2	1.21	0.545
Sex/age x activity	2	45.99	**0.000**
Locality x season x sex/age	2	6.10	**0.047**

CHAPTER 4

Predicting forest management effects on oak-rodent mutualisms

Morán-López T.[1], Wiegand T.[2], Morales J.M.[3],
Valladares F.[1] and Díaz M.[1]

(1) Department of Biogeography and Global Change (BCG-MNCN). Museo Nacional de Ciencias Naturales, CSIC. Madrid, Spain.
(2) Department of Ecological Modelling, Helmholtz Centre for Environmental Research—UFZ, Leipzig, Germany
(3) Laboratorio Ecotono, INIBIOMA-CONICET, Universidad Nacional del Comahue, Black River, Argentina

Chapter under review in Oikos

ABSTRACT

Wood mice (*Apodemus sylvaticus*) are the main dispersers of acorns in highly managed Mediterranean holm-oak woodlands. Mice mobilize and cache acorns to store them for winter consumption. They carry acorns away from potential competitors; face predation risks during mobilization, and cache them in areas where pilfering risks are low. However, mice can act either as net predators or as moderately efficient dispersers, depending on the way landscape management affects intraspecific competition for acorns and shelter availability. To assess the influence of landscape structure and mice behavior on acorn dispersal we used abundant field data to develop an agent-based model (ABM). More specifically, we (i) used pattern orientated modeling to determine uncertain model parameters, (ii) validated the model with independent data from five landscapes with largely different structure, (iii) conducted sensitivity analyses regarding mice behavior and landscape management, and (iv) assessed the effect of shrub encroachment as a management tool to enhance dispersal service in savanna-like landscapes (dehesas).

The model was able to accurately predict acorn dispersal patterns in a wide range of forest management practices based on information on forest habitat availability, stem density and shrub cover. Sensitivity analysis revealed that caching rates emerged from the interplay between intraspecific competition for seeds and predation risk accepted during mobilization. It also showed that intraspecific competition for acorns decreased with increasing habitat loss (due to positive edge effects on acorn production) while landscape resistance to mouse movements increased. As a result, the net benefits of caching declined and acorn predation became the dominant strategy. Finally, the model predicted non-linear responses to shrub encroachment of dehesas, with a 65% threshold of shrub cover to achieve relatively high levels of high-quality acorn dispersal.

Key words: *Apodemus sylvaticus, Quercus ilex,* acorn dispersal, management, agent based model

INTRODUCTION

Seed dispersal is a key component of plant population dynamics since it determines the potential area for recruitment and establishes the initial template for important post-dispersal process such as predation, competition and the spatial structure of mating network (Nathan and Muller-Landau 2000). In temperate and Mediterranean systems, between 20% and 60% of plant species depend on animals to disperse their seeds (Willson et al. 1990). Therefore, animal-generated seed shadows and the factors conditioning them have been a longstanding topic in ecological research.

However, unraveling which factors drive plant regeneration potential is particularly challenging because seed dispersal patterns arise from complex interactions between plant and animal traits, animal behavior and the environment (Morales and Carlo 2006, Carlo and Morales 2008, Cortes and Uriarte 2013). In fact, despite that it is well established that environmental conditions can modify seed dispersal effectiveness (*sensu* Schupp et al. 2010), the behavioral mechanisms underlying such changes remain elusive (reviewed in Cousens et al. 2010). We live in a world with rapidly changing landscapes in which animals are forced to face new conditions of food and habitat availability, local competition for sources and degree of (hostile) matrix permeability to their movements. Under these new conditions animals may move and deposit seeds differently (reviewed in McConkey et al. 2012). Therefore, analyzing seed dispersal from a behavioral perspective will allow for a more realistic assessment of the vulnerability of plants to global change in anthropogenic habitats, for detecting possible causes of seedling recruitment bottlenecks and for developing more adequate management practices.

Mechanistic models of seed dispersal by animals have provided new insights about the nature of seed dispersal kernels, have been used for predicting long-distance dispersal events and also have been crucial in detecting critical gaps in our knowledge of the seed dispersal processes (Westcott et al. 2005, Morales and Carlo 2006, Will and Tackenberg 2008, Morales et al. 2013). They have rapidly evolved from context-dependent models parameterized for specific environmental conditions to new approaches in which seed shadows emerge as the result of the interplay between the behavior of dispersal agents and the limitations imposed by landscape structure (see Cousens et al. 2010 for a review). Thanks to these new models, it has been possible to assess which environmental factors have major effects on dispersers' foraging decisions and thus modulate seed shadows (i.e. Morales and Carlo 2006, Levey et al. 2008, D'Hondt et al. 2012, Bialozyt et al. 2014).

However, to evaluate the effects of land use changes on seed dispersal patterns in a dynamic way we need to integrate dispersal with landscape models. This approach will translate management decisions into changes in key environmental factors that drive the behavior of seed dispersers. Here we use such an integrated landscape-dispersal model to address management effects on the holm oak-rodent mutualism. Holm oak (*Quercus ilex)* forests are widely distributed in the western Mediterranean basin where they play an important ecological and socioeconomic role. Most of these woodlands are highly managed, either by understory removal and tree thinning or by forest fragmentation due to agricultural expansion (Santos and Tellería 1998, Campos et al. 2013). These management practices preclude holm oak recruitment due to dispersal failure and increased seed predation (Santos and Telleria 1997, Pulido and Diaz 2005). In small forest fragments and savanna-like woodlands acorn dispersal mostly depends on wood mice (*Apodemus sylvaticus*) due to the disappearance of Eurasian jays (*Garrulus glandarius*), the main acorn disperser in Europe, (Bossema 1979), (Andren 1992, Brotons et al. 2004). However, oak-rodent interaction is not always mutualistic. Depending on environmental conditions, rodents can act as net seed predators or as moderately efficient acorn dispersers (Den Ouden et al. 2005, Gómez et al. 2008). The main drivers of mouse foraging decisions are (1) intraspecific competition for acorns, which is related to direct competition for acorns as well as the likelihood of cache pilfering by conspecifics (Theimer 2005 , Vander Wall 2010), and (2) the presence of shelter (i.e. shrubs), which determines mouse perception of predation risks while mobilizing acorns (Perea et al. 2011). Recent observational work has shown that management effects on acorn dispersal quality by rodents can be explained by its net effects on these two environmental factors (Morán-López et al. 2015).

We developed an agent based model (ABM) to simulate acorn dispersal by mice in response to forest thinning and fragmentation. Forest management modifies local intraspecific competition for acorns and shelter availability, and depending on the balance between these two processes mice adapt their foraging strategies, which results in different acorn dispersal patterns. We assume that the main motivation for mice to mobilize and hoard acorns far from mother trees is to store them for winter consumption. For this purpose, mice carry seeds outside areas with high probability of cache pilfering by conspecifics but they do this only taking an acceptable amount of predation risks during acorn mobilization.

The objectives of this study were to (1) show how management effects on an oak-rodent mutualism can be described and analyzed through an integrated landscape-dispersal model; (2) assess the influence of mouse behavior and of landscape features on the resulting acorn dispersal patterns; and (3) illustrate the power of this approach as management decision tools. To achieve these goals we (i) we parameterized our model through pattern orientated modeling on data from one study area; (ii) we validated our model using five independent study sites that included forest interior areas with contrasting stem densities, savanna-like woodlands (dehesa), forest edges and small forest fragments; (iii) we performed sensitivity analyses of mice behavioral decisions and landscape features; and (iv) we assessed the effect of shrub encroachment in dehesas as a potential a management practice to enhance seedling recruitment.

METHODS

Field observations

Field data were collected in three study sites of holm oak woodlands of the Iberian Peninsula: in Lerma (northern plateau; 42°5'N, 3°45'W), Quintanar de la Orden (southern plateau; 39° 35’ N, 3°02’W) and Cabañeros (southern plateau, 39°39′N, 4°28′W). In these three study sites there are six different landscape scenarios (see below). One of them was used for model construction and calibration and the other five for model validation.

Lerma and Quintanar correspond to holm oak archipelagos located in an extensive treeless agricultural region where cereal cultivation have reduced the original forest cover to smaller woodland patches ranging in size between 0.1 and 2000 ha (Santos and Tellería 1998). Field data from these sites were collected in winter 2012-2013 within the framework of an experiment in which fragmentation effects on acorn dispersal by mice were evaluated (Morán-López et al. 2015). Cabañeros is a National Park in which two contrasting landscape configurations can be found, holm oak forests and savanna-like woodlands (dehesas). Dehesas are characterized by a very low stem density (12 trees ha^{-1}) within an open grassland matrix with almost no shrub cover (<1%). Seed dispersal patterns were measured in winter 2011-2012 in two dehesas (Díaz et al. in prep.).

In Lerma and Quintanar we monitored acorn dispersal in three fragmentation levels- forest interior areas, forest edges and small fragments. We offered and tracked 405 acorns per locality and fragmentation level (2430 in total). In Cabañeros we tracked 446 acorns.

Information of dispersal patterns included acorn mobilization distances, caching rates and microhabitat selection by mice. Besides, field data at the three sites included information of acorn production of oaks, local mouse abundance and understory cover structure. See Morán-López et al. 2015 for further details.

From the observed data we derived information to directly parameterize the effects of holm-oak intraspecific competition on acorn production, the effects of canopy and shrub cover on mouse abundance, in situ predation rates and the probability of depositing a seed under canopy or shrub cover at the end of the mobilization process (see Appendix 4.A submodels section). Additionally, we used the dataset of northern plateau (Lerma) forest edges to determine uncertain model parameters because it contained the largest diversity of landscape structures. The other five datasets (forest interiors of Quintanar and Lerma, forest edges of Quintanar, small forest fragments of both localities and Cabañeros dataset) were used to evaluate the predictive performance of the model.

Modeling approach

To model the effects of landscape management on acorn dispersal by mice, we developed and agent-based model implemented in Netlogo 5.0.4 (Wilensky 1999) a free platform for building ABMs. The Netlogo code is available in supplementary material (Appendix 4.B, in CD attached). The model description follows the Overview and Design Concepts and Details (ODD) protocol for communicating agent-based simulation models (Grimm et al. 2006, Grimm et al. 2010). In the following sections, we present the overview and design concepts, for details see Appendix 4.A.

Entities, state variables and scales

This ABM comprises five different entities: landscape, trees, shrubs, acorns and mice. The landscape consists of a two-dimensional grid with a cell size of 1 m. It has an area of 5.76 ha, 1 ha in the center corresponding to the study area and a buffer around it of 70 m width (which corresponds to the average home-range radius of *Apodemus sylvaticus* observed in Mediterranean areas (Rosalino et al. 2011) and also to the maximum dispersal distances observed in our study (Morán-López et al. 2015). This buffer avoids artificial edge effects. Each grid cell is characterized by two variables: habitat type (forest or cropland) and microhabitat (open land, shrub or canopy).

Trees are randomly placed within the landscape, but keeping a realistic 4m minimum distance to each other. Each tree is characterized by its canopy radius and acorn production. Acorns are initially placed on trees and are characterized by the coordinates of their initial and final positions and by their final seed fate (“predated in situ”, “mobilized and predated” or “dispersed”). Shrubs are randomly placed within the landscape. Mice are randomly placed on the landscape but this placement is constrained by realistic home-ranges areas and home-ranges overlap (see Appendix 4.A.1, Mouse abundance submodel). Then, mice located close to oak trees are asked to mobilize seeds while the rest of them create a map of local mouse abundance.

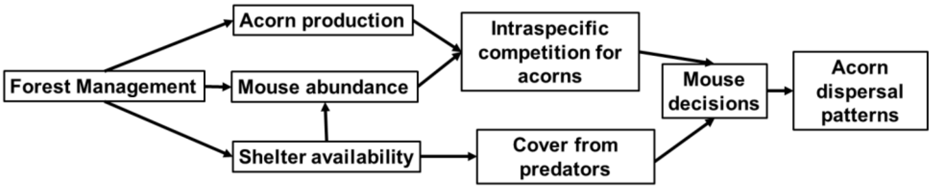

Fig.4.1. Basic structure of the model. Forest management modifies local mouse abundance, acorn production and habitat structure which entails changes in intraspecific competition for acorns as well as availability of cover from predators. Mice modify their foraging strategies according to these new environmental conditions, thereby affecting acorn dispersal patterns.

Design concepts, process overview and scheduling

Figure 4.1 shows how forest management influences the local environmental conditions and how mice adapt their behavior accordingly. From field data we parameterized the effects of landscape structure on acorn production of trees and on local mouse abundance. Acorn production by individual trees in the model is negatively related to intraspecific competition for water sources (see Appendix 4.A.1, Acorn production submodel). As a consequence, trees located in areas with lower stem densities or in forest edges surrounded by croplands show higher acorn production. Local mouse abundance is positively related to canopy and shrub cover in forest interiors and it depends on the amount of habitat availability in fragmented areas (see Appendix 4.A.1, Mouse abundance submodel). Therefore, the effects of forest management on intraspecific competition for acorns will depend on its net effects on the ratio between local acorn production and mouse abundance (Fig 4.1; for further details see Appendix 4.A.1). Finally, open microhabitats represent areas of high predation risks for mice. Thus, our model assumes that landscape permeability to mouse movements depends on the amount of open land cover it has. Depending on forest management effects on intraspecific competition for acorns and the amount of open land cover in the landscape, mouse modify their foraging decisions resulting in different acorn mobilization patterns.

In our model, mouse foraging decisions follow three objectives: (1) mobilize seeds away from potential competitors, (2) avoid moving through risky habitats, and (3) cache seeds in areas where the probability of pilfering by conspecifics is low (Fig. 2B). During the first meters of acorn mobilization mouse decisions are governed by intraspecific competition for acorns. Then, mobilization continues until risk perception exceeds a certain threshold. Finally when acorns are deposited, the decision between predation and seed caching depends on the risk of cache pilferage by conspecifics and the effort invested in seed mobilization.

Mouse decisions are made according to three internal variables- intraspecific competition for seeds, competition radius and risk perception. The first two variables represent foraging strategies related to direct competition for acorns and the avoidance of cache pilfering by conspecifics. The third variable defines the amount of risks perceived by mice while mobilizing seeds. Once carried acorns have been deposited, mice return to the source tree and the whole dispersal process restarts. A model run finishes when all acorns within the study area are dispersed (see Appendix 4.A. for further details).

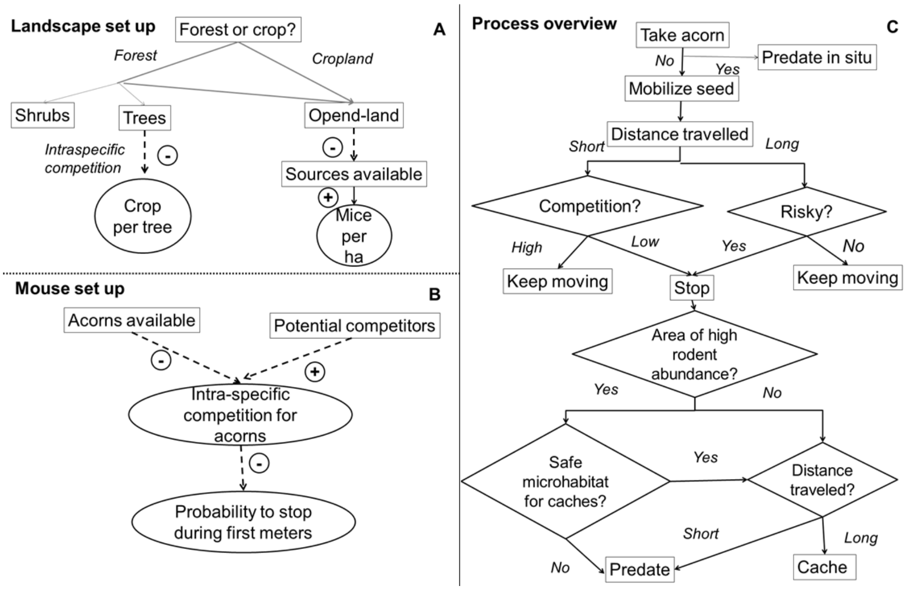

Fig. 4.2. Flow diagrams showing the structure of the model. (A) Procedure to generate landscapes, (B) decision process of mice before starting acorn mobilization, (C) process overview of mouse foraging decision. Dashed lines and circles represent parameters that depend on local environmental characteristics. Grey lines represent input values. In figure C diamonds indicate decision points

Initialization- Our model needs three input data: proportion of forest habitat loss within the landscape, number of stems per hectare and proportion of shrubs in the understory cover.

Observation- Within the model, acorn mobilization distances as well as their final state (cached vs. predated) is recorded (main model output). Caching rates are estimated taking into account in situ acorn predation while dispersal distances are estimated only taking into account mobilized seeds.

Model parameterization

Pattern-oriented modeling was used for model parameterization (Wiegand et al., 2003; Hartig et al., 2011 and Railsback and Grimm 2011). We parameterized the model with the data from the results of a field experiment conducted in Lerma in which 405 acorns were tracked in three independent edge areas of large forest fragments (> 100 ha; (Morán-López et al. 2015). Four output variables were used for model parameterization, including the maximum dispersal distances, the shape and the rate parameters of a gamma distribution fitted to dispersal distances, and the proportion of cached acorns. A total of 16000 combinations of parameters were sampled from uniform distributions within biologically plausible ranges for all parameters (see Table 4.1). For each parameter combination, five model simulations were run (variance of mean global values among replicates stabilizes with a sample size of 5). We then estimated global cost of parameter sets. Cost was defined as the sum of the squared relative deviations to the mean value of the acceptable value range over the four different criteria (when model output fell within the acceptable value range its cost was 0; Thiele et al. 2014- eq. 1-4). Following and Approximate Bayesian Computing (ABC) approach, the optimal model parameter combination was then selected from the median of the approximate posterior distributions of parameter sets with low global costs (rejection filter, global cost < 0.15). In the case of risk threshold, the value of maximum frequency was chosen (since this parameter is an integer).

