TESIS DOCTORAL

PROCESOS IMPLICADOS EN LA REGENERACIÓN DE BOSQUES MIXTOS MEDITERRÁNEOS AFECTADOS POR DECAIMIENTO

UNVERSIDAD PABLO DE OLAVIDE
CONSEJO SUPERIOR DE INVESTIGACIONES CIENTÍFICAS

Beatriz Ibáñez Moreno
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Memoria que la Ingeniera Beatriz Ibáñez Moreno presenta para optar al Grado de Doctora por la Universidad Pablo de Olavide

Esta memoria ha sido realizada bajo la dirección de:
Dra. Lorena Gómez Aparicio, Dr. Teodoro Marañón Arana y
Dr. Luis Ventura García Fernández

Esta memoria ha sido realizada bajo la tutela de:
Dr. Antonio Gallardo Correa

Ing. Beatriz Ibáñez Moreno
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Dra. Lorena Gómez Aparicio, Investigador Científico del Consejo Superior de Investigaciones Científicas (CSIC)

Dr. Teodoro Marañón Arana, Investigador Científico del Consejo Superior de Investigaciones Científicas (CSIC)

Dr. Luis Ventura García Fernández, Investigador Científico del Consejo Superior de Investigaciones Científicas (CSIC)

CERTIFICAN

Que los trabajos de investigación desarrollados en la presente Memoria de Tesis Doctoral: "Procesos implicados en la regeneración de bosques mixtos mediterráneos afectados por decaimiento", **han sido realizados bajo su dirección y son aptos para ser presentados por la Ing. Beatriz Ibáñez Moreno ante el Tribunal que en su día se designe, para optar al grado de Doctora por la Universidad Pablo de Olavide.**

Y para que así conste, y en cumplimiento de las disposiciones legales vigentes, extendemos el presente certificado a __ de _______ de 2014

Dra. Lorena Gómez Aparicio

Dr. Teodoro Marañón Arana   Dr. Luis Ventura García Fernández

Dr. Antonio Gallardo Correa, Catedrático de Ecología de la Universidad Pablo de Olavide

CERTIFICA

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Dr. Antonio Gallardo Correa

Para la realización de esta Tesis Doctoral he disfrutado de una Beca Predoctoral de Formación de Personal Investigador del Ministerio de Economía y Competitividad asociada al proyecto: *Interacciones árbol-suelo y funcionamiento del bosque mediterráneo: una aproximación espacialmente explícita usando modelos de vecindad* (INTERBOS- CGL2008-04503-C03-03).

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RESUMEN

En las últimas décadas se han descrito síndromes de decaimiento forestal en bosques de todo el mundo. El incremento en la frecuencia y magnitud de eventos climáticos extremos (ej. sequías), así como del ataque de plagas y patógenos, son algunas de las causas últimas identificadas. La mayoría de los eventos de decaimiento descritos presentan cierta especificidad, afectando en distinto grado a las distintas especies arbóreas coexistentes. Estos procesos tendrán por tanto una alta capacidad para alterar la composición y estructura de la comunidad de plantas no solo a corto plazo (disminuyendo la abundancia relativa de adultos de la especie afectada) sino también a largo plazo a través de sus efectos sobre las dinámicas de regeneración. El **objetivo general** de esta tesis doctoral es evaluar los efectos del decaimiento de *Quercus suber* (alcornoque) sobre la regeneración de especies leñosas en bosques mixtos del sur de la Península Ibérica, y en base a ello determinar las trayectorias sucesionales más probables de estos sistemas.

En primer lugar (**capítulo 2**) se realizó un estudio a escala de toda Andalucía para evaluar el efecto del clima y su interacción con otras variables abióticas (suelo) y bióticas (interacción con individuos vecinos) sobre la mortalidad de adultos y la abundancia de plántulas y juveniles de *Q. suber*. Para ello se utilizaron datos del Segundo y Tercer Inventario Forestal Nacional Español. Los resultados obtenidos mostraron respuestas diferenciales de adultos y regenerado de *Q. suber* a las variables climáticas. La supervivencia de adultos disminuyó al aumentar la temperatura de primavera, mientras que la regeneración se vio afectada positivamente por inviernos cálidos. Se encontró además un importante efecto modulador de la textura del suelo sobre los efectos de la precipitación en la supervivencia de adultos, los cuales fueron positivos en suelos arenosos pero negativos en suelos arcillosos. Los resultados obtenidos indican que la sostenibilidad de los bosques de *Q. suber* va a depender no solo de las condiciones climáticas futuras, sino también de sus interacciones con otros factores clave (ej. propiedades del suelo) que podrían modular los efectos del clima sobre las tasas demográficas de esta especie.

En los siguientes capítulos de la tesis (capítulos 3-6) se analizó a escala local el impacto del decaimiento de *Q. suber* sobre los patrones de abundancia y funcionamiento de plántulas y juveniles de especies leñosas, analizando de forma específica la relevancia para la regeneración de los cambios inducidos por el decaimiento sobre las comunidades de organismos del suelo (patógenos y micorrizas). Para ello se desarrollaron trabajos de campo experimentales y observacionales en seis parcelas del Parque Natural de los Alcornocales (Cádiz), tres de ellas situadas en bosques abiertos dominados por *Q. suber* y *Olea europaea* var. *sylvestris* (acebuche), y otras tres situadas en bosques cerrados de *Q. suber* y *Q. canariensis* (quejigo). Los datos obtenidos en estos capítulos fueron analizados mediante *modelos de vecindad* en los que las variables demográficas y edáficas de interés fueron predichas en función de la distribución, tamaño, identidad y estado de salud de los árboles y matorrales vecinos.

En el **capítulo 3** se realizó un experimento de siembra de semillas con las principales especies arbóreas (*Q. suber, Olea europaea* y *Q. canariensis*) para analizar el efecto de la composición y estado de salud del dosel arbóreo-arbustivo sobre la emergencia,

supervivencia y crecimiento de plántulas. De forma complementaria, en el **capítulo 4** se realizó un estudio observacional para cuantificar los patrones espaciales de abundancia y riqueza de regenerado de especies leñosas. Los resultados obtenidos en ambos capítulos mostraron la importancia de la identidad y el estado de salud de los árboles del dosel para la dinámica de plántulas en los dos tipos de bosque estudiados. Se encontró un efecto negativo generalizado del decaimiento de *Q. suber* en la supervivencia y abundancia de plántulas y juveniles de especies arbóreas, particularmente de las especies de *Quercus*. El decaimiento no afectó sin embargo negativamente a otros grupos funcionales como los matorrales o las lianas, los cuales incluso presentaron mayor abundancia en vecindades dominadas por alcornoques defoliados o muertos que en vecindades dominadas por alcornoques sanos. Los resultados obtenidos sugieren por tanto que el decaimiento de *Q. suber* implica una serie de cambios en el regenerado que podrían conllevar una pérdida de dominancia y cobertura de la especie a largo plazo, promoviendo la conversión de estos bosques hacia sistemas más abiertos con menor cobertura arbórea y mayor cobertura de matorral.

En los **capítulos 5** y **6** se analizaron los patrones espaciales de oomicetos patógenos y hongos micorrícicos (respectivamente) en los bosques de estudio, así como sus posibles causas y consecuencias para la emergencia y supervivencia de plántulas de *Q. suber* y *Q. canariensis*. Encontramos que la identidad y estado de salud de las especies arbóreas fueron unos de los principales factores determinantes de la variabilidad espacial existente en la abundancia de patógenos y micorrizas. Lo que es más, dicha variabilidad afectó a la probabilidad de emergencia y supervivencia de plántulas. Específicamente, la abundancia de patógenos afectó negativamente a la emergencia y supervivencia de *Q. suber* (pero no de *Q. canariensis*), mientras que la colonización por hongos endo- y ecto-micorrícicos tuvo efectos neutros o negativos sobre la supervivencia de ambas especies de *Quercus*. En general, estos resultados indican que el decaimiento de *Q. suber* implica cambios en las comunidades edáficas que pueden afectar a la dinámica del bosque vía procesos de retroalimentación planta-suelo.

En conjunto, la investigación realizada en el marco de esta Tesis Doctoral pone de manifiesto el fuerte impacto que el decaimiento de *Q. suber* puede tener en las comunidades de plantas y organismos del suelo de los bosques mixtos de estudio. Los efectos detectados parecen apuntar hacia una disminución de la cobertura arbórea -particularmente de *Q. suber*- en el futuro, lo cual pone de manifiesto la vulnerabilidad de estos importantes sistemas y la necesidad de llevar a cabo actuaciones de manejo que incrementen su resiliencia frente a los distintos motores de cambio.

Índice

Capítulo 1

INTRODUCCIÓN

Capítulo 1. Introducción

MARCO CONCEPTUAL

El decaimiento forestal en un contexto de cambio global

La composición y estructura de bosques en todo el mundo están siendo afectadas por algunos de los motores de cambio asociados al cambio global (Peñuelas y Filella, 2001; Lovett *et al.*, 2006; Allen *et al.*, 2010). Sequías, plagas, enfermedades o la introducción de especies exóticas, actuando aislada o simultáneamente, han sido causantes de la mortalidad extensiva de árboles adultos en múltiples sistemas forestales en las últimas décadas, alterando sus dinámicas (e.g. Peñuelas *et al.*, 2001; Lovett *et al.*, 2006; Loo, 2009; Van Mantgem *et al.*, 2009; Allen *et al.*, 2010; Carnicer *et al.*, 2011). El fenómeno de mortalidad extensiva asociado a diversos factores abióticos y bióticos es conocido como decaimiento forestal, y puede presentar cierta especificidad afectando en distinto grado a las distintas especies arbóreas coexistentes, con una alta capacidad para alterar la composición y estructura de la comunidad de plantas (e.g. Clifford *et al.*, 2011; Collins *et al.*, 2011). El número de estos episodios de decaimiento podría verse incrementado a raíz de la alteración de la frecuencia y la intensidad de las perturbaciones asociadas al cambio global, aumentando la vulnerabilidad de los bosques (Allen *et al.*, 2010). Al tener el declive de una especie un gran impacto en el funcionamiento y dinámica del ecosistema (Adams *et al.*, 2010; Allen *et al.*, 2010; Anderegg *et al.*, 2012), se hace necesario llevar a cabo una investigación profunda para entender cuáles son las respuestas más probables de los bosques al cambio global

El caso específico del decaimiento de las especies de Quercus

Uno de los géneros de plantas más castigado por decaimiento es el género *Quercus*. En el último siglo, diversas especies de *Quercus* han sufrido la muerte de decenas de miles de árboles tanto en Norte América (e.g. Rizzo y Garbelotto, 2003; Kabrick *et al.*, 2008; Brown y Allen-Diaz, 2009; Nagle *et al.*, 2010), como en Europa (Brasier *et al.*, 1993; Brasier, 1996; Jung *et al.*, 2000). Esta mortalidad extensiva de árboles es producida por una combinación de factores abióticos, como episodios de sequía ligados al cambio climático, y factores bióticos, como el ataque de patógenos exóticos del suelo (fundamentalmente oomicetos de los géneros *Phytophthora* y *Pythium*) que limitan la capacidad de las plantas de absorber agua al destruir las raíces finas (Sánchez *et al.*, 2006; Romero *et al.*, 2007). Estos eventos de mortalidad no solo afectan a árboles débiles o dominados como suele ocurrir en los procesos de sucesión natural, sino que pueden afectar (a veces incluso de forma mayoritaria) a árboles vigorosos o dominantes (Hansen y Goheen, 2000), pudiendo implicar cambios de gran magnitud sobre las condiciones de su entorno (Lovett *et al.*, 2006). Conocer los efectos y las implicaciones del decaimiento de las especies de *Quercus* en los bosques afectados permitirá avanzar en el entendimiento de los impactos que el declive arbóreo tiene en las comunidades ecológicas, lo cual, a pesar de su extrema importancia, ha sido hasta ahora poco explorado (Anderegg *et al.*, 2012).

El decaimiento de Quercus *spp. en la Península Ibérica*

En el caso concreto de la Península Ibérica durante las últimas décadas se ha observado el decaimiento de *Q. suber* (alcornoque) y *Q. ilex* (encina) en el fenómeno conocido como “la seca” (Brasier *et al.*, 1993; Sánchez *et al.*, 2002; Tuset y Sánchez, 2004). Factores abióticos como sequías (Peñuelas *et al.*, 2001; Corcuera *et al.*, 2004), y factores bióticos como la acción del oomiceto *Phytophthora cinnamomi* (Brasier *et al.*, 1993; Brasier, 1996), son las principales causas de este fenómeno que data de la década de los 90. Por ejemplo, las dos especies de *Quercus* han presentado síntomas de decaimiento en la Península Ibérica tras las sequías de 1994 (Peñuelas *et al.*, 2001; Carnicer *et al.*, 2011) y 2005 (Carnicer *et al.*, 2011), causando la debilitación y muerte de individuos adultos. Por otro lado, desde que fue detectado en los 90, diversos estudios han confirmado el papel de *Phytophthora cinnamomi* en el decaimiento de *Quercus* en el suroeste de España y sur de Portugal (e.g. Sánchez et al 2002, 2006, Moreira y Martins 2005). Este oomiceto puede llegar a matar al árbol en pocos meses desde la infección al destruir las raíces propagándose a través del floema y el cambium. *Phytophthora cinnamomi* es una especie exótica en la Península Ibérica procedente de Nueva Guinea y Sudáfrica (Zentmyer, 1980), introducido en Europa a principios del siglo XIX. Desde entonces se ha expandido por todo el continente afectando a diversos géneros, como *Castanea* y *Quercus* (Brasier, 1996). Se propaga por el suelo, siendo beneficiado en condiciones húmedas y cálidas, aunque puede sobrevivir durante periodos secos (Shearer and Tippett, 1989), por lo que puede atacar al árbol durante varios años consecutivos.

Además del problema de decaimiento, la regeneración de las especies de *Quercus* en estos bosques está limitada por diversos factores bióticos y abióticos que afectan a las distintas fases del reclutamiento (e.g. semillas, plántulas, Pausas *et al.*, 2009). Por ejemplo, existe una elevada depredación de semillas por parte del ganado (Pulido y Díaz, 2005), especialmente en el caso de las dehesas, así como de insectos (Pérez-Ramos, 2007), y roedores (Pérez-Ramos y Marañón, 2008), aunque estos últimos también contribuyen a la dispersión de semillas. La supervivencia de plántulas se ve comprometida por la alta herbivoría existente (Pausas *et al.*, 2009), así como la sequía estival característica de los sistemas mediterráneos (Gómez-Aparicio, 2008). El problema de la continuidad de estos bosques por falta de regeneración podría verse agravado como consecuencia de la mortalidad extensiva de árboles adultos.

Un caso específico de bosques afectados por decaimiento con una importante repercusión ecológica y socioeconómica son los alcornocales de la Península Ibérica. Durante siglos estos sistemas han sido explotados por el ser humano para el aprovechamiento de la corteza de esta especie de *Quercus*, el corcho. Fue durante el siglo XVIII cuando el comercio de este material natural cobró especial importancia para su uso como tapón de botellas, incrementando su interés en el mundo económico (Parejo, 2004). Por esta razón se ha promovido su expansión en detrimento de otras especies arbóreas con las que convive (Urbieta *et al.*, 2008). Los alcornocales constituyen sistemas antropogénicos y culturales, cuyo aspecto socioeconómico es fundamental en relación a su conservación y gestión (Aronson *et al.*, 2009). Además, estos bosques se encuentran situados en uno de los puntos calientes (“hotspots”) de biodiversidad del mundo, la Cuenca Mediterránea, cuya conservación es considerada prioritaria (Myers *et al.*, 2000). Por todo ello, los alcornocales de la Península Ibérica son sistemas donde es imprescindible ampliar el conocimiento del impacto del decaimiento.

La relación mortalidad-regeneración: clave en la determinación de la composición futura de bosques afectados por decaimiento

En bosques afectados por decaimiento conocer el balance entre la mortalidad de árboles y la regeneración es imprescindible para evaluar si el sistema tiene capacidad de sobreponerse a los impactos del decaimiento, o si por el contrario es esperable un cambio en la composición relativa de las especies (Lloret *et al.*, 2012). La probabilidad de que ocurran cambios en la vegetación tras el declive va a estar en gran parte determinada por las dinámicas de regeneración tras el evento de mortalidad (e.g. Suarez y Kitzberger, 2008; Kayes y Tinker, 2012; Galiano *et al.*, 2013; Redmond y Barger, 2013). Por un lado, la capacidad de sobreponerse a la pérdida de individuos adultos de la especie afectada, y por otro lado la respuesta de las otras especies coexistentes a las nuevas oportunidades tras la apertura del dosel, son los factores clave que van a determinar la composición futura de bosques con decaimiento. Estudiar cómo las plántulas de las principales especies leñosas responden al estado del dosel en un bosque afectado, así como evaluar si los cambios producidos han impactado en las dinámicas de regeneración de estos bosques permitirá evaluar si es previsible que exista un reemplazamiento sucesional a largo plazo.

ESCALA DE TRABAJO DE LA IMPLICACIÓN DEL DECAIMIENTO EN LA REGENERACIÓN

El estudio de la relación entre el decaimiento y las dinámicas de regeneración puede enfocarse desde distintas escalas espaciales. El uso de distintas escalas permite evaluar desde diversos enfoques la dinámica de bosques en relación a los motores de cambio asociados al cambio global (Levin, 1992; Urban, 2005). Por ejemplo, el empleo de grandes escalas constituye una primera aproximación para entender cómo el bosque de estudio está siendo o puede ser afectado por el cambio global. El uso de una escala amplia, por ejemplo a nivel regional, permitirá detectar de forma general cómo distintas variables ambientales afectan a los procesos de mortalidad de árboles y a la regeneración. Conocer a gran escala la magnitud de los efectos ambientales en los dos estadios de vida de la planta permitirá definir el estado de los bosques a lo largo de un gradiente ambiental, y predecir las posibles tendencias futuras de la especie afectada en los bosques de estudio (Thomas *et al.*, 2004; Bradley *et al.*, 2009). Así, mediante este tipo de estudios se han encontrado evidencias del papel del cambio climático (i.e. incremento de temperaturas, aumento de sequías) en procesos de decaimiento forestal (Peñuelas *et al.*, 2001; Van Mantgem *et al.*, 2009; Allen *et al.*, 2010), pronosticándose el incremento de la vulnerabilidad de estos sistemas ante las condiciones climáticas predichas (Allen *et al.*, 2010). El uso de escalas más pequeñas, sin embargo, proporcionará información sobre los factores abióticos e interacciones bióticas que afectan a la dinámica del bosque a escala local, mostrando por ejemplo las dinámicas de reemplazamiento individuo a individuo. El empleo de estas escalas permitirá detectar qué especies se verán beneficiadas o perjudicadas, y cuáles son los factores que intervienen en los mecanismos por los que el decaimiento afecta a la regeneración, con lo que se podrá discernir parte de las consecuencias del declive arbóreo en la composición futura del bosque (Suarez y Kitzberger, 2008; Redmond y Barger, 2013), al influir las dinámicas de regeneración en las trayectorias sucesionales y la composición de la comunidad del bosque (Spurr y Barnes, 1980; Pacala *et al.*, 1996). Ambas escalas tienen sus limitaciones (Pearson y Dawson, 2003; Denny y Benedetti-Cecchi, 2012), pero su empleo conjunto para evaluar el impacto del decaimiento en la regeneración a lo largo de gradientes ambientales, permitirá obtener unos resultados consistentes que amplíen con solidez el estado de conocimiento sobre las dinámicas de bosques afectados por decaimiento.

- *Escala regional*

Los Inventarios Forestales

Una herramienta útil para el estudio a escala regional de la importancia de los efectos de decaimiento en los procesos demográficos del bosque son los Inventarios Forestales. Un Inventario Forestal (IF) se define como "un proyecto encaminado a obtener el máximo de información posible sobre la situación, (…), probable evolución y capacidad productora de todo tipo de bienes de los montes de un país" (http://www.magrama.gob.es/). Los Inventarios Forestales constituyen una fuente de información de gran valor que permite detectar patrones espacio-temporales en la dinámica forestal a gran escala, los cuales pueden ser de gran utilidad para predecir futuras tendencias de las masas forestales. Analizando las bases de datos de estos inventarios se han desarrollado estudios a lo largo de todo el mundo valorando el crecimiento (e.g. Elfving y Tegnhammar, 1996; Eitzel *et al.*, 2013), la productividad (e.g. Jenkins *et al.*, 2001; Charru *et al.*, 2010), las tasas de mortalidad (e.g. Kromroy *et al.*, 2008; Lines *et al.*, 2010; Dietze y Moorcroft, 2011) o los patrones de regeneración (e.g. Schweiger y Sterba, 1997; Plieninger *et al.*, 2010) de masas boscosas. Concretamente en España, hasta la fecha se han publicado tres Inventarios Forestales Nacionales (IFN1-1966/1975, IFN2-1986/1996, IFN3-1997/2007). A partir del análisis de los datos del Segundo y Tercer Inventario se han producido numerosos trabajos en los últimos años, arrojando importantes resultados sobre la situación y tendencias futuras de nuestras masas forestales, constituyendo una contribución de valor incalculable a la ciencia (e.g. Lloret *et al.*, 2007; Carnicer *et al.*, 2011; Gomez-Aparicio *et al.*, 2011; Urbieta *et al.*, 2011; Vilà-Cabrera *et al.*, 2011b; Vilà-Cabrera *et al.*, 2011a; Ruíz-Benito *et al.*, 2013; Vayreda *et al.*, 2013).

Identificar las dinámicas de una población a la escala que permiten los Inventarios Forestales supone el primer paso para ampliar el estado de conocimiento de un sistema., permitiendo realizar predicciones de gran importancia. Complementar estos trabajos con estudios a escalas menores que incluyan aproximaciones experimentales y observacionales permitirá conocer con mayor precisión cómo va a responder una comunidad a los impactos de cualquier perturbación. Trabajar a estas escalas hace posible operar en un nivel donde las interacciones entre la vegetación establecida y diversas propiedades del sistema son detectables, posibilitando conocer los impactos de cualquier perturbación a nivel de población.

- *Escala local*

Las interacciones planta-planta

Uno de los determinantes de la regeneración en los bosques son las plantas adultas. Las dinámicas de regeneración en los sistemas forestales están determinadas en gran medida por los árboles y matorrales establecidos al actuar, por una parte, como fuentes de semillas, y por otra parte como moduladores del medio (HilleRisLambers *et al.*, 2002; Queenborough *et al.*, 2007; Gómez-Aparicio *et al.*, 2008; Comita y Hubbell, 2009; McCarthy-Neumann y Kobe, 2010), dada la gran dependencia de las plántulas del ambiente que las rodea (Harper, 1977; Kitajima y Fenner, 2000). Distintas especies del dosel arbóreo-arbustivo crean ambientes determinados en lo que se conoce como "la huella" del árbol, los cuales pueden repercutir en las propias plantas directa o indirectamente, positiva o negativamente, en lo que se conoce como procesos de retroalimentación. Por ejemplo, la sombra cerrada creada bajo el dosel arbóreo puede limitar el crecimiento de brinzales (Finzi y Canham, 2000), donde un incremento de luz por la apertura parcial o total del dosel podría favorecer la regeneración de especies menos tolerantes a la sombra (e.g. Canham *et al.*, 1994; Beckage *et al.*, 2000), confiriendo diversidad al sistema. Además, ambientes más húmedos bajo la cobertura arbórea comparados con espacios abiertos pueden favorecer el establecimiento de plántulas (Callaway, 2007), especialmente relevante en ambientes caracterizados por sequía estival (Pugnaire *et al.*, 1996; Maestre *et al.*, 2001). También en estos ambientes es relevante el papel del matorral en la regeneración, al proporcionar a las plántulas protección frente al estrés producido por las altas temperaturas y radiación del verano (Castro *et al.*, 2004; Gómez-Aparicio *et al.*, 2005; Rodríguez-García *et al.*, 2011). Las distintas especies leñosas modifican de forma diferente el contenido en nutrientes del suelo (Aponte *et al.*, 2012) y pueden a su vez modificar los patrones de crecimiento y supervivencia de plántulas (Callaway, 2007). Junto a los efectos del dosel sobre los factores abióticos, también su influencia en los factores bióticos, como por ejemplo las comunidades de microorganismos del suelo, pueden repercutir en las dinámicas de regeneración. Por ejemplo ha sido ampliamente descrito el efecto negativo que los árboles pueden ejercer sobre las plántulas de la misma especie al favorecer la presencia de patógenos especialistas en el suelo de su entorno (Augspurger, 1984; Packer y Clay, 2000; Packer y Clay, 2003; Reinhart y Clay, 2009). Por el contrario, la presencia de árboles adultos puede favorecer la relación de plántulas conspecíficas con hongos mutualistas que faciliten el establecimiento de dichas plántulas (Dickie *et al.*, 2002; O'Brien *et al.*, 2011).

Perturbaciones en el dosel arbóreo-arbustivo: efectos del decaimiento en la regeneración

El importante papel que árboles y matorrales juegan en las dinámicas de regeneración del bosque está por tanto ampliamente reconocido. Debido a esta gran influencia, cualquier perturbación en el dosel puede tener un gran impacto en los patrones de regeneración del bosque. Uno de los fenómenos más frecuentes en las dinámicas de sistemas forestales que conllevan una perturbación es la muerte del árbol y la consecuente apertura del dosel. Este es un proceso crucial por el que el dosel arbóreo y las condiciones en el sotobosque son modificados de forma natural (Canham *et al.*, 1985; Pickett y White, 1985; Gray y Spies, 1996; Kneeshaw y Bergeron, 1998), al desencadenarse una cascada de cambios en las condiciones ambientales. Así, por ejemplo, los niveles de luz en el sotobosque se ven incrementados (Canham *et al.*, 1990), modificando la temperatura y humedad del suelo (Denslow y Hartshorn, 1994; Gray *et al.*, 2002), que a su vez afectará a los microorganimos descomponedores (Meentemeyer, 1978; Pastor y Post, 1986) de una materia orgánica que se verá puntualmente incrementada por la caída de hojas y el aporte de ramas y detritus del árbol, modificando el contenido de nutrientes del suelo (e.g. Orwig *et al.*, 2008). Los cambios en las condiciones del medio (i.e. temperatura, humedad, nutrientes) van a influir a su vez en las comunidades de organismos patógenos (Augspurger *et al.*, 1990) y micorrícicos (Erland y Taylor, 2003) del suelo. Todos estos cambios pueden repercutir directamente en el éxito de establecimiento de plántulas y brinzales, modificando los patrones de regeneración del bosque. Tras la muerte de un individuo adulto se puede favorecer un incremento en la heterogeneidad espacial de nichos ecológicos, beneficiando el reclutamiento de las especies menos frecuentes y contribuyendo así a la coexistencia de las especies (Tilman y Pacala, 1993; Pacala y Tilman, 1994; Beckage *et al.*, 2000).

Cuando el fenómeno de mortalidad arbórea ocurre de forma masiva y continua, la escala espacial y la magnitud del proceso de mortalidad va a producir cambios muy rápidos y drásticos que pueden llevar a grandes modificaciones en la comunidad. Este tipo de eventos, dada su gran magnitud, tiene mayor capacidad de alterar la estructura y composición del bosque incluso llevándolo a estadios sucesionales distintos, en comparación con el proceso natural de mortalidad. Por ejemplo, el decaimiento de una determinada especie puede modificar a medio-largo plazo la identidad de la especie dominante del bosque y las comunidades asociadas a esa especie (e.g. Mueller *et al.*, 2005; Suarez y Kitzberger, 2008; Redmond y Barger, 2013), en algunos casos acelerando o modificando la dinámica sucesional del bosque (Clifford *et al.*, 2011; Collins *et al.*, 2011). En los trabajos que se han realizado hasta la fecha en todo el mundo analizando el impacto del decaimiento en la regeneración, se ha detectado el potencial que tienen los fenómenos de decaimiento de infligir cambios en la composición del bosque. Por ejemplo, en las Montañas Rocosas de Estados Unidos y en la Columbia Británica de Canadá, se han desarrollado varios estudios en bosques donde la especie dominante de pino (*P. contorta* y/o *P. edulis*) ha mostrado una alta mortalidad debido a plagas de insectos. Algunos de estos trabajos vaticinan un cambio en la composición de estos bosques a largo plazo, donde podrían pasar a dominar otras especies que no son afectadas por las plagas (Veblen *et al.*, 1991; Axelson *et al.*, 2009; Vyse *et al.*, 2009; Collins *et al.*, 2011; Kayes y Tinker, 2012)., aunque también se sugiere la continuidad en la predominancia del pino en algunas zonas en función de las características del sitio (Diskin *et al.*, 2011) o del grado de afección por la plaga (Axelson *et al.*, 2009). Al SO de Colorado, en Estados Unidos, la continuidad de *P. edulis* tras el declive por plagas de insectos va a depender de la presencia de matorral que facilite el establecimiento de plántulas (Redmond y Barger, 2013). Cambios en la composición relativa del bosque tras un proceso de declive también se han detectado en bosques de la Patagonia Argentina tras la mortalidad generalizada de árboles por sequía, donde la especie *Nothofagus dombeyi* podría a pasar a ser dominante en bosques previamente dominados por *Austrocedrus chilensis*, especie fuertemente afectada por la sequía (Suarez y Kitzberger, 2008; Amoroso *et al.*, 2012). En sistemas sub-mediterráneos, Galiano *et al*. (2013) han mostrado un reemplazo de *Pinus sylvestris* por individuos de *Quercus* sp. tras la muerte generalizada de individuos adultos de pino, también como consecuencia de un episodio de sequía extrema.

Los posibles cambios en la composición y estructura de los bosques tras fenómenos de decaimiento van a estar determinados por las dinámicas de regeneración tras el declive arbóreo. Por un lado, estas dinámicas van a depender de la capacidad de regeneración de las especies bajo las nuevas condiciones creadas tras el decaimiento. Por ejemplo, el incremento en los niveles de luz o estrés por sequía en los espacios abiertos tras la muerte de los árboles, podría evitar el establecimiento de plántulas de aquellas especies tolerantes a la sombra, favoreciendo el establecimiento de especies pioneras, más tolerantes a esas condiciones (Diskin *et al.*, 2011; Amoroso *et al.*, 2012). Por otro lado, los patrones de regeneración tras el declive podrían no depender solo de las nuevas plántulas, sino también de la regeneración avanzada (“advance regeneration”), esto es, plántulas y brinzales establecidos en el sotobosque antes del fenómeno de decaimiento. Para estos individuos, la apertura de huecos en el dosel podría suponer una oportunidad de ocupar un espacio donde antes estaban oprimidos, lo que permitiría a esas especies seguir dominando, limitando así el establecimiento de las especies pioneras demandantes de luz (Collins *et al.*, 2011; Kayes y Tinker, 2012; Redmond y Barger, 2013). Para esclarecer el posible impacto del declive sobre todo el ecosistema estos trabajos ponen de manifiesto la importancia de estudiar, por una parte, las posibilidades de establecimiento de nuevas plántulas bajo las condiciones de cambio desencadenadas por el decaimiento. Y por otra parte, la composición de la comunidad de plantas a nivel de sotobosque en el momento previo, durante y después del decaimiento.

Perturbaciones en el dosel arbóreo-arbustivo: efectos del decaimiento en organismos patógenos y mutualistas del suelo y su implicación en la dinámica de plántulas

Dado que los organismos del suelo no se encuentran distribuidos aleatoriamente sino que presentan patrones espaciales predecibles (Ettema y Wardle, 2002), afectados por factores bióticos y abióticos (Agrios, 2005; Smith y Read, 2010), cualquier perturbación local puede llevar a producir variaciones en las comunidades de estos organismos (Ettema y Wardle, 2002). Por esta razón, es esperable que el decaimiento de una especie en el bosque dibuje los patrones espaciales de los organismos del suelo. Al producirse la defoliación y muerte del árbol, las condiciones abióticas en su entorno van a ser modificadas (e.g. variación en la luz, temperatura, humedad, nutrientes), lo cual puede tener una influencia directa sobre estos organismos. Por ejemplo, en un bosque mediterráneo de pino con decaimiento por episodios de sequía extrema, en los suelos de los espacios abiertos tras la muerte de los árboles se han encontrado variaciones de las comunidades de organismos del suelo, asociado a cambios en las condiciones (Yuste *et al.*, 2012). Además, en el caso de aquellos organismos que se relacionan directamente con las raíces de las plantas, como patógenos oomicetos y micorrizas, la muerte del individuo arbóreo va a suponer la muerte y pérdida de las raíces donde esos organismos se establecen, por lo que es esperable que se produzca un cambio en sus abundancias en los suelos entorno a esos individuos. Establecer las relaciones entre el decaimiento y la distribución espacial de organismos del suelo ofrece una oportunidad para avanzar en el conocimiento de los factores que estructuran las comunidades de plantas y los mecanismos de coexistencia en bosques en declive.

Los patrones espaciales de organismos patógenos del suelo van a responder en gran medida a la distribución de los individuos vegetales con los que pueden asociarse, a la vez que la dinámica y distribución de las plantas van a estar influidas por los contenidos de patógenos en el suelo (Holdenrieder *et al.*, 2004). Por ejemplo, en un bosque cuyo decaimiento se pueda atribuir presumiblemente a la acción de un determinado organismo patógeno, sería esperable encontrar mayores abundancias de ese patógeno en las cercanías de árboles debilitados por decaimiento comparado con árboles sanos, al estar produciendo la muerte de las raíces (Brasier, 1996; Jung *et al.*, 1996). Además, el propio efecto de los patógenos en los árboles puede generar un proceso de retroalimentación que favorezca al patógeno. Así, debido al efecto negativo sobre las raíces del árbol se producirá una pérdida de cobertura foliar, llevando a cambios ambientales tales como incremento de la temperatura o modificación en los contenidos de materia orgánica del suelo. Estos cambios pueden beneficiar a su vez al patógeno, incrementando su abundancia y produciendo en última instancia la muerte del árbol. A su vez, el hecho de que las plántulas sean muy vulnerables a los patógenos dada la poca lignificación de sus raíces (Augspurger, 1984; Augspurger *et al.*, 1990; Romero *et al.*, 2007), y que la respuesta a los patógenos varía entre especies (Augspurger y Wilkinson, 2007; Reinhart *et al.*, 2010), va a producir que los bancos de plántulas y brinzales estén definidos en gran medida por la distribución espacial de la abundancia del patógeno. Por tanto la heterogeneidad de los patrones espaciales de patógenos, modulada por árboles sanos y afectados, puede tener importante consecuencias ecológicas al repercutir en el éxito de establecimiento de las plántulas.

Similarmente, el fenómeno de decaimiento puede afectar a las comunidades de mutualistas del suelo. Aunque hasta ahora ha sido poco estudiado, los trabajos que evalúan los efectos del decaimiento en las micorrizas muestran cómo las comunidades de estos hongos varían en tipo, abundancia o composición en los suelos entorno a árboles afectados en comparación con árboles sanos (Perrin y Estivalet, 1989; Causin *et al.*, 1996; Montecchio *et al.*, 2004; Swaty *et al.*, 2004; Ishaq *et al.*, 2013; Lancellotti y Franceschini, 2013). Estos efectos pueden estar relacionados con la pérdida de hojas de los árboles afectados, que puede afectar negativamente a la fijación de C en las raíces y por tanto a la cantidad de carbohidratos solubles que la planta aporta a la micorriza (Gehring y Whitham, 2003). O bien las micorrizas pueden responder a los cambios abióticos desencadenados tras la apertura del dosel. Los efectos del decaimiento en la comunidad de micorrizas pueden a su vez repercutir en la propia especie vegetal, ya que pueden influir en la asociación plántula-micorriza y por tanto en las probabilidades de establecimiento de la plántula. Por tanto, la identidad de las especies así como el grado de decaimiento de los árboles pueden influir en la distribución de las micorrizas, que potencialmente marcarán el éxito de reclutamiento de las plántulas (O'Brien *et al.*, 2011), influyendo en la variación espacial de los patrones de regeneración.

CONSIDERACIONES METODOLÓGICAS EN EL ESTUDIO DEL DECAIMIENTO Y LAS DINÁMICAS DE REGENERACIÓN

Aplicación de modelos de vecindad

En bosques mixtos va a ser el efecto simultáneo de todas las especies en torno a una plántula el que va a definir las características del micrositio en el que se establece. Estos efectos pueden ser no aditivos, al producirse interacciones espaciales. Por ello, para estudiar cómo una plántula es afectada por el dosel arbóreo es necesario incorporar conjuntamente los efectos de todos los individuos situados alrededor de esa plántula. Los modelos de vecindad son una aproximación que incorpora de forma espacialmente explícita las interacciones entre las dinámicas de poblaciones y los procesos del ecosistema (Gómez-Aparicio *et al.*, 2014). Estos modelos permiten regular la variación espacial de propiedades del ecosistema (como por ejemplo las tasas demográficas) en función de la distribución espacial de las especies. En los modelos de vecindad la estimación de los parámetros está basada en datos de campo. Por ejemplo, si consideramos *y* una medida de tasa demográfica en el punto p, como por ejemplo supervivencia de plántulas, el modelo de vecindad más simple sería una función aditiva de la forma general (Canham y Uriarte, 2006):

$$y(\mathrm{p}) = \mathrm{g}(\mathrm{p})\sum \mathrm{f}(\mathrm{x}_i) + \varepsilon$$

para i = 1…n árboles dentro de una distancia máxima (r), y donde g(p) es una función de características del punto p. A cada árbol le corresponde un vector de rasgos propios como pueden ser la especie, el estado de salud, el diámetro normal (diámetro a la altura del pecho) y su distancia al punto p. La distancia máxima r será lo suficientemente grande para incluir a todos los individuos que puedan potencialmente influenciar el proceso estudiado en el punto p. Estos modelos son muy flexibles ya que permiten adaptar la función $\mathrm{f}(\mathrm{x}_i)$ a la forma más adecuada (i.e. no lineares) para describir lo más aproximado posible el proceso en cuestión. La función $\mathrm{f}(\mathrm{x}_i)$ describe cuál es la “huella” del individuo en el punto de estudio, en función de su tamaño y de la distancia, fundamental para poder predecir las consecuencias que los cambios en la composición de la vegetación pueden tener sobre el ecosistema.

Estos modelos han sido fundamentalmente aplicados en bosques tropicales y templados, pero hasta ahora apenas han sido empleados para cuantificar el efecto de árboles en bosques mediterráneos (Gómez-Aparicio *et al.*, 2014). Además, estos estudios se han basado en la identidad del individuo, considerando árboles de la misma o distinta especie, pero no ha sido aplicado en el caso de individuos con distintos estados de salud. La aplicación de este método en un bosque afectado por decaimiento puede permitir discernir los efectos del decaimiento en procesos ecosistémicos o demográficos en un contexto en el que individuos de otras especies también se encuentran interactuando.

Aproximaciones estadísticas

La estimación de los parámetros de los modelos se puede abordar con el uso de distintas aproximaciones estadísticas: frecuentista, máxima verosimilitud y bayesiana. El uso de distintas aproximaciones en ecología ha encendido un amplio debate en los últimos años (Dennis, 1996; Ellison, 1996; Anderson *et al.*, 2000), dadas las diferencias entre éstas en su definición de probabilidad (Senn, 2003; Kéry, 2010). En estadística frecuentista la probabilidad se define como la frecuencia relativa de observar un resultado determinado al repetir un hecho un número elevado de veces, mientras que en estadística bayesiana la probabilidad es usada para expresar la incertidumbre sobre el valor más probable de un parámetro sin necesidad de la replicación hipotética de los datos (Kéry, 2010). La aproximación de máxima verosimilitud se encuentra entre ambas, con características propias de las dos (Senn, 2003).

Más específicamente, la estadística frecuentista calcula la probabilidad de obtener un resultado concreto en un procedimiento experimental, definido como la frecuencia con la que se obtendría ese resultado en una secuencia repetida del experimento. Se basa en el planteamiento de una hipótesis nula y busca confirmarla o rechazarla a partir de la distribución de posibles respuestas. Calcula un *p-valor* que informa sobre la probabilidad de obtener esos resultados u otros más extremos dada la hipótesis nula inicial (Bolker, 2008; Kéry, 2010). Los métodos de máxima verosimilitud tienen la misma base filosófica, pero en este caso plantea un modelo y busca el set de parámetros que hace que los datos observados sean los más probables de haber ocurrido, en ocasiones adaptándose mejor esta aproximación comparada con el método frecuentista para responder cuestiones ecológicas (Bolker, 2008). Con la aproximación de máxima verosimilitud se obtiene una medida explícita del apoyo de los datos al modelo propuesto mientras que los p-valores de la estadística frecuentista no ofrecen una medida directa del apoyo de los datos a otras hipótesis alternativas (Gómez-Aparicio *et al.*, 2014). En el caso de la estadística bayesiana se establece que lo que es real es lo observado, y son los parámetros o las hipótesis los que tienen distribuciones de probabilidad. Es decir, las respuestas que se obtienen con esta aproximación no dependen de observaciones hipotéticas si no de lo realmente observado, y lo que se obtienen son conclusiones acerca de las distintas probabilidades de los parámetros y las hipótesis (McCarthy, 2007; Bolker, 2008; Kéry, 2010). Esto hace que la interpretación de los resultados usando esta aproximación sea más sencilla. Los métodos bayesianos aportan gran flexibilidad a modelos que no podrían ser desarrollados con métodos tradicionales (Clark, 2005), y además permiten incorporar al modelo información previa (*priors*) (McCarthy, 2007), siendo éste uno de los puntos más criticados de estos métodos (e.g. Dennis, 1996).

En ausencia de “priors” y en el caso de modelos sencillos, las tres aproximaciones producen resultados similares (Bolker, 2008). Sin embargo, la interpretación de estos resultados es lo que diferencia a las tres aproximaciones. La elección de uno u otro método va a depender de las preguntas que se buscan resolver, en relación con la complejidad del modelo, y su uso no debe ser exclusivo sino que puede ser complementario (Bayarri y Berger, 2004; Little, 2006). En palabras de Bolker (2008) en cuanto a qué aproximación usar: “la actitud debe ser eclética y tratar de entender los puntos fuertes y débiles de cada una y usarlas de forma apropiada”. Con este objetivo se han utilizado métodos de máxima verosimilitud y bayesianos en esta tesis, como parte de un proceso de aprendizaje con el que adquirir familiaridad con cada uno de ellos, adaptando el método más conveniente para cada uno de los tipos de preguntas y modelos desarrollados.

OBJETIVOS Y ESTRUCTURA DE LA TESIS

El objetivo principal de esta Tesis es entender la dinámica de bosques dominados por *Q. suber* afectados por decaimiento, analizando su estado actual y la relación entre la mortalidad de árboles adultos y la regeneración en las dinámicas sucesionales de estos bosques. El estudio se realiza usando dos escalas de trabajo. A escala regional se analizan las dinámicas de árboles y regenerado a lo largo de gradientes ambientales. Se trata de conocer qué factores están relacionados con la supervivencia de árboles adultos y los patrones de regeneración del alcornoque, y así poder predecir el impacto que el cambio climático podría tener en la dinámica de estos sistemas. A escala local, el trabajo se centra en el estudio de las relaciones del dosel arbóreo-arbustivo con procesos demográficos; es decir, la caracterización de la "huella" de distintas especies leñosas en las dinámicas de regeneración de los bosques de estudio.

Para el análisis a escala regional se emplearon datos del Segundo y Tercer Inventario Forestal Nacional. Para el análisis a escala local se hicieron trabajos descriptivos y experimentales en condiciones de campo. Esta parte se llevó a cabo en el Parque Natural de los Alcornocales, en las provincias de Cádiz y Málaga (Figura 1). Se establecieron seis parcelas de estudio, tres situadas en bosques mixtos abiertos donde el alcornoque convive con el acebuche (*Olea europaea* var. *sylvestris*), y las otras tres situadas en bosques cerrados donde el alcornoque convive con el quejigo andaluz (*Q. canariensis*) (Figura 1).

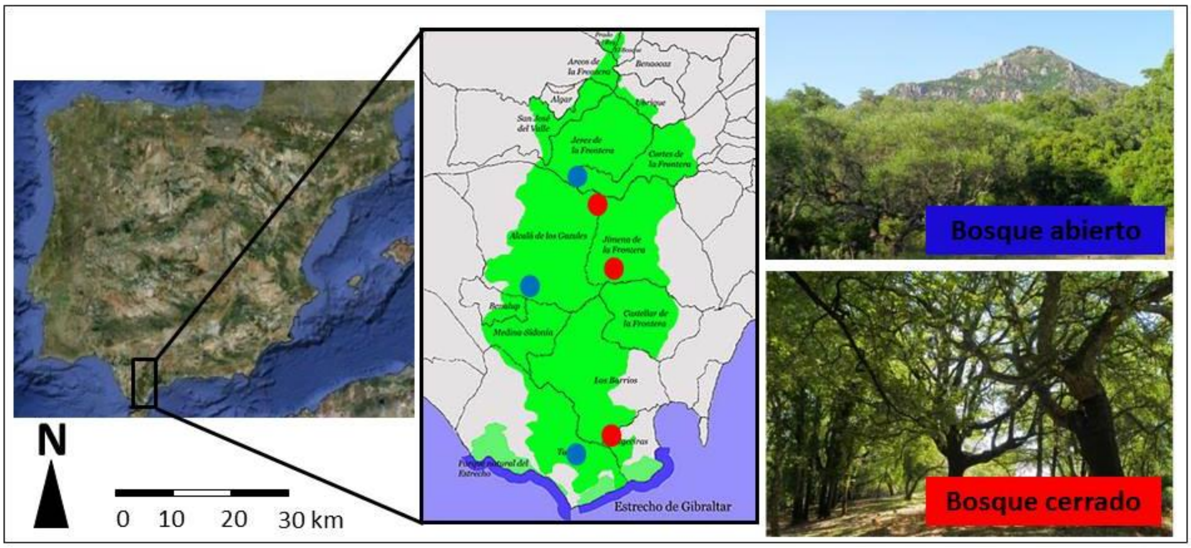

Figura 1. Localización de las seis parcelas de estudio en el Parque Natural de los Alcornocales. Los puntos azules corresponden con las tres parcelas de bosque mixto *Q. suber*-*O. europaea* (bosque abierto). En rojo, las tres parcelas de bosque mixto *Q. suber*-*Q. canariensis* (bosque cerrado).

En cada una de las parcelas se establecieron 49 puntos de muestreo, distanciados 10 metros entre sí formando una malla de 60m x 60m (Figura 2). En cada uno de los puntos se llevó a cabo la siembra de semillas con el seguimiento de las plántulas emergidas, la evaluación del ambiente abiótico (luz, humedad, nutrientes y textura del suelo) y biótico (patógenos y micorrizas), y se estableció un cuadrado permanente 1m x 1m para el seguimiento de la regeneración natural. En estas parcelas se mapearon todos los árboles y matorrales incluidos en un radio de 15 metros (árboles) y 5 m (matorrales) en torno a cada punto, registrando la especie y el tamaño (diámetro normal para los árboles, proyección del área de copa para los matorrales). Además, en el caso del alcornoque, se diferenciaron árboles con distintos estados de salud (sanos, afectados por decaimiento y muertos) (Figuras 3 y 4).

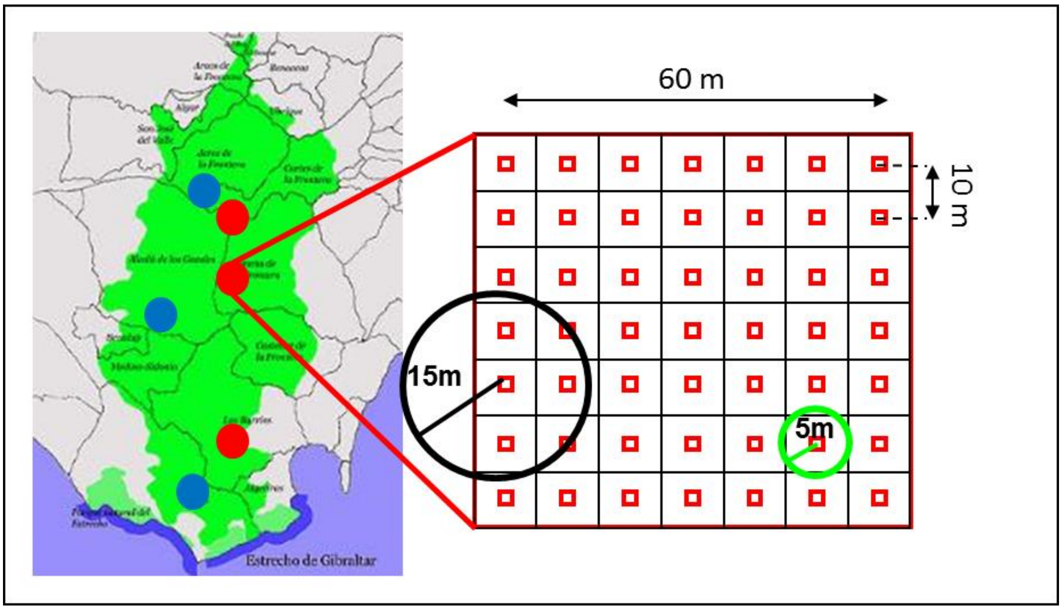

Figura 2. Esquema de los puntos de muestreo situados en cada una de las parcelas de estudio. Se indican los círculos empleados en cada punto para mapear los árboles (en negro, 15 m de radio) y los matorrales (en verde, 5 m de radio).

Figura 3. Detalle de árboles de alcornoque sano (a), en decaimiento (b) y muerto (c).

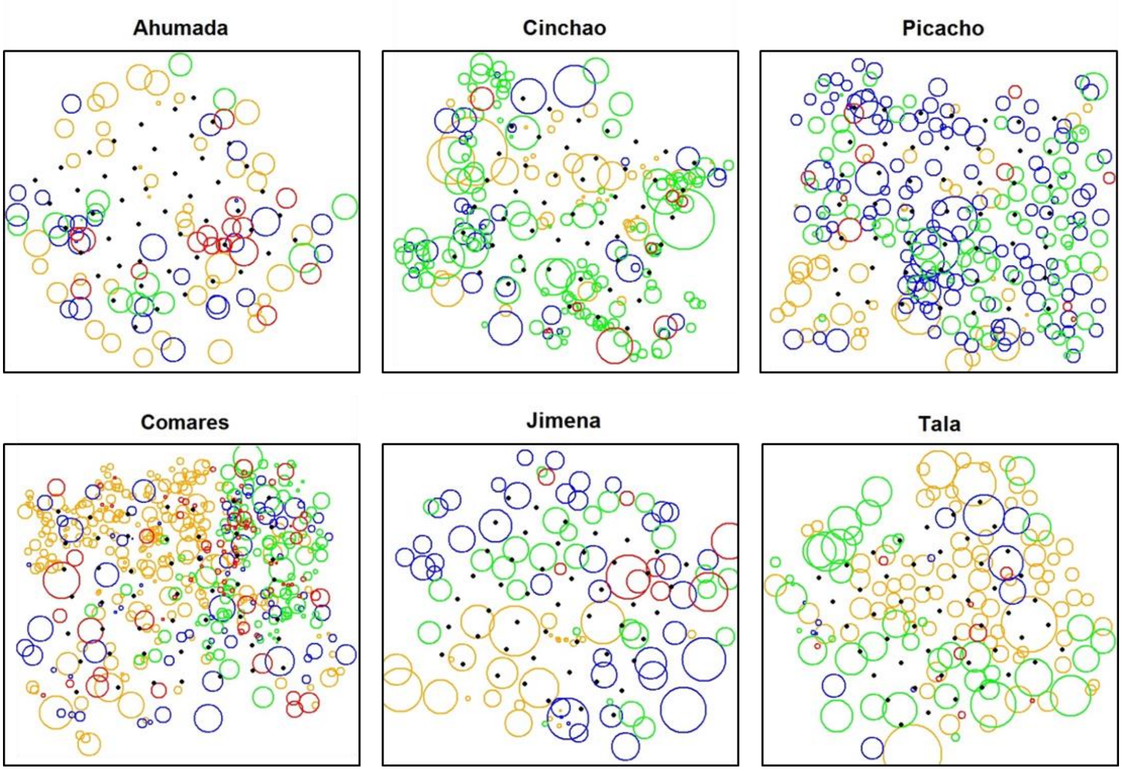

Figura 4. Distribución de los árboles en las seis parcelas de estudio. De izquierda a derecha se muestran las parcelas situadas en el sur, centro y norte, respectivamente, de los bosques de *Q. suber*-*O. europaea* (paneles superiores) y *Q. suber*-*Q. canariensis* (paneles inferiores). Se representan los árboles sanos (verde), en decaimiento (azul) y muertos (rojo) de *Q. suber*, y *O. europaea* o *Q. canariensis* (naranja) según el tipo de bosque. El tamaño de los círculos es proporcional al diámetro normal de los árboles. En negro, los puntos de muestreo.

Esta Tesis se ha organizado por capítulos en formato de artículos científicos. Se presentan cinco capítulos en inglés cada uno con sus secciones de introducción, material y métodos, resultados y discusión, con un resumen en castellano e inglés. Los capítulos 2 y 5 se encuentran publicados (en *Diversity and Distributions* y *New Phytologist* respectivamente), el 3 en revisión y los capítulos 4 y 6 en preparación. La Tesis finaliza con el capítulo 7 donde se desarrolla una discusión general, y el capítulo 8 donde se muestran las conclusiones de esta Tesis Doctoral. Cada capítulo tiene su propia sección de referencias. A continuación se ofrece una descripción del contenido y los objetivos específicos de cada capítulo.

En el **capítulo 2** se presenta un estudio de los patrones de supervivencia de árboles adultos y las dinámicas de regeneración de bosques de alcornoque en Andalucía. Se desarrollaron modelos estadísticos para evaluar el estado de los bosques de alcornoque, utilizando el IFN2 e IFN3, a lo largo de un gradiente ambiental. Se incluyeron factores climáticos (temperaturas medias y precipitaciones mensuales), factores edáficos (textura, materia orgánica, pH, capacidad de retención de agua) y factores topográficos (pendiente, orientación) con que cada parcela de estudio fue caracterizada a partir de información independiente (e.g. mapas y modelos digitales de información geográfica). El análisis se desarrolló con el objetivo de evaluar las respuestas específicas de esta especie en distintas fases de vida a diversos factores ambientales, para proporcionar una descripción de sus tendencias presentes y futuras. La importancia de este estudio recae en la necesidad de entender futuras tendencias poblacionales para evaluar la sostenibilidad de los bosques ante los cambios previstos en las condiciones climáticas. Se emplearon métodos bayesianos para la estimación de los parámetros de los modelos.

Las preguntas específicas fueron:

1- ¿Son las dinámicas de supervivencia de árboles adultos y de regeneración equivalentes en parcelas con distintos regímenes de temperatura y precipitación?

2- ¿Cómo afectan distintas variables bióticas y abióticas y su interacción con el clima a las dinámicas del alcornoque?

3- ¿Cómo podrían afectar los cambios predichos en temperatura y precipitación a la supervivencia de árboles y a la regeneración?

A escala local, en el **capítulo 3** se trata de evaluar la capacidad de establecimiento de las especies arbóreas en las condiciones de decaimiento. Se llevó a cabo una aproximación experimental, donde semillas de las tres especies arbóreas principales de los bosques de estudio fueron sembradas en los 49 puntos de cada una de las seis parcelas establecidas en el Parque Natural de los Alcornocales durante dos años consecutivos, y monitorizadas durante tres años. Usando una aproximación espacialmente-explícita se desarrollaron modelos de vecindad para explicar los patrones observados en la variación espacio-temporal de la emergencia, supervivencia, crecimiento y eficiencia fotosintética de plántulas en función del tamaño, identidad, estado de salud, abundancia y distribución de los árboles y arbustos en torno a la plántula.

Las preguntas específicas de este capítulo fueron:

1- ¿Cómo afectan la composición y el estado de salud de los árboles vecinos al comportamiento de las plántulas de especies coexistentes?

2- ¿Cuál es el papel relativo de los matorrales vecinos comparado con los árboles en el comportamiento de las plántulas?

3- ¿Son los efectos de los vecinos consistentes entre años con condiciones climáticas contrastadas?

4- ¿Varían los efectos de los árboles y matorrales en la dinámica de plántulas con la ontogenia?

5- ¿Cuáles son las implicaciones de las interacciones dosel-plántulas en las dinámicas sucesionales de bosques de alcornoque en decaimiento?

El **capítulo 4** evalúa la composición de la regeneración de las especies leñosas en relación con el estado actual de decaimiento. Se usa una aproximación de modelos de vecindad desarrollando modelos demográficos basados en estimadores de máxima verosimilitud para estudiar las respuestas de las distintas especies al dosel. Se trata de estudiar si diferentes especies del dosel, así como árboles de alcornoque con distintos grados de decaimiento, tienen efectos predecibles en los patrones naturales de regeneración, para responder a la cuestión de si la pérdida de árboles de alcornoque en el dosel es compensado con su propia regeneración, o si otras especies coexistentes muestran potencial para pasar a dominar estos bosques.

Las preguntas específicas de este capítulo fueron:

1- ¿Es capaz el alcornoque de compensar la pérdida de árboles adultos con su propia regeneración?
2- ¿Cómo afecta la mortalidad del alcornoque a la regeneración de las otras especies arbóreas con las que convive?
3- ¿Supone el decaimiento del alcornoque una oportunidad para la regeneración de especies arbustivas?
4- ¿Cuál es la implicación del decaimiento en la dinámica sucesional de estos bosques?

El **capítulo 5** se centra en los patrones espaciales de distribución de patógenos de suelo, en concreto de los oomicetos *Phytophthora cinnamomi*, y especies del género *Pythium*. En este capítulo hay dos objetivos principales. En primer lugar, se busca avanzar en el entendimiento de la distribución de patógenos en el suelo desarrollando modelos de vecindad espacialmente explícitos para explicar la importancia que los factores abióticos (como la textura del suelo) y bióticos (las comunidades de árboles y matorrales) tienen en los patrones de abundancia de patógenos del suelo en estos bosques mediterráneos afectados por decaimiento. El segundo objetivo busca explorar cuáles son los efectos de estos patógenos del suelo en la emergencia y supervivencia de plántulas de las especies arbóreas principales considerando su grado de tolerancia a la sombra. Los parámetros de los modelos fueron estimados usando máxima verosimilitud.

Las preguntas específicas fueron:

1- ¿Afectan los factores abióticos como la textura del suelo a la abundancia de patógenos del suelo?
2- ¿Existe un patrón esperable de la distribución de patógenos del suelo en relación a las especies de árboles y el decaimiento del alcornoque?
3- ¿Cómo afecta el matorral a la distribución de estos organismos?
4- ¿Cuál es el papel de los patógenos del suelo en las dinámicas de regeneración de estos bosques?