The six parameters estimated were (1) CR of the competition-area radius function, which defines the area in which mouse foraging decisions are governed by intraspecific competition (eq.4, Appendix 1.2); (2) the parameter PS of the probability to stop function, that modulates the strength of intraspecific competition effects on mouse foraging decisions (eq. 5 Appendix 1.2, intraspecific competition for acorns submodel); (3) the risk threshold during acorn mobilization ($N_{R;}$ Appendix 4.A.2 Risk threshold submodel), (4-5) the parameters C1 and C2 of caching probability function, which determine maximum caching rates and the strength of the effects of mobilization distances on the probability of acorn caching, respectively (eq. 7 Appendix 4.A.2) and (6) edge-belt width, which defines the areas of increased pilfering risks due to increased mouse abundance in forest edges (EW; Appendix 4.A.2. Hoarding vs.predation submodel). For further details see Appendix 4.A.2.

The RNetLogo package was used for inverse parameterization (Thiele et al. 2012) following guidelines specified in (Thiele et al. 2014). For fitting the gamma distribution we used the fitdistribution plus package (Delignette-Muller et al. 2014).

Table 4.1. Parameter values estimated during model parameterization and their ranges employed during the sensitivity analysis.

Global Process	Process	Sub-process	Parameter	Range during parameterization	Value in base model	Values in sensitivity Test
Forest management	--	Fragmentation	Habitat loss	0.50	--	[0.1, 1]
		Forest thinning	Stems / ha	400	--	[50, 350]
		Understory development	Shrub cover	0.25	--	[0.1, 1]
Mouse foraging decisions	Acorn mobilization	Intraspecific competition effects	Competition area radius	[0, 20]	3 m	--
			Probability to stop (PS parameter)	[0.10- 0.60]	0.40	[0.10-0.60]
		Predation risk effects	Risk perception threshold (N_R)	[0, 4]	1 m	[0, 4]
	Predation vs Caching	Pilfering risk effects	Edge-belt width	[0, 60]	35 m	--
		Distance travelled effects	Maximum caching rates (C1)	[0.5, 1]	0.75	[0.5, 1]
			Distance effects (C2)	[0.1, 0.2]	0.16	[0.1, 0.2]

Model validation

We validated our model with five independent datasets, including forest interiors of the northern plateau (Lerma; N = 3 forest interiors) and the southern plateau (Quintanar; N = 3 forest interiors), forest edges of the southern plateau (Quintanar; N= 3 forest edges), small woodlots within croplands of both plateaus (N= 5 areas of small forest fragments) and a Spanish dehesa (N = 2 dehesas). We simulated acorn dispersal by mice based on the optimal model parameterization and on the landscape parameters (habitat availability, stem density and shrub cover) of these study areas. In field data of the northern and southern plateaus each observation corresponds to 135 seeds offered and tracked (Morán-López et al. 2015). In the case of the dehesa 202 and 244 seeds were offered and tracked per observation (Díaz et al. in prep). In the case of the Spanish dehesa *Mus spretus* was the main disperser instead of *Apodemus sylvaticus*. Although the model structure remained the same, we needed to adapt the home range radius to 15 m (Gray et al. 1998) and the weight-ratio to 0.24 (field data from Díaz et al. in prep, see eq. 5 Appendix 4.A.2).

For each landscape we run 100 independent simulations. To validate acorn mobilization distances, we calculated for both, observed and simulated data the mean and the standard error of mean and maximum dispersal distances, the shape and rate parameters of the gamma distribution fitted to dispersal distances, and the distance for 0.95 quantiles. We assumed an acceptable model prediction when mean values of 100 simulations were within the 95% percentiles of the observed data. We also evaluated the variance explained by the model by regressing observed *vs* simulated data of the proportion of seeds deposited at a given distance in annuli of 5 m (log-transformed, with a fixed slope of 1) and obtained the R^2.

To evaluate the models' ability to predict mouse hoarding activity we evaluated if the proportion of cached acorns differed between simulated and observed data. In this case the experimental units were sampled trees instead of forest areas (N=15 trees for forest interiors and edges, N=30 for small woodlots). Out of the simulated and observed data we calculated mean and standard errors of caching rates (defined as the percentage of cached seeds). We assumed an acceptable model prediction when the mean values of 100 simulations were within the 95% percentiles of the observed data.

Sensitivity analyses

Two sensitivity analyses were performed. Firstly, we evaluated the sensitivity of the predicted dispersal pattern to parameters governing mice behavior (decision sensitivity test, hereafter). We used here all parameters that were determined by pattern-oriented modeling, (except the edge-belt width EW) and landscape scenario corresponded to Northern forest edges (see Table 1 for parameter ranges). In a second analysis we evaluated the net effects of landscape features (landscape sensitivity test, hereafter) based on the standard parameter set shown in Table 1. We varied in this analysis all three parameters used to define a landscape, habitat availability (0.1 to 1), stems per ha (50 to 350), and a proportion shrub cover (0.1 to 1).

We analyzed as output variables the shape and rate parameter of the gamma distribution fitted to the simulated dispersal kernels, maximum dispersal distances and the percentage of mobilized seeds cached. The shape parameter *k* describes the location of the maximum probability ($k = 1$: maximum at $x = 0$). The rate parameter describes the tail of the dispersal kernel ($\mathrm{Var}(x) \sim 1/\mathrm{rate}^2$) lower values imply broader probability distributions with longer tails. This way, we could evaluate which part of the foraging decision process (intraspecific competition, risks assumed during mobilization, or cache pilfering avoidance) influence different aspects of seed dispersal quality (proportion of acorns dispersed close to the mother trees, potential colonization distances and amount of seeds finally cached). To detect linear and non-linear monotonic associations between model parameters being evaluated and output variables, global sensitivity analysis was performed following a partial correlation rank test using sensitivity package in R (Pujol et al. 2014, Thiele et al. 2014).

Landscape scenarios- dehesa shrub encroachment

To illustrate the potential of ABMs as a tool for the development of adequate management policies we simulated shrub encroachment in a dehesa (savanna-like woodlands with 15 stems per ha), a suggested management practice to foster recruitment of holm-oaks, and evaluated its effects on seed dispersal patterns. In particular, its effects on mean and maximum dispersal distances as well as caching rates were evaluated. Preliminary scatterplots showed non-linear responses in the case of mean and maximum dispersal distances. Therefore, the data was fit with a two parameter exponential growth curve and a four parameter sigmoidal curve (mean and maximum dispersal distances respectively). In the case of caching rates a linear regression was adjusted. These analyses were performed using Sigmaplot 12.0.

RESULTS

Model calibration

ABC parameterization based on the data for forest edges from the northern plateau showed that the model could be parameterized to yield mobilization distances and caching rates patterns close to those of observed data. Regarding mobilization patterns, almost all summary statistics of the simulated data fell within the 95 % confident interval of observed data (see Table 4.2; Northern forest edge, mean and maximum dispersal distances, rate parameter, quantile of probability 0.95). The model slightly underestimated the proportion of seeds that were deposited in the first 5 m (Fig 4.3A) and the shape parameters of the gamma distributions fitted to dispersal distances were slightly higher than those of the observed data (Table 4.2). However, there was a general good agreement between observed and simulated data (R^2=0.88 fit between log-transformed data of observed and expected seed deposition at a given distance). Besides, caching rates fell within the 95% confidence interval of observed data (Table 4.3, Northern forest edge).

Model validation

Our parameterized model predicted acorn dispersal distances (Fig. 4.3; Table 4.2) and caching rates (Table 4.3) that agreed well with the data from the five independent landscape scenarios tested. Our model yielded similar acorn mobilization patterns than those observed in Southern forest edges (Fig.4.3B, Table 4.2, R^2= 0.88, between log-transformed data of observed and expected seed deposition at a given distance, slope fixed to 1). In northern forest interiors, our model overestimated short-range mobilization distances (0-5 m; Fig. 4.3C). However, the fit between observed and expected seed deposition at a given distance was high (R^2=0.95). Furthermore, predicted mean and maximum dispersal distances, dispersal kernel parameters and the distance corresponding to for 0.95 quantile of the probability all fell within the 95% interval of observed data. Simulated data of Southern forest interiors accurately reproduced field-observed patterns (Fig. 4.3D, R^2=0.91, Table 4.2). Although the fit between observed and simulated data was high for small forest fragments (R^2=0.99 Fig. 4.3E), the proportion of seeds deposited close to the source point was overestimated and kernel tails were thinner (shape and rate parameter, Table 4.2). Finally our model was able to reproduce the field data of the dehesa accurately (Fig. 4.3F, Table 4.2; R^2= 0.99). In all cases the mean values of the simulations caching rates fell within the 95% interval of observed data (Table 4.3). However, mean values of caching rates in small forest fragments were in the lower limit of the confidence interval and caching rates in dehesas were in the upper limit.

Table 4. 2. Model parameterization and model evaluation. The data from the northern forest edges were used for model parameterization, all other data sets were used for model evaluation. The table shows summary statistics of seed dispersal distances of observed and simulated data. Values of observed data correspond to 95% confidence interval. Values of simulated data represent mean ± SE. Mean = mean dispersal distance, max = maximum dispersal distance, shape= shape parameter of gamma distribution fit, rate = rate parameter of gamma distribution fit, 0.95= distance for quantile of probability 0.95. Northern and Southern forests correspond to Lerma and Quintanar datasets respectively, small forest fragments correspond to data set of both localities and Dehesa corresponds to Cabañeros National Park dataset.

Landscape	**Type**	**Mean**	**Max**	**Shape**	**Rate**	**0.95**
*Northern forest edge***	Observed	[1.00, 4.90]	[9.88, 53.07]	[0.50, 0.57]	[0.10, 0.18]	[4.26, 25.38]
	Simulated	4.35±0.06	44.03±0.93	0.63±0.00	0.15±0.00	6.78±0.30
Southern forest edge	Observed	[1.25, 3.42]	[23.70, 38.15]	[0.58, 0.73]	[0.17, 0.45]	[4.80, 20.86]
	Simulated	2.69±0.02	26.07±0.70	0.77±0.07	0.29±0.04	8.73±0.17
Northern forest interior	Observed	[4.77. 10.63]	[34.63, 71.33]	[0.51, 0.64]	[0.04, 0.13]	[17.02, 35.90]
	Simulated	4.10±0.05	45.63±1.03	0.62±0.04	0.15 ± 0.00	15.32±0.27
Southern forest interior	Observed	[1.25, 4.16]	[16.15, 39.37]	[0.46, 0.75]	[0.07, 0.50]	[4.83, 23.03]
	Simulated	2.19±0.03	14.46 ±0.34	0.90±0.01	0.42±0.04	5.86±0.05
Small fragment	Observed	[1.43, 2.60]	[6.37, 13.85]	[0.86, 1.20]	[0.37, 0.77]	[4.21, 8.4]
	Simulated	2.00±0.01	14.61±0.61	2.83±0.05	1.42±0.03	4.37±0.03
Dehesa	Observed	[0.98, 1.26]	[2.95, 7.12]	[1.96, 2.43]	[1.52, 2.42]	[2.44, 2.76]
	Simulated	1.63±0.02	7.20±0.11	1.81±0.25	1.13±0.17	3.68±0.11

*The simulated data consist on 100 independent model runs. In forest interiors and forest edges field data consist on three indepent dispersal kernel estimations (offered seeds = 135 in each observation). For small forest fragments field data consist on five independt kernel estimations (offered seeds= 135 each observation). In dehesa, field data consist on two independent estimation of dispersal kernels (offered seeds= 202 and 244).**Data set used for inverse modeling parameterization

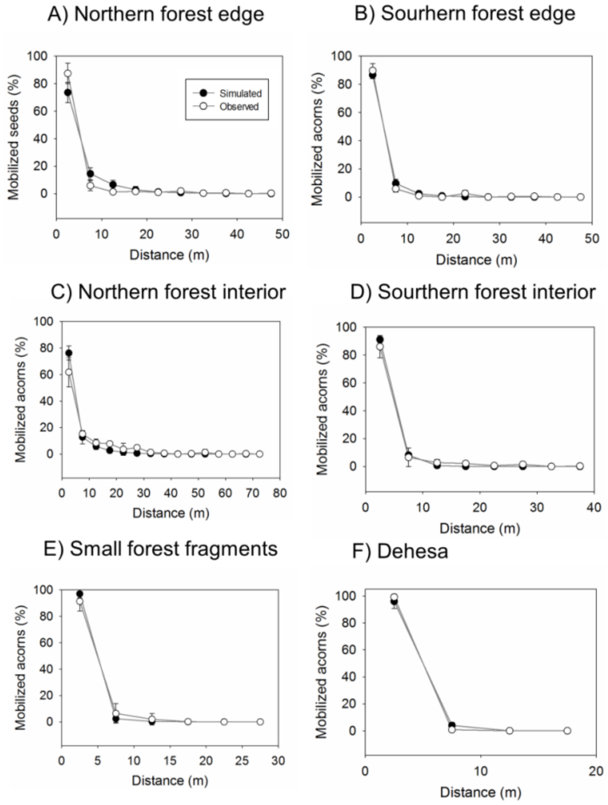

Fig.4.3. Comparison of seed dispersal kernels from simulated (black, filled circles) and observed (open circles). The simulated data consist on 100 independent model runs. In forest interior and edges field data consist on three independent dispersal kernel estimations (offered seeds = 135 in each observation). For small forest fragments field data consist on five independent kernel estimations (offered seeds= 135 each observation). In dehesa, field data consist on two independent estimation of dispersal kernels (offered seeds= 202 and 244). Northern and Southern forests correspond to Lerma and Quintanar datasets respectively, small forest fragments correspond to data set of both localities and Dehesa corresponds to Cabañeros National Park dataset. Bars represent 95percentiles (unless eclipsed by the symbol).

Table 4.3. Model parameterization and model evaluation - Summary statistics of mice hoarding activity of observed and simulated data. Data represent the percentage of mobilized seeds that were cached by rodents. Values of observed data correspond to 95% confidence interval. Values of simulated data represent mean ± SE. Northern and Southern forests correspond to Lerma and Quintanar datasets respectively, small forest fragments correspond to data set of both localities and Dehesa corresponds to Cabañeros National Park dataset.

Landscape	**Type**	**Cached acorns**
*Northern forest edge***	Observed	[3.65, 13.70]
	Simulated	9.46±0.23
Southern forest edge	Observed	[2.4, 10.03]
	Simulated	5.91±0.14
Northern forest interior	Observed	[11.03, 22.72]
	Simulated	15.19±0.26
Southern forest interior	Observed	[2.40, 17.12]
	Simulated	8.18±0.15
Small forest fragments	Observed	[2.25, 7.07]
	Simulated	2.35±0.11
Dehesa	Observed	[0, 1.83]
	Simulated	1.84±0.14

* Field data corresponding to forest interiors and edges consist on 15 trees located in three indepent locations (offered seeds = 27 per tree). For small forest fragments field data consist on 30 trees located in 16 independent small woodlots (offered seeds= 27 per tree). In dehesa, field data consist on two indepent dehesas (offered seeds= 202 and 244 per dehesa). **Data used in inverse modeling parameterization.

Sensitivity analysis

Model parameters driving mouse foraging decisions were correlated differently to short-range mobilization patterns, maximum mobilization distances and caching rates (Fig. 4.4). In general, seed dispersal distances were sensitive to both, the importance of intraspecific competition on acorn mobilization (parameters CR and PS) and the predation risks accepted by mice during acorn mobilization (parameter NR). However, the relative importance of the parameters CR, PS and NR differed between dispersal kernel estimates and maximum dispersal distances. The shape and rate parameters of the kernels were most strongly correlated to the CR and PS parameters (Fig. 4.4A, B) and the shape and rate parameters of the dispersal kernel increased when both parameters increased. These results fit our expectation that mice tend to mobilize seeds closer to the parent tree when intraspecific competition effects are relaxed. This translates into dispersal kernels characterized by higher probabilities of mobilization events close to the source point as well as shorter and thinner tails (higher shape and rate parameters).

However, maximum dispersal distances were mainly correlated with predation risks accepted during mobilization (parameter NR; Fig. 4.4C). When mice accepted a higher risk the landscape matrix became more permeable to mouse movements and hence maximum mobilization distances increased. Shape and rate parameters of dispersal kernels were more robust to changes in model parameters than maximum dispersal distances. This is due to the fact that kernel estimates collect information about all mobilization events; hence, changes in these parameters imply great differences in overall mobilization patterns.

Caching rates were related to all decision points, however, they were correlated to a greater extent to the parameters PS and the maximum caching rate (C1) (Fig. 4D). The former result is in accordance to our expectation that mice invest higher efforts in safeguarding acorns for winter consumption.as the effects of intraspecific competition increases. The second is simply related to the maximum of the caching probability function (eq. 7, Appendix 4.A.2).

Landscape sensitivity analysis (Fig. 4.5) revealed that forest habitat loss is a key factor for seed dispersal quality. Higher habitat loss was related to overall shorter mobilization distances (shape, rate parameters) as well as lower caching rates. Shrub cover was highly correlated to maximum dispersal distances. Stem density showed the lowest effects on all parameters except for caching rates. Thus, our landscape sensitivity analysis revealed that parameters related to changes in both- intraspecific competition for acorns and matrix permeability had the greater overall effects on acorn mobilization distances and caching rates.