El **capítulo 6** se centra en las comunidades de organismos mutualistas, las micorrizas, y su asociación con las plántulas. Se analiza cómo el dosel arbóreo-arbustivo influye en los patrones de distribución de la asociación plántula-micorriza considerando distintas especies de árboles y matorrales, y estados de salud del alcornoque, y cómo la asociación plántula-micorriza afecta al establecimiento de las plántulas. Usando un marco bayesiano en la estimación de parámetros, se combinan datos espacialmente-explícitos de la colonización de plántulas por micorrizas con la distribución de la comunidad leñosa establecida y variables abióticas, para responder las siguientes preguntas:

1- ¿Influyen la composición y el estado de salud del dosel en la colonización de plántulas por micorrizas?

2- ¿Afecta el ambiente abiótico (i.e. humedad del suelo, luz, nutrientes, textura) a la relación plántula-micorriza?

3- ¿Cuál es la importancia relativa de la colonización por micorrizas y factores abióticos en la supervivencia de las plántulas?

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Capítulo 2

LOS EFECTOS CONTRASTADOS DEL CAMBIO CLIMÁTICO EN DISTINTAS FASES DE VIDA DE UNA ESPECIE ARBÓREA DOMINANTE: LA IMPORTANCIA DE LAS INTERACCIONES CLIMA-SUELO

Este capítulo reproduce el siguiente manuscrito:

Ibáñez, B., Ibáñez, I., Gómez-Aparicio, L., Ruiz-Benito, P., García, L.V., Marañón, T. *Contrasting effects of climate change along life stages of a dominant tree species: the importance of soil-climate interactions*. Diversity & Distributions, DOI: 10.1111/ddi.12193.

Los efectos contrastados del cambio climático en distintas fases de vida de una especie arbórea dominante: la importancia de las interacciones clima-suelo

RESUMEN

Los principales procesos que determinan la composición y estructura del bosque son la supervivencia de árboles adultos y las dinámicas de regeneración de plántulas y brinzales. Por ello, para poder predecir las tendencias futuras de las poblaciones en estos sistemas es crítico estudiar cómo estas dos fases de la vida pueden ser afectadas por el cambio climático en el contexto de otras variables bióticas y abióticas.

El objetivo de este estudio es evaluar la sostenibilidad de bosques de alcornoque (*Q. suber*) en el núcleo de su rango de distribución ante las futuras condiciones climáticas predichas. El estudio es llevado a cabo en el sur de España, usando datos del Inventario Forestal Nacional 2 y 3. Se realiza un amplio análisis para evaluar el papel de diferentes factores abióticos y bióticos en la supervivencia de árboles adultos y en los patrones de regeneración.

Se encontraron respuestas contrastadas entre los árboles adultos y el regenerado a las condiciones climáticas. La supervivencia de árboles adultos disminuyó con mayores temperaturas en primavera, mientras que la abundancia de plántulas aumentó con mayores temperaturas en invierno. La textura del suelo mostró un importante papel como modulador de los efectos de la precipitación. Con mayores precipitaciones la supervivencia de árboles adultos aumentó en suelos arenosos, pero disminuyó en suelos arcillosos. Por lo tanto, en los futuros escenarios climáticos predichos con inviernos más lluviosos y temperaturas más elevadas, la presencia del alcornoque podría quedar relegada a zonas más arenosas. También se encontró un efecto negativo de otras especies para el alcornoque tanto en la fase adulta como en la fase plántula. En general, la sostenibilidad de los bosques de estudio va a depender no solo de las condiciones climáticas futuras sino también de sus interacciones con otros factores clave, como la textura del suelo, que podrían modular los efectos del clima en las tasas demográficas.

Contrasting effects of climate change along life stages of a dominant tree species: the importance of soil-climate interactions

Beatriz Ibáñez[*,a], Inés Ibáñez[b], Lorena Gómez-Aparicio[a], Paloma Ruiz-Benito[c,d], Luis V. García[a], Teodoro Marañón[a]

a. *Instituto de Recursos Naturales y Agrobiología de Sevilla, Avda Reina Mercedes 10, 41012, Seville, Spain*
b. *School of Natural Resources and Environment, University of Michigan, 440 Church Street, Ann Arbor, MI 48109, United States*
c. *Forest Ecology and Restoration Group, Department of Life Sciences, University of Alcalá, 28871 Alcalá de Henares (Madrid), Spain*
d. *Biological and Environmental Sciences, School of Natural Sciences. University of Stirling. FK9 4LA, Stirling, United Kingdom*

ABSTRACT

For tree species adult survival and seedling and sapling recruitment dynamics are the main processes that determine forest structure and composition. Thus, studying how these two life stages may be affected by climate change in the context of other abiotic and biotic variables is critical to understand future population trends. The aim of this study was to assess the sustainability of cork oak (*Quercus suber*) forests at the core of its distributional range (Southern Spain) under future climatic conditions.

Using forest inventory data collected at two periods 10 years apart, we performed a comprehensive analysis to evaluate the role of different abiotic and biotic factors on adult survival and recruitment patterns.

We found that both life stages were influenced by climatic conditions, but in different ways. Adult tree survival was negatively impacted by warmer spring temperatures, while recruitment was positively affected by warmer winter temperatures. Our results also revealed the importance of soil texture as a modulator of winter precipitation effects on adult survival. With higher winter precipitation adult survival increased in sandy soils, and decreased in clayish soils. Therefore, under predicted future climate scenarios of wetter winters and warmer temperatures, the presence of cork oaks is more likely to occur in sandy soils versus clayish soils. Biotic conditions also affected these life stages. We found a negative effect of heterospecific but not conspecific trees on both adult survival and seedling recruitment.

Overall, the sustainability of the studied forests will be highly dependent not only on future climatic trends, but also on their interaction with other key factors - soil properties in particular - that modulate the effects of climate on demographic rates.

Key-words Bayesian analysis, declining forest, demographic rates, establishment, forest inventory data, Mediterranean region

INTRODUCTION

In forest ecosystems, mature tree survival and regeneration dynamics have long been recognized as the underlying processes determining forest structure and composition (Franklin *et al.*, 1987; Kobe, 1996; Lewis *et al.*, 2004) and hence, as the drivers of forest properties (Canham & Pacala, 1994; Pacala *et al.*, 1996). Thus, changes in demographic rates at any of these stages could have great impact on the overall dynamics of forest ecosystems (Kobe, 1996). In the last decades, many forests have experienced a decrease in adult tree survival and/or recruitment because of global change-related events (Peñuelas *et al.*, 2007; Lloret *et al.*, 2009; Allen *et al.*, 2010). In particular, increasing temperatures and drought events linked to climate change have been proposed as the likely drivers of recent tree decline in temperate ecosystems (van Mantgem *et al.*, 2009; Carnicer *et al.*, 2011; Vilà-Cabrera *et al.*, 2012). Tree seedling recruitment has also been shown to be negatively affected by drier conditions (Lloret *et al.*, 2004; Ibañez *et al.*, 2007). As a species' response to environmental stressors may differ, in direction and magnitude, among its different life stages (Cavender-Bares & Bazzaz, 2000; He *et al.*, 2005; Niinemets, 2010), its persistence would depend on the net effect across all stages (Phillips & Gentry, 1994). Still, there is a surprising lack of studies exploring how a given global change driver (e.g. increase in temperature or reduced water availability) could simultaneously affect different life stages in the plant cycle, hampering our ability to predict the effects of future climate on forest ecosystems.

In an era of global change, with heavily modified landscapes and unprecedented rates of climate change, understanding how demographic rates of dominant species in forest systems could be affected by the future trends will be critical to successfully conserve and manage these ecosystems. Many forests worldwide have been highly modified by humans, giving rise to semi-natural forest types (Noble & Dirzo, 1997; Axelsson & Ostlund, 2001), frequently characterized by a dominant woody species (Bengtsson *et al.*, 2000) whose persistence will depend on human activities (Urbieta *et al.*, 2008; Brudvig & Damschen, 2011; Bugalho *et al.*, 2011). In the south-west of the Iberian Peninsula (Portugal and Spain), humans have highly impacted forest composition for centuries, increasing the dominance of sclerophyllous *Quercus* species (mainly *Q. suber*, cork oak) forming either agro-forestry systems known as 'montado' in Portugal or 'dehesa' in Spain (Olea & San Miguel-Ayanz, 2006) or closed forests in areas with higher precipitation (Urbieta *et al.*, 2008). In both ecosystems, dehesa and close canopy forest, the dominant woody species are a major structural element in these forests, frequently considered a 'keystone species'. Oak trees maintain ecosystem functions and services, such as protection from soil erosion, enhancement of plant and animal diversity (Marañón *et al.*, 1999; Reyes-López *et al.*, 2003; García *et al.*, 2011), provisioning resources (e.g. cork, livestock feed) and cultural services (e.g. hunting, recreation) (Olea & San Miguel-Ayanz, 2006; Marañón *et al.*, 2012). Although these forests have been managed and sustained for hundreds of years (Plieninger *et al.*, 2003; Bugalho *et al.*, 2011), their long-term viability could be threatened by the current decline in adult oak trees, arising from both abiotic (e.g. recurrent drought periods) and biotic (e.g. soil-borne pathogens) factors (Brasier, 1995; David *et al.*, 2004). This phenomenon, together with the lack of regeneration mainly due to seed predation (Pausas *et al.*, 2009; Pérez-Ramos & Marañón, 2012), massive seedling mortality during the summer (Gómez-Aparicio *et al.*, 2008) and seedling predation by domestic and wild herbivores (Pulido & Díaz, 2005; Pausas *et al.*, 2009), highlight the uncertainty of the sustainability of this ecosystem and the services it provides.

Cork oak is distributed along the Mediterranean Basin, this is a region expected to undergo substantial increases in temperature and aridity in the next decades (IPCC, 2007; Planton, 2012), and it is considered one of the most vulnerable areas in the world under the predicted scenarios of climate change (Brunet *et al.*, 2007; Giorgi & Lionello, 2008). To assess the future of cork-oak forests at the core of the species' distributional range we carried out a comprehensive study that focused on the two main processes determining the future of this species: mature tree survival and regeneration patterns. Specifically, we used forest inventory data collected across Southern Spain to answer the following questions: (1) Are adult tree survival and recruitment dynamics equivalent along sites with different temperature and precipitation regimes? (2) How do other abiotic and biotic variables, and their interactions with climate, affect cork oak dynamics? (3) How will predicted changes in temperature and/or precipitation potentially affect adult tree survival and/or regeneration? By answering these questions we aim to evaluate the specific life-stage responses to environmental factors of *Q. suber*, and to provide an overview of the current and likely future trends of this important declining species.

METHODS

Study area and tree species

The study area, Andalusia, is located in the West Mediterranean region, at the southern portion of Spain (7º 31'W-1º 39'W, 37º 33'N-37º 23'N, Fig S1 in Supporting Information). It covers 87268 km^2 and the climate is typical Mediterranean, with cool, humid winters and warm, dry summers. Forested areas in Andalusia cover near 40% of the total surface, *Quercus* being the predominant tree genus in these forests (Urbieta *et al.*, 2011).

Quercus suber, the study species, is a dominant tree in these landscapes. This is an evergreen species of great economic and ecological importance, present across 240000 ha in the region. Cork oaks have low tolerance to extremely cold temperatures (frost) and severe droughts (they are rare in areas below 600 mm of annual rainfall) and they tend to prefer sandy soils (Aronson *et al.*, 2009). In Andalusia *Q. suber* is distributed in two main sub-regions with varying precipitation: Alcornocales Natural Park (1031.8±172.5 mm of annual precipitation, hereafter referred to as *wet region*), and Sierra Morena (767.3±96.6 mm, hereafter *dry region*). In the *wet region* forests have predominantly closed canopies (mean basal area ± standard deviation15.27±8.84 m^2/ha), while the *dry region* is mainly a savannah-like scrubland (10.21±6.98 m^2/ha; see Table S1 for a summary of the main characteristics of the studied plots).

Cork oak can form mono-specific stands but it is also frequently found intermingled with other species. *Olea europaea* var. *sylvestris* and *Quercus canariensis*, a winter deciduous oak, are the most common companion tree species in the *wet region*, while *Quercus ilex* is dominant in the *dry region*. Cork oak trees are extensively managed for cork production, except in highly protected reserves (García *et al.*, 2011).

Forest Inventory data

We used the Spanish National Forest Inventory (SNFI) dataset to investigate patterns in adult tree survival and natural regeneration of *Q. suber* in this region. We used the Second and Third SNFI censuses, where data were collected during the years 1995-1996 (SNFI2) and 2006-2008 (SNFI3). Stands were located on a grid of 1 x 1 km in forested areas, and of 2 x 2 km in savannah-like scrublands (Villaescusa & Díaz, 1998). The stands are circular and composed of four concentric sub-circles with radii 25, 15, 10 and 5 m each, defining four different areas where trees are sampled according to size (minimum diameter at breast height [dbh] threshold of 42.5, 22.5, 12.5 and 7.5 cm respectively). Trees within the stand were identified, measured (dbh) and mapped within the stand. The datasets contain information on recruitment as well (seedlings and saplings smaller than 1.30 m or dbh < 7.5 cm), measured within the 5 m radii circle (Villaescusa & Díaz, 1998; Villanueva, 2004).

Stands were included in the analysis of adult tree survival if at least one mature cork oak tree (dbh > 7.5 cm) was measured. We discarded those stands with evidences of forest management (cutting or thinning) in the SNFI3 (accurately detailed in the data base), resulting in a total of 755 stands used in the analysis. We then analyzed changes in the number of trees present in each stand at time 1 (SFNI2), N_1, and at time 2 (SFNI3), N_2. As individuals were identified by their position within the concentric circles we were able to discard in-growth trees, i.e., those individuals with diameters growing above the 7.5 cm threshold during the two censuses.

For the analysis of natural regeneration, based on the SFNI3 census, we discarded the stands with reforestation activities. We worked with a total of 737 stands. The number of seedlings and saplings was recorded in ordinal categories: small seedlings (height < 0.30 m), large seedlings (height between 0.30 m and 1.30 m), small saplings (height > 1.30 m and dbh < 2.5 cm) and large saplings (height >1.30 m and 2.5<dbh<7.5 cm).

Abiotic and biotic predictors

The selected stands were characterized by 20 abiotic and two biotic variables. The abiotic factors included ten climatic, eight edaphic and two topographic variables. The ten climatic variables, calculated from Gonzalo's (2008) map with a 1-km^2 spatial resolution, were annual precipitation (mm) and seasonal precipitation (spring, summer, fall and winter); and mean annual and seasonal temperature (ºC) (see Table S2). We carried out a preliminary analysis and ran different models (see below for an in-depth description of the type of models used) that we parameterized with each one of the climatic variables. We compared those models to evaluate the most influential temperature and precipitation measurements within the year, which were then selected for further analysis. The eight edaphic variables were estimated from different maps and models developed for the study area (De la Rosa *et al.*, 2002; De la Rosa & Monge, 2006; Monge *et al.*, 2008, see Table S2), calculated for the first 50 cm of soil and included pH, clay, sand and silt content (%), organic matter (%), soil water content at field capacity (g/100g), soil bulk density (g/cc) and available water capacity (g/100g). In order to avoid convergence problems during parameter estimation we applied a principal component analysis (PCA) followed by a varimax rotation to discard those soil variables which were highly correlated (R Development Core Team, 2009). This approach was chosen in order to minimize the shared variance among the selected predictors. Given the results of the PCA (see Table S3) we decided to include sand content (as representative of soil capacity to retain and percolate water), soil bulk density and organic matter content as variables representative of the edaphic conditions in each stand. The topographic variables were calculated from a SRTMV1 digital elevation model with a 1-km^2 spatial resolution (Shuttle Radar Topographic Mission, http://www2.jpl.nasa.gov/srtm/) and included slope (degrees) and a topographic radiation index. This last variable was calculated from the slope and aspect (degrees) as cos(aspect)*slope/100, with a value of zero for a flat surface, negative for a southern exposure and positive for a northern exposure (Dietze & Moorcroft, 2011).

The biotic variables considered were conspecific (*Q. suber*) and heterospecific (all other tree species) basal area in each stand (m^2 ha^{-1}). Correlation between all potential predictors was lower than 0.4. In an exploratory analysis we found that the proportion of dead trees in the selected sites was similar across size classes, so we did not include size as a factor in the analysis. To improve model runs and to be able to make direct comparisons among parameter values, previous to the analysis, we standardized all the continuous explanatory variables by subtracting the mean and dividing by the standard deviation.

Data analysis

We tried several combinations of explanatory variables and of model structure (e.g., hierarchical estimation of the parameters, inclusion of spatial random effects). We first included climatic variables only, as temperature and precipitation are recognized as the main environmental variables associated with the decline processes (Carnicer *et al.*, 2011), and then included additional explanatory variables (edaphic, topographic and biotic) and their interactions with climate. We describe our final models below, these were the model structures and combination of explanatory variables that best fitted the data based on predicted loss (D, Gelfand & Ghosh, 1998) which considers the goodness of fit of the model and a penalty term (the predictive variance). Models with the smallest D were a better fit to the data (for a list of other alternative models and combination of explanatory variables we tried see Tables S4 and S5).

Analysis of tree survival - To analyze tree survival as a function of several environmental and biotic variables we used adult census data for the two times, N_1 and N_2 in a binomial likelihood where trees survived between censuses with probability θ. We related θ to the explanatory variables using a logit link function (see Appendix S1 for further explanation).

Analysis of regeneration patterns –For the analysis of recruitment data (SFNI3), we split the data in two groups: seedlings less than 1.30 m height (*seedling group* hereafter; we considered together the two first categories in SFNI3, see Table S6) and saplings, individuals higher than 1.30 and dbh smaller than 7.5 cm (*sapling group* hereafter, considering together categories three and four in SFNI3, see Table S6). We separated between seedlings and saplings, as plants within these two life stages can respond differently to environmental factors (Plieninger *et al.* 2010). For the analysis of both seedling and sapling abundance we considered that analyzing the number of individuals at one time (i.e. SFNI3) for the two life stages was appropriate to get accurate insights on the success or failure of recruitment at these stages. This approach may have some limitations relating to saplings, whose differences between inventories could have been more precise to evaluate their performance. Nevertheless, due the nature of the data, we could not have discerned the reason of the differences in rates (i.e. sapling mortality rate or sapling recruitment rate, Vayreda *et al.*, 2013) and thus a survival analysis between the two censuses and the abundance analysis for just one would be equivalent. As counts were recorded in ordinal categories we used the average count for each of them: zero for plots without recruits, 2 for low (1-4), 10 for medium (5-15) and 20 for high (>15), and the exact number of saplings in category 4 of the SIFN3. Models were fitted to each group separately. For the analysis of the *sapling group,* we considered as an additional explanatory variable the seedlings and saplings in category 1 in the first census (SFNI2, see Table S6). This is because it can influence sapling abundance by acting as a “recruit bank” (Plieninger *et al.* 2010).

In the analysis of the *seedling group,* we defined the likelihood using a zero inflated Poisson (Zuur *et al.*, 2009) distribution with mean parameter μ. For the final model, the probability of a zero count was given by ω. We then related the parameter μ from the Poisson distribution to the explanatory variables using a log link function (see Appendix S2 for more detail).

For the analysis of the *sapling group* we evaluated the abundance of saplings in those stands where they were present (71 stands in total). We used a Poisson likelihood (with parameter μ) to model the abundance of saplings recorded in the second census (SFNI3). We related the parameter μ from the Poisson distribution to the explanatory variables using a log link function (see Appendix S3 for more detail).

We followed a Bayesian approach to estimate the parameters of the adult tree survival and recruitment models (see Appendix S4). Bayesian modeling allowed us to track the different sources of uncertainty inherent in the analysis, i.e., the data, the process and the parameters (Clark, 2005). Parameters were estimated from non-informative prior distributions (see Appendix S4). Posterior densities of the parameters were obtained by Gibbs sampling (Geman & Geman, 1984) using OpenBUGS 3.1.2. (Thomas *et al.*, 2006). Models were run until convergence of the parameters was reached (~150,000 iterations) and parameters and their confidence intervals were estimated after discarding pre-converge “burn-in” iterations (~10000). Plots of predicted versus observed values were also used to evaluate the fit of the model (unbiased model having a slope of unity). R^2 of observed versus predicted values was used as a measure of goodness-of-fit. Fixed effects coefficients whose 95% credible intervals did not include zero were considered statistically significant.

Prediction of climate change effects

We also sought to forecast the most likely trends on the dynamics of this species under future conditions, in particular how the interaction between climate and other factors might affect cork oak dynamics. We used parameter values (mean, variances and covariances) from the model runs to predict changes in tree survival and recruitment under different climatic scenarios. To do this, we used a space-for time substitution approach where variations in *Q. suber* demography along spatial climatic gradients reflected in our data were used to infer potential species responses to future changes in climate. Hence, in order to examine the potential effects of forecasted temperature increases (IPCC, 2007; Planton, 2012), we used a mean predicted increase of 3ºC within each stand (mean of A2 and B2 regional predictions for 2070-2100) to predict survival and regeneration and compared these predicted values with current conditions.

RESULTS

Tree survival patterns

The fit of the best model predicting the data had an $R^2 = 0.54$ and a slope = 1.00 (Table 1, Table S4). The final model included: winter precipitation, spring temperature, slope, topographic radiation index, sand content, sand*winter precipitation and heterospecific basal area. In this model temperature in spring and the interaction between winter precipitation and soil sand content were the most important variables affecting the survival of adult cork oak (Table 1, Figure 1). In sandy soils, the effect of increased winter precipitation was positive, whereas in heavier soils the effect was the opposite (i.e. tree survival decreased for higher precipitation, Figure 2). In flat areas there was a tendency for higher survival, whereas steeper soils translated into lower probability of survival (Figure 1). Similarly, there was a tendency of lower probability of survival at northern exposure compared with southern exposure (negative value of the parameter, Figure 1). We also found that the presence and abundance of other species was associated with a decrease in the probability of cork oak survival (Table 1, Figures 1 and 3).

Regeneration patterns

In the analysis of the *seedling group* the best model’s R^2 between observed and predicted values was 0.18 and slope 0.92 (Table 2, Table S5). The final model included: winter precipitation, winter temperature, their interaction, slope and heterospecific basal area (Table 2).

Increasing winter temperatures had a positive effect on recruitment (Figure 1), and there was a trend, although not significant, for higher precipitation favoring seedling recruitment. However the winter temperature x precipitation interaction term was negative, meaning that recruitment would be favored under warmer temperatures and drier conditions, diminishing the positive effect of warmer temperatures under wetter conditions (Figures 1 and 4). Given the parameter values and the credible intervals, the effect of the slope, although not statistically significant, was of biological relevance, showing less recruitment in steeper areas (Figure 1). The presence of heterospecific trees had negative effect on this stage of recruitment (Figure 3). Actual parameter values, standard deviation and 95% confidence interval are reported in Table 2.

Table 1 Parameter estimates for the best model analyzing mature tree survival. Values are posterior means ± sd and 95% credible intervals. Bold values indicate coefficients that do not include zero in their credible intervals and denote a significant effect of the variable on survival. Letters indicate comparison: same letter indicates not differences among regions and different letter indicate differences between regions.

Parameter	**Values**
α1, wet region intercept	3.90 ± 0.25 a
	3.42,4.42
α2, dry region intercept	3.65 ± 0.37 a
	2.94,4.41
β1, winter precipitation	-0.09 ± 0.39
	-0.87,0.61
β2, winter temperature	**-0.89 ± 0.30**
	-1.48,-0.26
β3, slope	-0.44 ± 0.24
	-0.91,0.04
β4, topographic radiation index	**-0.42 ± 0.18**
	-0.79,-0.06
β5, sand content	0.02 ± 0.24
	-0.44,0.49
β6, sand content * precipitation in winter	**1.25 ± 0.54**
	0.19,2.30
β7, heterospecific basal area	**-0.71 ± 0.24**
	-1.16,-0.12
σ^2, wet region	2.56 ± 0.39
	1.96,3.57
σ^2, dry region	2.08 ± 0.57
	1.38,3.85
ρ, wet region	**0.99 ± 0.91**
	0.02,3.51
ρ, dry region	**0.99 ± 1.01**
	0.03,2.86

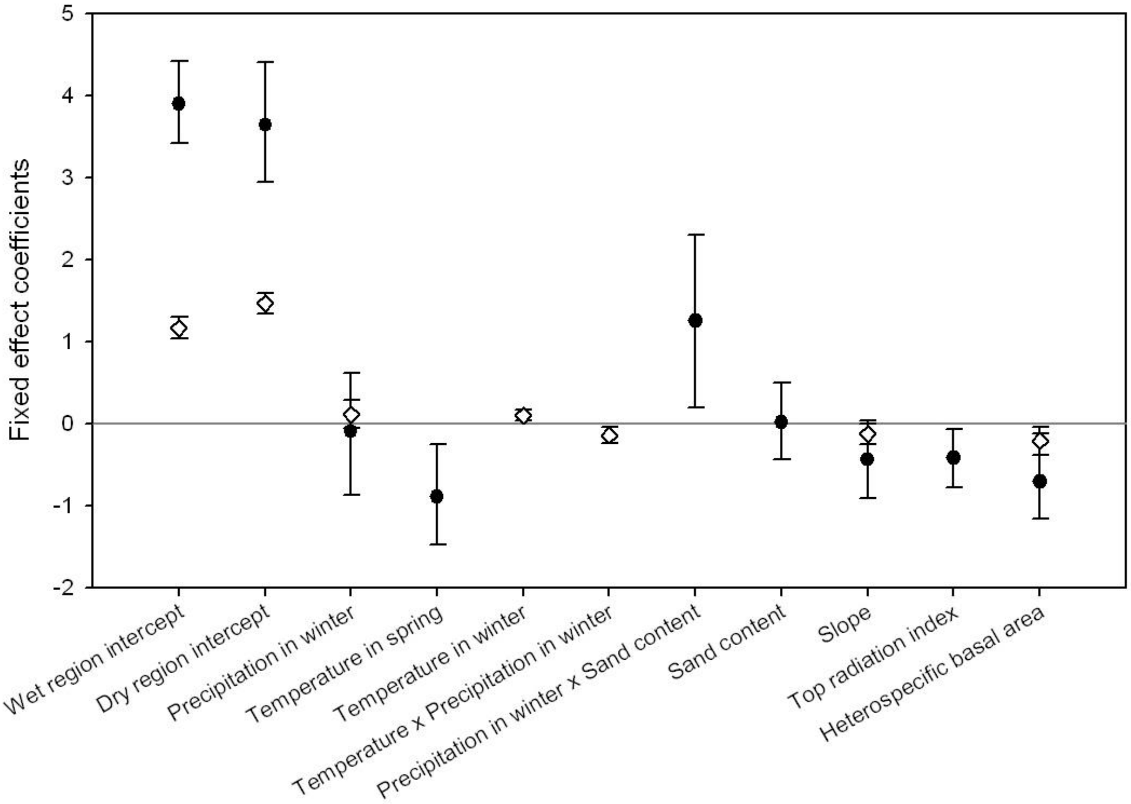


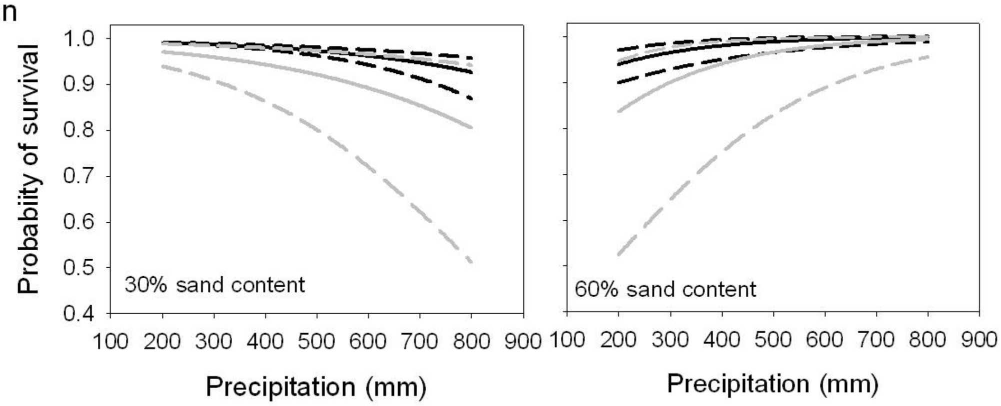
Figure 1 Posterior mean parameter values for each of the variables included in the adult tree survival (black dots) and seedling recruitment (white diamonds) analyses. Symbols for each variable are shown only when the variable was included in the final model. Bars indicate the 95% credible interval. Coefficients that do not include zero in their credible intervals are considered statistically significant.

From the analysis of the *sapling group* for which we had 74 plots, the value of predicted loss for all of the models did not improve the fit of the model when compared with the climate only model (see Table S7). However, the variables included in this model (mean annual temperature and spring precipitation) were not significant (i.e. the 95% confidence interval included zero, Table 2). Despite the findings on seedling patterns affected by different environmental factors, the scarcity of individuals found at the sapling stage could have hampered the detection of any effects at this stage.

Prediction of climate change effect

Based on the response of the studied variables along spatial environmental gradients, we predicted that under an intermediate scenario of 3°C temperature increase, the probability of tree survival decreased compared to current conditions (Figure 2); whereas recruitment abundance increased, especially noticeable under drier conditions (Figure 4). Changes in precipitation would affect adult tree survival differently depending on the texture of soil, increasing in sandy soils and decreasing in heavier soils. Increase in precipitation would favor recruitment abundance, but this benefit would be less clear under higher temperatures.

a) wet region



b) dry region

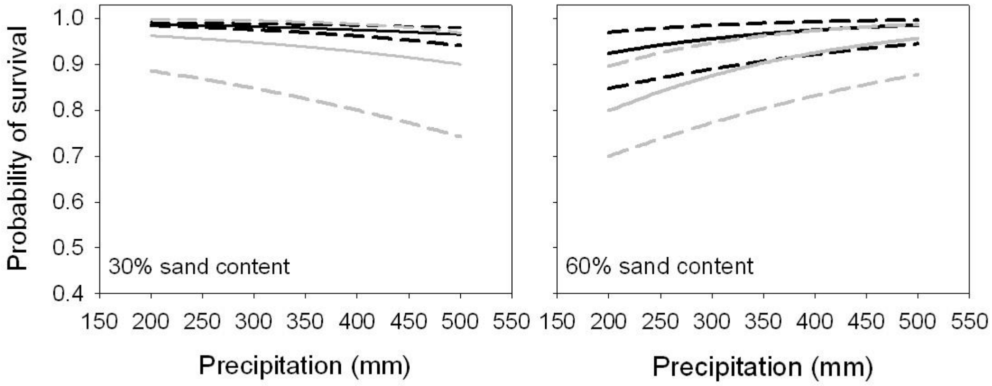


Figure 2 Predicted mean effect of precipitation on the probability of adult survival for soils with different sand content in the *wet region* (a) and the *dry region* (b). Effect under the mean temperature (black color) and the effect of 3° C temperature increase (grey color) are shown. The solid line is the mean of the posterior predictions and the broken lines represent the 95% predicted interval, for the two regions. Winter precipitation is limited to the range found for this variable in each region.

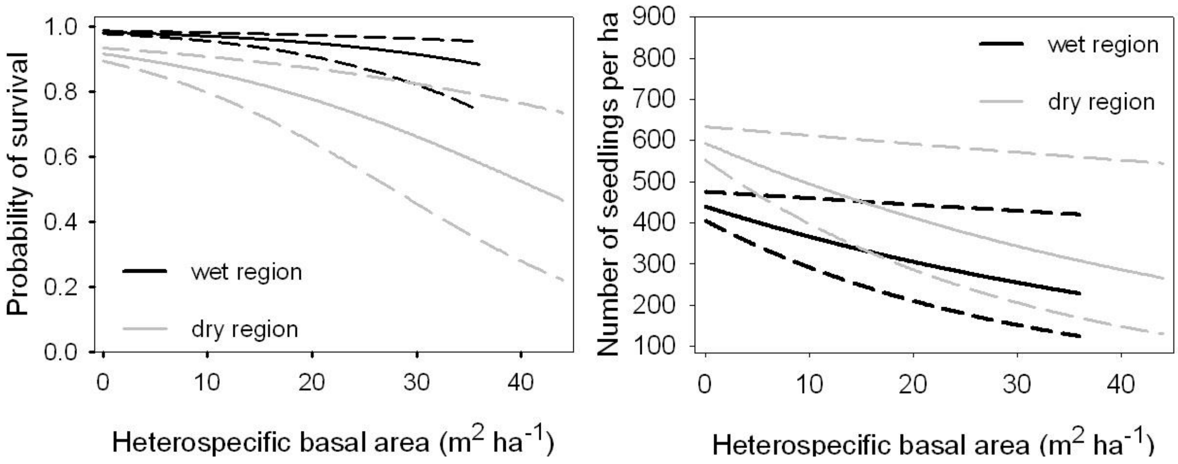


Figure 3 Mean effect of heterospecific abundance (basal area) on mature tree cork oak survival, left panel, and seedling recruitment, right panel, in the wet (black line) and dry (grey line) regions. The solid line is the mean of the posterior predictions and the broken lines represent the 95% predicted interval. Heterospecific basal area is limited to the range found for this variable in each region.

Table 2 Parameter estimates for the best model analyzing seedling and sapling abundance. Values are posterior means ± sd and 95% credible intervals. Bold values indicate coefficients that do not include zero in their credible intervals and denote a significant effect of the variable on abundance. Letters indicate comparison: same letter indicates not differences among regions and different letter indicate differences between regions.

Parameter	Values
Seedling group	
γ_1, wet region intercept	1.17 ± 0.07 a 1.031,1.303
γ_2, dry region intercept	1.47 ± 0.06 b 1.341,1.591
φ_1, winter precipitation	0.11 ± 0.09 -0.05,0.29
φ_2, winter temperature	**0.10 ± 0.03** **0.03,0.16**
φ_3, winter temperature * winter precipitation	**-0.14 ± 0.05** **-0.24,-0.05**
φ_4, slope	-0.12 ± 0.06 -0.25,0.00
φ_5, heterospecific basal area	**-0.21 ± 0.09** **-0.38,-0.04**
σ^2, wet region	0.05 ± 0.01 0.03,0.08
σ^2, dry region	0.06 ± 0.02 0.02,0.13
ρ, wet region	**1.025 ± 0.99** **0.02,3.51**
ρ, dry region	**0.93 ± 0.92** **0.02,3.31**
Sapling group	
γ_1, wet region intercept	1.44±0.18 a 1.09,1.80
γ_2, dry region intercept	1.50±0.19 a 1.12,1.87
φ_1, anual temperature	0.10±.24 -0.37,0.56
φ_2, precipitation in spring	-0.20±0.30 -0.79,0.41

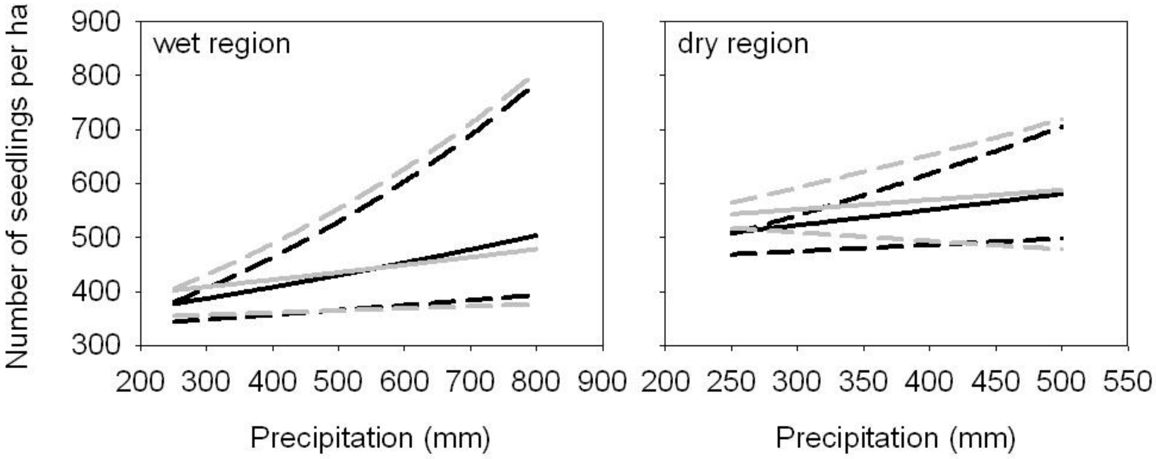


Figure 4 Predicted mean effect of precipitation on seedlings abundance (number of seedlings per hectare). Effects under the mean temperature (black color) and under a 3° C temperature increase (grey color) are shown. The solid line is the mean of the posterior predictions and the broken lines represent the 95% predicted interval, for the two regions. Winter precipitation is limited to the range found for each variable in each region.

DISCUSSION

There is the potential that future climatic trends will differently affect the life stages of organisms. It will be then the net effect along the life span of individuals that will determine the overall population response to future conditions. In this study we investigated how climatic conditions influence *Q. suber* adult survival and seedling recruitment. Interestingly, our analysis showed contrasting responses of the two life-stages studied (adult versus seedling regeneration) to an increase in temperature, being detrimental for adult trees but beneficial for seedling recruitment. Furthermore, we found that soil conditions seem to modulate the effect of climate on adult tree survival by regulating the availability of water during the dry season. These results emphasize the need for simultaneously evaluating different life-stages when studying plant population dynamics in response to varying environmental factors and highlight the importance of considering climate together with other interacting variables, in our case soil properties, when studying forest responses to future climates.

Tree survival patterns

Our results illustrate how adult tree survival was not only influenced by climate, in this case temperature in the spring having a negative effect, but also by the interaction between winter precipitation and soil texture. Spring is the season when Mediterranean plants reach their maximum photosynthetic rates (Ogaya & Peñuelas, 2003), thus plants in this region are especially sensitive to environmental conditions during this season (Peñuelas *et al.*, 2002; Gordo & Sanz, 2010). Increased spring temperature may accelerate depletion of starch pools leading to carbon starvation and subsequent mortality during a drought year, according to the C-starvation hypothesis (McDowell & Sevanto, 2010).

One of the main results derived from our study is the important role played by soil texture as a modulator of winter precipitation effects on adult survival. Soil texture determines soil hydrological properties (water infiltration, retention and runoff) and, ultimately, soil water availability (Weltzin *et al.*, 2003). As expected, our results showed higher tree survival with higher winter precipitation, but surprisingly only in sandier soils. The positive effect of increase precipitation on sandy soils is probably due to the fact that rainfall percolates to deeper soil layers, ensuring the availability of water in the dry season (Brady & Weil, 1996). On the contrary, on clayish soils, characterized by poor drainage capacity, water tends to accumulate and produce temporal waterlogging conditions. Waterlogging negatively affects cork oak survival both directly due to lack of aeration (Gaertig *et al.*, 2002) and indirectly by favoring the accumulation of aggressive soil-borne pathogens (Gómez-Aparicio *et al.*, 2012) such as *Pythopthora cinnamomi*, the main soil-borne pathogen related to the decline of cork oak in the area (Tuset & Sánchez, 2004). Altogether, our results corroborate that soil texture is a key variable regulating the effects of varying climatic conditions on this species (Fernandez-Illescas *et al.*, 2001; Piedallu *et al.*, 2012). Consequently, although precipitation may be a good proxy for soil water availability to plants at very large scales, i.e. regionally, soil hydrological properties have to be taken into account at smaller scales to fully describe the effects of changes on precipitation regime on plants.

In our analyses we also found that biotic factors, in this case density of heterospecific species, had an effect on cork oak's adult survival. Unlike cool temperate forest systems where light is recognized as the major limiting factor for growth (e.g. Canham, 1988), in Mediterranean climates water availability is generally the most limiting resource (Carnicer *et al.*, 2011). The negative relationship between the abundance of heterospecifics and cork oak survival could then be related to competition for water resources. This result agrees with previous studies that have found an increase in the sensitivity of evergreen oaks to competition with decreasing precipitation (Gomez-Aparicio *et al.*, 2011). Nevertheless, we did not find any effect of conspecific trees on cork oak survival suggesting that interspecific competition for cork oak may be greater than intraspecific competition (Gomez-Aparicio *et al.*, 2011).

Recruitment patterns

Similar to what we found for adult survival, climatic variables had the most influence determining *Q. suber* regeneration dynamics. Nevertheless, the effects of climatic factors on recruitment of new individuals did not completely match with those from the adult trees analysis: seedling abundance was mainly affected by temperature in winter, with a positive response to warmer conditions, while adult tree survival responded negatively to spring temperatures. In addition, while our model provides very useful information for assessing recruitment, the R^2 obtained suggests that other factors are likely affecting the observed recruitment patterns.

The different response to seasonal temperatures between seedlings and adult trees may be due to the high sensitivity of cork oak seedlings to low winter temperatures (Aranda *et al.*, 2005). In fact, low temperatures have a more negative impact on the photochemistry of cork oak leaves than do low water availability and high temperatures in summer (Aranda *et al.*, 2005). Contrary to what we expected, the interaction between temperature and precipitation showed in our models could indicate that the positive effect of precipitation on the abundance of seedlings may be weaker under warmer temperatures. This surprising result seems to indicate that the effect of climate on cork oak recruitment could be largely mediated by indirect mechanisms related to the presence of soil-borne pathogens, whose abundance is favored by soil moisture and warmer temperatures (Hendrix & Campbell, 1973; Sánchez *et al.*, 2002).

Here again our models showed a negative effect of heterospecific trees on seedling recruitment. In the case of seedling recruitment the negative effect that heterospecific trees seemed to have on recruitment may be due to competition for light. Some of the most common heterospecific species in our study sites (e.g. *Quercus canariensis*) create deep shade microsites under their canopy. Cork oak is a species of intermediate shade tolerance, and at low light levels seedlings tend to allocate resources to leaves at the expense of the root system, preventing roots from reaching deeper water sources (e.g. Lloret *et al.*, 1999; Cardillo & Bernal, 2006). Still, the apparently lack of effect from conspecific adults on seedling abundance could be the result of several factors acting simultaneously with an overall neutral effect, a positive effect as seed producers but a negative effect due to the accumulation of host specific enemies like soil pathogens or herbivores according to the Janzen-Connell hypothesis (e.g. Clark & Clark, 1984).

Predictions under forecasted climate change scenarios

According to our model results adult trees would respond negatively to warmer springs, and therefore the predicted changes in climatic conditions could threaten the persistence of this species and the ecosystems it supports (see examples of other forest systems around the world in van Mantgem *et al.*, 2009; Allen *et al.*, 2010; Vilà-Cabrera *et al.*, 2012). Thus, our simulation forecasts illustrate how cork oak, a key species in the Mediterranean, would be affected by the predicted rise in temperature during the year (Brunet *et al.*, 2007). Global warming would affect both adult tree survival (influenced negatively by higher temperature in spring) and potentially recruitment patterns (influenced positively by higher temperature in winter) and it will be the net effect that will determine future dynamics. What is more, in these Mediterranean forests, the inherent low abundance of seedlings and saplings resulting from their limiting climatic (e.g. high seedling mortality during summer) and management (e.g. overgrazing) characteristics, makes the process of transition exceedingly slow, which highlights the important consequences that the increase in tree mortality and lack of recruitment may have on the continuity of these forests.

While there is a clear trend of increasing seasonal average temperature, the predicted seasonal changes in precipitation are more variable for the Mediterranean Region. Although decreases are expected in the annual average and in average precipitation for most months, winter precipitation, our key variable, is expected to increase up to 30-40%, particularly in December and January (Brunet *et al.*, 2007; Planton, 2012). Our results suggest that the predicted changes in precipitation could have very different effects on tree survival patterns depending on the characteristics of the soils, which modulate the influence of climate. Therefore, under the predicted future climate scenarios, cork oak persistence is more likely to occur in sandy soils compared to clayey soils.

Most studies forecasting future plant distributions are based only on climate, neglecting the role of soils explaining distribution patterns. In our study we have shown how soil characteristics are of crucial importance when determining the influence of climate on tree dynamics. Furthermore, for a more accurate assessment on plant dynamics, different life-stages should be studied simultaneously as their different responses to environmental factors could determine the sign of the overall effect with great implications on the community.

Our models provided us with important information about underlying drivers of regeneration and mortality processes along large-scale climatic gradients, which shows contrasting trends at different life-stages. However, other underlying drivers of these processes, such as herbivory in regeneration patterns (e.g. Pulido *et al.* 2013) or biotic agents in mortality processes (e.g. Brasier *et al.* 1993), could alter the observed trends. In addition, our approach, a space for time substitution, has several relevant limitations. Specifically, local adaptation of tree species and the interaction of climate with biotic factors might lead to departures from the forecasted results. Still, this approach is valuable and informative, as it provides us with realistic insights of the potential consequences of climate change on plant populations (e.g. Pearson & Dawson, 2003; Thomas *et al.*, 2004; Bradley *et al.*, 2009; Gomez-Aparicio *et al.*, 2011).

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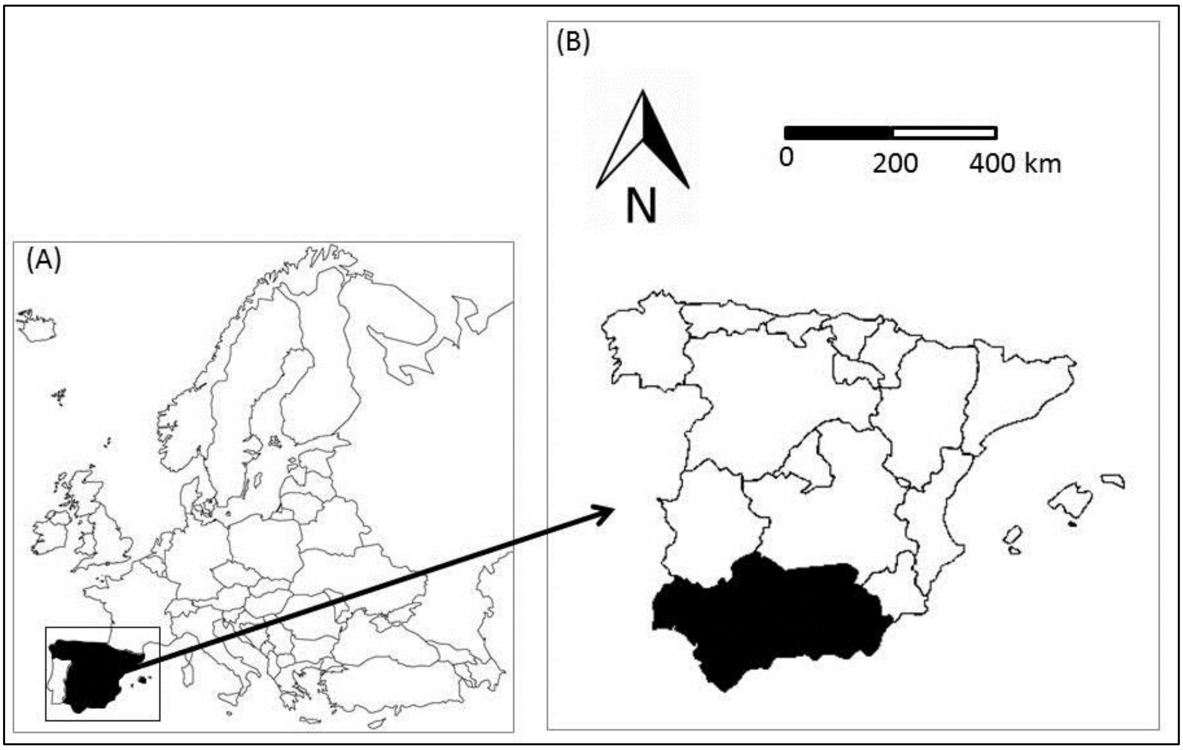
SUPPORTING INFORMATION

Figure S1 Map showing the location of Spain within Europe (A), and of the study area (Andalusia, (B)).



Appendix S1 Analytical methods _ *Analysis of tree survival*
To analyze tree survival as a function of several environmental and biotic variables we used adult census data for the two times, N1 and N2 in a binomial likelihood where trees survived between censuses with probability Θ. Then for stand i:

N_{2i} ~Binomial(N_{1i}, Θ_i)

And process model:

$logit(\Theta_i) = \alpha_{region(i)} + \beta X_i + b_i$

where α is the intercept (estimated for each region, wet and dry), β represents the vector of fixed effect coefficients associated with each of the exploratory variables included, Xi is the matrix of explanatory variables (the final model included: winter precipitation, winter temperature, slope, topographic radiation index, sand content, sand*winter precipitation and heterospecific basal area, Table 1), and bi is a spatially explicit random effect.

Appendix S2 Analytical methods _ *Analysis of the seedling group*
In the analysis of the *seedling group*, we defined the likelihood using a zero inflated Poisson distribution (Zuur *et al.* 2009) with mean parameter μ, due to the excess zero-counts in the data. We tried other types of models, i.e. zero inflated negative binomial, and

approaches to the ordinal data, through inclusion of a latent variable for each count (Table S5). For the final model, the probability of a zero count was given by ω. The likelihood in stand *i* with count y_i was:

$\Pr(y_i = 0)$ $\quad Poisson(\omega_i + (1 - \omega_i) \times e^{-\mu_i})$

$\Pr(Y_i{=}y_i \mid y_i > 0)$ $\quad Poisson((1 - \omega_i) \times e^{-\mu_i} \times \left(\frac{\mu_i^{y_i}}{y_i!}\right))$

And process model:

$$\ln(\mu_i) = \gamma_{region(i)} + \varphi \times X_i + \epsilon_i + b_i$$

with an intercept γ for each region, fixed effect coefficients φ and a matrix of explanatory variables, X_i that for the final model included: winter precipitation, winter temperature, their interaction, slope and heterospecific basal area (Table 2). We also included individual error term per stand, ε_i, and spatial random effects, b_i.

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Appendix S3 Analytical methods _ *Analysis of the sapling group*

For the analysis of the *sapling group* we evaluated the abundance of saplings in those stands where they were present (71 stands in total). We used a Poisson likelihood (with parameter µ) to model the abundance of saplings recorded in the second census (SFNI3):

$\Pr(Y_i = y_i)$ $\quad Poisson(e^{-\mu_i} \times \left(\frac{\mu_i^{y_i}}{y_i!}\right))$

And process model similar to the model used for seedlings:

$$\ln(\mu_i) = \gamma_{region(i)} + \varphi \times X_i + \epsilon_i + b_i$$

In this case the explanatory variables included in X_i for the best model were annual temperature and precipitation in spring, but none of them were significant (Table 2, Table S7).

Appendix S4 Analytical methods _ Parameter estimation

We followed a Bayesian approach to estimate the parameters of the adult tree survival and recruitment models, *α, β,* γ, φ, ω, ϵ and *b*. Bayesian modeling allowed us to track the different sources of uncertainty inherent in the analysis, i.e., the data, the process and the parameters (McCarthy, 2007). Parameters were estimated from non-informative prior distributions, α, β, γ and φ ~Normal(0,1000), ϵ_i ~Normal (0, σ^2) with $1/\sigma^2$ ~Gamma(0.01,0.01) and

$\omega_i \sim$Beta(1,1). The spatial random effects b_i were estimated using Bayesian Gaussian kriging models, where the spatial random effects were estimated separately for each region as:
$b_i|b_{j,\, j\neq i} \sim Normal(exp(-(\rho d_{ij})^{\kappa}),\ \sigma_b^2)$
where d_{ij} is the distance between two stands, ρ is the rate of decay estimated from $\rho \sim Gamma(1,1)$, the smoothing parameter, κ, was set up to 1, and $1/\sigma_b^2 \sim Gamma(0.1,0.1)$.
Posterior densities of the parameters were obtained by Gibbs sampling (Geman & Geman, 1984) using OpenBUGS 3.1.2. (Thomass *et al.* 2006). Models were run until convergence of the parameters was reached (~150,000 iterations) and parameters and their confidence intervals were estimated after discarding pre-converge “burn-in” iterations (~10000). Plots of predicted versus observed values were also used to evaluate the fit of the model (unbiased model having a slope of unity). R^2 of observed vs predicted values was used as a measure of goodness-of-fit. Fixed effects coefficients, *β and φ parameters, whose 95% credible intervals did not include zero,* were considered statistically significant.

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Table S1 Number of stands and number of *Q. suber* trees (total and dead between SFNI2 and SFNI3) considered for the analysis of tree survival. Number of stands where seedlings and saplings were present considered in the analysis of recruitment.

	Andalusia	*Wet region*	*Dry region*
Analysis of tree survival			
Total			
Stands in SNFI2	755	408	347
Q. suber trees	4964	3541	1423
Mean trees/stand	6.6	8.7	4.1
Tree Mortality			
Number of stands	170	114	56
(Percentage total stands)	22.5	27.9	16.1
Trees	347	271	76
(Percentage total trees)	7.0	7.7	5.3
Maximum (tree/stand)	28	28	6
Mean (tree/stand in stands were mortality was recorded)	2.0	2.4	1.4
Analysis of recruitment			
Seedling			
Stands (with present individuals)	396/736	254/405	142/331
Sapling			
Stands (with present individuals)	71/736	35/405	36/331

Table S2 Mean (± sd) and minimum and maximum values of the exploratory variables for each region.

Variables		Wet region			Dry region		
		mean±sd	min	max	mean±sd	min	max
Climatic	Annual temperature (ºC)	16.8±1.1	12.8	18.7	16.0±1.0	13.1	18.6
	Spring temperature (ºC)	14.8±1.2	10.5	16.9	14.0±1.0	10.7	16.7
	Summer temperature (ºC)	23.4±1.0	20.5	25.5	24.2±0.9	21.8	26.6
	Fall temperature (ºC)	18.1±1.1	13.2	19.9	17.0±1.0	13.8	20.0
	Winter temperature (ºC)	10.9±1.3	6.8	13.3	8.8±1.1	5.4	11.7
	Annual precipitation (mm)	1031.8±172.5	472.0	1756.0	767.3±96.6	532.0	1092.0
	Spring precipitation (mm)	237.4±42.4	116.0	390.0	196.6±23.1	131.0	257
	Summer precipitation (mm)	30.1±9.7	8.0	57.0	38.3±7.7	20.0	62.0
	Fall precipitation (mm)	280.3±46.8	121.0	506.0	216.0±29.07	133.0	314.0
	Winter precipitation (mm)	484.0±82.5	214.0	812.0	315.9±47.4	204.0	468.0
Topographic	Slope %	3.3±2.2	0.1	11.3	2.0±1.4	0.2	5.3
Edaphic*	Sand content %	36.3±9.6	31.7	70.1	44.2±7.5	30.2	63.5
	Silt content %	23.7±4.3	5.6	33.8	27.3±6.1	15.6	34.8
	Clay content %	39.4±8.6	19.4	56.7	27.2±4.1	19.6	35.8
	Soil bulk density (g/cc)	1.5±0.1	1.05	1.7	1.5±0.2	1.1	1.7
	Organic matter %	1.2±0.1	0.6	1.4	1.2±0.2	0.8	1.4
	Soil water content (g/100g)	28.4±5.7	12.1	36.3	20.9±3.3	12.1	24.7
	Available water capacity (g/100g)	18.3±6.2	3.0	21.4	9.7±5.1	5.9	31.6
	pH	6.7±1.0	6.1	7.0	6.4±0.3	6.1	7.1
Biotic	Conspecific basal area3 (m^2/ha)	11.5±6.8	0.4	42.1	5.5±4.9	0.4	25.8
	Heterospecific basal area3 (m^2/ha)	3.8±6.3	0.0	38.0	4.7±6.6	0.0	54.2

* For soil bulk density, soil water content and available water capacity the spatial resolution was 1:400.000. The other soil variables were estimated by the SEISnet system. The estimates come from three levels of information: regional level, landscape levels and field soil profiles. Average values of the soil properties of interest were estimated by using a model based on three main information sources: (1) a Geological Mining map and (2) a FAO soil-classes map, both at 1:400.000 scale; and (3) a wide array of detailed soil data stored in a soil profile database of the study area (SDBm Plus, de la Rosa et al 2002). Using pedotransfer functions (de la Rosa et al 2001) and interpolation techniques for spatial data, average values of several soil properties of interest, for a given geo-edaphic unit and location, were estimated (Monge et al. 2008). For a more detailed description see:

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Table S3 Factor loadings of varimax-rotated factors for the soil variables. The most representative variables for each axis are shown in bold.

Variables	Factor 1	Factor 2	Factor 3
pH	0.48	-0.03	-0.01
Clay content	**0.92**	-0.07	0.20
Silt content	-0.06	0.32	0.11
Sand content	**-0.93**	-0.23	-0.05
Organic matter	0.30	-0.14	**0.94**
Soil water content	**0.92**	-0.18	0.17
Soil bulk density	0.60	**0.94**	-0.21
Available water capacity	**0.92**	-0.16	0.17
Importance of components			
Standard deviation	3.82	1.49	1.09
Proportion of variance	0.42	0.17	0.12
Cumulative proportion	0.42	0.59	0.71

Table S4 Selected models to evaluate the probability of mature tree survival. Predictive loss (D) and description of the best models in each group of variables (smallest value of D). We included only the interactions that were significant. To account for spatial autocorrelation we added a spatially random effect b_i. Temperature and precipitation in the models including topographic, soil and biotic variables correspond to temperature in spring and precipitation in winter. α_i are the intercepts for each region, β_i are the parameters of the covariates Xi.