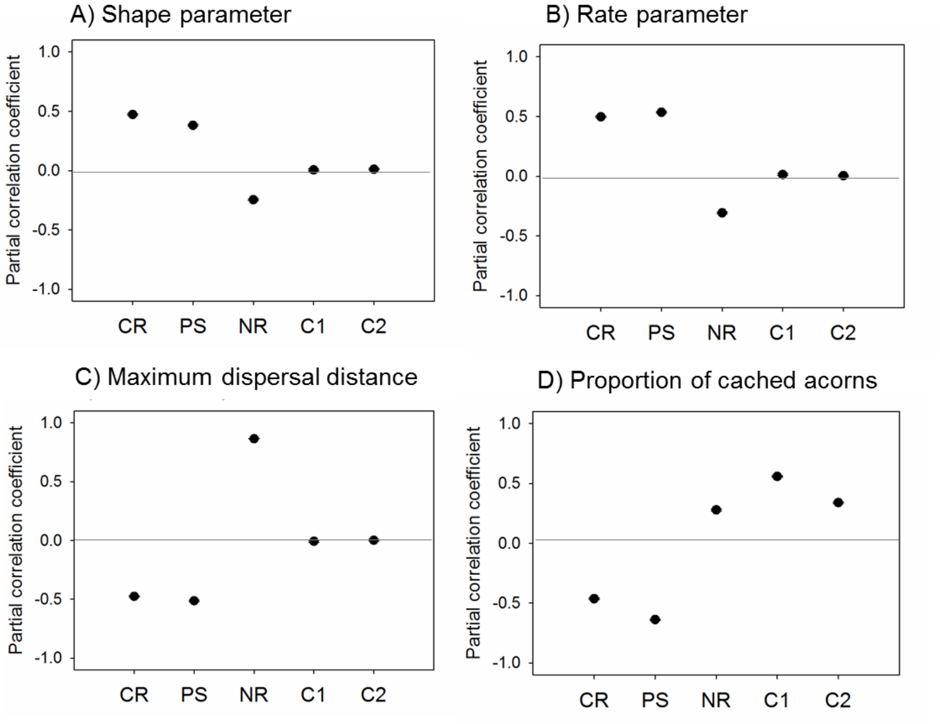

Fig. 4.4. Sensitivity analysis of mouse foraging. Results show the partial rank correlation (PRCC) between mouse foraging decisions parameters and the following model output variables: (A) the shape and (B) the rate parameter of the gamma distribution fitted to mobilization distances, (C) maximum dispersal distance, and (D) proportion of cached acorns. Circles represent PRCC values and bars indicate bootstrapped (n = 100) 95% confidence intervals corresponding to sensitivity indices (unless eclipsed by the symbol). CR: competition radius (Appendix 4.A.2, eq.4); PS: parameter of probability to stop function (Appendix 4.A.2, eq. 5) , NR: risk-treshold giving the maximal number of consecutive movement steps in the risky open land, C1: maximum caching rates with distance, C2: effects of distance on the probability of acorn caching (Appendix 4.A.2, eq.7).

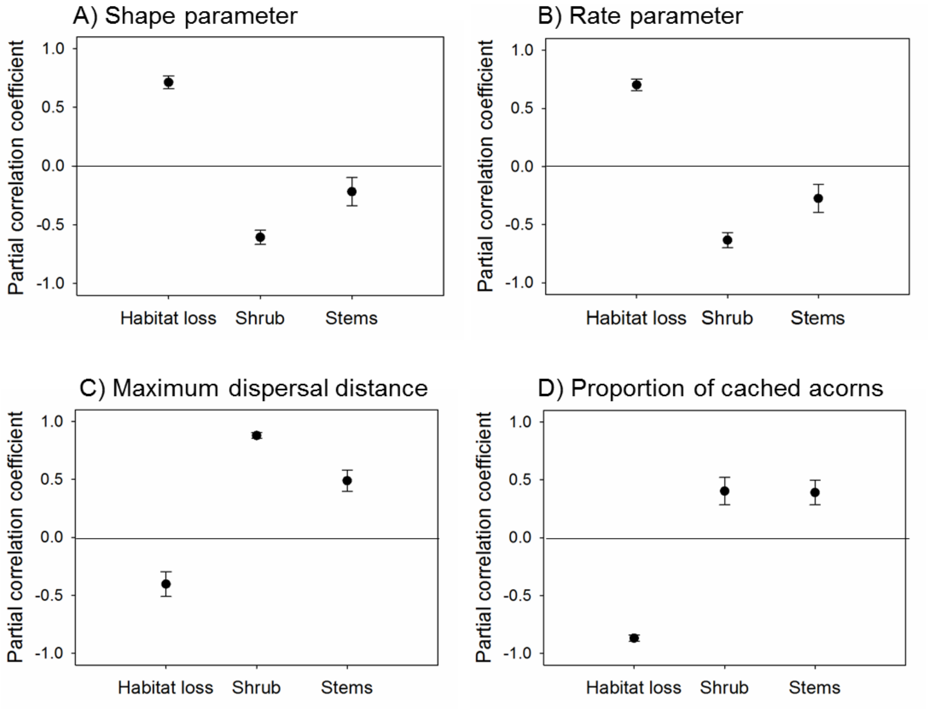

Fig.4.5. Sensitivity analysis of landscape parameters. Results show the partial rank correlation (PRCC) between landscapes attributes and the following model output variables: (A) the shape and (B) the rate parameter of the gamma distribution fitted to mobilization disances, (C) maximum dispersal distance, and (D) proportion of cached acorns. Circles show PRCC values and sticks show bootstrapped (n= 100) 95% confidence intervals corresponding to sensitivity indices (unless eclipsed by the symbol). Landscape parameters: forest habitat loss (%), shrub cover (proportion) and stems per ha.

Landscape scenarios- dehesa shrub encroachment

Shrub encroachment effects in a typical dehesa produced non-linear responses for dispersal distances. The two parameter exponential curve and the three parameter sigmoidal curve fitted well our simulations of shrub encroachment effects on mean and maximum dispersal distances (Fig. 4.6A and 4.6B, R^2 = 0.89; R^2=0.96, respectively). In both cases, shrub encroachment effects did not become evident until shrubs represented between a 50 and a 65% of understory cover. In the case of caching rates, encroachment effects became evident straight away. However, caching rates did not reach a 10% until shrub cover was greater than a 40% (Fig. 4.6C). In summary, our results show that shrub encroachment has minor effects on seed dispersal quality if understory shrub cover is below 40% and that these effects don’t become evident until shrubs represent more than a 65% of the understory cover.

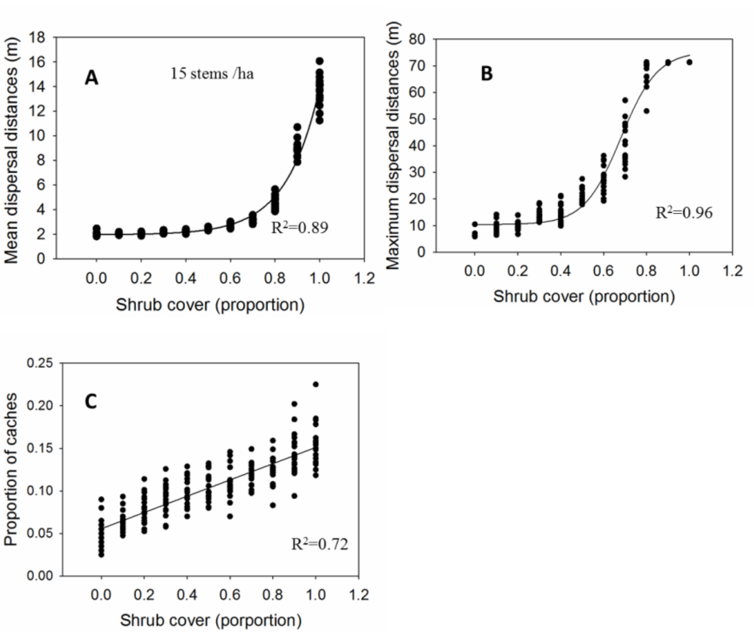

Fig.6. Model predictions of shrub encroachment effects on a savanna-like woodland (dehesa) on (A) mean and (B) maximum dispersal distances and (C) caching rates. Lines represent fitted curve (A) $\mathrm{mean} = 0.33 \times \mathrm{e}^{3.64\times\mathrm{shrub}}$ (B) $max = 10.35 + \frac{65.08}{1 + e^{(-(shrub-0.68)/0.09)}}$ (C) $caching = 0.05 + 0.10 \times shrub$

DISCUSSION

Animal-generated seed shadows in human-modified woodlands emerge from complex interactions between management effects on environmental conditions and animal behavior (Cortes and Uriarte 2013). Here, we analyzed effects of land-use changes on acorn dispersal patterns in holm oak woodlands using an approach that integrates an individual-based model with a landscape model. Previous work on holm oak woodlands from different perspectives, including acorn production, mouse population dynamics and oak-rodent mutualisms provided an understanding of the mechanisms that potentially drive acorn dispersal patterns. Including these processes into our model allowed us to reproduce simultaneously several key features of acorn dispersal patterns in a variety of forest management scenarios that were not used for model parameterization. Besides, successful application of a slightly modified model version to Dehesa landscapes where acorns are dispersed by *Mus spretus* (instead of *Apodemus sylvaticus*) showed that the model incorporates rather general decision processes of rodent species since the same environmental factors seem to modulate their foraging behavior (Theimer 2005 , Vander Wall 2010).

Mouse foraging decisions effects on seed dispersal patterns

Sensitivity analysis helped in previous modeling work to disentangle the behavioral mechanisms behind the main attributes of seed dispersal kernels (Morales and Carlo 2006; Bialozyt, Flinkerbusch et al. 2014). Our “decision sensitivity test” aimed at identifying those foraging decisions with greater effects on different aspects of seed dispersal quality. This approach allowed us to interpret large-scale management effects on seed rain patterns from a behavioral perspective.

Our results showed that a higher proportion of acorns were deposited closer to the mother tree when the effects of intraspecific competition for seeds were relaxed. This result is in accordance with previous observational work (Puerta-Piñero et al. 2010, Morán-López et al. 2015). As pointed out by Moore (2007), when sources are abundant, rodents depend less on the stored food and pilfering pressure decreases. In such cases, optimal cache distances are determined by minimizing energy costs rather than by minimizing cache pilfering risks resulting in shorter mobilization distances and higher clumping of caches. In contrast, maximum dispersal distances mainly depended on the risks assumed by mice while mobilizing seeds. This is in agreement with the idea that maximum dispersal distances are largely determined by matrix permeability to seed-vector movement (Schurr et al. 2008). In our model when mice took riskier decisions landscape matrix turned more permeable and consequently maximum dispersal distances increased.

The aim of scatter-hoarders is to store seeds for winter consumption and, hence, rodents act as dispersers only when seed caches escape retrieval or pilfering (Den Ouden et al. 2005). In general, seed dispersal models focus on how environmental factors modulate animal movement and the effects of seed handling are rarely taken into account (reviewed in Cousens et al. 2010, but see D'Hondt et al. 2012). However, when modeling oak-rodents mutualistic relationship the difference between seed caching and predation needs to be included. In fact, initial caching rates in forest habitats ranges from 7 to 40 percent and seed survival until late autumn from 9 to 20 percent (Gómez et al. 2008, Perea et al. 2011, Morán-López et al. 2015). As pointed out by our sensitivity analysis, caching rates emerge from the interplay between intraspecific competition for seeds and the risks taken during mobilization. There was a good agreement between predicted and observed values in all landscape scenarios, which suggests that the main drivers of seed caching by wood mice were included in the model. When intraspecific competition for seeds is high mice carry seeds far from the mother tree and cache them in areas where the risk of pilfering by conspecifics is relatively low (Den Ouden et al. 2005, Gómez et al. 2008, Puerta-Piñero et al. 2010, Perea et al. 2011).

Management effects on seed dispersal patterns

Mice were able to adapt their behavior to environmental conditions, resulting in different seed dispersal patterns that were similar to field observations. Forest habitat loss had a great effect on seed dispersal kernels as well as on caching rates. When habitat loss occurs two processes take place, intraspecific competition is relaxed and landscape becomes less permeable to mice movements. Despite that local mouse abundance is higher at forest edges (García et al. 1998), increments in acorn production are much higher resulting in lower intraspecific competition for acorns (Morán-López et al. 2015). As a result, rodents invest less effort in moving and caching seeds (Moore et al. 2007). Besides, in fragmented areas predation risks incurred by mice when moving across croplands are particularly high (Tew and Macdonald 1993). Therefore, as habitat loss progresses the benefits of safeguarding caches from competitors by mobilizing seeds outside forest fragments decline and acorn predation rather than caching becomes the dominant strategy (Morán-López et al. 2015). Shrub cover was tightly related to maximum dispersal distances, and to a lesser extent to shape and rate parameter of the dispersal kernel. In the light of the “decision sensitivity test”, shrub encroachment effects on shape and rate parameters may be mediated by its positive effects on local mouse abundance and hence intraspecific competition for acorns. In contrast, its effects on maximum dispersal distances would be mediated by mouse perception of lower predation risks while mobilizing seeds. Likewise, in field studies shrub cover has been found to enhance acorn mobilization distances (Morán-López et al. 2015).

Landscape scenarios- shrub encroachment of dehesas

Dehesas are savanna-like woodlands that cover 3.1 million hectares in the Iberian Peninsula playing an important economic role (reviewed in Campos et al. 2013). Despite of having been considered as sustainable due to their stability over long periods of time, dehesas suffer from chronic tree regeneration failure (Pulido and Diaz 2005). Shrub encroachment has been proposed by several studies as the best way of promoting oak recruitment in this system (i.e. Alberto Ramirez and Diaz 2008, Pulido et al. 2010, Mario 2014). Most of these studies have focused on the role of shrubs in buffering stressful abiotic conditions during early recruitment stages (Smit et al. 2008, Rolo et al. 2013). However, shrubs can also enhance local mouse abundance by providing shelter to rodents (Muñoz et al. 2009). Our model predicts that a high proportion of shrub cover is needed (50-65%) in order to restore dispersal distances and caching rates. Shrub covers below this threshold would be almost ineffective due to non-linear responses. Our model predicts that mice act as seed dispersers only when local mouse abundance and matrix permeability increases greatly in dehesas. This may result from to a very low intraspecific competition for seeds due to the large acorn production of trees. Shrub cover needed to restore moderately efficient acorn dispersal may not be compatible with the exploitation of dehesas since it would dramatically decrease pasture productivity (Rivest et al. 2011). As pointed out in previous work (Ramírez and Díaz, 2007; Díaz 2014), rotation strategies at farm or landscape scales should be developed to integrate regeneration and productive uses of this habitat.

Model limitations and caveats

During simulations mice mobilize seeds following a correlated random-walk depositing acorns along a preferential direction. However, the choice of such direction is random. Previous observational work suggests that wood mice deposit seeds in clumped patterns and it has been suggested that enhanced mobilization distances are related to lower aggregation of caches (Puerta-Piñero et al. 2010). Therefore, mobilization distances could be reflecting both aspects of seed dispersal quality. Nonetheless, it is unlikely that rodents select a preferential direction of seed mobilization irrespectively of habitat characteristics. For instance, in agro-forest systems wood mice preferentially use habitats that ensure food acquisition or encounters with potential mates (Rosalino et al. 2011). Collecting new data that combine tracked mice during the fruiting period and seed deposition patterns are needed to find out if wood mice use preferential seed dispersal paths in highly heterogeneous landscapes. Such data may allow us to parameterize a more realistic movement model that can create anisotropic two dimensional maps of the probability of seed dispersal (see (Santamaria et al. 2007, Rodriguez-Perez et al. 2012).

For the sake of simplicity, our model used randomly distributed shrubs and did not include microhabitat effects on seedling recruitment. However, it is well known that microhabitat of acorn deposition has important effects on post-dispersal predation and seedling dry out (main bottlenecks for acorn-seedling survival in Mediterranean areas (Gómez 2004, Smit et al. 2008). Seed-sowing experiments in different management scenarios that include information about local mouse abundance and acorn production will help to easily include seedling recruitment in the model.

CONCLUSIONS

We developed a model that integrates an individual-based model with a landscape model thanks to the wealth of empirical studies about the main processes involved in holm oak regeneration. We could assess which environmental factors are critical for mouse foraging decisions, estimate the mechanisms underlying forest management effects on such factors and forecast the main behavioral responses of rodents to such changes. Our model is able to predict acorn dispersal patterns in a wide range of management scenarios with a few empirical variables. In fact, the only input variables required by the parameterized model are the proportion of forest habitat within the landscape, the density of stems and the cover of shrubs.

However, despite that recruitment cannot occur without seed arrival, seedling establishment also depends on post-dispersal process like post-dispersal seed predation, seedling survival to summer drought or seedling intraspecific competition (Wang and Smith 2002). Therefore, future work that estimates clumping of dispersed acorns and microhabitat effects on final seed fate will help to evaluate to what extent changes in seed dispersal patterns are reflected in the demographic structure of oak populations.

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APPENDIX

Appendix 4.A.

1.Landscape management effects on local environment

Acorn production-Holm oak acorn production is negatively affected by local intraspecific competition for water sources (Moreno and Cubera 2008, Carevic et al. 2010). In our model, acorn production of individual trees depends on the maximum crop production of the year and the proportion of canopy cover of neighbors within a buffer of 20 m. This approach allows therefore in principle inter-annual variability on acorn production which is a natural process in holm oaks (Koenig et al. 2013).

$$Ap = \begin{cases} 1 & if\ canopy\ cover < 0.25 \\ (1.74 - 2.84 * Cover) * Maximum\ acorn\ production & if\ canopy\ cover \geq 0.25\ and \leq 0.6 \\ 0.1 & if\ canopy\ cover > 0.6 \end{cases} \quad (1)$$

Acorn production (Ap) is represented as a semi-quantitative measure that ranges from 0 to 24 (Koenig et al. 2013, Morán-López et al. 2015). Intercept and slope parameters were estimated empirically with data from a monitoring program (2011-2013) of acorn production in two fragmented landscapes (Morán-López in prep.). Finally, in simulations presented in this paper maximum acorn production is fixed to 10 which is the average of maximum acorn production of eighteen plots monitored from 2011 to 2013 (180 trees; Teresa Morán López, Alicia Forner Sales and Dulce Flores Rentería unpublished data).