Model description	Process model	D
Hierarchical		
A model with the form $P(Y\mid y)$= αjs + βjs x Xj where αjs and βjs are the parameters for each X1 to Xj covariates in each s region, allowed us to combine data from the two regions to estimate the overall response of cork oak to the climatic variables while allowing for variation in this response among the two regions. Parameter estimation for one region was informed by data from the other region through the hyperparameters aj and bj. αjs and βjs were estimated from prior distributions αjs~Normal(a,σa2) and βjs~Normal(b,σb2) respectively. Prior parameters for this distributions were estimated from un-informative distributions: a~Normal(0,1000), σa~Uniform(0,1000), b~Normal(0,1000), σb~Uniform(0,1000).	logit(p_i)= $\alpha_{1,S}+\alpha_{2,S}$*Winter Precipitation$_i$+$\alpha_{3,S}$*Spring Temperature$_i$ Observations: high values of the standard deviation of the hypermarameters leaded us to discard the hierarchical model and work with the two regions independently.	1402
Simple Bayes		
Climate	logit(p_i)= $\alpha_{[regionS]}+\alpha_2$* Precipitation$_i$+$\alpha_3$* Temperature$_i$	
	Annual temperature	1733
	Winter temperature	1878
	Spring temperature	1560
	Summer temperature	1771
	Fall temperature	2185
	Spring temperature-annual precipitation	1560
	Spring temperature-winter precipitation (selected)	1511
	Spring temperature-spring precipitation	2087
	Spring temperature-summer precipitation	1827
	Spring temperature-fall precipitation	1964
Climate+Topography	logit(p_i)= $\alpha_{[regionS]}+\alpha_2$*Winter Precipitation$_i$+$\alpha_3$*Spring Temperature$_i$+$\alpha_4$*Slope$_i$+$\alpha_5$*Topographic radiation index$_i$	1387
Climate+Soils	logit(p_i)= $\alpha_{[regionS]}+\alpha_2$* Winter Precipitation$_i$+$\alpha_3$*Spring Temperaturei+$\alpha_4$*Sand content$_i$+$\alpha_5$*Soil bulk density$_i$+$\alpha_6$*Organic matter$_i$	1461
Climate+Biotic variables	logit(p_i)= $\alpha_{[regionS]}+\alpha_2$*Winter Precipitation$_i$+$\alpha_3$*Spring Temperature$_i$+$\alpha_4$*Slope$_i$+$\alpha_5$*Topographic radiation index$_i$+α_6*Sand$_i$+α_7*Sand$_i$*Winter Precipitation$_i$+α_8*Heterospecific basal area$_i$	1496

Climate + Topographic + Soils + Biotic variables	logit(p_i)= $\alpha_{[\text{regionS}]+}\alpha_2$*Winter Precipitation$_i$+$\alpha_3$*Spring Temperature$_i$+$\alpha_4$*Slopei+$\alpha_5$*Topographic radiation index$_i$+α_6*Sand$_i$+α_7*Sand$_i$* Winter Precipitation$_i$+α_8*Heterospecific basal area$_i$	1269
Model accounting for spatial autocorrelation Climate + Topographic + Soils + Biotic variables+spatially random effect	logit(p_i)= $\alpha_{[\text{regionS}]}$+$\alpha_2$*Winter Precipitation$_i$+$\alpha_3$*Spring Temperature$_i$+$\alpha_4$*Slope$_i$+$\alpha_5$*Topographic radiation index$_i$+α_6*Sand$_i$+α_7*Sand$_i$*Winter Precipitation$_i$+α_8*Heterospecific basal area$_i$+b_i	493

Table S5 Selected models to evaluate the number of *Q. suber* seedlings less than 1.30 m tall. We included only the interactions that were significant. Temperature and precipitation in the models including topographic, soil and biotic variables correspond to temperature in winter and precipitation in winter. Mean μi of the positive count data is calculated as a function of the covariates. γi are the intercepts for each region, φi are the parameters of the covariates Xi. ωi was estimated with a prior distribution Beta(1,1). ki is a parameter from the negative binomial distribution and it represents the number of failures until a certain number of successes. D: predictive loss calculated for each model. To account for spatial autocorrelation we added to the best models a spatially random effect b_i. To account for the overdispersion of the non-zero data we tried two different approximations: in a first approach, we added a stand level random effect ϵ into the linear predictor for the Poisson intensity, μ. As a second approach, we specified a negative binomial (ZINB) distribution that is overdispersed relative to the Poisson (Kéry 2010). Zero-inflated Poisson distributions (ZIP) resulted in a better fit to the data compared with ZINB and accordingly we used the ZIP model. We also considered the number of counts, y_i as a latent variable, where the true value of counts was estimated from a normal distribution with mean y_i and a variance constrained to reflect the maximum and minimum values of that ordinal level (e.g., the low ranged from 1 to 4, we used a mean of 2 and a variance of $(4-1)^2/12$, variance of the uniform distribution). We tried several model structures and combination of explanatory variables, and once the best model was selected we accounted for spatial auto-correlation by adding a spatially explicit random effect, defined above.

References

Kéry, M. (2010) *Introduction to WinBUGS for Ecologists: A Bayesian Approach to Regression, ANOVA and Related Analyses*. Academic Press.

Model description	**Process model**	**D**
Selection of the likelihood distribution		
Zero-inflated negative binomial (explanatory variables annual precipitation and temperature)	$Pr(y_i = 0)$ $\omega_i+(1-\omega_i)*(k_i/(\mu_i+k_i))k_i$ $Pr(Y_i=y_i \mid y_i > 0)$ $(1-\omega_i)*(\Gamma(y_i+k_i)/(\Gamma(k_i)*\Gamma(y_i+1))*(k_i/(\mu_i+k_i))k_i*(1-k_i/(\mu_i+k_i))y_i$ $\mu_i = \exp(\alpha_0+\alpha_1*X_{1i}+\ldots..+\alpha_n*X_{ni}+\varepsilon_i)$	215100
Zero-inflated Poisson number of seedlings/saplings as a latent variable (explanatory variables annual precipitation and temperature)	$Pr(y_i = 0)$ $\omega_i+(1-\omega_i)*\exp(-\mu_i)$ $Pr(Y_i=y_i \mid y_i > 0)$ $(1-\omega_i)*\exp(-\mu_i)*(\mu_i^{ylatenti}/ylatent_i!)$ $\mu i = \exp(\gamma_0+\varphi_1*X_{1i}+\ldots..+\varphi_n*X_{ni}+\varepsilon_i)$	30270
Zero-inflated Poisson number of seedlings/saplings as a fix variable (explanatory variables annual precipitation and temperature)	$Pr(y_i = 0)$ $\omega_i+(1-\omega_i)*\exp(-\mu_i)$ $Pr(Y_i=y_i \mid y_i > 0)$ $(1-\omega_i)*e-\mu_i*(\mu_i y_i/y_i!)$ $\mu i = \exp(\gamma_0+\varphi_1*X_{1i}+\ldots..+\varphi_n*X_{ni}+\varepsilon_i)$	15070
Alternative groups of models with a Zero Inflated Poisson likelihood		
Hierarchical		
A model with the form $P(Y \mid y)= \alpha1s + \beta js$ x Xj where αjs and βjs are the parameters for each X2 to Xj covariates in each s region, allowed us to combine data from the two regions to estimate the overall response of cork oak to the climatic variables while allowing for variation in this response among the two regions. Parameter estimation for one region was informed by data from the other region through the hyperparameters aj and bj. αjs and βjs were estimated from prior distributions αjs~Normal(a,σa2) and βjs~Normal(b,σb2) respectively. Prior parameters for these distributions were estimated from un-informative distributions: a~Normal(0,1000), σa~Uniform(0,1000), b~Normal(0,1000), σb~Uniform(0,1000).	$Pr(y_i = 0)$ $\omega_i+(1-\omega_i)*\exp(-\mu_i)$ $Pr(Y_i=y_i \mid y_i > 0)$ $(1-\omega_i)*e-\mu_i*(\mu_i y_i/y_i!)$ $\mu i = \exp(\gamma_{1,S}+\gamma_{2,S}*\text{Winter Precipitation}_i+\varphi_{1,S}*\text{Winter Temperature}_i+\varepsilon_i)$	14950
Simple Bayes		
	Annual temperature	15070

	Winter temperature	15030
	Spring temperature	15210
	Summer temperature	15080
	Fall temperature	15040
	Spring temperature-annual precipitation	15030
	Winter temperature-winter precipitation (selected)	14980
	Winter temperature-spring precipitation	15040
	Winter temperature-summer precipitation	15050
	Winter temperature-fall precipitation	15000
	$\mu i = \exp(\gamma_{[regionS]+}\varphi_1 * \text{ Winter Precipitation}_i+\varphi_2*\text{Winter Temperature}_i+\varphi_3*\text{ Winter Precipitation}_i*\text{ Winter Temperature}_i+\varepsilon_i)$	14980
Climate+topography	$\mu i = \exp(\gamma_{[regionS]+}\ \varphi_1 * \text{ Winter Precipitation}_i+\ \varphi_2 * \text{ Winter Temperature}_i+\ \varphi_3 * \text{ Winter Precipitation}_i * \text{ Winter Temperature}_i+\ \varphi_4 * \text{Slope}_i+\varphi_5 * \text{Top radiation index}_i+\varepsilon_i)$	14960
Climate + edaphic variables	$\mu_i = \exp(\gamma_{[regionS]+}\varphi_1 * \text{ Winter Precipitation}_i+\varphi_2 * \text{ Winter Temperature}_i+\varphi_3 * \text{ Winter Precipitation}_i * \text{ Winter Temperature}_i+\varphi_4 * \text{Sand content}_i+\varphi_5 * \text{Soil bulk density}_i+\varphi_6 * \text{Organic matter}_i+\varepsilon_i)$	15130
Climate+ biotic variables	$\mu_i = \exp(\gamma_{[regionS]+}\varphi_1 * \text{ Winter Precipitation}_i+\varphi_2 * \text{ Winter Temperature}_i+\varphi_3 * \text{ Winter Precipitation}_i * \text{ Winter Temperature}_i+\varphi_4 * \text{Conspecific basal area}_i+\varphi_5 * \text{Heterospecific basal area}_i+\varepsilon_i)$	14950
Climate + Topography + Biotic variables	$\mu i = \exp(\gamma_{[regionS]+}\varphi_1 * \text{ Winter Precipitation}_i+\varphi_2 * \text{ Winter Temperature}_i+\varphi_3 * \text{ Winter Precipitation}_i * \text{ Winter Temperature}_i+\varphi_4 * \text{Slope}_i+\varphi_5 * \text{Heterospecific basal area}_i+\varepsilon_i)$	14890
Model accounting for spatial autocorrelation Climate + Topographic + Biotic variables+spatially random effect	$\mu_i = \exp(\gamma_{[regionS]+}\varphi_1 * \text{ Winter Precipitation}_i+\varphi_2 * \text{ Winter Temperature}_i+\varphi_3 * \text{ Winter Precipitation}_i * \text{ Winter Temperature}_i+\varphi_4 * \text{Slope}_i+\varphi_5 * \text{Heterospecific basal area}_i+\varepsilon_i\ +b_i)$	14680

Table S6 Classification of small seedlings (height < 0.30 m), large seedlings (height between 0.30 m and 1.30 m), small saplings (height > 1.30 m and dbh < 2.5 cm) and large saplings (height >1.30 m and 2.5<dbh<7.5 cm) in SFNI2 and SFNI3. The semi-quantitative scale corresponds to low: 1-4 seedlings or saplings, medium: 5-15 seedlings or saplings, or high: >15 seedlings or saplings. To make a unique category of saplings we add the exact number of saplings in category 4 of the SIFN3 and the average count for each of the ordinal categories for category 3 in the SIFN3 (low = 2, medium = 10, and high = 20). The *corresponding recruitment stage group* column shows the two different groups (seedlings and saplings) considered in the analysis.

Height	dbh	quantification	SIFN2	SIFN3	corresponding recruitment stage group for the analysis
< 0.30 m	-	semi-quantitative scale	category 1	category 1	seedlings
0.30-1.30 m	-	semi-quantitative scale	category 1	category 2	seedlings
>1.30 m	<2.5 cm	semi-quantitative scale	category 1	category 3	saplings
>1.30 m	2.5-7.5 cm	exact number of saplings	category 2	category 4	saplings

Table S7 Predictive loss (D) for the models run in the analysis of saplings (>1.30 m high).

Alternative models		D
Climate	Annual temperature	849.5
	Winter temperature	857.4
	Spring temperature	855.8
	Summer temperature	850.9
	Fall temperature	850.8
	Annual temperature-annual precipitation	849.6
	Annual temperature-winter precipitation	851.3
	Annual temperature-spring precipitation	**847.9**
	Annual temperature-summer precipitation	853.9
	Annual temperature-fall precipitation	851.4
Topography		853.2
Soil		850.5
Biotic		852.8
Previous recruitment census		857.1
Soil, biotic		854.5
Soil, biotic + spatially explicit random effect		850.1

EFECTO DE LOS VECINOS EN LAS DINÁMICAS DE REGENERACIÓN DE BOSQUES MEDITERRÁNEOS AFECTADOS POR DECAIMIENTO: LA ESPECIE Y EL ESTADO DE SALUD INFLUYEN

Este capítulo reproduce el siguiente manuscrito:

Ibáñez, B., Gómez-Aparicio, L., Stoll, P., Ávila, J.M., Pérez-Ramos, I.M., Marañón, T. *How neighbours influence seedling dynamics in declining Mediterranean forests: tree identity and health condition matter*. Enviado a Journal of Ecology. En revisión.

Efecto de los vecinos en las dinámicas de regeneración de bosques mediterráneos afectados por decaimiento: la especie y el estado de salud influyen

RESUMEN

En los sistemas forestales la cobertura arbórea puede ejercer una gran influencia sobre las plántulas al modificar las condiciones de su entorno. La estrecha relación existente entre esta cobertura y las dinámicas de regeneración indican que cualquier alteración en los árboles adultos podría impactar profundamente en la regeneración. En un contexto de declive arbóreo, se aborda cómo el decaimiento de árboles puede influenciar la composición del bosque a través de cambios en las dinámicas de regeneración.

En dos bosques mediterráneos afectados por el decaimiento de la especie dominante, *Quercus suber*, se sembraron semillas de las tres especies arbóreas coexistentes en seis sitios durante dos años consecutivos y se monitorizaron durante tres años. Usando un análisis de vecindad espacialmente-explícito se desarrollaron modelos para explicar cómo el dosel arbóreo y el sotobosque interactúan. Se exploró la variabilidad espacio-temporal en el efecto de vecindades complejas (árboles y matorrales de distintas especies y con distintos estados de salud) en varios procesos demográficos.

Los efectos de la vecindad en las plántulas fueron comunes y predominantemente positivos para la emergencia, probablemente relacionado con mecanismos de protección frente al encharcamiento. Para la supervivencia los efectos fueron muy variables en el espacio y el tiempo, presumiblemente respondiendo a la influencia de los árboles en las abundancias de patógenos del suelo y mecanismos denso-dependientes. Unos de los principales resultados de este estudio fue el efecto negativo generalizado que tuvo el decaimiento en la regeneración de las especies de *Quercus*. La supervivencia de plántulas de todas las edades fue menor en vecindades dominadas por árboles de *Q. suber* en decaimiento que en vecindades de árboles sanos.

Los resultados sugieren que los cambios actuales en la abundancia relativa de las especies de árboles en estos bosques podrían alterar las trayectorias sucesionales a través de los impactos específicos de los vecinos en las dinámicas de plántulas. En estos sistemas con limitación de agua, los espacios abiertos tras la muerte del alcornoque podrían ser espacios no adecuados para la regeneración de estas especies arbóreas, pero sí beneficiar a otras especies más adaptadas a la escasez de agua. Esto sugiere que podría producirse la matorralización de estos bosques. El incremento predicho de episodios de decaimiento en el futuro como consecuencia del aumento de temperaturas resalta la importancia de estos resultados, y la necesidad de tener más información sobre las dinámicas de regeneración para predecir las trayectorias sucesionales más probables de bosques afectados, así como sus posibilidades de recuperación.

How neighbours influence seedling dynamics in declining Mediterranean forests: tree identity and health condition matter

Beatriz Ibáñez*[a], Lorena Gómez-Aparicio[a], Peter Stoll[b], José M. Ávila[a], Ignacio M. Pérez-Ramos[a] and Teodoro Marañón[a]

a. *Instituto de Recursos Naturales y Agrobiología (IRNAS, CSIC), PO Box 1052, Sevilla 41080, Spain.*
b. *Institute for Environmental Sciences, Section Conservation Biology, University of Basel, St. Johanns-Vorstadt 10, CH-4056 Basel, Switzerland.*

ABSTRACT

In forests, the highly vulnerable seedling stage is largely influenced by the canopy as modifier of the surrounding environment. Consequently, any alteration in the characteristics of the adult neighbourhood, such as those promoted by forest dieback, might profoundly impact regeneration dynamics. In this work we analyse the interaction between canopy neighbours and seedlings in two Mediterranean forest types (woodland and closed forest) affected by the decline and mortality of its dominant species (*Quercus suber*). Our ultimate objective was to understand how neighbour-specific effects could affect the future dynamics of these declining forests. Seeds of three tree species (*Q. suber*, *Olea europaea* and *Q. canariensis*) were sown in three sites per forest type during two consecutive years. We used a spatially-explicit, neighbourhood approach to develop models that explained the observed spatial variation in seedling emergence, survival, growth and photochemical efficiency as a function of the size, identity, health status, abundance and distribution of adult trees and shrubs in the immediate neighbourhood.

We found strong neighbourhood effects in the two forest types and for all the performance estimators measured, particularly for emergence and survival. Neighbourhood effects on seedling emergence were predominantly positive, likely due to mechanisms involving protection against soil waterlogging. For survival, on the contrary, neighbourhood effects were highly variable in space (different forest and neighbour types) and time (different years and seedling ages). The most consistent pattern detected was the negative effect of defoliated and particularly dead *Q. suber* trees across seedling species.

Ongoing changes in the species relative abundance and health of the studied forests might alter their successional trajectory through neighbour-specific impacts on seedling performance. The recruitment failure of dominant oak species in the gaps opened after *Q. suber* dead would indirectly favour the establishment of other coexisting woody species, such as drought-tolerant shrubs, fostering the conversion of current forests into more open systems with lower tree cover. Because global change is expected to increase the risk of forest die-off, more information on post-mortality regeneration dynamics is urgently needed to predict the successional trajectories and possibilities of recovery of disturbed forest ecosystems.

Key-words Forest dieback, mixed oak forests, neighbourhood models, plant interactions, *Quercus suber*, regeneration, seedling emergence and survival, seedling growth, spatiotemporal variability, tree mortality

INTRODUCTION

The seedling stage is one of the most vulnerable stages in the life cycle of plants as it is highly dependent on the surrounding environment (Harper 1977; Kitajima and Fenner 2000; Silvertown, Doust and Lovett-Doust 2001). The characteristics of the environment where seedlings establish can be largely influenced by plant canopy cover, which acts as a key modifier of biotic (e.g. pathogen abundance, mycorrhizal diversity, herbivory pressure) and abiotic (e.g light, temperature, soil fertility) conditions in the understory (Binkley and Giardina 1998; Ayres *et al.* 2009; Aponte *et al.* 2010; Gómez-Aparicio *et al.* 2012). For example, it has been widely suggested that canopy tree species can negatively affect conspecific recruitment due to the accumulation of host-specific natural enemies, namely seed predators, pathogens and herbivores (i.e. the Janzen-Connell hypothesis; Janzen 1970; Connell 1971). Moreover, seedlings of coexisting species can respond in contrasting ways to the local abiotic environment generated by a certain canopy species due to differences in their functional traits and patterns of resource acquisition (i.e. the niche differentiation hypothesis, Tilman and Pacala 1993; Queenborough *et al.* 2009). These non-exclusive hypotheses that tightly link the dynamics of canopy trees and understory seedlings clearly indicate that any alteration in the abundance, composition or health status of adult trees might profoundly impact forest regeneration dynamics.

The death of a tree and the imminent opening of a gap is a crucial process by which canopy cover and local understory conditions are naturally changed (Canham and Marks 1985; Gray and Spies 1996; Kneeshaw and Bergeron 1998). However, in the last two decades the process of gap opening in forests has been magnified due to the combined effect of several global change drivers (e.g. climate change, exotic pathogens and pests) that have caused extensive decline and mortality of several tree species worldwide (e.g. Battles and Fahey 2000; Allen *et al.* 2010; Koepke, Kolb and Adams 2010; Carnicer *et al.* 2011). Selective mortality of particular tree species could drive long-term vegetation shifts due to increased seed limitation in the die-off species or due to changes in microhabitat conditions that impair its regeneration or favour the establishment of competing species (Battles and Fahey 2000; Suarez and Kitzberger 2008; Redmond and Barger 2013). Despite the fact that understanding changes in ecological communities following forest die-off is crucial to predict future function of forest ecosystems, very few studies have specifically addressed how tree decline and mortality might influence forest composition through changes in the performance of the seedling bank (Anderegg, Kane and Anderegg 2012).

One of the main tree genus affected worldwide by die-off is *Quercus* sp. (Brasier 1996; Rizzo and Garbelotto 2003; Kabrick *et al.* 2008). In the Iberian Peninsula in particular, a severe decline affecting evergreen oak forests dominated by *Quercus ilex* and *Quercus suber* has been reported since the early 1990s (Brasier 1992; Brasier 1996). Underlying causes are the combination of abiotic and biotic stressors such as on-going drought linked to global warming and the attack of exotic soil-borne pathogens (*Phytophthora* and *Pythium* sp.) that limit plant water uptake by destroying fine roots (Sánchez *et al.* 2006; Romero *et al.* 2007; Carnicer *et al.* 2011). A fundamental characteristic of this type of drought-induced mortality is that it is not restricted to small dominated trees, as is usually the case for background mortality in Mediterranean forests (e.g. Vilà-Cabrera *et al.* 2011; Ruíz-Benito *et al.* 2013), but mainly affects medium to large size canopy trees. Thus, it constitutes a process with unprecedented capacity to modify patterns of seedling emergence and survival in a type of system (the Mediterranean forests) inherently affected by severe regeneration problems (Gómez-Aparicio 2008; Pérez-Ramos and Marañón 2012).

In this work we aim to analyse the interaction between canopy neighbours and understory seedlings in Mediterranean forests affected by the decline and mortality of their dominant species (*Quercus suber*), in order to understand how neighbour-specific effects could affect the future dynamics of these declining forests. For this, we sowed seeds of the three dominant tree species (*Quercus suber*, *Olea europaea* var. *sylvestris* and *Quercus canariensis*) in six forest sites during two consecutive years, and monitored seedling emergence, survival, growth and physiology during three years (2010, 2011 and 2012). We used a spatially-explicit, neighbourhood analysis to develop models that explain the observed spatial variation in seedling performance as a function of the size, identity, health status, abundance and distribution of adult trees and shrubs in the immediate neighbourhood. Previous observational studies have explored species-specific effects of neighbouring trees on seedlings in tropical and cool temperate forests (e.g. HilleRisLambers, Clark and Beckage 2002; Queenborough *et al.* 2007; Gómez-Aparicio, Canham and Martin 2008; Comita and Hubbell 2009). However, to our knowledge, this is the first experimental study that explores the spatiotemporal variability that complex neighbourhoods (i.e. composed by trees and shrubs of different species and health status) have on several consecutive plant demographic processes (emergence, survival and growth) in water-limited forests. By using a neighbourhood approach with multiple sites and years we sought to answer the following questions: (1) How do composition and health status of neighbours affect performance of coexisting seedling species?; (2) What is the relative role of neighbouring shrubs compared to trees on seedling performance?; (3) Are neighbourhood effects on seedlings consistent among years with contrasting climatic conditions?; (4) Do neighbourhood effects on seedling dynamics change through plant ontogeny?; and (5) What are the implications of neighbourhood interactions on the successional dynamics of declining oak forests?

MATERIAL AND METHODS

Study sites and species

The study was conducted in the Alcornocales Natural Park (36º22'N-5º34'W), a protected area in Southwestern Spain approximately of 170000 ha in extent. The climate is Mediterranean-type, with cool, humid winters and hot, dry summers. Mean annual rainfall is 970 mm (mean 1951–1999). Mean annual temperature ranges from 14.6 to 18.4 ºC, with a mean monthly maximum of 36ºC (July) and a mean monthly minimum of 2.8ºC (January). The three study years (2010, 2011 and 2012) had contrasting weather conditions. The year 2010 was especially wet with a higher than average annual and summer rainfall (1346 mm and 40 mm, respectively), 2011 was an average year in terms of both annual and summer rainfall (1037 mm and 16 mm, respectively), whereas 2012 was an extremely dry year with 474 mm annual rainfall and 0 mm summer rainfall. The bedrock is dominated by Oligo-

Miocenic sandstone that is frequently interspersed with layers of marl sediments, yielding soils rich in clay.

The Alcornocales Natural Park is situated in the Baetic-Rifean biogeographic region, which is considered a *hot spot* of biodiversity in the Mediterranean Basin (Médail and Quézel 1997). This protected area contains the largest and best conserved *Quercus suber* forests of Europe (Anonymous 2005). In drier and clayish lowlands, *Q. suber* forms mixed open woodlands with the evergreen, drought-tolerant *Olea europaea* var. *sylvestris*, whereas in sandier, wetter areas *Q. suber* coexists with the semi-deciduous, shade-tolerant *Quercus canariensis* Willd. (Algerian oak) forming closed forests (Urbieta, Zavala and Marañón 2008). The shrubby understory is diverse and rich in endemic taxa (Ojeda, Marañón and Arroyo 2000).

Experimental design

The field experiment was conducted in six study sites distributed across the whole Natural Park. Three of the sites were located in open woodlands of *Q. suber* and *O. europaea* (hereafter woodland sites), and the other three sites were located in closed forests of *Q. suber* and *Q. canariensis* (hereafter closed forest sites). The six sites covered a gradient of climate and soil conditions (see Table S1 in Supporting Information). At each site we established a 70 x 70 m permanent plot in a topographically uniform area situated within large-scale exclusions used by Park managers to avoid ungulate access. Each plot was subdivided in 49 10 x 10 m subplots (6 sites x 49 subplots, 294 sampling points).

Seed sowings were conducted during the winters (January) of 2010 (first cohort) and 2011 (second cohort). Seeds of each of the three tree species were collected from at least 10 different trees throughout the Natural Park during the previous autumn and combined to make a common pool of seeds. Viable seeds were selected by flotation and stored in moist substrate at 4ºC until sowed. Sterilized seeds were sown at each site in two adjacent 30 x 30 cm^2 quadrats at the centre of each of the 49 subplots. Each quadrat contained three lines of seeds that were separated from each other and from the border of the quadrat by 7.5 cm. In the woodland sites, we alternatively sowed each line with three seeds of *Q. suber* or six seeds of *O. europaea*. The larger number of *Olea* seeds was chosen based on their lower germination rates (Voyiatzis and Porlingis 1987; Rey *et al.* 2004). In the closed forest sites, we alternatively sowed each line with three seeds of *Q. suber* or *Q. canariensis*. Sowing quadrats were protected with 1-cm mesh to exclude seed predators. Overall, we sowed 2646 seeds of *Q. suber,* 2646 seeds of *O. europaea* and 1323 seeds of *Q. canariensis*.

To characterize local neighbourhoods, we mapped and identified all live and dead trees and shrubs around each sampling subplot. In particular, we used a Leica TC 407 to map all trees with a diameter at breast height (dbh) > 2 cm located within a 15 m radius of each subplot, as well as shrubs within a 5 m radius around the subplots. We considered a radius of 5 m to be sufficiently large to detect shrub effects as most shrubs in these forests are small (height usually < 3 m) (Gómez-Aparicio *et al.* 2012). We measured the diameter at breast height of each of the trees mapped (n = 1341 trees). Due to its multi-stem growth form, shrub size was characterized by measuring the two diameters of the elliptical projection of its crown (n = 3005 shrubs). Additionally, we divided *Q. suber* trees into different categories according to health based on a standardized semi-quantitative scale widely used in the region to monitor oak decline (e.g. García *et al.* 2011): (1) healthy reference trees; (2) defoliated trees; and (3) dead trees. No other tree or shrub species in the study area showed symptoms of decline.

Seedling measurements

We used seedling emergence, survival, height increment and photochemical efficiency as response variables to evaluate seedling performance. Seedling emergence was monitored in early June to ensure that most seedlings had emerged (Pérez-Ramos and Marañón 2012). Seedlings were revisited in early October to record survival after the summer, the main period of seedling mortality in Mediterranean systems (Gómez-Aparicio 2008; Pérez-Ramos *et al.* 2012). Survival of each emerged seedling was followed during the whole duration of the experiment (three years for the first cohort and two years for the second cohort).

To estimate seedling growth, stem height was measured in all seedlings at the end of the growth period of the three study years. The relative growth rate in height (cm) was calculated for each seedling as the fraction of height increment observed in each growing season (two growing seasons for the first seedling cohort and one for the second cohort). During the summers of 2010 and 2011, we performed in-situ chlorophyll fluorescence measurements on attached leaves using a portable, pulse-modulated fluorometer (PAM-2000, Walz Effeltrich, Germany). The photochemical efficiency of photosystem II (Fv/Fm) was measured at midday (i.e. between 12:00 and 14:00) after a 30 min dark adaptation in one 1-year old seedling per species and subplot.

Data analyses

We used a model selection procedure (Johnson and Omland 2004) to estimate seedling emergence, survival, height growth and physiological condition (measured by photochemical efficiency) as a function of the characteristics of the neighbourhood. We fit separate models for each combination of forest type (woodland and closed forest), seedling cohort (2010 and 2011) and seedling species (*Q. suber* and *Q. canariensis*). Unfortunately, emergence of *O. europaea* was virtually nil in all sites (data not shown), which precluded us from testing neighbourhood effects on this tree species.

Our simplest model (*Null* model, eqn 1) estimates seedling emergence, survival, growth or photochemical efficiency using a single mean, thereby assuming that the site and the spatial distribution of woody neighbours have no impact on seedling performance. For observation *i*, this model has the form:

$$Y_{(i)} = \alpha + \varepsilon_{(i)} \qquad \text{eqn 1}$$

where α represents the mean for the seedling performance estimator Y in each forest type, and ε is the error term. We then fit a *Site* model (eqn 2) that considered potential differences in seedling performance among the three sites of each forest type:

$$Y_{(i)} = \alpha_{Site(i)} + \varepsilon_{(i)} \qquad \text{eqn 2}$$

Finally, the effects of neighbouring trees and shrubs were incorporated into the model by adding a simple linear term:

$$Y_{(i)} = \alpha_{Site\ (i)} + \beta_{Neighbour\ type(i)} * NI_{(i)} + \varepsilon_{(i)} \qquad \text{eqn 3}$$

where NI (neighbourhood index) is the combined effect (quantified below) of woody neighbours on seedling performance and β is the slope of the effect of each neighbour type. A main motivation for this study was to compare models that make different assumptions about the nature of neighbourhood interactions between canopy neighbors and tree seedlings in declining Mediterranean forests. Thus, we explicitly tested four alternate models of increasing complexity. The simplest model assumed that all neighbours had equivalent effects on the target regardless of species or health status (*All trees* model), and therefore calculated a single general β parameter. A second model differentiated between conspecific and heterospecific neighbours, and calculated separate values of β for the two classes (*Species* model). The third model separated neighbours of different species and also calculated different βs for healthy, defoliated, and dead *Q. suber* trees (*Species + Health* model). The final neighbourhood model added the effect of shrubs to the best tree model, by including a separate β for shrubs (*Shrubs* model).