Mouse abundance. In forest habitats mouse density depends on the proportion of canopy and shrub cover (Muñoz et al. 2009):

$$Mice\ per\ hectare = Maximum \Big/ (1 + e^{-((canopy+shrubs)-a)/b} \quad (2)$$

In our simulations “maximum” represents the carrying capacity of the system which is fixed to 10 mice per ha (average vales between November and January in Mediterranean areas, (Rosario and Mathias 2004). Parameters a and b were estimated empirically with field data and fixed to 0.16 and 0.07 respectively.

Home range radiuses are fixed to 70 m (Rosalino et al., 2011). However, core areas of home ranges can shrink when mouse densities area high (Godsall et al., 2004) and they overlap more as habitat availability decreases (Tattersall et al. 2001)

$$Corea.area\ radius = \sqrt{{(Area/Mice)}/{\pi}} \quad (3.1)$$

$$Restricted\ radius = Core.area\ \ radius * [(Habitat\ availability * 0.8) + 0.1] \quad (3.2)$$

In eq.3.1 Mice is number of mice in the landscape (mice per hectare* 5.76, eq.2) and Area is the area of the landscape ($5.76 * 10^4$). The center of home range radiuses of mice is placed in their warrens. To avoid unrealistic home-range overlaps, once a warren is created other warrens cannot be located in patches within a restricted area (eq 3.2). In equation 3.2., habitat availability represents the proportion of forest habitat in the landscape. In forest interiors, where habitat availability is 1, maximum overlap of core areas is 10% (Rosalino et al. 2011). In small forest fragments (<0.1 ha) maximum core-areas overlap is about 90%, values comparable to those found in literature (small woodlots after harvest, Tattersall et al. 2001) and reproduces values of mouse abundance similar to those found in small fragments of the study areas (Morán-López et al.

2015). Finally, mice do not place their warrens in open microhabitats. Therefore when fragmentation occurs, mice warrens concentrate in small woodlots and edge areas where mice density is higher (Ylonen et al. 1991, García et al. 1998).

2.Mouse foraging decisions

Mouse foraging decisions occur through three consecutive steps. During the first meters of acorn mobilization mouse decisions are governed by intraspecific competition for acorns. Afterwards, mobilization continues until risk perception exceeds a certain threshold. Finally when acorns are deposited, the decision between predation and seed caching depends on the risk of cache pilferage by conspecifics and the effort invested in seed mobilization (Fig. 4.2B).

Predation in situ- when mice handle an acorn they predate it in situ with a probability of 0.25 (value directly parameterized with field data). No effects of intraspecific competition or shelter availability in “predation in situ” are included in the model because such effects were not observed in the field.

Mouse movement- Mice move following a correlated random walk (Benhamou 1990). The direction (grid) of the first movement is chosen randomly, in the following steps the direction is chosen favoring moves toward grid cells located in line with the previously performed move (Fig. 4A1).

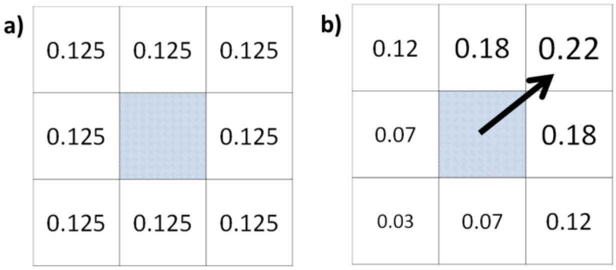

Fig. A1 Probability partition for the correlated random walk for (A) the first step of acorn mobilization and (B) all following steps. The middle cell represents the current position; the arrow indicates the direction of the last move and numbers correspond to the probability of moving

Intraspecific competition for acorns- The importance of intraspecific competition on seed dispersal depends on two parameters, the competition area radius and the probability to stop moving (within the competition area). The competition area radius defines the area in which mouse foraging decisions are driven by intraspecific competition for acorns. Our model assumes some flexibility in the competition area. When inhabiting forest fragments mice are able to use harvested croplands (to a certain extent) despite of their increased predation risks (Tattersall et al. 2001). Therefore, in our model each mouse calculates its competition area radius depending on the amount of cropland within its home range. This way, unrealistic sharp barriers for acorn dispersal in croplands are avoided.

$$Competition\ area\ radius = CR + CR * (proportion\ of\ cropland\ within\ the\ home.range) \quad (4)$$

The parameter CR was determined with pattern-oriented modeling (see Material and Methods).

Within the competition area mouse decide in each movement step whether to stop moving or not. The probability to stop moving depends on the variable competition for acorns (defined as the ratio between potential competitors and acorn production within home-ranges) and is scaled by the weight-ratio that represents the ratio between the average weight of acorns and the average weight of mice:

$$Mouse\ probability\ to\ stop = PS * e^{-Weight.ratio * Competition} \quad (5)$$

In our case the weight-ratio is fixed to 0.1 in *Apodemus sylvaticus* (on the basis of field data; (Morán-López et al. 2015). The parameter PS was determined using pattern-oriented modeling (see 2.3; Material and Methods). In the extreme cases in which no competitors are found within the home range the probability to stop is fixed to 0.6 to ensure that all acorns are dispersed within the core-are of mouse home-ranges. Note that the probability to stop does not change with the distance travelled because it depends on the intraspecific competition within the home-range. However, the probability that a mouse moves i steps decreases with the number i-1 of movements previously done:

$$Prob(reaching)i = (1 - \mathrm{prob.stop})^{i-1} * (\mathrm{prob.stop}) \quad (6)$$

Risk threshold - Once acorns have been mobilized beyond the competition area, risk perception by mice determines the dispersal process. If mice move through risky microhabitats (open land) for more than N_R consecutive movement steps they stop mobilizing the seed. N_R was parameterized through pattern-oriented modeling (see Material and Methods).

Hoarding vs predation- When mice stop mobilizing the seed (either due to low intraspecific competition for acorns or to too high predation risks perceived) they move it to nearby shrubs or tree canopies with probability of 0.7 (estimated from field data). If the microhabitat of all neighbor patches is open land mice just drop the acorn. With this rule we avoid that all dispersed acorns are deposited on open land patches and favor mouse activity in safe microhabitats (Pons and Pausas 2007, Gómez et al. 2008, Perea et al. 2011). At the end of the dispersal process mice can eat or cache the mobilized acorn. Our model assumes that this decision depends on the risk of cache pilferage by conspecifics and the distance travelled. This decision is made in three consecutive steps (Fig 2B). Firstly mice evaluate if they are in an area of high mouse abundance or not (forest edges vs. forest interiors; (García et al. 1998). If they are in forest interiors and acorns have been mobilized beyond the canopy of the source tree the probability of caching an acorn depends on the distance travelled through a saturation curve.

$$Probability\ of\ caching = C1 * \left(1 - e^{(-C2*distance)}\right) \quad (7)$$

In eq.7 the parameters C1 and C2 represent the maximum and the slope of the curve, respectively. Both parameters were calibrated through pattern-oriented modeling (see Material and Methods). This equation reflects that higher dispersal distances enhance caching rates (Morán-López et al. 2015).

If mice are located in areas of high mouse abundance (forest edges, defined by the edge-belt width, EW parameter), our model assumes that acorns mobilized under shrubs or canopies are predated since these microhabitats present high mouse activity which in forest edges leads to an unacceptable risk of cache pilferage (Gómez 2004, Muñoz and Bonal 2011). This model rule captures the observation that despite that many mobilization events end up under shrubs or tree canopies, the probability of acorn caching is much higher in open land microhabitats (Perea et al. 2011, Morán-López et al. 2015). If acorns are deposited on open land microhabitats then the probability of caching depends on distance (eq. 7). The parameter edge-belt width (EW) was calibrated through pattern-oriented modeling (see Material and Methods).

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CHAPTER 5

Functional connectivity on fragmented holm oak woodlands, the importance of local acorn dispersal

Morán-López T.[1], Robledo-Arnuncio J.J.[2], Díaz M.[1], Morales J.M.[3], Lázaro-Nogal A.[1], Lorenzo Z.[2]and Valladares F.[1]

(1) *Department of Biogeography and Global Change (BCG-MNCN). Museo Nacional de Ciencias Naturales, CSIC. c/Serrano 115 bis, 28006 Madrid, Spain.*

(2) *Department of Forest Ecology & Genetics, INIA-CIFOR, Ctra. de la Coruña km*
7.5, 28040 Madrid, Spain.

(3) *Ecotono, INIBIOMA-CONICET, Universidad Nacional del Comahue, Quintral 1250, 8400,Bariloche, Río Negro, Argentina.*

ABSTRACT

Demographic and genetic connectivity of widespread patchy holm oak (*Quercus ilex)* populations will depend on their potential for effective propagule flow across the landscape. Here, we analyzed functional connectivity in a holm oak fragmented landscape by considering three important stages driving recruitment: effective pollination, acorn production and acorn dispersal. We used a network approach to (1) determine if pollen-mediated gene exchange across the landscape was spatially structured; (2) estimate the effects of limited acorn dispersal on functional connectivity; (3) identify which landscape traits drive source-sink dynamics of gene flow.

Despite that long distance dispersal was relatively frequent, most effective pollen flow occurred over short distances (< 100 m).This resulted in a higher gene flow among nearby fragments. Negative edge effects on mouse hoarding activity had a strong impact on landscape connectivity, decreasing immigration rates into forest patches by one order of magnitude. In addition, our results show that big forest fragments (>10 ha) are the main pollen sources, while small ones (<1 ha) are important pollen sinks. Hence, big fragments are critical to maintain functional connectivity, while small forest fragments may provide acorn crops better representing regional genetic diversity. In addition to area effects, isolation and centrality modulated the role of forest fragments within the landscape. In spite of a clear source-sink dynamics, complex interactions between habitat availability, landscape configuration and edge effects call for caution before translating patch-level management guidelines to the landscape scale. Overall our study suggests that costly large-scale conservation strategies to enhance functional connectivity may not be effective if local processes, such as effective seed dispersal, are not explicitly considered.

Key words Quercus ilex, functional connectivity, acorn dispersal, seed dispersal, pollen dispersal

INTRODUCTION

Land use changes have led to the intense fragmentation of many temperate woodland ecosystems, replacing large continuous forests by a mosaic of isolated fragments embedded in agricultural or urban matrices (Riitters et al. 2000). The demographic and genetic connectivity of fragmented plant populations will depend on their potential to effectively disperse pollen and seed across the landscape (Sork et al. 1999, Sork and Smouse 2006). The intensity and scale of seed and pollen dispersal across forest fragments is thus central to the decade-long debate about the extent to which tree populations are resilient to fragmentation (Kramer et al. 2008). High tree genetic diversity and outcrossing rates and extensive long distance pollen movement may buffer the negative effects of forest fragmentation (Hamrick 2004). However, effective seed dispersal limitations can create genetic bottlenecks, because seed dispersal determines plant recruitment patterns, the successful establishment of both male and female migrant gametes, and the final distribution of genotypes (Sork and Smouse 2006). Pollen dispersal sets the template of male gametic gene flow, which necessitates and is subsequently shaped by effective seed dispersal (Fig. 5.1). The negative genetic effects of restricted seed dispersal may counteract the positive ones of extensive pollen flow, potentially jeopardizing the maintenance of genetic diversity in fragmented landscapes (Sork and Smouse 2006, Jordano 2010). Thus, an effective integration of the synergic effects of pollen and seed dispersal is needed in order to gain realism in studies evaluating tree species resilience to fragmentation effects (Sork and Smouse 2006, Bacles and Jump 2011).

Analyzing forest fragmentation effects on tree populations using a metapopulation perspective is a daunting task, given their long life span, delayed maturity, high recruit mortality, and long generation times (Bacles and Jump 2011). Functional connectivity provides a middle way between data-expensive (and sometimes unaffordable) metapopulation models and topological measures not underpinned by biological processes. Using a species-centered approach, functional connectivity measures the extent to which a certain landscape facilitates biological flow among habitat patches (Taylor et al. 1993). In plants, functional connectivity usually refers to demographic and genetic exchange among fragmented populations (Rico et al. 2012). The application of graph theory (reviewed in Laita et al. 2011), together with the development of methods for estimating effective pollen and seed dispersal (Smouse and Sork 2004, Robledo-Arnuncio et al. 2006), has allowed the quantification of functional connectivity (Dyer and Nason 2004, Dyer et al. 2010). This has paved the way for evaluating which factors govern mating patterns and effective pollen- and seed-mediated gene flow at a landscape scale, and to detect genetic bottlenecks on fragmented populations (Fortuna et al. 2008, Dyer et al. 2010, Herrera-Arroyo et al. 2013). However, few studies (if any) have integrated the compound process of pollen movement, effective mating, seed dispersal, and post-dispersal seed mortality when assessing landscape connectivity in plants, even if it is clear that connectivity patterns may be substantially altered when accounting for subsequent recruitment stages (Rico et al. 2012) Fig.5.1

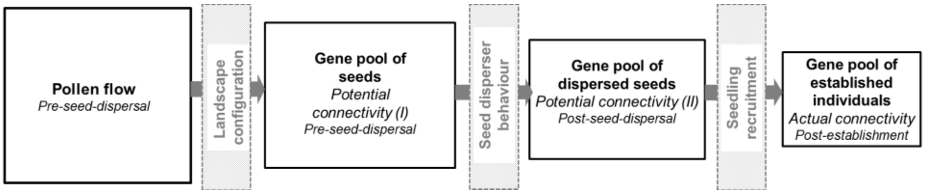

Fig.5.1. Conceptual model of functional connectivity including changes along different recruitment stages (modified from Rico et al. 2012)

Holm oak (*Quercus ilex)* forests are a suitable study system for addressing the effects of limited seed dispersal in functional connectivity. It is a monoecious wind-pollinated, gravity- and animal-dispersed species. Likewise other *Quercus*, holm oaks exhibit leptokurtic distributions of pollen dispersal distances, combining a rapid decay at short-distances with a rather fat tail enabling significant proportion of long-distance mating (Hampe et al. 2013, Ortego et al. 2014a). However, forest management typically hampers effective acorn dispersal (Santos and Telleria 1997, Pulido and Diaz 2005, Morán-López et al. 2015), and thus may compromise the successful establishment of long-distance male gametic migrants. Eurasian jays (*Garrulus glandarius),* the main long distance acorn disperser in Europe, are absent in small forest fragments (Andren 1992, Brotons et al. 2004). Under this scenario, acorn dispersal can be safely assumed to be mostly local, and relies on wood mice (*Apodemus sylvaticus*), a moderately efficient acorn disperser. Most acorns handled by mice remain within close range of mother trees (< 5m), and many of them are finally predated (Gomez et al. 2008). Therefore, functional connectivity of fragmented oak woodlands at a landscape scale will depend on both- effective pollen flow among fragments and subsequent mouse-mediated effective local acorn dispersal. Besides to these theoretical considerations, the study of functional connectivity in holm oak woodlands is interesting from a conservation perspective. It is a widely spread species across the western Mediterranean, where it plays important socio-economic roles over large areas, and most of its forests are heavily altered by habitat loss (Santos and Tellería 1998).

The main goal of this study was to quantify functional connectivity of a holm oak fragmented landscape and detect bottlenecks in gene exchange. For this purpose we built spatial networks of gene flow among forest patches taking into account effective pollination, acorn production and acorn dispersal. This allowed us to (1) gauge if pollen-mediated gene exchange within the landscape is spatially structured; (2) estimate mouse activity effects on functional connectivity; (3) determine which patch traits define source-sink dynamics and (4) evaluate if conclusions drawn from patch-level approaches can be directly scaled up to management guidelines at a landscape scale. We expected (a) a modular structure of the gene exchange network due to a non-negligible amount of local pollen flow (Ortego et al. 2014a) (b) a significant decrease of landscape connectivity due to restricted effective acorn dispersal (Gómez et al. 2008, Rico et al. 2012), (c) an important effect of the area, centrality and isolation of fragments on pollen source-sink dynamics but (d) a not feasible direct implementation of these findings at a landscape scale due to emergent properties in the connectivity network (Baguette et al. 2013).

METHODS

Study area

Field work was carried out in a Holm oak *(Quercus ilex)* archipelago located in the southern plateau of central Spain, near Quintanar de la Orden (39°35′N, 3°02′W, 870 m a.s.l.). Extensive cereal cultivation has reduced forest cover to ≈8%, with patches ranging in size between 0.02 and 793 ha. The dominant tree is holm oak and the understory is composed of shrubby kermes oak (*Quercus coccifera*) and typical shrub species from xeric Mesomediterranean localities (e.g. *Rhamnus lycioides, R. alaternus, Cistus ladanifer, Asparagus acutifolius*). Annual precipitation and mean temperature are 421 mm and 14°C, respectively. We chose this study site because it is representative of holm oak woodlands in central Spain (Santos and Tellería 1998).

Sampling design

In autumn 2012, we simultaneously measured acorn production, acorn dispersal patterns by wood mice (*Apodemus sylvativus)* (Morán-López et al. 2015) and pollen flow. In order to ensure that Eurasian jays could be ruled out from our connectivity analysis we surveyed corvid abundance by walking along trasects of 2 to 5 km stopping every 100 m. Monitoring was performed during the dawn and sunset. . Monitoring was performed during the dawn and sunset. We detected the presence of magpies *Pica pica* and carrion crows *Corvus corone* but not of Eurasian jays. Jay absence from the study area was further corroborated by interviews to farm keepers and local hunters.

We selected three large (> 100 ha) and 10 small (0.05 ha on average) forest fragments. Within large fragments, we defined interior and edge areas considering a 60 m threshold distance to the cultivated border (García et al. 1998). We thus considered three fragmentation categories: large fragment interior, large fragment edge, and small fragment, which allowed us to assess global patterns of acorn production and seed and pollen dispersal taking into account edge effects. We monitored acorn production of 90 focal trees (30 per fragmentation category) and its four nearest mature trees in random directions, whenever possible. We visually estimated acorn crop with a semi-quantitative measure ranging from 0 (no crop) to 4 (more than 90% of canopy producing acorns), acorn score hereafter (Koenig et al. 2013). Acorn dispersal patterns by mice were evaluated in 45 focal trees (15 trees per fragmentation category). In each focal tree we offered 27 acorns to rodents (1250 acorns in total) and we monitored acorn predation, seed movement distances and seed caching microhabitat (see Morán-López et al. 2015 for further details). Finally, to estimate pollen dispersal distances we selected and georeferenced 28 mother trees, collecting young leaves and 15-20 fully mature acorns from each of them (460 seeds in total; see next section).

Pollen dispersal kernel estimation

We used mother-embryo diploid genotypic data and the KINDIST model to estimate the probability density function of pollen dispersal locations from a source tree (pollen dispersal kernel), which was used to parameterize landscape connectivity models. KINDIST relies on the expected decay with distance of a normalized measure of correlated paternity among maternal sibship pairs (Robledo-Arnuncio et al. 2006, Robledo-Arnuncio et al. 2007). To gauge such decay empirically, sampled mother trees should cover as many pairwise-distance classes as possible, from neighboring to long-distance pairs. Guided by this requirement and by viable acorn availability, the 28 sampled mother trees were distributed as follows: 10 in the interior of large fragments, 6 in large fragment edges, and 12 in small fragments. Pairwise inter-mother distances ranged from 4 to 5477 m. We initially intended to estimate a separate kernel for each fragmentation category, since changes in canopy structure associated to fragmentation are expected to alter air movement (and thus pollination) patterns (Dyer and Sork, 2001; Bacles et al. 2005). However, sample sizes were insufficient to achieve good fits (results not shown), so we pooled all 28 mothers together for analysis, yielding a pollen dispersal kernel averaged over fragmentation categories.

Acorns were soaked for 24 hours and then placed in a germination chamber. Because some acorns contained not viable embryos, the final number of offspring per mother was 12 ± 0.32 (mean±S.E). We used Invisorb DNA Plant HTS 96 Kit/C to extract and purify genomic DNA from adults and progeny. A total of ten nuclear microsatellites transferred from other *Quercus* species were used to genotype all mothers and embryos (see table 5.A1). Primers were dyed labeled (FAM, PET, VIC, NED) and DNA was amplified following (Ortego et al. 2014). Amplification products were sent to an ABI Genetic Analyzer (ABI, St. Louis, MO) and genotypes were scored using Genemarker (Holland and Parson 2011).

The rank correlation coefficient between correlated paternity and inter-mother distance was negative and significant ($r_s = -0.13$; $p<0.01$), meeting the minimum requirements to estimate the pollen dispersal kernel with POLDISP software (Robledo-Arnuncio et al. 2007). We fit a two-parameter, two-dimensional exponential-power pollen dispersal kernel (Clark 1998, Austerlitz et al. 2004):

$$P(r|a,b) = \frac{b}{2\pi a^2\,\Gamma(2/b)}\exp(-({}^{r}/_{a})^{b}) \quad \text{eq.1}$$

where r is the pollination distance, Γ is the gamma function, b is the shape parameter, and a is the scale parameter. Two-parameter dispersal kernels allow estimating the kurtosis and the shape of the tail of the distribution of dispersal distances (Austerlitz et al. 2004). The effective number of pollen donors was estimated as the inverse of likelihood that two randomly selected offspring from a single mother share the same father (Ne = 1/rp) (Ritland 1990). It was calculated separately for trees located at small and big forest fragments. See Appendix 1 for further details on pollen dispersal kernel estimation.

Design of landscape connectivity network

We constructed the functional connectivity network of our landscape through three consecutive steps:(1) computation of expected pollen migration rates among fragments, based on the empirically estimated pollen dispersal kernel; (2) simulation of the number of acorns produced and the realized number of effective pollination (mating) events within fragments and among fragment pairs, given the expected pollen migration rates; and (3) simulation of dispersed acorn caching (*vs* predation) rates by rodents.

Expected pollen migration rates

A digital ortophotography of the study area (20 x 7.2 km) was used to create a gvSIG shape file (Steiniger and Hay 2009) of all fragments. For each forest fragment, we calculated its centroid, area and perimeter. There were 401 forest fragments in the study area, ranging from 0.02 to 793.52 ha. The shape file was then imported to Netlogo and rasterized (Wilensky 1999). Final pixel size was 20x20m (1000x360 pixels within the landscape) and each pixel contained information of its habitat (cropland vs forest) and the forest fragment it belonged to.

For each pair of fragments *i* and *j*, we defined the expected pollen migration rate from *j* to *i* (M_{ij}) as the probability that an acorn produced by a mother in the *i*-th fragment has been fertilized by pollen dispersed from the *j*-th fragment (see Fig.5.2), which was calculated as

$$M_{ij} = \frac{1}{n_{\chi_i}} \sum_{\chi_i=1}^{n_{\chi_i}} m_{\chi_i,j} = \frac{1}{n_{\chi_i}} \sum_{\chi_i=1}^{n_{\chi_i}} \left(\frac{\sum_{\chi_j=1}^{n_{\chi_j}} P_{\chi_i\chi_j}}{\sum_{k=1}^{K} \sum_{\chi_k=1}^{n_{\chi_k}} P_{\chi_i\chi_k}} \right) \qquad \text{eq. 2}$$

where $P_{\chi_i\chi_j}$ is the probability of pollen transport between the centres of recipient pixel χ_i and source pixel χ_j (from the *i*-th and *j*-th fragments, respectively), given by the assumed pollen dispersal kernel (eq. 1); and where n_{χ_i} is the total number of pixels in the *i*-th fragment and *K* the total number of fragments. Note that the term $m_{\chi_i,j}$ is the probability that an acorn produced by a mother in the χ_i-th pixel of the *i*-th fragment has been fertilized by pollen dispersed from (any of the pixels of) the *j*-th fragment, and thus that M_{ij} is calculated as an average probability of pollen immigration from fragment *j* across all pixels of the recipient fragment *i*, accounting for edge effects. Note also that M_{ii} yields the probability of local mating within the *i*-th fragment. All the M_{ij} values are stored in the *K* x *K* matrix **M.**

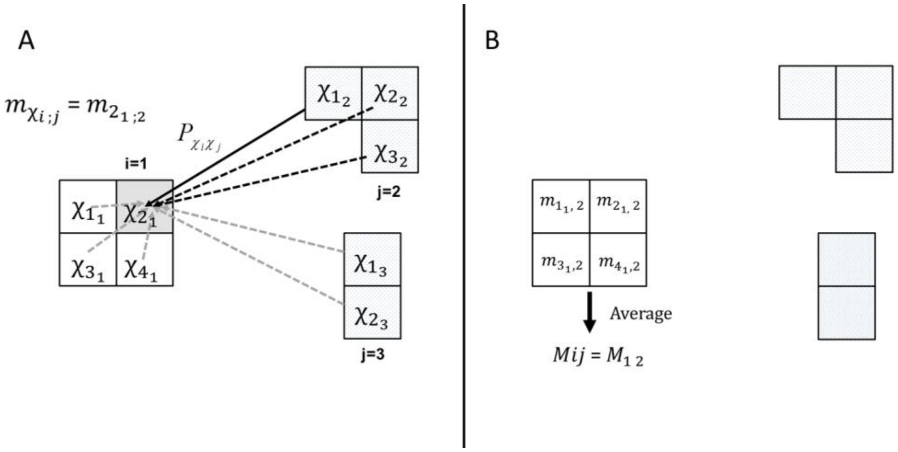

Fig.5. 2. Theoretical landscape with three forest fragments in which migration rates of pollen from forest fragment 2 to fragment 1 is calculated. In the first step (A) $m_{\chi_{1;2}}$ is calculated for all pixels of fragment 1 taking into account pollen flow from all potential sources; in a second step (B) average migration rates of pixels in fragment 1 are calculated to obtain the global migration rate from fragment 2 to fragment 1 (M_{12}). $P_{\chi_i\chi_j}$ represents the probability of arrival of pollen which depends on the dispersal kernel. $m_{\chi_i,j}$ is the probability that an acorn produced in pixel qr of fragment i is fertilized by a grain of pollen coming from pixel qe of fragment j. Mij is the average migration rates of pollen from fragment j to fragment i.

Simulating acorn production and mating events

We estimated acorn production at the landscape scale in 2012. Each pixel was assigned to one of the three forest fragmentation categories. The number of acorns produced in the *i*-th fragment ($Prod_i$) was estimated as:

$$Prod_i = \sum_{\chi_i=1}^{n_{\chi_i}} Prod_{type,\chi_i} \times 28.75 \times (\pi 2.5^2) x\, 5 \qquad \text{eq. 3}$$

where $Prod_{type,\chi i}$ is the obtained average semi-quantitative field measure of acorn production (see above) for the fragmentation category of the χ_i-th pixel of fragment *i* (1.28±0.03, 2.28±0.07 average acorn score of forest interior and edges respectively; N=171 and N=153 trees respectively); 2.5 is the average canopy radius in our study area (±0.01 m; N= 96; 32 per fragmentation category), 5 is the estimated number of stems per pixel (corresponding to an average stem density of 125 stems/ha). The constant 28.75 converts the semi-quantitative acorn score data into acorns per square m of canopy projection, following the regression study by Díaz et al. (2011) in the National Park of Cabañeros during 2008-2010, who obtained the equation acorns/m^2 = 28.75* acorn score ($p<0.01$, R^2= 0.87). .

The mating network was then constructed by simulating acorn fertilization. For each (recipient) forest fragment, we generated the number of acorns sired by pollen donors from each of the potential *K* (source) fragments by randomly drawing from a multinomial distribution with *K* classes with probabilities given by vector **M**[*i*,], and $Prod_i$ trials. We used multinomRob package for this purpose (Walter R. Mebane 2013). This way, we constructed a mating network in which the expected link weights corresponded to expected pollen migration rates (eqn. 2). By replicating realized numbers of mating events using the multinomial distribution (rather than the multinomial frequencies themselves), we could assess the sensitivity of network structure to stochastic mating, conditional on differences in acorn production (including acorn limitation) and caching rates between fragmentation categories.

Simulating acorn caching vs predation

We obtained average acorn caching rates per fragmentation category from our field acorn predation/removal experiments. We calculated the number of acorns cached per fragment using the equation:

$$Cached_i = \sum_{\chi_i=1}^{n_{\chi_i}} Prod_i \times Cached_{type,\chi_i} \quad \text{eq.4}$$

in which $Cached_i$ is the estimated number of acorns cached in a pixel of forest fragment i, $Cached_{type,\chi i}$ is the caching rate corresponding to the fragmentation category of the χ_i-th pixel of the i-th fragment (0.12±0.05 large fragment interior; 0.09±0.03 large fragment edge; 0.02±0.01 small fragment). $Prod_i$ is acorn production, as calculated using eq.3.

The post-acorn-dispersal (effective) mating network was built in the same way as the pre-acorn-dispersal mating network, but using $Cached_i$ (instead of $Prod_i$) as the number of trials of the corresponding multinomial for the i-th fragment. In this case, the weights of network links (i, j) corresponded to migration rates after mouse activity (fig.1), i.e., the proportion of acorns cached within fragment i that were fertilized with pollen from fragment j.

Quantifying network structure

We explored the structure of the two mating networks (before and after acorn dispersal) by constructing 100 replicates for each and performing modularity analyses. For each network, we calculated the following parameters of functional connectivity: (1) connectance, defined as the ratio between the number of realized links and the number of possible links; (2) number of isolated (unconnected) patches; (3) modularity of the network (raw and relative; see below); (4) number of modules; (5) mean number of nodes per module; (6-7) minimum and maximum module size; and (8) mean immigration rates.

The modularity function (M) determines if the network is organized in well-defined separate modules, and was calculated using Newman and Girvan (2004) algorithm, as implemented in the igraph R package (Csardi 2006):

$$M = \sum_{s=1}^{Nm} \left[\frac{ls}{L} + \left(\frac{ds}{2L} \right)^2 \right] \quad \text{eq. 5}$$

where *Nm* is the number of modules, *L* is the number of links in the network, *ls* is number of links between nodes in module *s*, and *ds* is the sum of degrees (total number of links) of module *s*. A higher modularity implies that the density of links inside each module is higher than that expected from the total number of links. In our case, it implies an uneven distribution of among-fragment effective pollination within the landscape. To test the significance of modularity we compared the observed M value with values of 100 randomization of the network, keeping the same connectance, (Guimera and Amaral 2005) using the package tnet (Opsahl 2009). The modularity of the networks depends on their connectance and hence, to control for this difference when comparing modularity between networks, we calculated relative modularity following (Fortuna et al. 2008).

$$M^{*} = {(M_{real} - \bar{M}_{random})}\Big/{\bar{M}_{random}} \quad \text{eq. 6}$$

Wilcoxon rank sum tests were used for comparing topological parameters (connectance, relative modularity, number of isolated nodes etc.) between pre- and post-acorn-dispersal mating networks. To compare immigration rates we used generalized binomial regression models (link logit). Besides, to evaluate the impact of seed dispersal by mice on functional connectivity (Fig. 5.1), we calculated the percentage of variation between pre- and post-acorn-dispersal mating networks for each parameter *P* ($\Delta_{pre\text{-}post}$).

$$\Delta_{pre-post} = \left(\frac{P_{pre} - P_{post}}{P_{pre}}\right) \times 100 \quad \text{eq. 7}$$

Factors determining effective pollen source-sink dynamics

We evaluated which factors determined the role of forest fragments as sources and/or sinks of effective pollen across the landscape (i.e. source *vs* sink nodes within the network). Our response variables were immigration and emigration rates and the degree of the fragments within the network. The degree of a node is defined as its number of outgoing and ingoing links, which in our case translates into the number of source or recipient fragments exchanging effective pollen with the target fragment. We divided out forest fragments into five size categories: ≥

100, [10, 100), [1, 10), [0.1, 1) and ≤ 0.1 ha. Our fixed effects were fragment area, distance to the center of the archipelago, mean distance to other forest fragments (isolation) and their interaction. Distance to the center of the archipelago and isolation were not correlated ($P = 0.22$, Pearson correlation = -0.06). We used generalized quasibinomial and quasipoisson models for the analysis of migration rates and fragment degrees, respectively.

Scaling up to regional-scale management from patch-level measures

To explore whether the aforementioned fragment-level analyses can be extrapolated to landscape management guidelines, we generated six alternative landscape scenarios: (1) Control landscape, in which the centroid and the area of forest fragments are equal to those of the real landscape; (2) Area reduction landscape, in which the area of large forest fragments (>10 ha) is reduced by 10%; (3) Uniform landscape, in which centroids of large forest fragments are uniformly distributed within the landscape, while keeping the same area; (4) Clumped landscape, in which centroids of big fragments are aggregated in the center of the archipelago following an exponential decay function; (5) Combined uniform and area reduction landscape (6) Combined clumped and area reduction landscape. The first step of landscape generation was to locate the centroid of the fragment in a pixel, and then forest habitat spread to neighbor cells until a certain area was reached producing a tumor-like shape. In order to avoid shape effects in our connectivity analysis the control landscape was created. A 10% of area reduction corresponds to reported values of habitat loss (per decade) in evergreen woodlands of the Iberian Peninsula (Costa et al. 2014). In the six landscape scenarios we built a pollen network following the same protocol as for the real landscape. Then, we calculated functional connectivity parameters of each theoretical network and compared them with the control (Δcontrol $_{\text{landscape}}$).

To assess the impacts of enhanced caching rates on the maintenance of landscape connectivity, we built two post-acorn-dispersal mating networks in the control landscape: a control one, in which caching rates were the same as those observed in the study area and an alternative increased-caching network in which caching rates were fixed to 0.17 for all pixels, which corresponds to caching rates observed in the interior of well-preserved forests (Morán-López et al. 2015). As before, we calculated landscape connectivity parameters and compared them between both caching scenarios (Δcontrol $_{\text{increased}}$).

RESULTS

Structure of pollen and acorn-dispersal networks

The estimated dispersal kernel was fat-tailed (b= 0.16) which lead to a very high average pollen dispersal distance (1148.68 m). However, it was highly positively skewed and most of pollen dispersal occurred within the neighborhood (< 100 m, Fig. 5.A1). Effective pollen movement across the landscape was significantly modular, both for the pre- and post-acorn-dispersal networks (Table 5.1). In the pre-acorn-dispersal mating network, Newmans' algorithm detected an average of seven modules over independent replicates, of highly variable size (ranging from 5.87 - 129.66 nodes per module, Fig 5.3A). Almost no isolated fragments were detected in any of the replicates of the network, even if only 22% of potential links between fragments were realized on average (Table 5.1).

Post-acorn-dispersal mating network was globally less connected (-36.62%), more spatially structured (61.62%), and with one order of magnitude lower immigration rates, relative to the mating network before seed dispersal (Table 5.1). Besides, the probability distribution of effective pollen immigration rates became substantially positively skewed after acorn dispersal, with one third of fragments showing very low (≤2 %) immigration rates (Fig. 5.3B, 5.3C). Overall, post-seed-dispersal demographic filters resulted in a more labile effective mating network, due to the disappearance of low probability links and a lower strength of the remaining ones.

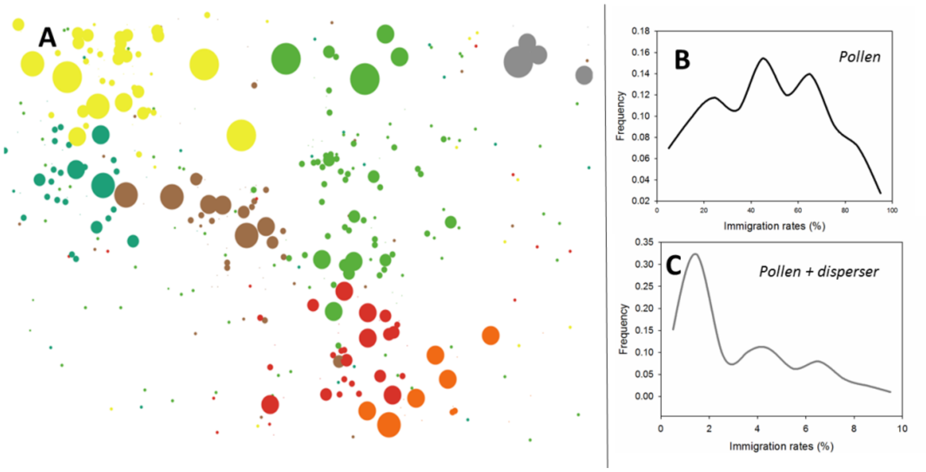

Fig.5.3 (A) Modular organization of the pollen network of *Quercus ilex* population (pre-acorn-dispersal). Nodes represent forest fragments. Each color depicts a module detected by the algorithm (areas of higher estimated gene flow). (B-C) Frequency distribution of immigration rates of the pre and post-acorn-dispersal networks.