We tested three alternative forms of the neighbourhood index (NI) where the effect of neighbours on seedling performance was: 1) exclusively a direct function of neighbour size (eqn 4); 2) a direct function of the size and an inverse function of the distance to the neighbour (eqn 5); and 3) a direct function of the size and an inverse function of the square distance to the neighbour (Weiner 1984) (eqn 6):

$$NI = \sum S_i \qquad \text{eqn 4}$$

$$NI = \sum \frac{S_i}{d_i} \qquad \text{eqn 5}$$

$$NI = \sum \frac{S_i}{d_i^2} \qquad \text{eqn 6}$$

In these equations, S_i is the size of the tree or shrub i within the neighbourhood and d_i its distance to the target subplot. The size of trees and shrubs was quantified differently (dbh for trees and area projection for shrubs), so we normalized size measurements and gave a value of 1 to the biggest tree and shrub to make parameter estimates comparable. Models were run with increasing neighbourhood radii to test whether there was an optimal neighbourhood radius and whether different types of neighbours influenced seedling performance at different distances (Gourlet-Fleury and Houllier 2000; Peters 2003; Phillips *et al.* 2003; Stoll and Newbery 2005). The radii tested were from 1 to 15 m in steps of 1 m for trees, and from 1 to 5 m in steps of 1 m for shrubs.

We used the Akaike Information Criterion corrected for small sample sizes (AIC_c) to select the best model, with lower AIC_c values indicating stronger empirical support for a model (Burnham and Anderson 2002). We allowed radii that yielded the minimum AIC_c to be different for each type of neighbour included in the model. Only variables that explained a significant amount of deviance (p-value < 0.05) were retained in the final best models.

Seedling emergence and survival were modelled using a binomial or quasibinomial (to account for overdispersion) error distribution, and seedling growth and photochemical efficiency using a normal distribution. In growth models, where seedlings of the same subplot were considered independent, subplot was included as a random factor to control for pseudoreplication. We used pseudo R^2 as a measure of goodness of fit in the emergence and survival models (Mittlbock and Schemper 1996), and the R^2 of observed vs. predicted values in the growth and photochemical efficiency models. All analyses were performed using R (R Development Core Team 2009).

RESULTS

Models that included the effects of neighbouring trees or shrubs on seedling performance were a better fit to the data than models that ignored them in 83% (30/36) of the combinations of forest type, seedling species, seedling cohort, year and performance estimator tested (Tables 1 and 2). Moreover, 60% of these best models (18/30) offered support for idiosyncratic effects of trees differing not only in their identity but also in their health status (*Species* + *Health* model). Shrubs were only included in 16% (5/30) of the best neighbourhood models (*Shrubs* model, Tables 1 and 2). The majority of the best neighbourhood models (27/30) included the simplest neighbourhood index (NI), where neighbour effects were exclusively a function of their size (i.e. it did not consider a distance decay of neighbour effects). This indicates that the spatial configuration of neighbours was less important for seedling establishment than their overall abundance within the neighbourhood. In the optimal neighbourhood radius included in the best models there was large variability among forest and neighbour types, which ranged from 1 to 15 m (see Tables S2 and S3 in Supporting Information). In general, optimal neighbourhood radii were lower in woodland than in closed forest sites, probably due to the lower tree height in woodlands. In these sites, most neighbour effects were constrained to < 10 m, whereas in closed forests roughly half of the detected effects were >10 m. We did not detect any consistent trend regarding different optimum radius among neighbour types (see Tables S2 and S3).

Seedling emergence

Models that considered the effect of tree neighbours of different species and health status (*Species* + *Health* model) were the best fit for emergence of the two *Quercus* species in all combinations (6/6) of forest types and seedling cohorts, and explained a percentage of variation in the data that ranged from 15.2% to 25.2% (Tables 1 and 2, Fig. 1). Adding shrub effects to the best tree model substantially improved model fit (i.e. decreased AIC_c values > 2 units) in only 33% (2/6) of the cases (first cohort *Q. suber* emergence in woodlands and *Q. canariensis* emergence in closed forests). Positive effects on emergence were detected for all type of woody neighbours in woodland sites (i.e. positive β values; see Table S4). On the contrary, in closed forests, neighbour effects on emergence were predominantly neutral. Only *Q. canariensis* trees had a consistent positive effect on the emergence of *Q. suber* and *Q. canariensis* seedlings in this type of forests. For both seedling species, neighbour effects on emergence were more frequently found during the extremely wet spring of 2010 than during the normal 2011 (Fig. 1).

Table 1 Comparison of alternate models for performance variables of *Quercus suber* seedlings in the woodland sites. The first two models calculate an average value of seedling performance that varies (*Site* model) or not (*Null* model) among the three woodland sites. The other four models include an additional term that accounts for the effect of neighbours on seedlings, either considering all individual trees as equivalent (*All trees* model), separating among species (*Species* model) and health status (*Species + Health* model), or adding the effect of shrubs to the best tree model (*Shrubs* model). The most parsimonious model (indicated in bold) is the one with the lowest AIC$_c$. Significant explanatory variables included in the best models are detailed: TREES, all trees; CON, conspecific trees; HET, heterospecific trees; HEA, healthy *Q. suber* trees; DEF, defoliated *Q. suber* trees; DEA, dead *Q. suber* trees; SHR, shrubs. R^2 or pseudo-R^2 of the best model is also given. NI indicates the form of the neighbourhood index included in the best model; S, size; D, distance.

		AICc								
Cohort	Variable	Null	Site	All trees	Species	Species + Health	Shrubs	NI	R^2	Explanatory variables
Cohort 1	Emergence	668.2	667.5	657.4	650.4	638.7	**628.2**	S	15.2	HET+HEA+DEF+DEA+SHR
	First-year survival	316.3	291.7	289.4	281.7	**275.5**	292.3	S	22.4	Site+HET+DEA
	Second-year survival	274.0	250.4	245.0	**236.5**	242.9	248.6	S	21.0	Site+HET+CON
	Third-year survival	255.0	**235.6**	234.8	234.2	234.1	235.8	-	11.7	Site
	First-year growth	74.5	**66.5**	66.4	67.4	67.1	66.4	-	18.4	Site
	Second-year growth	**-230.0**	-227.8	-226.4	-226.8	-225.3	-227.0	-	1.2	-
	Fv/Fm	-710.0	-716.1	**-725.2**	-726.3	-723.5	-716.2	S/D	12.6	Site+TREES
Cohort 2	Emergence	690.1	653.5	626.5	624.6	**621.0**	623.9	S	20.1	Site+HEA+DEF+DEA
	First-year survival	384.4	369.8	371.3	366.2	**336.3**	350.0	S/D	20.6	Site+HET+DEF+DEA
	Second-year survival	192.9	190.8	**185.1**	187.0	185.5	186.5	S	9.2	Site+TREES
	First-year growth	65.0	59.0	58.5	59.5	**53.8**	58.0	S/D^2	39.0	Site+DEF+DEA
	Fv/Fm	**-330.2**	-330.1	-331.3	-329.3	-331.8	-330.0	-	1.9	-

Table 2 Comparison of alternate models for performance variables of *Quercus suber* and *Quercus canariensis* seedlings in the closed forest sites. The first two models calculate an average value of seedling performance that varies (*Site* model) or not (*Null* model) among the three closed forest sites. The other four models include an additional term that accounts for the effect of neighbours on seedlings, either considering all individual trees as equivalent (*All trees* model), separating among species (*Species* model) and health status (*Species + Health* model), or adding the effect of shrubs to the best tree model (*Shrubs* model). The most parsimonious model (indicated in bold) is the one with the lowest AIC_c. Significant explanatory variables included in the best models are detailed: TREES, all trees; CON, conspecific trees; HET, heterospecific trees; HEA, healthy *Q. suber* trees; DEF, defoliated *Q. suber* trees; DEA, dead *Q. suber* trees; SHR, shrubs. R^2 or pseudo-R^2 of the best model are also given. NI indicates the form of the neighbourhood index included in the best model; S, size; D, distance.

Species	Cohort	Variable	AIC_c						NI	R^2	Explanatory variables
			Null	Site	All trees	Species	Species+ Health	Shrubs			
Q. suber	Cohort 1	Emergence	568.3	515.9	514.5	510.7	**504.1**	511.2	S	24.4	Site+HET+DEA
		First-year survival	304.6	291.6	292.1	290.0	**288.0**	292.1	S	12.7	Site+DEA
		Second-year survival	281.7	219.8	211.9	**208.1**	212.1	219.9	S	39.5	Site+HET
		Third-year survival	160.5	150.2	147.6	145.0	**140.4**	150.9	S	23.6	Site+HEA+DEA
		First-year growth	284.0	278.7	276.6	**273.4**	275.9	275.3	S	37.9	Site+HET
		Second-year growth	**-30.5**	-29.1	-30.4	-30.1	-28.8	-28.8	-	2.1	-
		Fv/Fm	-191.4	-203.2	**-207.3**	-206.2	-201.8	-204.6	S	29.8	Site+TREES
	Cohort 2	Emergence	453.5	429.8	422.2	418.1	**415.0**	419.0	S	18.1	Site+DEA
		First-year survival	194.5	191.2	191.8	187.4	**179.4**	181.6	S	14.7	DEA
		Second-year survival	98.7	96.6	90.6	86.9	**80.9**	98.5	S	40.0	Site+HET+HEA+DEF
		First-year growth	74.0	66.7	**61.0**	60.9	61.9	67.8	S	24.2	Site+TREES
		Fv/Fm	-328.6	-342.4	-343.1	-342.5	-351.2	**-356.9**	S	36.8	Site+HEA+DEA+SHR
Q. canariensis	Cohort 1	Emergence	584.5	541.3	529.1	527.3	522.6	**516.9**	S	25.2	Site+CON+DEA+SHR
		First-year survival	398.6	375.1	371.7	365.8	**353.4**	375.8	S	22.1	Site+CON+DEF+DEA
		Second-year survival	348.8	262.5	255.9	251.1	**245.7**	263.7	S	44.3	Site+HEA+DEF+DEA
		Third-year survival	185.4	183.1	181.5	178.6	**145.5**	183.2	-	32.4	Site+HEA+DEA
		First-year growth	227.7	219.6	219.3	**215.4**	215.6	220.5	S	16.8	Site+CON
		Second-year growth	-287.3	-293.2	**-303.4**	-303.5	-303.3	-294.5	S	14.7	Site+TREES
		Fv/Fm	-408.2	-418.7	-419.5	-419.8	-420.4	**-422.2**	S	20.5	Site+SHR
	Cohort 2	Emergence	380.6	366.8	363.4	362.9	**355.7**	358.3	S	20.5	Site+DEF
		First-year survival	199.4	188.3	**177.1**	181.4	186.1	187.3	S	19.0	Site+TREES
		Second-year survival	113.5	98.8	99.0	94.0	**90.9**	95.1	S	36.3	Site+HEA+DEF
		First-year growth	23.1	**16.5**	17.2	18.1	15.4	15.4	-	9.0	Site
		Fv/Fm	-176.0	-183.1	-183.2	-183.1	-182.5	**-186.1**	S	17.3	Site+SHR

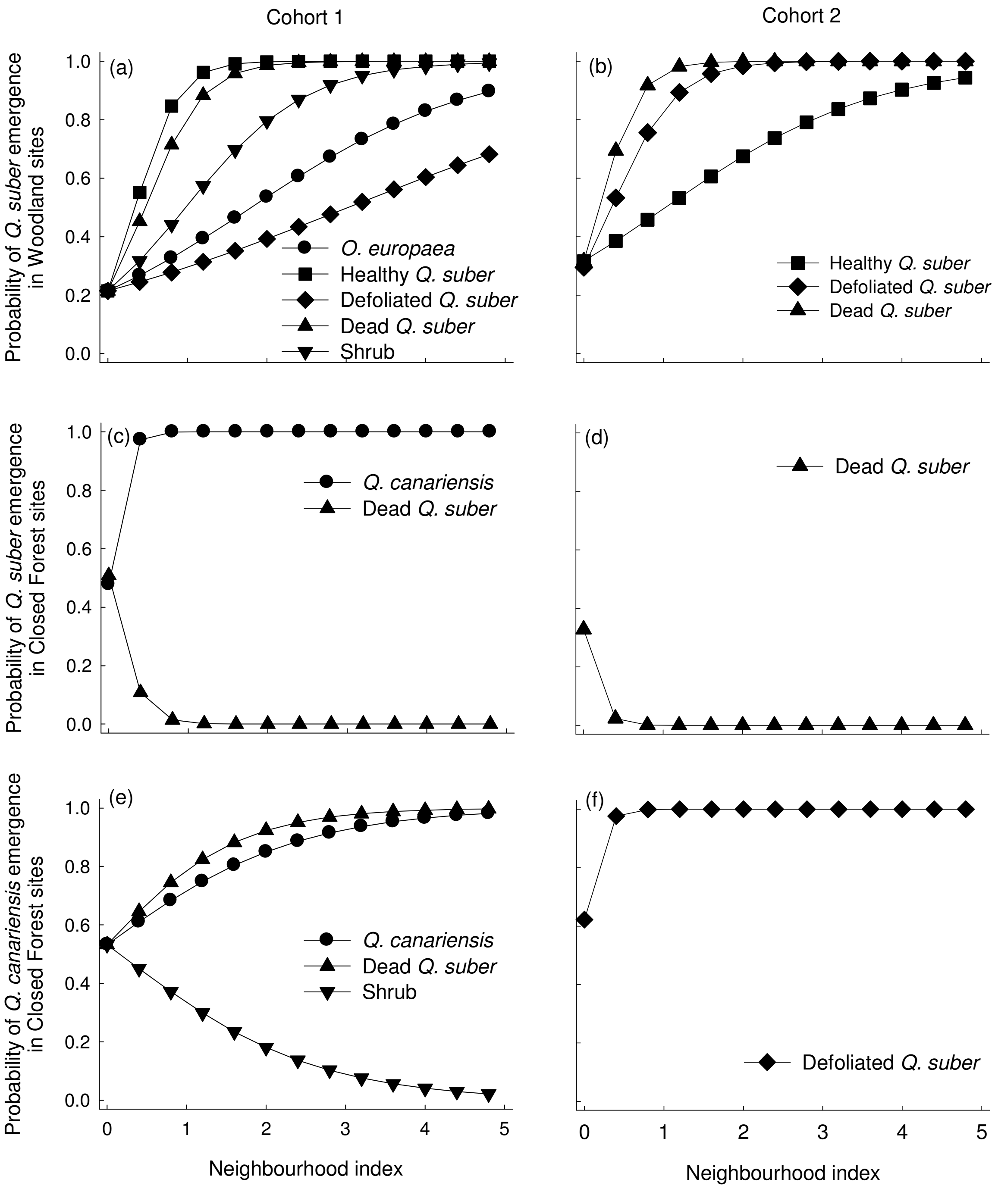

Figure 1 Predicted probability of emergence of *Quercus suber* seedlings in the woodland (a, b), and of *Q. suber* (c, d) and *Q. canariensis* (e, f) seedlings in the closed forest, calculated as a function of the neighbourhood index (NI) using the most parsimonious models and parameters given in Tables S4, S5 and S6. The Y-intercepts show the predicted mean emergence for the three sites in the absence of neighbours. Only neighbour types with a significant effect on emergence are shown.

Seedling survival

For 93% (14/15) of the possible combinations of forest type, seedling species, seedling cohort and year, the best models included the effect of neighbour trees on seedling survival (Tables 1 and 2). Moreover, most of these best models (10/14) separated the effect of neighbour trees of different species and health status (*Species* + *Health* model, Tables 1 and 2). Including shrubs never improved the fit of the best tree model (i.e. lower AIC_c for the *Shrub*s model in Tables 1 and 2), indicating that shrubs did not influence seedling survival during the course of the experiment. Model R^2 for the best neighbourhood model ranged between 9.2% and 44.3%. In woodland sites, heterospecific *O. europaea* trees had a general, positive effect (i.e. positive β values, see Table S4) on 1- and 2-year old *Q. suber* seedling survival in the two cohorts, whereas the effect of heterospecific *Q. canariensis* in closed forests was neutral (for 1-year old seedlings) or negative (for 2-year old seedlings; Figs 2 and 3). Adult *Q. canariensis* trees had similar negative or neutral effects on conspecific *Q. canariensis* seedlings. The effect of *Q. suber* trees on seedling survival varied depending on its health status, with healthy trees having predominantly neutral or positive effects and defoliated and particularly dead trees having negative impacts (Figs 2 and 3). Neighbourhood effects were not always consistent among years. For example, tree effects on survival of 2-year old *Q. suber* seedlings in woodlands varied from strongly negative in 2011 to positive in the dry 2012 (Figs 2b and 3b). Similar stronger positive effects in 2012 compared to 2011 were found for *Q. suber* and *Q. canariensis* seedlings of the second cohort when comparing the survival of 2-year vs. 1-year old seedlings (Fig. 3).

Three-year old seedling survival was only measured for the first cohort and in general showed fewer responses to the different neighbour types than younger seedlings. Neighbourhood effects on third year survival were only detected in closed forests (Tables 1 and 2). Healthy *Q. suber* trees had strong positive effects (positive β values) and dead trees strong negative effects (negative β values) on the two seedling species, particularly on *Q. canariensis* (larger β values, see Tables S5 and S6).

Seedling growth

A growth model that included tree neighbour effects was the best model for 55% (5/9) of the different combinations of forest type, seedling species, seedling cohort and year tested (Tables 1 and 2). Most of these best neighbourhood models pooled all trees together or differentiated only among species (*All trees* and *Species* models, Tables 1 and 2), with only one best model separating the effect of *Q. suber* trees by health status (1-year old *Q. suber* seedlings of the second cohort in woodland sites, Table 1). Including shrubs never improved the fit of the best tree model. Best neighbourhood models explained a proportion of the variance that ranged between 14.7% and 39.0%. In woodland sites, neighbour effects on growth were mainly restricted to the positive effects of dead trees (large positive β value, see Table S4). In closed forests, all trees (particularly *Q. canariensis*) had negative effects on seedling growth of the two seedling species (negative β values, see Tables S5 and S6).

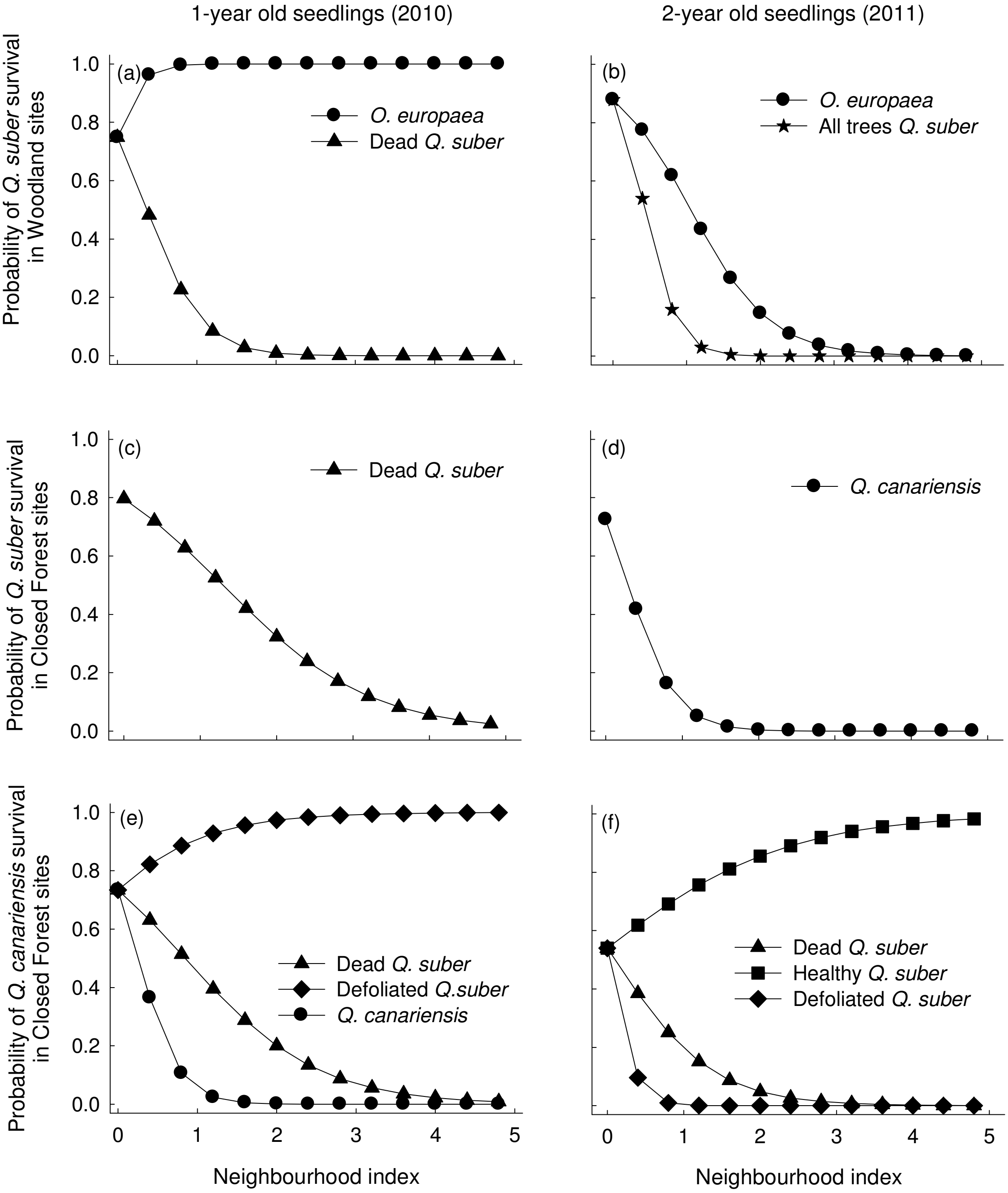

Figure 2 Predicted probability of survival of seedlings from the first cohort (sown in 2010) of *Quercus suber* in the woodland (a,b), and of *Q. suber* (c,d) and *Q. canariensis* (e,f) in the closed forest, calculated as a function of the neighbourhood index (NI) using the most parsimonious models and parameters given in Tables S4, S5 and S6. The Y-intercepts show the predicted mean survival for the three sites in the absence of neighbours. Only neighbour types with a significant effect on survival are shown.

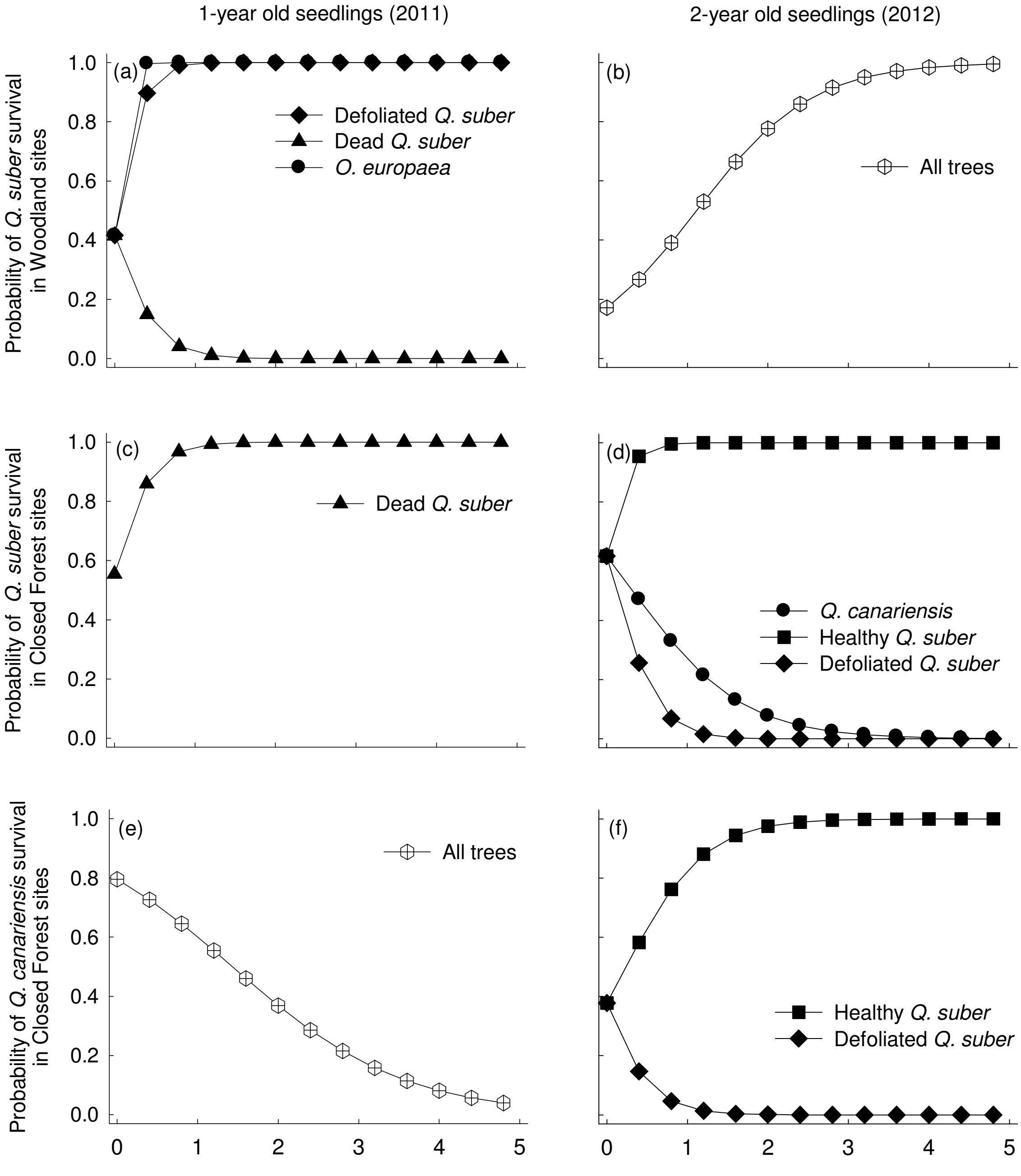

Figure 3 Predicted probability of survival of seedlings from the second cohort (sown in 2011) of *Quercus suber* in the woodland (a,b), and of *Q. suber* (c,d) and *Q. canariensis* (e,f) in the closed forest, calculated as a function of the neighbourhood index (NI) using the most parsimonious models and parameters given in Tables S4, S5 and S6. The Y-intercepts show the predicted mean survival for the three sites in the absence of neighbours. Only neighbour types with a significant effect on survival are shown.

Seedling photochemical efficiency

Models that considered the effect of tree and shrub neighbours were the best fit for seedling photochemical efficiency (Fv/Fm) in 83% (5/6) of the different combinations of forest types, seedling species and seedling cohorts tested. However, only one best model separated the effect of *Q. suber* trees by health status (*Q. suber* seedlings of the second cohort in closed forest sites, Table 2). According to this best model, healthy *Q. suber* trees had positive effects on seedling photochemical efficiency whereas dead *Q. suber* trees had negative effects (see Table S5). Neighbour shrubs had consistent positive effects on seedling photochemical efficiency during the summer for all seedling species and cohorts, but only in closed forest sites (see Tables S5 and S6). Model R^2 for the best models ranged between 12.6% and 36.8%.

DISCUSSION

EFFECTS OF NEIGHBOUR TREES AND SHRUBS ON SEEDLING PERFORMANCE

Tree community effects on seedlings

Our results clearly indicate that the composition and health status of the tree community can largely influence the success of tree recruitment in the understory of Mediterranean forests due to local neighbourhood effects on the magnitude of seedling emergence, survival, growth and physiological performance. The most consistent positive effects of all type of tree neighbours were found for the process of emergence. This supports previous studies in the area that show higher tree seedling emergence under the canopy than in forest gaps (Gómez-Aparicio *et al.* 2008; Urbieta, Zavala and Marañón 2008). Rainfall interception by canopy trees seems to mitigate the negative effects of excess water on seedling emergence during the rainy season, particularly in forests with clayish soils of high water-holding capacity and therefore prone to suffer temporal waterlogging (Pérez-Ramos and Marañón 2009). This could explain why the influence of neighbours on seedling emergence was particularly obvious in woodland sites, characterized by soils much richer in clay than closed forests, and where even declining trees had a positive effect on seedling emergence.

Tree neighbours also had prevalent effects on seedling survival, although these effects varied from highly positive to strongly negative depending on neighbour species and health. Among tree species, (healthy) *Q. suber* and particularly *O. europaea* neighbours had largely positive effects on seedling survival, whereas the effects of *Q. canariensis* trees were mainly negative on the two *Quercus* species. Interestingly, these inter-specific differences perfectly matched the results of a recent study that showed contrasting patterns of soil-borne pathogen abundance under the canopy of the three tree species (*O. europaea* < healthy *Q. suber* < *Q. canariensis*; Gómez-Aparicio *et al.* 2012). Thus, the positive effects of *Olea* neighbourhoods on seedling survival could be related to the fact that they seem to suppress pathogens, while *Q. canariensis* trees seem to act as reservoirs without showing any apparent disease symptoms (Gómez-Aparicio *et al.* 2012). However, we cannot rule out the possibility that neighbor effects were also driven by species-specific impacts on key abiotic factors, such as light (B. Ibáñez, unpublished data) or soil nutrients (Aponte *et al.* 2011). Regardless of what causes seedling mortality, our findings suggest contrasting differences among the two coexisting oak species in the importance of density- or distance-dependent mechanisms of seedling establishment (i.e. Janzen-Connell effects), in agreement with previous observational studies (Pérez-Ramos and Marañón 2012). Interestingly, *Q. canariensis* was the only species showing lower survival in conspecific neighbourhoods, despite its higher shade tolerance (Quero *et al.* 2006) and resistance to pathogen attack (Gómez-Aparicio *et al.* 2012) than *Q. suber*. Our results therefore do not support theoretical expectations that predict shade-tolerant, well-defended species to experience less severe density-dependent mortality than shade-intolerant species (Kobe and Vriesendorp 2011).

A main finding of our study is the broadly negative impact that tree decline had on oak establishment. Survival of *Q. suber* and *Q. canariensis* seedlings of all ages was lower in neighbourhoods dominated by defoliated and particularly dead *Q. suber* trees than in healthy neighbourhoods. In Mediterranean ecosystems, summer drought has been addressed as the most general and important cause of seedling mortality (Gómez-Aparicio 2008). Seedling survival is frequently found to be higher under established vegetation than in open gaps due to the amelioration of extreme microclimatic conditions by woody neighbours (Gómez-Aparicio *et al.* 2008; Ameztegui and Coll 2013). Therefore, it would be possible that after the death of a tree, the loss of leaves in the crown would translate into higher light levels and evapotranspiration demand (Gray, Spies and Easter 2002; Royer *et al.* 2011). These changes would in turn increase abiotic stress on oak seedlings (as shown by the lower photochemical efficiency) and summer mortality rates in neighbourhoods dominated by dead trees.

Species replacement in gaps is shaped by the species-specific ability to colonize the space opened after tree mortality (Kneeshaw and Bergeron 1998; McCarthy 2001). Our two oak species differed in several relevant physiological and morphological functional traits (Pérez-Ramos *et al.* 2012) which lead us to expect species-specific responses to the process of *Q. suber* decline. In particular, we expected seedlings of the moderately shade-intolerant *Q. suber* to have a relative advantage over shade-tolerant seedlings of *Q. canariensis* in neighbourhoods dominated by dead trees. However, we did not detect substantial support for this hypothesis, since recruitment of both species was subjected to collapse in unhealthy neighbourhoods, particularly in dry years (see *Variation of neighbourhood effects among years*) (e.g. Fig. 3d,f). Our results therefore suggest that in water-limited forests where positive plant-plant interactions are frequent, forests gaps that open after tree decline might not be suitable microhabitats for recruitment of dominant oak species.

Shrub effects on seedlings

One of the significant and novel aspects of our neighbourhood approach was the inclusion of the shrub community, which is frequently ignored in neighbourhood models. We decided to include shrubs in our models because they constitute an important fraction of the total vegetation biomass in many Mediterranean systems, and play a key role as nurse plants that increase the success of tree seedling establishment (e.g. Gómez-Aparicio *et al.* 2004; Rodríguez-García, Bravo and Spies 2011). Accordingly, we found evidence for positive shrub effects on seedling performance in our oak forests. In woodlands, shrubs increased seedling emergence, probably by alleviating the negative effect of excess water during the rainy season, as suggested for the tree community. In closed forests, on the other hand, shrubs improved the seedling physiological performance of the two species during the summer. Shrubs have been shown to decrease light and increase relative air humidity regardless of canopy cover (Beckage *et al.* 2000; Rodríguez-García, Ordóñez and Bravo 2011), which might have protected seedlings from photoinhibition and thermal stress (Valladares *et al.* 2005; Gómez-Aparicio, Valladares and Zamora 2006). However, such physiological changes did not translate into higher survival or growth for any combination of site, species or year. Our results therefore suggest that in forests with a relatively high tree cover (as those of this study) the role of shrubs as nurse plants is strongly attenuated and trees become the main structural drivers of seedling dynamics.

TEMPORAL VARIATION OF NEIGHBOURHOOD EFFECTS ON RECRUITMENT

Variation of neighbourhood effects among years

Although we found significant neighbourhood effects on seedling performance in each year of study, the sign and magnitude of these effects did not always remain constant among years. The clearest example is the strong change in the general effect of the tree canopy on second-year survival of *Q. suber* seedlings in woodland sites, which varied from highly negative in 2011 (an average year in precipitation terms) to strongly positive in the extremely dry 2012 (Figs 2b and 3b). This result agrees with previous studies that show weather conditions to strongly influence the outcome of plant-plant interactions in water-limited systems (Gómez-Aparicio, Gómez and Zamora 2005; Cuesta *et al.* 2010), and with the prevalence of net positive interactions under stressful conditions as suggested by the Stress Gradient Hypothesis (SGH, Bertness and Callaway 1994). Moreover, our findings imply that neighbourhood studies would benefit from including a multi-year perspective in their analyses to take account of the variability shown by understory processes not only in space but also in time.

Variation of neighbourhood effects through plant ontogeny

Our models showed that neighbourhood effects on recruitment varied both in magnitude and sign as seedlings emerged, established and grew. Specifically, neighbourhood effects on seedlings varied from common and predominantly positive for emergence, through highly variable in space and time for survival and photochemical efficiency, to infrequent and predominantly negative for growth. Additionally, seedling age played an important role on how neighbours affected seedling survival. Three-year old seedlings were in general more independent of the composition of the neighbourhood than 1- and 2-year old seedlings, in agreement with previous studies showing neighbourhood effects to decrease with target size (Hubbell et al. 1990). A likely explanation for this pattern would be the high vulnerability and dependence of young seedlings from local environmental conditions, which rapidly decreases as they develop lignified stems and larger root systems that confer higher stress tolerance (Lloret, Peñuelas and Ogaya 2004; Gómez-Aparicio 2008). Interestingly, one of the few neighbour effects found for 3-year old seedlings was a decrease in survival due to the presence of dead trees. The lasting negative effect of dead trees on seedling survival across ages confirms the importance that tree decline could have for recruitment in these forests. Overall, our findings support the well-known notion that the most favourable conditions for one regeneration stage (e.g. seed) might not be the most favourable for others (e.g. seedlings of different ages), leading to ontogenetic conflicts (*sensu* Schupp 2007). However, this study is one of the few describing life-stage conflicts in neighbourhood effects (see also Gómez-Aparicio, Canham and Martin 2008), offering a venue to reconcile contrasting conclusions obtained in neighbourhood studies with a focus on different ontogenetic stages (HilleRisLambers, Clark and Beckage 2002).

IMPLICATIONS FOR THE DYNAMICS OF FOREST AFFECTED BY OAK DECLINE

Our modelling approach enabled us to identify how seedlings of two co-existing oak species respond to the composition of the tree and shrub neighbourhood in Mediterranean forests affected by *Q. suber* decline. Our results suggest that the ongoing changes in the species relative abundance and health of these forests might alter their successional trajectory through neighbour-specific impacts on seedling performance. Theoretically, canopy gaps have been considered to provide recruitment opportunities for tree seedlings in tropical and temperate forests, allowing establishment of shade-intolerant species and increasing the diversity of tree regeneration (Shugart 1984; Pickett and White 1985). However, our results offer a different picture for water-limited forests, where recruitment failure of dominant oak species in the gaps opened after *Q. suber* dead would leave space and resources for the establishment of other coexisting woody species, such as drought-tolerant understory shrubs, with better regeneration ability and capacity to survive in open, dry microsites (Pérez-Ramos and Marañón 2012). A likely consequence would be the conversion of current forests into more open woodlands with lower tree cover and higher shrub cover, in a process of shrub encroachment already suggested for other water-limited forests (Acácio *et al.* 2007; Mendoza *et al.* 2009; Koepke, Kolb and Adams 2010).

At our study sites and in much of the Iberian Peninsula, mortality of *Q. suber* and other evergreen oaks (e.g. *Quercus ilex*) is an increasing problem but has not affected extensive forest surfaces yet. However, we suggest that because plants interact at local scales, mortality consequences could be larger than expected based on total abundance at regional scale. In fact, we found that high local densities of dead trees within 15-m neighbourhoods consistently lead to strong negative effects on seedling performance in space (i.e. different forest types) and time (i.e. different years and seedling ages). The decline of the adult canopy would therefore represent and additional threat to add to the list of factors already limiting recruitment in *Quercus* forests worldwide (e.g. massive seed and seedling predation; Pulido 2002; Pausas *et al.* 2009). Because changes in temperature, precipitation, and insect and pathogen dynamics are expected to increase the risk of forest die-off in the future (Adams *et al.* 2009; Allen *et al.* 2010), more information on post-mortality regeneration dynamics is urgently needed to predict the most likely successional trajectories and possibilities of recovery of disturbed forest ecosystems.

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SUPPORTING INFORMATION

Table S1 Description of main characteristics of the six study sites located in the South (S), Center (C) and North (N) of the Alcornocales Natural Park. Values of texture (percentage of clay), tree basal area (m^2/ha) and shrub crown area (m^2/ha) represent median [P10 – P90, 10th and 90th percentiles] for the 49 sampled neighborhoods at each site. Neighborhoods are circles of 15-m (for trees) and 5-m (for shrubs) radius around each sample point. Shrub crown area is given for the most common species across the six study sites.

	Woodlands			Closed forests		
	South Site	Center Site	North Site	South Site	Center Site	North Site
Latitude (N)	36º 04′ 38″	36º 04′ 38″	36º 31′ 69″	36º 06′ 09″	36º 23′ 10″	36º 28′ 13″
Longitude (W)	05º 33′ 05″	05º 33′ 05″	05º 38′ 08″	05º 30′ 53″	05º 31′ 52″	05º 35′ 31″
Annual rainfall (mm)	948.9	726.4	973.1	1067.1	1022.6	1097.0
Mean annual T (ºC)	16.3	16.9	16.3	15.4	17.3	15.9
Texture	29.62 [25.01-35.57]	15.17 [11.76-18.21]	29.62 [22.99-41.97]	12.84 [10.03-16.71]	12.59 [10.01-15.59]	9.19 [7.72-11.73]
Tree basal area						
O. europaea/Q. canariensis	5.20 [2.72-7.49]	4.18 [2.37-11.59]	2.57 [1.26-5.09]	15.55 [7.93-24.01]	5.45 [0-13.39]	14.81 [10.22-22.06]
Q. suber $_{\text{Healthy}}$	2.43 [0-5.56]	19.02 [10.82-26.65]	10.26 [6.07-15.52]	5.45 [1.50-12.48]	5.61 [2.47-6.19]	9.56 [3.52-17.52]
Q. suber$_{\text{Defoliated}}$	5.33 [2.47-8.04]	3.91 [1.48-7.28]	19.44 [12.68-28.7]	7.18 [4.72-9.00]	7.61 [2.18-10.47]	0.26 [0-3.52]
Q. suber $_{\text{Dead}}$	2.14 [0-7.09]	0.00 [0-1.00]	0.89 [0-1.79]	5.52 [3.22-7.64]	0.00 [0-3.52]	0.44 [0-0.93]
Shrub crown area						
Pistacia lentiscus	198.6 [0.00-599.7]	1276.0 [0.00-2977.0]	1975.0 [1442.0-3106.0]	------	0.00 [0-0.00]	------
Erica spp.	0.00 [0-0.00]	0.00 [0-0.00]	------	648.1 [151.2-2472.0]	3358.0 [2116.0-7810.0]	0.00 [0-126.4]
Phillyrea latifolia	0.00 [0-0.00]	0.00 [0-0.00]	112.7 [0-1638.0]	0.00 [0-0.00]	0.00 [0-0.00]	112.7 [0-1638.0]
Crataegus monogyna	449.5 [150.2-714.3]	0.00 [0-0.00]	1013.0 [611.2-1458.0]	------	0.00 [0-0.00]	0.00 [0-0.00]

Table S2 Optimal neighborhood radius for each neighbour type in the best models (i.e. models with the lowest AIC_c, Table 1) for *Quercus suber* seedlings at the woodland sites. Values within brackets indicate the neighborhood radii at which neighbor effects were detected (i.e. models with AIC_c lower than the null).

Cohort	Variable	All trees	Heterospecific	Conspecific	Healthy *Q. suber*	Defoliated *Q. suber*	Dead *Q. suber*	Shrubs
Cohort 1	Emergence	-	14[11-15]	-	2[2-7]	11[5-15]	5[2-8]	5[3-5]
	First-year survival	-	4[4-6]	-	-	-	7[2-15]	-
	Second-year survival	-	14[9-15]	2[2]	-	-	-	-
	Third-year survival	-	-	-	-	-	-	-
	First-year growth	-	-	-	-	-	-	-
	Second-year growth	-	-	-	-	-	-	-
	Fv/Fm	6[3-7]	-	-	-	-	-	-
Cohort 2	Emergence	-	-	-	8[6-14]	3[1-15]	3[3-12]	1[1]
	First-year survival	-	5[3-12]	-	-	7[1-15]	15[3-15]	-
	Second-year survival	10[10-11]	-	-	-	-	-	-
	First-year growth	-	-	-	-	7[6-15]	4[1-15]	-
	Fv/Fm	-	-	-	-	-	-	-

Table S3 Optimal neighborhood radius for each neighbour type in the best models (i.e. models with the lowest AIC_c, Table 2) for *Quercus suber* and *Quercus canariensis* seedlings at the closed forest sites. Values within brackets indicate the neighborhood radii at which neighbor effects were detected (i.e. models with AIC_c lower than the null).

Species	Cohort	Variable	All trees	Heterospecifics	Conspecifics	Healthy *Q. suber*	Defoliated *Q. suber*	Dead *Q. suber*	Shrubs
Quercus suber	Cohort 1	Emergence	-	1[1-15]	-	-	-	3[1-15]	-
		First-year survival	-	-	-	-	-	15[15]	-
		Second-year survival	-	4[3-7]	-	-	-	-	-
		Third-year survival	-	-	-	12[11-14]	-	13[13-15]	-
		First-year growth	-	1[1]	-	-	-	-	-
		Second-year growth	-	-	-	-	-	-	-
		Fv/Fm	1[1]	-	-	-	-	-	-
	Cohort 2	Emergence	-	-	-	-	-	3[3]	5[5]
		First-year survival	-	-	-	-	-	8[4-9]	-
		Second-year survival	-	11[9-13]	-	5[4-8]	13[4-15]	-	-
		First-year growth	13[12-15]	-	-	-	-	-	-
		Fv/Fm	-	-	-	8[5-11]	-	14[12-15]	3[2-4]
Quercus canariensis	Cohort 1	Emergence	-	-	6 [4-15]	-	-	11[10-15]	5[4-5]
		First-year survival	-	-	2[2]	-	10[8-11]	15[10-15]	-
		Second-year survival	-	-	-	15[5-15]	3[3-6]	10[9-15]	-
		Third-year survival	-	-	-	6[4-11]	-	13[6-15]	-
		First-year growth	-	-	15[9-15]	-	-	-	-
		Second-year growth	1[1-2]	-	-	-	-	-	-
		Fv/Fm	-	-	-	-	-	-	2[1-2]
	Cohort 2	Emergence	-	-	-	-	2[1-4]	-	5[4-5]
		First-year survival	15[15]	-	-	-	-	-	-
		Second-year survival	-	-	-	12[4-15]	13[13-14]	-	-
		First-year growth	-	-	-	-	-	-	-
		Fv/Fm	-	-	-	-	-	-	2[1-2]

Table S4 Parameter estimates (Estimate), standard errors (SE), z-values (for emergence and survival analyses), t-values (for growth and photochemical efficiency analyses) and p-values of the partial regression coefficients, for the best models selected at the woodland sites for Cohorts 1 (2010) and 2 (2011) of *Quercus suber* seedlings. When a Site effect was found, the Intercept (α value for the South Site) and α values for the Center and North Sites are given.

Cohort 1 (2010)						Cohort 2 (2011)					
Variable	Parameter	Estimate	SE	z/t-value	p-value	Variable	Parameter	Estimate	SE	z/t-value	p-value
Emergence	Intercept	-1.30	0.16	-8.26	0.000	Emergence	Intercept	-0.60	0.10	-5.85	0.000
	$\beta_{\text{Heterospecific}}$	0.72	0.23	3.07	0.002		α_{Center}	-0.45	0.16	-2.74	0.006
	β_{Healthy}	3.76	0.99	3.80	0.000		α_{North}	-1.26	0.17	-7.24	0.000
	$\beta_{\text{Defoliated}}$	0.43	0.17	2.58	0.010		β_{Healthy}	0.75	0.24	3.18	0.001
	β_{Dead}	2.77	0.80	3.49	0.000		$\beta_{\text{Defoliated}}$	3.04	0.72	4.22	0.000
	β_{Shrub}	1.33	0.37	3.53	0.000		β_{Dead}	3.97	1.31	3.04	0.002
First-year survival	Intercept	0.96	0.23	4.22	0.000	First year survival	Intercept	0.31	0.21	1.45	0.147
	α_{Center}	-0.54	0.28	-1.88	0.060		α_{Center}	-1.14	0.26	-4.48	0.000
	α_{North}	0.93	0.31	2.99	0.003		α_{North}	-0.80	0.32	-2.48	0.013
	$\beta_{\text{Heterospecific}}$	5.36	2.13	2.51	0.012		$\beta_{\text{Heterospecific}}$	15.60	4.25	3.67	0.000
	β_{Dead}	-2.90	0.89	-3.25	0.001		$\beta_{\text{Defoliated}}$	6.24	1.39	4.48	0.000
							β_{Dead}	-4.06	1.53	-2.66	0.008
Second-year survival	Intercept	1.98	0.34	5.49	0.000	Second-year survival	Intercept	-0.75	0.38	-1.97	0.049
	α_{Center}	-0.88	0.35	-2.50	0.010		α_{Center}	-1.34	0.42	-3.19	0.001
	α_{North}	0.88	0.36	2.41	0.010		α_{North}	-1.13	0.45	-2.51	0.012
	$\beta_{\text{Heterospecific}}$	-1.87	0.54	-3.55	0.000		β_{All}	1.41	0.52	2.71	0.007
	$\beta_{\text{Conspecific}}$	-4.55	1.47	-3.12	0.000						
Third-year survival	Intercept	0.94	0.26	3.67	0.000						
	α_{Center}	-1.78	0.42	-4.24	0.000						
	α_{North}	-0.17	0.32	-0.54	0.590						
First-year growth	Intercept	0.27	0.03	8.05	0.000	First-year growth	Intercept	0.16	0.04	4.17	0.000
	α_{Center}	-0.21	0.05	-4.45	0.000		α_{Center}	-0.04	0.06	-0.76	0.451
	α_{North}	0.01	0.04	0.20	0.840		α_{North}	0.19	0.07	2.94	0.004
							$\beta_{\text{Defoliated}}$	-0.67	0.32	-2.10	0.039
							β_{Dead}	4.05	1.71	2.36	0.020
Second-year growth	Intercept	0.001	0.02	0.07	0.94						
	α_{Center}	0.004	0.03	0.13	0.89						
	α_{North}	0.004	0.02	0.19	0.85						
Fv/Fm	Intercept	-0.12	0.002	-62.71	0.000	Fv/Fm	Intercept	-0.18	0.01	-26.1	0.000
	α_{Center}	0.004	0.002	1.48	0.142		α_{Center}	0.02	0.01	1.89	0.062
	α_{North}	0.005	0.003	1.99	0.048		α_{North}	0.001	0.01	0.38	0.702
	β_{All}	0.03	0.009	3.08	0.002						

Table S5 Parameter estimates (Estimate), standard errors (SE), z-values (for emergence and survival analyses), t-values (for growth and photochemical efficiency analyses) and p-values of the partial regression coefficients, for the best models selected at the closed forest sites for Cohorts 1 (2010) and 2 (2011) of *Quercus suber* seedlings. When a Site effect was found, the Intercept (α value for the South Site) and α values for the Center and North Sites are given.

Cohort 1 (2010)						Cohort 2 (2011)					
Variable	Parameter	Estimate	SE	z/t-value	P-value	Variable	Parameter	Estimate	SE	z/t-value	P-value
Emergence	Intercept	0.21	0.11	1.96	0.050	Emergence	Intercept	-0.32	0.12	-2.63	0.009
	α_{Center}	0.26	0.17	1.54	0.120		α_{Center}	0.15	0.25	0.59	0.554
	α_{North}	-0.84	0.15	-5.53	0.000		α_{North}	-0.80	0.17	-4.84	0.000
	$\beta_{\text{Heterospecific}}$	7.61	2.58	2.95	0.000		β_{Dead}	-9.04	3.10	-2.91	0.003
	β_{Dead}	-5.72	1.92	-2.97	0.000						
First-year survival	Intercept	1.84	0.32	5.78	0.000	First year survival	Intercept	0.22	0.15	1.43	0.154
	α_{Center}	-0.12	0.33	-0.38	0.703		β_{Dead}	3.98	1.09	3.66	0.000
	α_{North}	-1.31	0.33	-3.91	0.000						
	β_{Dead}	-1.05	0.44	-2.41	0.016						
Second-year survival	Intercept	0.97	0.27	3.5	0.000	Second year survival	Intercept	3.76	1.17	3.20	0.001
	α_{Center}	1.34	0.38	3.5	0.000		α_{Center}	-3.07	0.95	-3.23	0.001
	α_{North}	-1.34	0.33	-4.0	0.000		α_{North}	-3.30	1.03	-3.19	0.001
	$\beta_{\text{Heterospecific}}$	-3.26	0.89	-3.7	0.000		$\beta_{\text{Heterospecific}}$	-1.48	0.68	-2.19	0.029
Third-year survival	Intercept	1.51	0.51	2.97	0.003		β_{Healthy}	6.41	6.41	3.11	0.002
	α_{Center}	-1.66	0.47	-3.56	0.000		$\beta_{\text{Defoliated}}$	-3.85	-3.86	-2.73	0.006
	α_{North}	-2.91	0.74	-3.91	0.000						
	β_{Healthy}	1.43	0.57	2.52	0.011						
	β_{Dead}	-1.98	0.77	-2.57	0.010						
First-year growth	Intercept	0.45	0.04	9.90	0.000	First year growth	Intercept	0.96	0.20	4.82	0.000
	α_{Center}	-0.23	0.06	-3.75	0.000		α_{Center}	-0.54	0.09	-5.65	0.000
	α_{North}	-0.27	0.09	-3.02	0.000		α_{North}	-0.49	0.11	-4.41	0.000
	$\beta_{\text{Heterospecific}}$	-1.98	0.76	-2.60	0.010		β_{All}	-0.32	0.12	-2.77	0.008
Second-year growth	Intercept	0.008	0.017	0.49	0.630						
Fv/Fm	Intercept	-0.12	0.01	-19.13	0.000	Fv/Fm	Intercept	-0.10	0.01	-15.68	0.000
	α_{Center}	-0.04	0.01	-4.41	0.000		α_{Center}	-0.05	0.01	-6.27	0.000
	α_{North}	-0.02	0.01	-1.51	0.140		α_{North}	-0.02	0.01	-3.55	0.001
	β_{All}	-0.19	0.08	-2.46	0.020		β_{Healthy}	0.03	0.01	3.10	0.003
							β_{Death}	-0.03	0.01	-2.70	0.008
							β_{Shrub}	0.07	0.03	2.38	0.020

Table S6 Parameter estimates (Estimate), standard errors (SE), z-values (for emergence and survival analyses), t-values (for growth and photochemical efficiency analyses) and p-values of the partial regression coefficients, for the best models selected at the closed forest sites for Cohorts 1 (2010) and 2 (2011) of *Quercus canariensis* seedlings. When a Site effect was found, the Intercept (α value for the South Site) and α values for the Center and North Sites are given.

Cohort 1 (2010)						Cohort 2 (2011)					
Variable	Parameter	Estimate	SE	z/t-value	P-value	Variable	Parameter	Estimate	SE	z/t-value	P-value
Emergence	Intercept	-0.42	0.12	-3.63	0.000	Emergence	Intercept	-1.44	0.12	-11.96	0.000
	α_{Center}	0.26	0.18	1.42	0.155		α_{Center}	0.56	0.17	3.23	0.001
	α_{North}	1.39	0.21	6.69	0.000		α_{North}	0.41	0.30	1.34	0.177
	$\beta_{\text{Conspecific}}$	1.03	0.29	3.52	0.000		$\beta_{\text{Defoliated}}$	8.00	2.29	3.50	0.000
	β_{Dead}	1.18	0.36	3.29	0.001						
	β_{Shrub}	-0.82	0.34	-2.39	0.017						
First-year survival	Intercept	0.24	0.16	1.48	0.137	First year survival	Intercept	3.98	0.56	4.51	0.000
	α_{Center}	1.39	0.31	4.45	0.000		α_{Center}	-0.78	0.51	-3.45	0.001
	α_{North}	0.94	0.27	3.52	0.000		α_{North}	-2.53	0.71	-2.03	0.042
	$\beta_{\text{Conspecific}}$	-3.93	1.47	-2.68	0.007		β_{All}	-1.95	0.56	-3.51	0.000
	$\beta_{\text{Defoliated}}$	1.29	0.46	2.82	0.005						
	β_{Dead}	-1.20	0.40	-3.00	0.003						
Second-year survival	Intercept	0.00	0.33	4.09	0.000	Second year survival	Intercept	1.47	0.98	3.56	0.000
	α_{Center}	1,83	0.38	8.41	0.000		α_{Center}	-2.43	0.82	-1.27	0.204
	α_{North}	-1.35	0.77	-4.93	0.000		α_{North}	-3.48	0.74	-2.72	0.007
	β_{Healthy}	0.81	0.29	2.81	0.005		β_{Healthy}	2.08	0.71	2.91	0.004
	$\beta_{\text{Defoliated}}$	-6.31	1.77	-3.57	0.000		$\beta_{\text{Defoliated}}$	-3.15	1.24	-2.54	0.011
	β_{Dead}	-1.57	0.61	-2.58	0.010						
Third-year survival	Intercept	2.22	0.92	1.92	0.050						
	α_{Center}	-0.02	0.84	-0.56	0.572						
	α_{North}	-1.77	0.81	0.55	0.581						
	β_{Healthy}	3.50	0.97	3.59	0.000						
	β_{Dead}	-3.93	1.03	-3.83	0.000						
First-year growth	Intercept	0.15	0.06	3.34	0.001	First year growth	Intercept	0.33	0.06	5.85	0.000
	α_{Center}	-0.09	0.05	-5.68	0.000		α_{Center}	-0.34	0.07	-5.00	0.000
	α_{North}	0.35	0.06	5.67	0.000		α_{North}	-0.14	0.11	-1.34	0.187
	$\beta_{\text{Conspecific}}$	-0.11	0.04	-2.50	0.014						
Second-year old growth	Intercept	0.10	0.01	7.26	0.000						
	α_{Center}	-0.08	0.02	-4.75	0.000						
	α_{North}	0.03	0.06	0.52	0.605						
	β_{All}	-0.48	0.13	-3.69	0.000						
Fv/Fm	Intercept	-0.11	0.003	-44.25	0.000	Fv/Fm	Intercept	-0.16	0.01	-13.50	0.000
	α_{Center}	-0.02	0.005	-4.50	0.000		α_{Center}	-0.07	0.02	-3.97	0.000
	α_{North}	0.00	0.004	-0.50	0.594		α_{North}	-0.03	0.02	-1.85	0.070
	β_{Shrub}	0.25	0.109	2.32	0.024		β_{Shrub}	0.17	0.08	2.21	0.031

Capítulo 4

REGENERACIÓN DE LAS ESPECIES LEÑOSAS DE BOSQUES EN DECAIMIENTO: EFECTOS DE LA MORTALIDAD DE ÁRBOLES EN LAS DINÁMICAS SUCESIONALES

Este capítulo reproduce el siguiente manuscrito:

Ibáñez, B., Gómez-Aparicio, L., Ávila, J.M., Pérez-Ramos, I.M., Marañón, T. *Woody-plant regeneration in declining forests: the effects of tree dieback on successional dynamics*. En preparación.

Regeneración natural de especies leñosas en bosques en decaimiento: los efectos de la mortalidad de árboles en las dinámicas sucesionales

RESUMEN

En las últimas décadas se han documentado fenómenos de mortalidad extensiva de árboles en bosques de todo el mundo. Estos eventos de mortalidad a menudo muestran cierto nivel de especificidad, afectando principalmente a una o pocas especies, traduciéndose en cambios rápidos en la composición relativa de la comunidad adulta de plantas. A pesar de estos cambios a corto plazo, aún se desconoce si estos eventos pueden suponer un cambio a largo plazo de la vegetación. La trayectoria de recuperación del bosque ante un evento de decaimiento y la probabilidad de que ocurran cambios permanentes en la vegetación van a estar determinados en gran medida por las dinámicas de regeneración tras la perturbación.

En este trabajo se usó una aproximación espacialmente explícita con modelos de vecindad para evaluar los patrones espaciales de regeneración natural de la comunidad de plantas leñosas en bosques mixtos mediterráneos afectados por el decaimiento de una de sus especies arbóreas dominantes, *Quercus suber*. Se predijo la abundancia, supervivencia y riqueza de los bancos de plántulas y brinzales en función de la distribución y estado de salud de la comunidad arbóreo-arbustiva.

Los resultados indicaron que el decaimiento de *Q. suber* tiene efectos detectables tanto en las plántulas como en los brinzales de las especies coexistentes pertenecientes a distintos grupos funcionales (árboles, matorrales y lianas), implicando cambios en el ranking de la abundancia de plántulas y brinzales de las distintas especies. Estos cambios en la abundancia relativa de especies podrían afectar a las trayectorias sucesionales, potencialmente produciendo un cambio a largo plazo en la vegetación. Debido a que estos cambios parecen indicar una pérdida de cobertura y dominancia de *Q. suber*, se necesitan tomar medidas de gestión que atenúen la mortalidad de árboles adultos y promuevan su regeneración, para intentar contrarrestar los efectos negativos de los motores de cambio asociados al cambio global (patógenos exóticos, cambio climático) en estos bosques de elevado valor.