Table 5.1. Summary of modularity analysis on pre-acorn-dispersal and post-acorn-dispersal network. Abbreviations: Connect. – connectance, Isol. – number of isolated patches; Mod- Newmans' modularity, S. – significance of the modularity of the network , M* - relative modularity, Nmod- number of modules of the network, $\overline{N}$ −average number of nodes per module, Min.Max – minimum and maximum number of nodes per module respectively, Mig.- immigration rates (%, with respect to acorns produced). Δpre-post- percentage of variation between pollen-mediated network and that filtered by mouse activity (pre and post-acorn-dispersal network, respectively). Significant results are in bold.

Network	**Filter**	**Connec.**	**Isol.**	**Mod**	**S**	**M***	**Nmod**	$\overline{N}$	**Min**	**Max**	**Mig.**
Pre-acorn dispersal	Landscape	0.22±0.00	0±0.00	0.47±0.00	**	0.91±0.00	6.88±0.22	62.63±1.49	5.87±0.18	129.66±0.81	46.64
Post.acorn -dispersal	Acorn predation	0.14±0.00	0±0.00	0.51±0.00	**	1.47±0.01	6.97±0-23	63.15±1.81	5.82±0.16	109.61±3.30	3.11
Δpre-post		**-36.62****	--	--	--	**61.62****	1.30	0.83	-0.85	**-15.46****	**-93.32****

Factors determining effective pollen source-sink dynamics

Considering first the pre-acorn-dispersal mating network, we found that big fragments (>10 ha) acted predominantly as sources of effective pollen, while small forest fragments (<0.1 ha) were mostly effective pollen sinks (Fig.5. 4A and B, grey bars). Fragment area positively affected the number of ingoing and outgoing links, though this effect was weak (Fig. 5.4C and D, grey bars), resulting in a lower link number to fragment area ratio in big forest fragments (mean±s.e. links per pixel, 17.69±1.14 and 0.01±0.00 in fragments <10 ha and >100 ha respectively). In agreement with these results, number of effective pollen donors was much higher in trees located at small forest fragments than those from big ones (32.29±9.74 *vs* 12.66±1.95 in small and big forest fragments respectively). Pollen emigration rates and the degree of fragments also depended on their spatial configuration. More isolated stands donated less pollen and to a lower number of neighbor fragments. In addition to isolation, distance negatively affected the number of ingoing and outgoing links. In general, spatial configuration effects were stronger in smaller fragments (Table 5.2, pre-acorn-dispersal network).

Considering now the post-acorn-dispersal mating network (Fig. 5.4 black bars), results were similar in terms of emigration rates and fragment degree (in and out). However, immigration rates showed a bell-shape response (Fig. 5.4A, black bars). Medium size fragments showed the highest immigration rates. In fact, as a consequence of strong post-dispersal seed mortality, small forest fragments showed rather low effective pollen immigration rates (<2%), relative to the high proportion of immigrant pollen at the seed-crop stage (>60%).

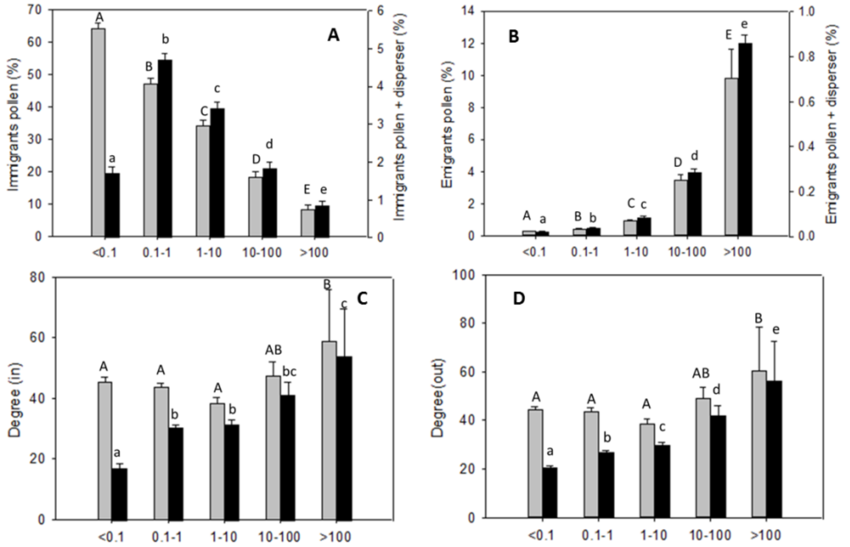

Fig. 5.4 Area effects on (A) Immigration and (B) emigration rates; (C) links arriving to the fragment (degree in); (D) links emerging from the fragment (degree out). Grey and black bars represent pre and post-acorn-dispersal network respectively. Letters represent groups of Tukey test (capitals- pre-acorn-dispersal, lower case- post-acorn-dispersal). Note that the axes of immigration and emigration rates have different scale for each network.

Table 5.2. Effects of patch area distance to the center of the archipelago and isolation on – immigration and emigration rates, number ingoing and outgoing links. Only significant effects are shown. Abbreviations: LRT- Likelihood ratio test, df- degrees of freedom, Sign- sign of the effect.

Network	Response	Effect	LRT	df	Sign	pseudoR2
Pre-acorn-dispersal (pollen)	Immigration rates	Area	4152.20	4	-	0.91
	Emigration rates	Area	1018.06	4	+	0.77
		Isolation	16.05	1	-	
		Area*Isolation	10.88	4	-	
	Degree(in)	Area	20.45	4	+	0.30
		Distance to center	87.00	1	-	
		Isolation	41.24	1	-	
		Area*Distance	9.12	4	-	
		Area*Isolation	15.00	4	-	
		Distance*Isolation	12.05	1	+	
	Degree(out)	Area	29.51	4	+	0.18
		Distance to center	42.92	1	-	
		Isolation	96.8	1	-	
		Area*Distance	11.36	4	-	
		Area*Isolation	15.75	4	-	
		Distance*Isolation	12.11	1	+	
Post-acorn-dispersal (pollen+mice)	Immigration rates	Area	5093	4	-/+	0.92
	Emigration rates	Area	1164.31	4	+	0.79
		Distance	3.69	1	-	
		Isolation	18.63	1	-	
		Area*Isolation	15.24	4	-	
	Degree (in)	Area	1141.54	4	+	0.29
		Distance	25.36	1	-	
		Isolation	12.00	1	-	
		Distance*Isolation	5.81	1	+	
	Degree(out)	Area	165.89	4	+	0.35
		Distance to center	34.95	1	-	
		Isolation	23.28	1	-	
		Area*Distance	33.25	4	-	
		Area*Isolation	14.17	4	-	

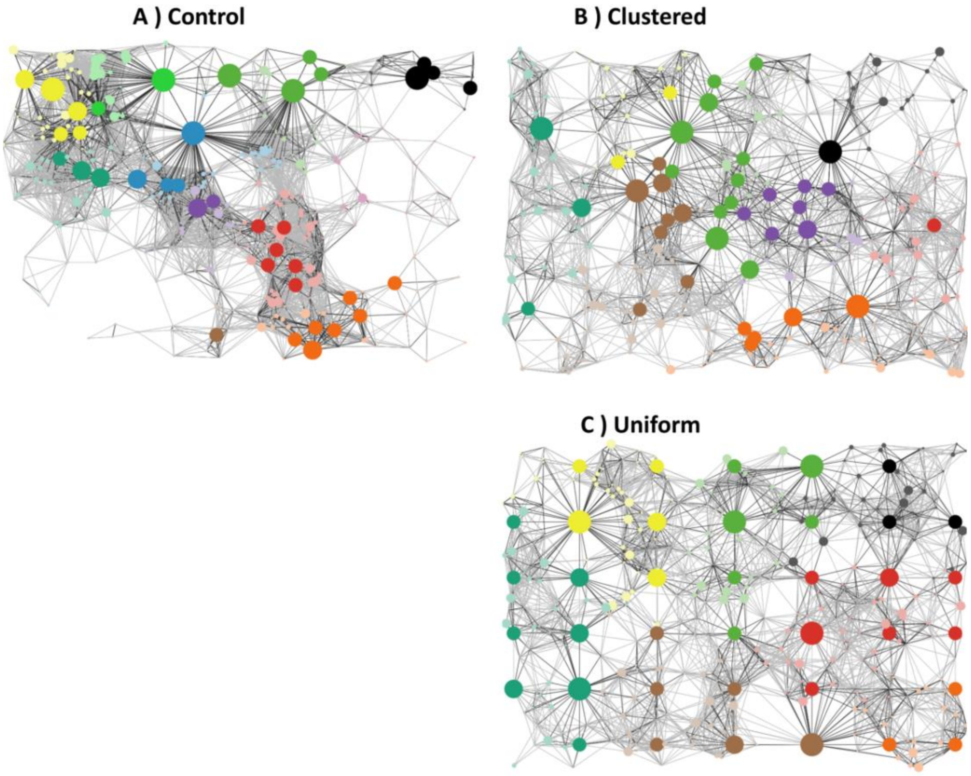

Fig 5.5. Modular organization of the landscape connectivity in theoretical landscapes. Nodes represent forest patches (N = 401; > 10 ha in matt color, <10 ha transparent color). Each color represents a module (group of patches highly connected detected by Newmans' algorithm). Lines indicate links between fragments mediated by pollen flow (darkness of grey color is proportional to migration rates of the link). (A) Control landscape preserving centroid of fragments and their area (B) Clumped landscape, centroids of big fragments are aggregated in the center of the archipelago following an exponential decay function (C) Uniform landscape, centroids of large forest fragments are uniformly distributed within the landscape

Scaling up to regional-scale management from patch-level measures

A 10% area reduction of large fragments (>10 ha) in the control landscape resulted in a lower number of links within the mating network (-9.36%), smaller modules (-6.99%) and weaker links (-3.13%). However, the modular structure of the network did not change significantly, as indicated by the relative modularity index (Table 5.3, see area reduction landscape). Contrary to our expectations, both clumped and uniform spatial distributions of large forest fragments negatively impacted landscape connectance (–36.60 and –33.99% respectively) and average immigration rates (–24.6 and –16.7%, respectively). However, links were more homogeneously distributed across the landscape (Fig. 5.5), resulting in a reduction of network modularity (–49.59 and–52.88% respectively). Besides, the size of the smallest modules was about three times larger (2.87 and 3.20, respectively) (Table5.3, clumped and uniform landscapes). Superimposing a fragment area reduction to the clumped or uniform landscapes had low additional impact on observed parameter changes (Table5.3, Uniform area and Clumped area landscapes).

The simulated enhancement of acorn caching rates fostered all connectivity parameters. It increased network connectance (15.51%), decreased the number of isolated patches decreased down to about 1 (*vs* 7 in the control network), and increased immigration rates by a factor of two (2.35% vs 5.15%). Besides, increased effective acorn dispersal relaxed the modular structure of the network (-8.99%), with bigger modules (12.33%) and in particular significantly larger size for the smallest module (100.36%) (Table 5.3, Increased caching effect).

Table 5.3. Landscape configuration effects on- connectance (Connect), number of isolated patches (Isol.), raw modularity (Mod), relative modularity (M*), number of modules (Nmod), mean number of nodes per module ($\bar{N}$), number of nodes of the smallest module (Min), number of nodes of the biggest module (Max) and migration rates (Mig.). Δcontrol $_{\text{lands.}}$ - percentage of variation of pre-acorn-dispersal network with respect to the control landscape, Δcontrol $_{\text{increase.}}$ percentage of variation between post-acorn-dispersal and increased-caching network in the control landscape. Significant differences are in bold. * p<0.05, ** p<0.05. S. depicts the significance of modular structure of the landscape in relation to null networks (see text.). Pre-disp (pre-acorn-dispersal network), post-disp (post-acorn-dispersal network)

Effect	**Landscape**	**Analysis**	**Connect.**	**Isol.**	**Mod**	**S.**	**M***	**Nmod**	$\bar{N}$	**Min**	**Max**	**Mig.**
No effect	Control	Pre-disp.	0.14	0.00	0.62	**	1.45	9.39	45.47	8.739	89.31	30.27
		Post-disp.	0.10	7.23	0.63	**	1.79	11.19	36.63	2.78	84.45	2.35
Area	Area reduction	Pre-disp.	0.12	0.03	0.63	**	1.45	9.88	42.29	10.10	91.41	29.33
		Δcontrol$_{\text{lands.}}$	**-9.34****	--	--	--	-0.04	5.16	**-6.99***	15.74	2.35	**-3.13****
Configuration	Clumped	Pre-disp.	0.09	0.00	0.63	**	0.73	8.59	48.86	25.95	72.49	22.83
		Δcontrol$_{\text{lands.}}$	**-36.30****	--	--	--	**-49.59****	**-8.56****	**7.43***	**197.34****	**-18.84****	**-24.6****
	Uniform	Pre-disp.	0.09	0.00	0.66	**	0.68	7.87	54.64	27.87	79.96	25.22
		Δcontrol$_{\text{lands.}}$	**-33.99****	--	--	--	**-52.88****	**-16.22****	**20.16****	**219.34****	**-10.47****	**-16.7****
Configuration & area	Clumped Area	Pre-disp.	0.09	0.00	0.61	**	0.65	8.64	49.18	24.38	72.30	21.12
		Δcontrol$_{\text{lands.}}$	**-34.54****	--	--	--	**-55.36****	**-8.03***	**8.14***	**179.35****	**-19.05****	**-30.23****
	Uniform Area	Pre-disp.	0.09	0.00	0.66	**	0.69	7.15	59.01	21.76	90.10	24.45
		Δcontrol$_{\text{lands.}}$	**-31.23****	--	--	--	**-52.11****	**-23.88****	**29.77****	**149.37****	0.88	**-19.43****
Increased caching	Control	Post-disp	0.12	0.84	0.63	**	1.63	10.13	41.15	5.57	82.43	5.15
		Δcontrol$_{\text{increas.}}$	**15.51****	**-88.38****	--	--	**-8.99****	**-9.47****	**12.33****	**100.36****	-2.39	**118.88****

DISCUSSION

This study aimed at analyzing functional connectivity in a holm oak fragmented landscape taking into account three important recruitment processes: effective pollen dispersal, acorn production and local acorn dispersal. Thanks to an extensive monitoring program of different aspects of fragmentation effects on holm oaks regeneration potential (Valladares et al. 2014), we could include in our connectivity networks processes that depend largely on the spatial configuration of forest patches (e.g. effective pollen dispersal rates) with others that are greatly influenced by edge effects (e.g. acorn predation rates). Our results show that limited seed dispersal can override extensive pollen flow jeopardizing landscape connectivity. Hence, effective seed dispersal needs to be integrated in large scale agro-environmental schemes.

As expected, effective pollen flow within the landscape was spatially structured. Likewise other *Quercus* species (Streiff et al. 1999, Pakkad et al. 2008, Pluess et al. 2009), most mating events occurred within the neighborhood, while showing at the same time a fat-tailed distribution. The modular structure of our mating network implies that there are landscape subareas within which effective pollen exchange is substantial and that show comparatively less frequent mating with other subareas. Decreased rates of effective local seed dispersal had a great impact on the landscape reproductive connectivity, diminishing the robustness of the mating network modules. Not only the number of connections in the mating network decreased after accounting for post-dispersal seed mortality, average effective pollen immigration rates were overall an order of magnitude lower. In line with previous work, our results show that limited acorn dispersal can have pervasive effects on the maintenance of reproductive and genetic connectivity of fragmented oak populations (Fernandez-M and Sork 2007, Grivet et al. 2009, Luisa Herrera-Arroyo et al. 2013). As pointed out by Ortego (2014), ecological factors such as poor recruitment, rather than restricted pollen flow, may be behind the reduced genetic diversity of younger cohorts of fragmented and savanna-like holm oak forest stands (Ortego et al. 2010) .

The role of forest fragments in the mating network was firstly determined by their area and secondly by their spatial distribution. Big fragments (>10 ha) were the main sources of effective pollen, enabling mating and thus pollen gene flow among fragments across the landscape. This result suggests that the system may become more genetically disjoint and fragile if a minimum number of large oak woodlands are not preserved. On the contrary, small forest fragments (<1 ha) acted as major pollen sinks, showing the highest effective pollen immigration rates. Likewise other anemophilous species, our model predicts that as population size decreases the paucity of local mating neighbors results in higher immigration rates, as a consequence of the mass-action law (reviewed in Sork and Smouse 2006)). In addition to the amount of immigrant pollen, the diversity of sources is important in maintaining the genetic diversity of the acorn pool. Although bigger fragments received migrant pollen from a higher number of external sources, the number of external pollen sources per area unit was larger for smaller fragments. Thus, individual trees within large fragments sampled less diverse pollen clouds. Despite that it has been advocated that small fragmented populations should be avoided in seed-collection management practices, due to impoverished genetic diversity of seed pools (Breed et al. 2013), our results suggest that potential trade-offs between fewer effective mothers and more effective fathers need not invariably result in reduced seed pool genetic diversity, a matter that deserves further empirical consideration. After seed dispersal, however, our results also showed that negative edge effects on acorn caching (a *proxi* for effective recruitment) may substantially reduce effective pollen immigration rates into small fragments. This could explain why previous empirical studies have shown extensive pollen flow but reduced genetic variability of oak seedlings established within fragments (Fernandez and Sork 2005, Fernandez-M and Sork 2007, Ortego et al. 2010, Ortego et al. 2014).

In addition to area effects, the spatial distribution of forest fragments across the landscape modulated the number of ingoing and outgoing links, as well as effective pollen migration rates. As would be expected, forest patches located in central areas and less isolated received pollen from a greater number of pollen sources and acted as more important pollen sources within the network. This suggests that a uniform or a clumped distribution of large forest fragments would enhance landscape connectivity. In the former case, gene flow would be more evenly distributed across the landscape. In the second one, a large central core area with a high number of patches and redundant connections would be created. However, functional connectivity may emerge from a complex interplay between habitat availability and landscape topology (Minor and Urban 2008, Laita et al. 2011, Baguette et al. 2013).

By simulating gene flow in theoretical landscape scenarios we were able to test whether fragment-level analyses can be directly scaled up to landscape management guidelines. In relation to area effects, the mating network was quite resilient to a ten percent area reduction of big forest fragments, even if the latter act as landscape hubs. Such an area decrement corresponds to reported values of habitat loss (per decade) in evergreen woodlands of the Iberian Peninsula (Costa et al. 2014). Although reproductive connectivity may not be disrupted by such an habitat loss, it is important to bear in mind that acorn dispersal limitations may be exacerbated by increasing edge areas (Costa et al. 2014, Morán-López et al. 2015). As expected, the spatial arrangement of large forest fragments significantly impacted the functional connectivity of the network. However, not all the effects followed the expected trend of landscape connectivity enhancement. For instance, a uniform distribution of large forest fragments decreased the modularity of the network and increased the size of the smallest module, but diminished the number of connections among patches and average immigration rates. Similar results were obtained in the clumped landscape scenario. Overall, these results suggest that translating patch-centered approaches into conservation planning strategies may not be straightforward, due to the interaction between landscape configuration, habitat availability and edge effects. On the contrary, caching rate enhancement in edge areas improved all connectivity parameters. Process-based models, like our network approach, can help to evaluate the potential effectiveness of costly, large scale conservation measures before their implementation (Bolliger et al. 2014, Humphrey et al. 2015). Besides, they draw the attention to the potential of local management practices in the maintenance of functional connectivity at the landscape scale.

Our network approach allowed us to evaluate concomitantly pollen and seed dispersal considering the structure of the entire landscape. However, several simplifying assumptions should be acknowledged. Due to sampling limitations, we estimated a single global pollen dispersal kernel, without considering potential variation in pollen movement probabilities associated with local heterogeneity in vegetation structure or wind direction. Therefore, our model could be underrating pollen flow in open areas or along certain directions (Robledo-Arnuncio et al. 2014). However, estimated pollen dispersal distances and simulated immigration rates were comparable to those found in previous studies developed in a variety of landscape scenarios and *Quercus* species (Streiff et al. 1999, Nakanishi et al. 2004, Pakkad et al. 2008, Pluess et al. 2009, Gerber et al. 2014, Ortego et al. 2014a). For the sake of simplicity, we did not include differences in male fecundity among individuals in our model. This assumption should not have biased our pollen dispersal kernel estimation, since the employed method has been shown to be accurate under non-uniform fecundity scenarios (Robledo-Arnuncio et al. 2006). The sensitivity of the mating network topology to potential variation in male fecundity among fragmentation categories, or across space, is more difficult to predict, and would be worth exploring theoretically and empirically. We additionally assumed that fragmentation did not induce pollen limitation. It is not clear whether pollen availability is a limiting factor of acorn production as density decreases in holm oak stands (Garcia-Mozo et al. 2007, Ortego et al. 2014), but the positive edge effect on acorn production observed in our study area may suggest that this is not the case in our landscape. Our model did not include fragmentation effects on seedling establishment, even if cropland ploughing will reduce recruitment success in edge areas and may act as a subsequent filter in functional connectivity (Fig 5.1). However, we were interested in evaluating the endogenous potential of patchy woodlands to maintain genetic connectivity. The massive disappearance of emerging seedlings due to ploughing would make unfeasible to tease apart differences in recruitment driven by changes in disperser behavior from purely anthropogenic impacts. Acorn tracking experiments in abandoned croplands would help to incorporate edge effects on potential seedling recruitment in the model. Finally, in long lived species like holm oaks, the contribution of individuals to population demography and genetics occurs over decades. Albeit our network approach is based on extensive field data, it is temporally fine-scaled and hence it is difficult to evaluate the overall impact of fragmentation on the long term population structure and dynamics. For instance, although seedlings of managed holm oak woodlands show lower genetic diversity (Ortego et al. 2010), recent studies suggest that long distance dispersal may prevent genetic erosion in extremely isolated populations (Hampe et al. 2013). Future approaches that include mechanistic demographic and genetic approaches will help to scale up our findings (Robledo-Arnuncio et al. 2014).

CONCLUSIONS

Our approach allowed us to evaluate fragmentation effects on pollen gene flow taking into account complex interactions between landscape configuration, habitat availability and edge effects. Our results showed that limited seed dispersal can constrain genetic cohesiveness of fragmented populations despite of extensive pollen flow. Besides, they suggest that the preservation of big forest fragment is essential to maintain functional connectivity, as they act as predominant pollen sources. By contrast, small forest fragments acted as pollen sinks and, hence, their acorn crops may potentially harbor higher genetic diversity. Despite the clear source-sink dynamics found here, our results highlighted the need for caution when scaling up patch-centered approaches into landscape conservation guidelines. Overall, our study shows that costly large scale management practices envisioned to enhance landscape connectivity may not be effective if local recruitment processes are disregarded

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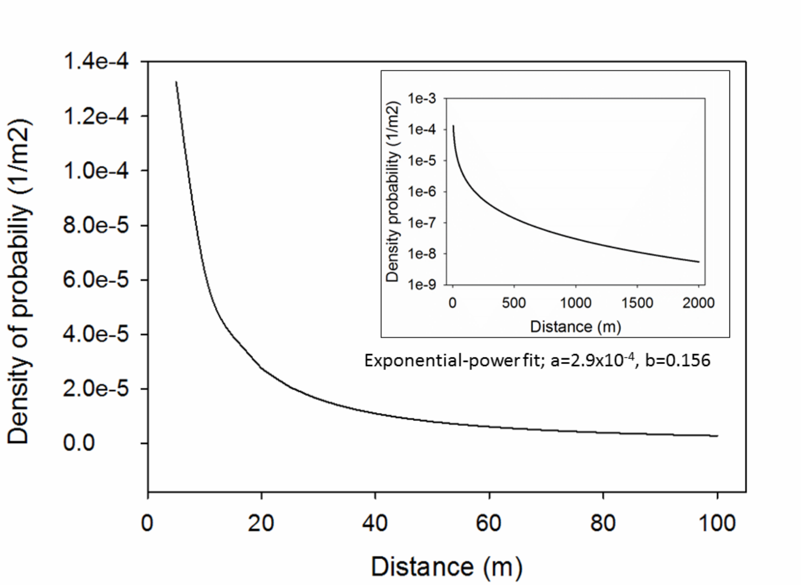
APPENDIX

Table 5.A1. Microsatellite loci used to genotype *Quercus ilex*. Ne = number of effective alleles, Ho: observed heterozygosity, He: unbiased expected heterozygosity, Ta = annealing temperature. Data corresponds to the analysis of the 28 mother trees.

Primer	**Ne**	**Ho**	**He**	**T_a**	**Primer origin**
MSQ13	5.92	1	0.85	50	Dow et al. (1995)
ZAG7	2.48	0.96	0.62	57	Kampfer et al. (1998)
ZAG9	4.98	0.64	0.76	55	Steinkellner et al. (1997)
ZAG11	1.55	0.43	0.36	50	Kampfer et al. (1998)
ZAG15	9.56	0.96	0.91	50	Steinkellner et al. (1997)
ZAG20	4.09	0.86	0.77	55	Kampfer et al. (1998)
ZAG112	2.88	0.64	0.66	55	Kampfer et al. (1998)
ZAG46	3.74	0.71	0.75	53	Steinkellner et al. (1997)
PIE020	2.27	0.57	0.57	50	Durand et al. (2010)
PIE258	6.37	0.68	0.86	55	Durand et al. (2010)



FigA1. Pollen dispersal kernel for *Quercus ilex* estimated with the exponential power function using the indirect method KINDIST. In the upper right corner is a log-plot version of the same curve providing a better representation of the tail.

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DISCUSIÓN GENERAL

Los cambios en el uso de suelo y la pérdida de bosque constituyen una amenaza para la biodiversidad a escala mundial debido a la extensión y velocidad del cambio (Sala et al. 2000, Hansen et al. 2010). En las últimas décadas se han hecho grandes avances a la hora de describir sus efectos sobre el funcionamiento de los ecosistemas (Fischer and Lindenmayer 2007, Selwood et al. 2015). Sin embargo, la comunicación entre la investigación ecológica y los gestores ambientales sigue siendo una asignatura pendiente (McConkey et al. 2012). Para poder diseñar pautas de manejo adecuadas es necesario conocer los procesos que subyacen a las respuestas ecológicas frente a la pérdida de bosque. En este contexto, centrar los esfuerzos sobre especies clave resulta una estrategia eficiente ya que el mantenimiento de sus poblaciones tiene consecuencias que trascienden a todo el sistema (Fischer and Lindenmayer 2007).

La encina es un ejemplo claro de este tipo de especies. Se encuentra ampliamente distribuida en el Mediterráneo occidental donde juega un papel importante como estructuradora del bosque (Barbero et al. 1992). Gran parte de los encinares están sujetos a algún tipo de manejo (adehesamiento, fragmentación o talas de monte bajo) (Campos et al. 2013, Santos and Tellería 1998) y se sabe que en zonas antropizadas presenta una regeneración empobrecida (Santos and Tellería 1997, Díaz 2014). Además se conocen qué factores regulan las distintas etapas de su ciclo de regeneración. Esto nos permitió traducir la fragmentación en cambios ambientales clave para las distintas etapas del ciclo y analizar sus efectos con un enfoque mecanicista. A través del desarrollo de la presente tesis doctoral creemos estar en disposición de contribuir al entendimiento de los impactos de la fragmentación sobre el potencial de regeneración de la encina y colaborar en el diseño de pautas de manejo más adecuadas.

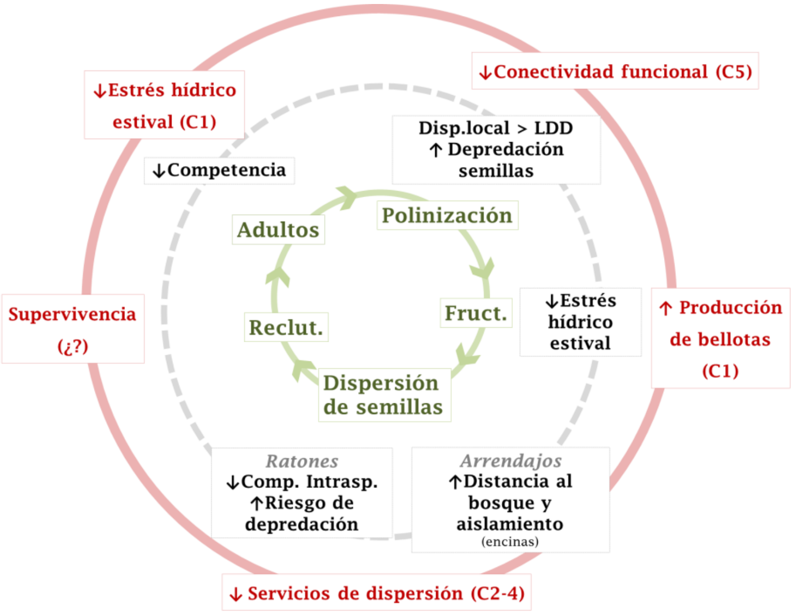

Fig. D.1. Esquema conceptual de la tesis doctoral en el que se indican qué fases del ciclo de regeneración de las encinas han sido abordadas en cada capítulo y los principales resultados. En rojo se indica la respuesta final, en negro los factores ambientales que la modulan en ambientes fragmentados. C1-C5 indican los capítulos.¿? Indica preguntas abiertas, no abordadas durante el desarrollo de la tesis LDD = dispersión a larga distancia.

EFECTOS DE BORDE Y LA PRODUCCIÓN DE BELLOTAS

Los efectos de la fragmentación sobre la producción de semillas supone cambios en el potencial de reclutamiento de las poblaciones de plantas (Selwood et al. 2015). En principio, éstos pueden deberse a la limitación de polen o a alteraciones en las condiciones microclimáticas. Sin embargo, descartamos el primero ya que las encinas se caracterizan por un flujo de polen extenso que asegura la reproducción en árboles extremadamente aislados (>30 km de otras masas forestales o 0.02 encinas por hectárea) (Hampe et al. 2013, Ortego et al. 2014).

Si bien existe una alta variabilidad inter-anual, la producción de bellotas depende en gran medida de la disponibilidad de agua durante las etapas de floración y maduración (Ogaya and Penuelas 2007, Espelta et al. 2008, Pérez-Ramos et al. 2010, Misson et al. 2011). En concreto, si el estrés hídrico estival supone una pérdida de conductividad hidráulica superior a un 70%, la falta de suministro de agua a las bellotas dispara las tasas de aborto y la cosecha final se ve comprometida (Carevic et al. 2014). Por tanto, a la hora de evaluar los efectos de la fragmentación nos centramos en los cambios ambientales relacionados con la disponibilidad de agua durante el verano. Nuestros resultados demuestran que en las áreas de borde la desaparición de cobertura vegetal circundante disminuye la competencia intraespecífica lo que hace que las encinas restantes sufran un estrés hídrico estival moderado y sean más productivas (Capítulo 1) (ver Moreno and Cubera 2008 para resultados similares en dehesas). De hecho, a pesar de que la localidad sur presenta en promedio un déficit hídrico acumulado un 43% más alto que la localidad norte, las grandes diferencias en los patrones de producción fueron encontradas entre niveles de fragmentación y no entre localidades. Nuestros resultados ilustran que los efectos del manejo sobre las condiciones abióticas a escala local pueden superponerse a las diferencias climáticas entre regiones. Además, advierten que el desarrollo de masas forestales especialmente densas podría aumentar la vulnerabilidad de las encinas frente a la sequía estival.

El hecho de que el efecto positivo de la fragmentación sobre la producción de frutos sea contra intuitivo, probablemente refleje más un sesgo en la literatura que en la frecuencia con la que esto se produce en la naturaleza. Cuando el polen no es limitante (revisado en Aguilar et al. 2006), la liberación de recursos asociado a la fragmentación podría mejorar la fertilidad en poblaciones de plantas en sistemas limitados por el agua o por la luz (ej. Neal et al. 2010). Este aspecto merece más atención cuando se analizan de manera global los efectos de la fragmentación sobre la fertilidad de las poblaciones de plantas.

ENTENDER EL COMPORTAMIENTO DE LOS DISPERSANTES

Si bien un aumento en la producción de bellotas aumenta la tasa potencial de crecimiento de la población, la tasa real depende asimismo de la efectividad en su dispersión (*sensu* Schupp et al. 2010). Para ello la encina cuenta con dos vectores caracterizados por requerimientos ecológicos y capacidades motoras dispares- los arrendajos y los ratones de campo.

Los arrendajos (*Garrulus glandarius*) son capaces de movilizar cientos de semillas durante el otoño-invierno, las distancias de movilización pueden llegar a las centenas de metros y en general las bellotas son depositadas en hábitats óptimos para el reclutamiento (Gómez 2003, Pons and Pausas 2007). Por ello, si los servicios de dispersión de los arrendajos se mantienen, éstos pueden amortiguar los impactos negativos de la fragmentación sobre el potencial de reclutamiento de las encinas y mejorar la cohesión genética entre las subpoblaciones. A pesar de que son capaces de explotar hábitats como olivares o matorrales para obtener distintas fuentes de alimento a lo largo del año (Rolando 1998) necesitan extensas áreas forestales para nidificar (Pons and Pausas 2008). De hecho, son mucho menos comunes en los pequeños fragmentos forestales (< 10 ha) e incluso pueden llegar a desaparecer (Andren 1994, Brotons et al. 2004).

La búsqueda de recursos nuevos o más abundantes en las matrices agrícolas puede alentar a las aves forestales a adentrarse en ellas (ej. DaSilva et al. 1996). Si esto no ocurre, se produce una caída importante en los servicios de dispersión a medida que nos alejamos del bosque (Luck and Daily 2003, Pizo and dos Santos 2011). Nuestros resultados mostraron que la producción de frutos en la dehesa a escala de paisaje es similar debido a la baja densidad de arbolado y sugieren que ésta es la causa principal del uso esporádico y tardío de las dehesas durante el otoño-invierno. Además, nuestro trabajo señala la necesidad de tener en cuenta la estructura del paisaje si queremos promover los servicios de dispersión de estas aves en las dehesas. Debe ser prioritario el mantenimiento de áreas de bosque cercanas para asegurar la presencia del dispersante y evitar densidades de árboles extremadamente bajas. Si esto no se cumple, las tasas de visita de los arrendajos serán prácticamente nulas independientemente de la calidad de la cosecha de los árboles. Con respecto a los patrones de deposición, si bien nuestros datos presentan ciertas limitaciones, apuntan a la incapacidad de los dispersantes de explotar de manera eficiente los árboles localizados en la dehesa. Contrario a lo que cabría esperar en un escenario de compensación de costes, la carga de bellotas por visita no fue mayor (Waite and Ydenberg 1996, Luck and Daily 2003) y la movilización de las semillas no se produjo hacia sus áreas de campeo habituales, los bosques (Yahner 2012). Esto conllevó distancias de movilización cuatro veces menores en la dehesa y la deposición de las bellotas en microhábitats *a priori* no óptimos para el reclutamiento (Capítulo 2).

El ratón de campo (*Apodemus sylvaticus)* es una especie generalista capaz de explotar hábitats muy antropizados (Fitzgibbon 1997, Díaz et al. 1999, Macdonald et al. 2000). Sin embargo, la relación de los roedores con la encina es ambigua. En función de las condiciones ambientales pueden actuar como depredadores de semillas (Santos and Telleria 1997) o como dispersantes a escala local (Gómez et al. 2008). A pesar de que no son capaces de transportarlas largas distancias y de que gran parte de las bellotas manipuladas son finalmente depredadas (80-90%) (Gómez et al. 2008, Perea et al. 2011b), al estar presentes en una gran variedad de hábitats su comportamiento como dispersante ha sido ampliamente estudiado (ej. Gómez et al. 2008, Puerta-Piñero et al. 2010, Perea et al. 2011b, Puerta-Piñero et al. 2012). Se sabe que los factores ambientales clave en el comportamiento de los roedores son- (1) la competencia intraespecífica por las bellotas, relacionada con los beneficios del consumo instantáneo *vs* el almacenamiento así como con el riesgo de robo de los almacenes (Theimer 2005 , Vander Wall 2010) y (2) la presencia de cobertura vegetal que actúe como refugio contra los depredadores durante la movilización (Perea et al. 2011b). Este conocimiento previo nos permitió evaluar si los efectos de la fragmentación sobre la relación roedor-encina estaban mediados por cambios en estos factores ambientales. Nuestros resultados (Capítulo 3) mostraron que los efectos negativos de la fragmentación sobre las distancias de movilización estaban determinados por un aumento de los microhábitats abiertos, donde el riesgo de depredación es mayor (Tew and Macdonald 1993). En consecuencia, las bellotas eran depositadas más cerca de los árboles focales y eran preferentemente depredadas. Sin embargo, en ambientes con más cobertura vegetal la toma de decisiones de los dispersantes dependió tanto de la estructura del hábitat como de la competencia intraespecífica. Cuando la competencia aumentaba los roedores movilizaban las bellotas más lejos y las almacenaban en mayor medida.

El siguiente objetivo fue desarrollar un modelo que combinaba los efectos del manejo sobre factores ambientales clave con un modelo basado en agente (ABM) (Grimm and Railsback 2005). En él la producción de bellotas estaba mediada por la competencia intraespecífica de las encinas (Capítulo 1), la abundancia de roedores dependía de la cantidad de hábitat forestal disponible y de la cobertura vegetal (Ylonen et al. 1991, García et al. 1998, Malo et al. 2013) y los microhábitats abiertos eran percibidos como zonas de alto riesgo por los roedores (Tew and Macdonald 1993, Perea et al. 2011a, Perea et al. 2011b, Capítulo 3). El principal objetivo de los roedores durante la toma de decisiones era transportar las semillas lejos de potenciales competidores pero aceptando un riesgo razonable durante la movilización. Este enfoque integrado nos permitió predecir los patrones de dispersión en una variedad de paisajes usando información ambiental relativamente simple (proporción de hábitat forestal en el paisaje, densidad de arbolado y cantidad de sotobosque). Además, los análisis de sensibilidad del modelo nos permitieron identificar qué parte de la toma de decisiones por parte del dispersante tiene mayor impacto sobre distintos atributos de los patrones de dispersión e interpretar los efectos del manejo desde el punto de vista del comportamiento.

A la luz de nuestros resultados, las distancias de mayor probabilidad de deposición están determinadas por la competencia intraespecífica. Si el alimento es abundante los roedores dependen menos de los almacenes y el riesgo de robo disminuye. Esto hace que adopten una estrategia de ahorro energético durante la movilización y, por tanto, que la mayor parte de las bellotas sean movilizadas cerca del árbol madre (Moore et al. 2007, Puerta-Piñero et al. 2010). Esta situación es típica en sistemas adehesados donde los árboles son muy productivos y la abundancia local de roedores baja (Díaz 2014). Por el contrario, las distancias máximas de movilización dependen en gran medida de la percepción de riesgo durante la movilización. Así, aquellas estrategias de manejo que provean a los roedores de zonas de refugio, como por ejemplo la matorralización, mejorarán la capacidad de las encinas de colonizar nuevos hábitats. Finalmente, las tasas de almacenamiento dependen tanto de la competencia intraespecífica como del riesgo percibido. Cuando la competencia es alta, los roedores necesitan acaparar el mayor número de bellotas posible en un corto periodo de tiempo lo que favorece una estrategia de almacenamiento siempre y cuando el riesgo durante la movilización sea razonable (Vander Wall 2010). En los pequeños fragmentos forestales las tasas de depredación se disparan (Capítulo 3) porque la competencia intraespecífica disminuye drásticamente (Capítulo 1 y 3) y los riesgos de adentrarse en la matriz agrícola desnuda son muy elevados (Tew and Macdonald 1993).

El hecho de que las relaciones mutualistas entre la encina y sus dispersantes sean contexto-dependientes hace que esta etapa del ciclo de regeneración sea particularmente sensible al manejo. Sin embargo, también permite recuperar los servicios de dispersión mediante políticas adecuadas. En nuestros trabajos (Capítulos 2, 3 y 4), intentamos observar los paisajes antropizados desde el punto de vista del dispersante para entender qué cambios ambientales modificaban su comportamiento dando lugar a servicios de dispersión empobrecidos. Este tipo de enfoques centrados en la toma de decisiones del animal ha ganado adeptos en los últimos años ya que permite detectar de manera temprana cuellos de botella en la regeneración y establecer puentes con las políticas de conservación (Cortes and Uriarte 2013).

CONECTIVIDAD FUNCIONAL: POLEN vs SEMILLA

En un paisaje fragmentado la capacidad de las plantas para mover sus genes a través del polen o las semillas determinará la cohesión genética entre las subpoblaciones (Sork et al. 1999, Sork and Smouse 2006). La encina, como ocurre con otras especies del género *Quercus*, se caracteriza por un flujo de polen extenso (Hampe et al. 2013, Ortego et al. 2014) pero una dispersión de las semillas limitada en zonas antropizadas (Capítulos 2, 3, 4). Ésta podría ser la causa de la menor diversidad genética de las plántulas en zonas fragmentadas (Ortego et al. 2010). Por tanto, para poder evaluar la conectividad funcional de encinares fragmentados es necesario tener en cuenta ambos procesos.

Discusión

Para cuantificar cómo era el flujo génico a través del paisaje usamos el marco conceptual de la teoría de grafos de (Fortuna et al. 2008) y medidas de tres etapas clave del reclutamiento: la dispersión efectiva de polen, la producción de bellotas (Capítulo 1) y su dispersión (Capítulo 3). Gracias a la dispersión de polen a larga distancia ningún fragmento quedó desconectado de la red a pesar de que los más aislados se encuentran a más de 3 km del resto. No obstante, nuestro modelo predijo un intercambio de polen espacialmente estructurado a escala de paisaje debido a que gran parte es depositado cerca del árbol focal (<100m). Las altas tasas de depredación de las bellotas hicieron que sólo una parte de la conectividad potencial recogida en las cosechas de los árboles pasara a los almacenes. La actividad de los roedores redujo un 36.62% el número de enlaces en la red y las tasas de migración de gametos masculinos disminuyeron un orden de magnitud. Estos resultados demuestran que la falta de dispersión efectiva puede frenar la conectividad funcional a pesar de que exista un flujo de polen extenso (Jordano 2010). Por tanto, el efecto borde negativo sobre las tasas de almacenamiento de las bellotas (Capitulo 3) puede tener repercusiones profundas en la diversidad genética de las plántulas. De hecho, nuestro modelo predijo tasas de migración en las bellotas almacenadas extremadamente bajas (<2%) en los pequeños fragmentos forestales (≤0.1 ha) a pesar de haber recibido una alta proporción de polen inmigrante (>60%).

Para poder valorar la efectividad de posibles políticas de manejo a escala de paisaje como las promovidas por lo esquemas agroambientales (Donald and Evans 2006) analizamos cómo el área y la configuración espacial de los fragmentos determinaban su papel en la red. Nuestros resultados mostraron que la cohesión genética de las subpoblaciones depende en gran medida del mantenimiento de un número mínimo de áreas de bosque en el paisaje (> 10 ha) ya que son las principales fuentes de polen. Por el contrario, los fragmentos pequeños actuaron como sumideros lo que sugiere que en sus cosechas queda recogida la diversidad genética a escala regional. Además del área, aquellos fragmentos menos aislados y en posiciones centrales tuvieron un papel más relevante. El hecho de que encontráramos un nexo claro entre las dinámicas fuente-sumidero y las características de los fragmentos nos hizo pensar que se podían generar paisajes con una conectividad óptima. Sin embargo, cuando diseñamos paisaje teóricos usando esta información los resultados no fueron concluyentes.

ESTABLECIENDO PUENTES CON LA CONSERVACIÓN

De entre todas las etapas del ciclo de regeneración la dispersión de las bellotas fue la más vulnerable a los impactos de la fragmentación. Además, el empobrecimiento de los servicios de dispersión tuvo consecuencias que trascendieron el reclutamiento neto de nuevos individuos. La falta de una dispersión efectiva puede generar cuellos de botella genéticos. Por tanto, su recuperación debe ser prioritaria. En el caso de los arrendajos preservar grandes fragmentos forestales (> 300 ha) (Brotons et al. 2004) intercalados entre las áreas de explotación agrícola o ganadera (< 2 km) es clave para asegurar su presencia. Además, dentro de la matriz es conveniente evitar fragmentos o encinas muy aisladas para mejorar las tasas de visita. Si bien nuestros resultados no nos permiten valorar qué estrategias de conservación son necesarias para mejorar la calidad de la dispersión (distancia y microhábitats de deposición), apuntan al riesgo de depredación como factor a tener en cuenta. Creemos que estudios que evalúen el mantenimiento de setos como áreas de refugio pueden dar información muy valiosa en este sentido. Además, cabe destacar la falta de arrendajos en los fragmentos grandes de Quintanar de la Orden cuando *a priori* son áreas adecuadas para la nidificación de estas aves debido a su extensa cobertura forestal y la heterogeneidad del hábitat a escala regional (Brotons et al. 2004, Pons and Pausas 2008). Esto sugiere que la estructura del bosque dentro de los parches puede ser importante. Un alto grado de manejo, estructuras multi-tronco en las encinas o cambios en la competencia con otras especies de córvidos podrían comprometer la presencia de estas aves (ver Pons and Pausas 2008 para un resultado similar). Poder determinar con mayor precisión las áreas de nidificación de los estas aves en paisajes antropizados es importante a la hora de establecer zonas de actuación prioritaria.

En relación a los roedores, dar pautas de conservación resulta algo más complejo ya que los patrones de dispersión dependen en gran medida de la competencia intraespecífica y tanto el adehesamiento como la fragmentación disparan la producción de bellotas. Durante el desarrollo del Capítulo 4 quisimos ilustrar cómo nuestro modelo puede ser usado para la evaluación o el diseño de políticas de manejo. La matorralización de las dehesas ha sido propuesta como la mejor estrategia para promover el reclutamiento (ej. Ramírez and Diaz 2008, Pulido et al. 2010, Díaz 2014). Provee de microhábitats que atemperan los efectos negativos sequía estival sobre la supervivencia de las plántulas (Smit et al. 2008, Rolo et al. 2013) y favorece la presencia de los roedores (Muñoz et al. 2009). Debido a respuestas no lineales nuestro modelo predijo la necesidad de un desarrollo de sotobosque de al menos un 65% de la cobertura total para restaurar servicios de dispersión moderados (tasas de almacenamiento mayores al 10% y distancias máximas en torno a 20 m). Estos porcentajes de matorralización no son compatibles con la explotación de la dehesa ya que disminuirían drásticamente la producción de pasto para el ganado (Rivest et al. 2011). Por tanto, tal y como se había señalado anteriormente (Ramírez and Díaz 2008, Díaz 2014) las políticas agroambientales en las dehesas deben incluir sistemas de rotación y abandono para integrar su regeneración natural y su uso productivo. Con respecto a los paisajes fragmentados, nuestros resultados apuntan a la necesidad de mantener fragmentos forestales de al menos 1 ha para que existan zonas de interior donde el aumento de la competencia intraespecífica estimule a los roedores a almacenar las bellotas y asegure el reclutamiento de nuevos individuos. Además, si queremos que estas medidas sean más efectivas deben tener un sotobosque bien desarrollado que favorezca el transporte de semillas lejos y aumente así la probabilidad de que los almacenes escapen a la depredación postdispersiva. A priori en los fragmentos forestales pequeños (<0.4 ha), no es posible recuperar los servicios de dispersión debido a una muy baja competencia intraespecífica y un riesgo de depredación muy elevado. Sin embargo, su presencia es importante ya que sus bellotas pueden albergar una alta diversidad genética y pueden actuar como catalizadores de la recuperación del bosque una vez la matriz agrícola sea abandonada y se vuelva más permeable al movimiento de los roedores.

Finalmente, nuestros análisis de la conectividad funcional de los encinares (Capítulo 5) apuntan a la necesidad de mantener grandes parches forestales (>10 ha) para asegurar la cohesión genética entre subpoblaciones. Además señalan que trasladar las conclusiones obtenidas con análisis a nivel de parche a políticas de manejo a escala de paisaje puede no ser realista debido a interacciones complejas entre la configuración del paisaje, la disponibilidad de hábitat y los efectos de borde (Minor and Urban 2008, Baguette et al. 2013). Asimismo, ilustran cómo políticas agroambientales a gran escala y de alto coste económico pueden no ser eficaces si la dispersión efectiva de las semillas a escala local no es tenida en cuenta.

NUEVOS HORIZONTES

Si bien la llegada de semillas es necesaria para que se produzca el reclutamiento ésta no garantiza su éxito (Nathan and Muller-Landau 2000). La efectividad en la dispersión (*sensu* Schupp et al. 2010) depende en muchos casos de procesos post-dispersivos como la depredación, la competencia intraespecífica o las condiciones microclimáticas. Por tanto, para poder evaluar la calidad de la dispersión en sentido estricto es necesario conocer el destino final de la semilla. En especies de ciclo de vida largo (como la encina) obtener esta información en campo puede resultar una tarea incosteable ya que presentan alta tasas de mortandad de sus semillas y una madurez sexual tardía (Bacles and Jump 2011). Además, en zonas donde los campos de cultivo son explotados resulta imposible discernir la mortandad de semillas debida a cambios en el comportamiento de los dispersantes de aquella que depende de actividades puramente antrópicas (ej. labranza). No obstante, incorporar información acerca de procesos postdispersivos podría ser de gran utilidad a la hora de evaluar si los cambios en los patrones de dispersión se traducen en cambios demográficos en el medio-largo plazo (Robledo-Arnuncio et al. 2014).

En el caso de la encina se sabe que la depredación y la mortandad por sequía son los principales limitantes en el éxito de reclutamiento de las semillas almacenadas (Gómez 2004). Asimismo, existe bastante información sobre los efectos de los microhábitats de deposición en estos dos procesos. En general, las áreas sin cobertura tienen tasas de depredación más bajas (Perea et al. 2011b) pero las plántulas suelen secarse durante el verano (Gómez 2004, Smit et al. 2008) y lo contrario ocurre bajo las copas de encinas (Gómez 2004). Los arbustos presentan propiedades intermedias. A pesar de ser zonas con una alta actividad de los roedores y por tanto con un consumo elevado de las bellotas almacenadas (Muñoz et al. 2009, Perea et al. 2011b) tienen un efecto neto positivo sobre el reclutamiento gracias a su papel como plantas nodriza (Pulido and Díaz 2005, Smit et al. 2008). Incorporar esta información en los modelos de dispersión ajustándola a la densidad de depredadores y a las condiciones climáticas de la zona sería relativamente sencillo y aportaría información muy valiosa.

Por otro lado, los patrones en el uso del hábitat por parte del dispersante es otro factor a tener en cuenta. La existencia de áreas o rutas preferentes puede dar lugar a una deposición anisotrópica de las semillas y a patrones de reclutamiento agregados (Santamaría et al. 2007, Puerta-Pinero et al. 2010) lo que aumentaría la competencia intraespecífica. La información proporcionada por técnicas de radio-marcaje sería de gran utilidad en este aspecto (ej. Rodríguez-Pérez et al. 2012).

CONSIDERACIONES FINALES

Evaluar los efectos de la fragmentación desde un enfoque mecanicista permite determinar cuáles son los procesos biológicos subyacentes y determinar qué factores los modulan. Si somos capaces de identificar qué etapas del ciclo de regeneración ponen en peligro la viabilidad de las poblaciones fragmentadas y de entender qué cambios ambientales causan estos cuellos de botella podremos establecer puentes con las políticas de manejo. A lo largo del desarrollo de esta tesis doctoral hemos utilizado este tipo de aproximación para evaluar los efectos de la fragmentación al potencial de regeneración de la encina. El principal factor limitante en la regeneración es el empobrecimiento de los servicios de dispersión que comprometen tanto el reclutamiento como la diversidad genética de los nuevos individuos. Por tanto, su restauración debe ser prioritaria en cualquier política de manejo. Para ello, necesitamos tener en cuenta la estructura del paisaje y la calidad del hábitat desde el punto de vista del dispersante. Finalmente, combinar modelos de dispersión con procesos post-dispersivos es un reto en el medio plazo que nos permitirá predecir los patrones de recuperación del bosque a lo largo de sucesivas generaciones.

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A lo largo de esta tesis doctoral estudiamos los efectos de la fragmentación sobre la regeneración de la encina (*Quercus ilex*). Se trata de una especia que domina la cobertura vegetal de extensas áreas del Mediterráneo occidental, se conocen bien los procesos que modulan las distintas etapas de su ciclo vital y el manejo forestal parece amenazar su sostenibilidad a largo plazo. Nuestros objetivos fueron (1) detectar qué etapas de su ciclo de regeneración (polinización, fructificación, dispersión de bellotas) son más vulnerables a la fragmentación y (2) determinar qué cambios ambientales general estos cuellos de botella.