Woody-plant regeneration in declining forests: the effects of tree dieback on successional dynamics

Beatriz Ibáñez[a], Lorena Gómez-Aparicio[a], José M. Ávila[a], Ignacio M. Pérez-Ramos[a], Teodoro Marañón[a]

a. *Instituto de Recursos Naturales y Agrobiología (IRNAS, CSIC), PO Box 1052, Sevilla 41080, Spain*.

ABSTRACT

In the last decades widespread tree dieback has been documented in forests of almost every bioregion of the world. These mortality events usually show certain level of host-specificity, translating into rapid changes in the relative abundance of the adult community. Despite these short-term changes, it is poorly understood whether these events are likely to result in long-term vegetation shifts. Trajectories of forest recovery after tree dieback and the probability of occurrence of permanent vegetation shifts are to a large extent determined by post-mortality regeneration dynamics.

Here we used a spatially-explicit neighborhood approach to evaluate the spatial patterns of natural regeneration of the woody plant community in mixed Mediterranean forests affected by the decline of their dominant tree species, *Quercus suber*. We predicted the abundance, survival and richness of the seedling and sapling bank as a function of the distribution and health status of the canopy tree and shrub community.

Our results indicated that the decline of *Q. suber* had detectable effects on both new seedlings and older saplings of coexistent woody species belonging to very different functional groups (trees, shrubs and lianas), implying shifts in the species ranking of seedling and sapling abundance. These rank shifts could affect successional trajectories, potentially leading to vegetation shifts. Because most of these changes pointed towards a loss of cover and dominance of *Q. suber*, management strategies are urgently needed in order to either attenuate adult mortality or promote its regeneration, counteracting the negative effects of global change drivers (exotic pathogens, climate change) on these valuable forests.

Key-words disturbance, forest gaps, Mediterranean forests, *Olea europaea*, *Quercus canariensis*, *Quercus suber*, seedling bank, sapling bank, shrubs.

INTRODUCTION

Over the last two decades widespread tree decline and mortality has been documented in forests of almost every bioregion of the world (Breshears *et al.*, 2009; Van Mantgem *et al.*, 2009; Allen *et al.*, 2010). Several global change drivers have been identified as potential causes, such as increasing drought frequency and severity, recurrent pest outbreaks or the spread of exotic pathogens (e.g. Axelson *et al.*, 2009; Loo, 2009; Carnicer *et al.*, 2011). A common feature to these mortality events is that they usually show certain level of host-specificity, some tree species being much more vulnerable to abiotic and biotic sources of stress than others. As a result, they have a large potential to induce selective species removals and changes in community composition (Allen & Breshears, 1998; Collins *et al.*, 2011). For example, in semi-arid *Pinus edulis-Juniperus monosperma* woodlands of southwestern USA, recent severe droughts have induced a shift towards *Juniperus* dominated communities due to the higher drought tolerance of this species (Mueller *et al.*, 2005; Koepke *et al.*, 2010). In coastal California forests, the emerging pathogen *Phytophthora ramorum* has caused a rapid decline of *Notholithocarpus densiflorus* and an increase in the relative dominance of coexisting *Umbellularia californica* or *Sequoia sempervirens* (Brown & Allen-Diaz, 2009; Ramage *et al.*, 2012). However, despite this evidence for rapid short-term changes in the relative abundance of the adult community, we still have limited information on trajectories of forest recovery after tree mortality events and whether they are likely to result in long-term vegetation shifts.

The probability of occurrence of permanent vegetation shifts is to a large extent determined by regeneration dynamics after tree dieback (Suarez & Kitzberger, 2008; Kayes & Tinker, 2012; Galiano *et al.*, 2013; Redmond & Barger, 2013). Tree defoliation and mortality can induce a series of changes in local environmental conditions that alters the probability of establishment of new tree seedlings, inducing shifts of species abundance rankings in the seedling bank. For example, an increase in radiation levels and drought stress in the gaps opened after tree death could preclude the establishment of late-successional shade-tolerant species, indirectly favoring pioneer drought-tolerant species (Ibáñez et al. submitted, Diskin *et al.*, 2011; Amoroso *et al.*, 2012). It has also been shown that trajectories of recovery after drought- or insect-driven tree mortality might depend not only on new seedling establishment, but also even more strongly on advance regeneration established prior to the disturbance (Collins *et al.*, 2011; Kayes & Tinker, 2012; Redmond & Barger, 2013). For example, tree dieback in mature forests could release suppressed saplings of shade-tolerant species, allowing late-successional species to keep dominating the stands and indirectly limiting the establishment of light-demanding pioneer species otherwise typical of disturbed sites (Veblen *et al.*, 1991; DeRose & Long, 2010). These examples illustrate the complexities inherent to post-mortality regeneration dynamics, with seedlings and saplings of different ages likely responding in different ways (e.g. Galiano *et al.*, 2013), and show the need for further research that helps to elucidate long-term changes in stand composition of disturbed forests.

The main objective of this study was to evaluate the spatial patterns of natural regeneration of the woody plant community in mixed oak forests of southwestern Spain affected by the decline of their dominant tree species, *Quercus suber*. The decline of this species has been reported throughout the Mediterranean Basin since the early 1990s (Brasier, 1992; Brasier, 1996). Several abiotic (e.g. extreme droughts) and biotic (e.g. insects and pathogens) factors are potentially involved in this decline (Tuset & Sánchez, 2004). However, in the study area, oomycete soil-borne pathogens (*Phytophthora cinnamomi* and *Pythium spiculum*) have been isolated from symptomatic *Q. suber* trees and are suggested to be the main drivers of the species decline (Brasier, 1996; Sánchez *et al.*, 2002; Sánchez *et al.*, 2006; Romero *et al.*, 2007). For the analysis of natural regeneration patterns, we used a spatially-explicit neighborhood approach (Canham & Uriarte, 2006; Gómez-Aparicio *et al.*, 2008a; Gómez-Aparicio *et al.*, 2008b) where the abundance, survival and richness of the seedling and sapling bank was predicted as a function of the distribution and health status of the canopy tree and shrub community. Previous studies have shown *Q. suber* to suffer from stronger recruitment limitation than coexistent trees or arborescent shrubs in Mediterranean forests (Pérez-Ramos & Marañón, 2012), mainly due to heavy post-dispersal seed predation and high seedling mortality due to summer drought (Gómez-Aparicio *et al.*, 2008b; Pérez-Ramos & Marañón, 2008). Moreover, in a parallel experimental study we found that defoliated and dead *Q. suber* trees generated unsuitable microsites for survival of conspecific seedlings (Ibáñez *et al. submitted*). Following this, we hypothesized that the process of *Q. suber* decline might cause the recruit bank to become even less *Q. suber* dominated, hampering the potential for self-replacement and favoring successional trajectories towards forests dominated by other co-existing woody species.

MATERIAL AND METHODS

Study sites and species

The study was conducted in Los Alcornocales Natural Park, a 170,000 ha protected area in Southwestern Spain. The climate is Mediterranean type, with cold and humid winters and warm and dry summers. Mean annual temperature varies from 14.6 to 18.4 °C, with a mean monthly maximum of 36°C (July) and a mean monthly minimum of 2.8°C (January). Mean annual precipitation is 975 mm (mean 1951–1999). Bedrock is dominated by Oligo-Miocenic sandstone. Our study was carried out during three consecutive years (2010, 2011 and 2012) which exhibited contrasted climatological conditions. The year 2010 was extremely wet in terms of precipitation (1346 mm annual rainfall, 40 mm summer rainfall), 2011 had an average precipitation (1037 mm annual rainfall, 16 mm summer rainfall) and 2012 was particularly dry (474 mm annual rainfall, 0 mm summer rainfall).

The flora in the Alcornocales Natural Park is dominated by mixed sclerophyll forests of *Q. suber*, located mainly on non-carbonated soils, at altitudes between 100-700 m. Within the park the structure of the forests and its diversity vary depending on orography and soil type. In low altitude sites with clayish soils, *Q. suber* forms mixed open woodlands with the evergreen drought-tolerant *Olea europaea* var. *sylvestris*. The shrub layer in these woodlands is usually dense and largely dominated by the evergreen *Pistacia lentiscus* L. and the deciduous *Crataegus monogyna* Jacq. In sandier, moister and colder sites *Q. suber* coexists with the deciduous, shade-tolerant *Quercus canariensis* forming closed forests. The shrubby understory is diverse and dominated by arborescent shrubs (*Arbutus unedo* L., *Phillyrea latifolia* L.) and heath species (*Erica arborea* L.,*Erica scoparia* L.) (Ojeda *et al.*, 1996).

Field sampling

The field work was conducted in six study sites within the Natural Park. Three of the sites were located in open woodlands of *Q. suber* and *O. europaea* var. *sylvestris* (hereafter woodland sites) and three in closed forests of *Q. suber* and *Q. canariensis* (hereafter closed forest sites). The six sites covered a gradient of climate and soil conditions (see Table S1 in Supporting Information). During winter 2009, we established a 70 x 70 m plot at each of the six study sites. Each plot was subdivided in 49 10 x 10 m subplots. Within each of the 49 subplots, a smaller 1 x 1 m quadrat was permanently set up for monitoring of natural regeneration (n = 147 sampling quadrats per forest type, 294 quadrats in total).

During early June in 2010, 2011 and 2012 we counted and marked all the seedlings (i.e. individuals emerged that spring) and saplings (i.e. > 1 year-old individuals smaller than 50 cm height) of woody species (i.e. trees, fleshy-fruited shrubs, dry-fruited shrubs, and lianas) in each of the 1 m^2 sampling quadrats. We chose this sampling date to ensure that most seedlings had emerged (Pérez-Ramos & Marañón, 2012). Additionally, for the three tree species, seedlings and saplings were revisited in early October 2010 to record survival after the summer, the main mortality period in Mediterranean systems (Gómez-Aparicio, 2008; Pérez-Ramos *et al.*, 2012). We also calculated species richness for each quadrat as the number of different woody plant species censured at seedling or sapling stage. Due to the low growth rates of oak species in Mediterranean systems and their resprouting ability, saplings smaller than 50 cm height can be as old as 30 years (Galiano *et al.*, 2013). Therefore, the sapling bank would represent the regeneration accumulated during the last decades and even before the first report of *Q. suber* decline in the area (Brasier, 1992; Brasier, 1996).

To characterize the local neighborhood of each plot, we identified and mapped all live and standing dead trees with a diameter at breast height (dbh) > 2 cm and all shrubs in the 70 x 70 m permanent plots, as well as in a buffer zone 15-m (for trees) or 5-m (for shrubs) wide around each plot. Tree neighborhoods of similar size have been shown to capture the most important aspects of neighborhood interactions in temperate forests (Gómez-Aparicio *et al.*, 2008a; Coates *et al.*, 2009). Although we did not have any reference to choose the maximum shrub neighborhood, we considered a size of 5 m to be big enough based on the small size of most shrubs in these forests (height usually < 3 m). We measured the dbh of each of the trees mapped (n = 1341 trees). Due to its multi-stem growth form, shrub size was characterized measuring the two diameters of the elliptical projection of its crown (n = 3005 shrubs). In addition, we visually evaluated the crown health status of *Quercus suber*, with a standardized semi-quantitative scale used routinely for monitoring purposes of oak decline (García *et al.*, 2011) : (1) healthy reference trees; (2) defoliated trees; and (3) dead trees. No other tree or shrub species in the study area showed symptoms of decline.

Data analysis

Neighborhood models of seedling and sapling performance and richness

We used likelihood methods and model selection for the analysis of our data (Johnson & Omland, 2004; Canham & Uriarte, 2006). Following the principles of likelihood estimation, we estimated model parameters that maximized the likelihood of observing the data measured in the field. We fit separate models for each combination of dependent variable (abundance, survival, and richness), life-stage (seedling and sapling), forest type (woodland and closed forest), and woody species/functional group. The dominant tree species were analyzed separately (*Q. suber*, *O. europaea* and *Q. canariensis*), whereas the remaining woody species were divided in three groups according to their life-form and dispersal syndrome: fleshy-fruited shrubs (with endozoochorous dispersal), dry-fruited shrubs (with dispersal syndromes other than endozoochory, mainly abiotic dispersal) and lianas (Table S2).

Our regeneration models predicted mean seedling/sapling performance in each quadrat as a function of three components: 1) the potential seedling/sapling performance at each of the three study sites in the absence of specific effects of neighboring trees (i.e. site effects); 2) the identity, size, health status and spatial distribution of the trees in the neighborhood (i.e. tree neighborhood effects); and 3) the size and spatial distribution of shrubs in the neighborhood (i.e. shrub neighborhood effects). We tested and compared two different model frameworks (additive vs. multiplicative) to describe neighbor effects (e.g. Baribault & Kobe, 2011):

Additive model $$Y = a_{Site} + b_{Year} * NI_{Tree} + c_{Year} * NI_{Shrub} + \varepsilon \tag{1}$$

Multiplicative model $$Y = a_{Site} * \exp(b_{Year} * NI_{Tree}) * \exp(c_{Year} * NI_{Shrub}) + \varepsilon \tag{2}$$

The first term in the models, a_{Site}, represents the site effect. The second term accounts for the tree neighborhood effects, which are assumed to vary as a function of a *neighborhood index* (NI_{Tree}). The parameter *b* defines the steepness of the variation in performance due to an increment in NI_{Tree} and was allowed to vary between years to account for inter-annual differences in tree effects. The tree neighborhood index quantifies the net effect of *j=1,...,n* neighboring trees of *i=1,...,s* species on seedling/sapling abundance, survival or richness, and was assumed to vary as a direct function of the size (dbh) and as an inverse function of the distance to neighbors:

$$NI_{Tree_{ij}} = \sum_{i=1}^{s} \sum_{j=1}^{n} \lambda_i \frac{dbh_{ij}^{\alpha}}{dist_{ij}^{\beta}} \tag{3}$$

where dbh_{ij} is diameter at breast height, $dist_{ij}$ is the distance to the sampling point of the *j*th neighboring tree of the *i*th species, and α and β are estimated parameters that determine the shape of the effect of the dbh (α) and the distance to neighbors (β) on the target variable. We used NI standardized ($0<NI_i/NI_{max}<1$) to facilitate comparisons across different seedling/sapling species. Because we were particularly interested in exploring whether tree effects varied between individuals of different species or health status, we multiplied the net effect of an individual tree by a *per-capita* coefficient (λ) that ranged from -1 to 1 and allowed for differences between neighbors in their effects (negative or positive) on the target variable. We grouped neighbors in four categories (and therefore estimated four different λ values): healthy *Q. suber* trees, defoliated *Q. suber* trees, dead *Q. suber* trees, and the coexisting tree species at each site (*O. europaea* or *Q. canariensis*),

The third term in equations 1 and 2 accounts for shrub neighborhood effects, and were calculated as a function of a shrub neighborhood index ($\mathrm{NI}_{\mathrm{Shrub}}$). The parameter *c* defines the steepness of the variation in performance due to an increment in $\mathrm{NI}_{\mathrm{Shrub},}$ and was allowed to vary between years to account for inter-annual differences in shrub effects. This index is a simplified version of the tree neighborhood index, and quantifies the net effect of *j=1,...,n* neighboring shrubs of *i=1,...,s* species on seedling/sapling abundance, survival or richness following the form:

$$NI_{Shrub_{ij}} = \sum_{i=1}^{s} \sum_{j=1}^{n} area_{ij} \qquad (4)$$

The $\mathrm{NI}_{\mathrm{Shrub}}$ was assumed to vary just as a direct function of the size (crown area) of neighbor shrubs in a 5-m radius neighborhood. We decided not to include distance in the calculation of the index given the already restricted area over which shrubs were mapped and to keep the number of parameters in the models manageable.

Parameter estimation and model selection

Following the principle of parsimony, we followed the strategy of systematically reducing the number of parameters in the full model (considering site, year, tree and shrub effects) to the simplest model that was not a significantly worse fit than any more complicated model. Additive and multiplicative models with the same number of parameters were also compared among them. We used the Akaike Information Criterion corrected for small sample sizes (AIC_c) to select the best model, with lower AIC_c values indicating stronger empirical support for a model (Burnham & Anderson, 2002). The error terms (ε) for the abundance data were modeled using a negative binomial distribution defined by a size parameter, a binomial distribution for survival, and a Poisson distribution for richness. We solved for the maximum likelihood parameter values with simulated annealing (Goffe *et al.*, 1994), a global optimization procedure. We used asymptotic 2-unit support intervals to assess the strength of evidence for individual maximum likelihood parameter estimates (Edwards, 1992). The slope of the regression (with a zero intercept) of observed versus predicted was used to measure bias (with an unbiased model having a slope of 1). The R^2 of the regression was used as a measure of goodness-of-it. Coefficients whose 95% credible intervals did not include zero were considered statistically significant. All analyses were performed using R (R Development Core Team, 2009).

RESULTS

Seedling and sapling abundance

A total of 4514 seedlings and 1865 saplings of 21 woody species were counted during the three sampling years at the six study sites (Table S2). Due to the scarcity of dry-fruited shrub seedlings and saplings, this group was only included in the analysis of seedling abundance in the woodlands. All models produced unbiased estimates of seedling and sapling abundance (slope ~1) and explained a percentage of the variation in the data that ranged from 0.02 to 0.15 (Table 1). Both the additive and multiplicative approaches were used in best models of seedling abundance, whereas most best models of sapling abundance involved a multiplicative approach (Table 1). Most best models of seedling (7/9) and sapling (7/8) abundance found differences among the three sites in regeneration abundance. All models detected tree neighborhood effects on seedling and sapling abundance, as indicated by significant λ values of one or more neighbor categories (Tables S3 and S4). These effects did not vary among years (Table 1). Our models did not detect any effect of shrubs on seedling abundance, and only in one species (*Olea europea*) for sapling abundance.

In general, seedling abundance was higher in healthy tree communities (as indicated by positive λ values) than in neighborhoods dominated by defoliated or dead trees (as indicated by neutral or negative λ values) (Table S3). However, the magnitude of the neighborhood effect varied among species/functional groups, causing shifts in rankings of species abundance among neighborhood types. In woodlands, whereas *Olea* was the dominant seedling species in healthy tree neighborhoods (both conspecific and heterospefic), *Q. suber* dominated the seedling bank in defoliated neighborhoods and fleshy-fruited shrubs in dead neighborhoods (Fig. 1). In closed forests, lianas and (to a lesser extent) fleshy-fruited shrubs were the dominant groups in all type of neighborhoods (Fig. 2). Among tree species, *Q. suber* and *Q. canariensis* dominated their respective conspecific healthy neighborhoods, whereas the abundance of both species was virtually null in defoliated and dead *Q. suber* neighborhoods (Fig. 2e,g). In most neighborhood models of seedling abundance (7/9), the exponent α of the Neighborhood Index (which controls how neighbor effects scale with tree size, Eq. 3) took high values (> 2), indicating that the effect of neighboring trees scaled roughly with biomass (Table S3). Low values of the β parameter (which controls the effect of distance to neighbors, Eq. 3) in most models indicated that neighbor effects on seedling abundance generally decreased steeply with distance (Table S3)

Sapling abundance of tree species was also generally lower in defoliated and dead neighborhoods than in healthy ones (Table S4). However, abundance of fleshy-fruited shrub and liana saplings was not negative affected by tree decline in most situations (as indicated by neutral or positive λ values; Table S4). Shifts in rankings of species abundance among neighborhood types were also found in the sapling community. In woodland sites, whereas healthy neighborhoods of both *Q. suber* and *O. europea* were dominated by conspecific saplings, the strong negative effects of defoliated and dead trees on *Q. suber* saplings (stronger than on any other species) caused these neighborhoods to be dominated by heterospecific *O. europaea* saplings (Fig. 1f,h). In closed forests, the sapling bank kept being dominated by lianas and fleshy-fruited shrubs in all type of neighborhoods (with the

Table 1 Summary of best models of seedling and sapling abundance, survival and richness. Model features include: model type (additive vs. multiplicative), existence of site effects on regeneration (YES/NO), variation among years in tree neighborhood effects (YES/NO), and existence of shrub neighborhood effects (YES/NO). The number of parameters (NP), slope (SL) and goodness of fit (R^2) are also given.

Variable	Life stage	Forest type	Species	Model features				NP	SL	R^2
				Model type	Site effects	Year effects	Shrub effects			
Abundance	Seedling	Woodland	*Q. suber*	AD	NO	NO	NO	9	1.05	0.04
			O. europaea	AD	YES	NO	NO	11	0.91	0.08
			Fleshy-fruited shrubs	MT	YES	NO	NO	11	1.02	0.03
			Dry-fruited shrubs	MT	YES	NO	NO	11	0.93	0.10
			Lianas	MT	YES	NO	NO	11	0.97	0.08
		Closed forest	*Q. suber*	AD	YES	NO	NO	11	1.05	0.08
			Q. canariensis	AD	NO	NO	NO	9	1.06	0.09
			Fleshy-fruited shrubs	AD	YES	NO	NO	11	0.92	0.02
			Lianas	MT	YES	NO	NO	11	0.96	0.13
	Sapling	Woodland	*Q. suber*	MT	YES	NO	NO	11	0.98	0.07
			O. europaea	MT	YES	NO	YES	12	1.00	0.06
			Fleshy-fruited shrubs	MT	YES	NO	NO	11	1.09	0.07
			Lianas	MT	YES	NO	NO	11	1.00	0.06
		Closed forest	*Q. suber*	MT	YES	NO	NO	11	1.07	0.15
			Q. canariensis	MT	YES	NO	NO	11	1.02	0.08
			Fleshy-fruited shrubs	MT	NO	NO	NO	9	1.07	0.03
			Lianas	AD	YES	NO	NO	11	1.08	0.08
Survival	Seedling	Woodland	*Q. suber*	AD	NO	YES	NO	9	0.90	0.25
			O. europaea	AD	NO	NO	NO	8	-	0.05
		Closed forest	*Q. suber*	AD	NO	NO	NO	8	-	0.23
			Q. canariensis	AD	NO	NO	NO	8	1.02	0.17
	Sapling	Woodland	*Q. suber*	AD	NO	NO	NO	8	0.96	0.08
			O. europaea	AD	YES	YES	NO	11	0.99	0.06
		Closed forest	*Q. suber*	AD	NO	YES	NO	9	0.97	0.17
			Q. canariensis	AD	YES	NO	NO	10	0.98	0.31
Richness	Seedling + sapling	Woodland	All woody species	AD	NO	NO	NO	8	0.97	0.04
		Closed forest	All woody species	AD	YES	YES	YES	15	0.97	0.39

exception of fleshy-fruited shrubs in *Q. canariensis* neighborhoods). Among tree species, *Q. canariensis* dominated the sapling bank in conspecific neighborhoods and was also slightly more abundant than *Q. suber* in healthy *Q. suber* neighborhoods. However, *Q. suber* dominated the sapling bank in defoliated and dead neighborhoods likely as a result of stronger negative effects of decline (more negative λ values) on *Q. canariensis* than on *Q. suber* seedling abundance (Table S4). In models of sapling abundance, the value of the α parameter was highly variable among species (Table S4), whereas the β parameter was generally close to 0 indicating that abundance was mostly proportional to neighbor density.

Seedling and sapling survival

All models produced unbiased estimates of tree seedling and sapling survival (slope ~1) and explained a percentage of variation in the data that ranged from 0.05 to 0.31 (Table 1). In all cases, additive models were a better fit to the data than multiplicative models (Table 1). Only 25% (2/8) of the best survival models found differences among sites in seedling and sapling survival (Table 1). All models detected tree neighborhood effects on seedling and sapling abundance, as indicated by significant λ values of one or more neighbor categories (Table S5). These tree effects remained mostly constant among years, with three exceptions (*Q. suber* seedlings and O. *europaea* saplings in woodlands, *Q. suber* saplings in closed forests; Table 1). Our models did not detect any effect of shrubs on seedling survival (Table 1).

In woodlands, neighbor effects on survival were of generally weak magnitude, as indicated by the low value of most significant λ (Table S5). Moreover, the sign of the effects on *Q. suber* seedlings and *Olea* saplings varied among years (see sign of parameter *b* in Table S5), with survival being higher in healthy than defoliated neighborhoods in 2012 (a very dry year) but lower in 2011 (a normal year in terms of rainfall). In closed forests, *Q. canariensis* neighborhoods had the most negative effect (lowest λ value, Table S5) on seedling survival of the two oak species, followed by healthy *Q. suber* neighborhoods. Although seedling survival was lower in healthy than in declining *Q. suber* neighborhoods, sapling survival was higher (more positive λ values) in healthy neighborhoods. This was particularly true for *Q. canariensis* saplings, which suffered from strong negative effects of defoliated and dead neighbors (Table S5). Values of parameters α and β in the Neighborhood Index (Eq. 3) showed a very high variability among best models of seedling and sapling survival (Table S5).

Seedling and sapling richness

The two richness models produced unbiased estimates of species richness (slope ~1), and explained a percentage of variation much higher in closed forests (R^2 = 0.39) than in woodlands (R^2 = 0.04, Table 1). In both cases, an additive approach offered a better fit to the data than a multiplicative approach (Table 1). In woodlands, the best model detected an effect of the tree community on richness values, but did not find any site, year o shrub effects (Table 1). In this forest type, species richness was higher in healthy tree communities of *Quercus* and *Olea* (large positive λ values) than in neighborhoods dominated by defoliated

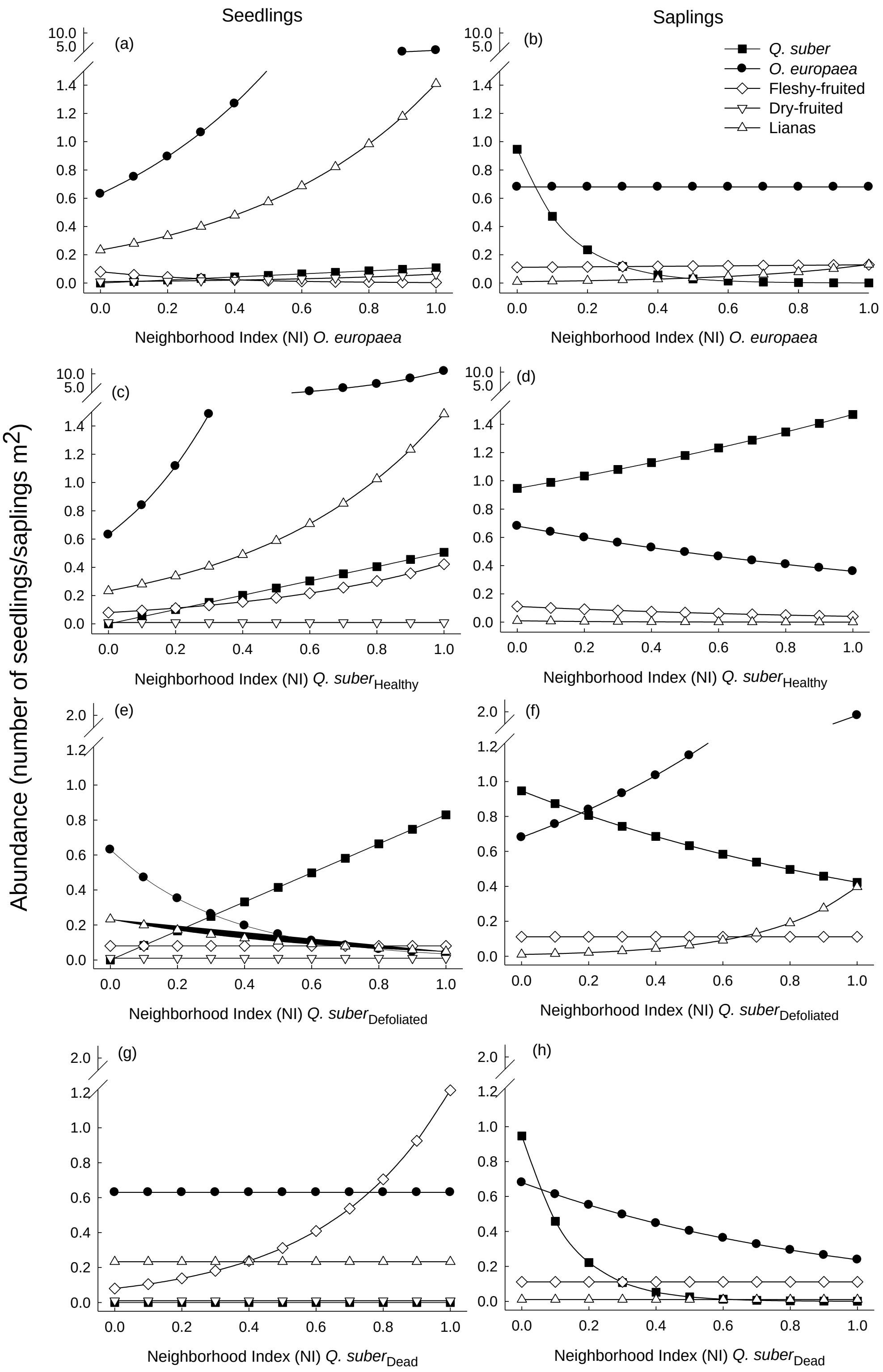

Figure 1 Predicted variation in the abundance of seedlings and saplings of different woody species (*Quercus suber*, *Olea europaea*, fleshly-fruited shrubs, dry-fruited shrubs, and lianas) as a function of the neighborhood index (NI) calculated for four different neighbor types (*O. europaea* [a,b], healthy *Q. suber* [c, d], defoliated *Q. suber* [e, f] and dead *Q. suber* [g,h]) in woodland sites. NI values of 0 represent neighborhoods in the data set without trees, whereas NI values of 1 represent, for each neighbor category, the neighborhoods with the highest observed value of NI (i.e. the highest influence of that neighbor type). Predicted abundance of seedlings and saplings was calculated using the values of the parameters *a*, *b* and *λ* in Eq. 1 or 2, given in Supporting Information Table S3 and S4.

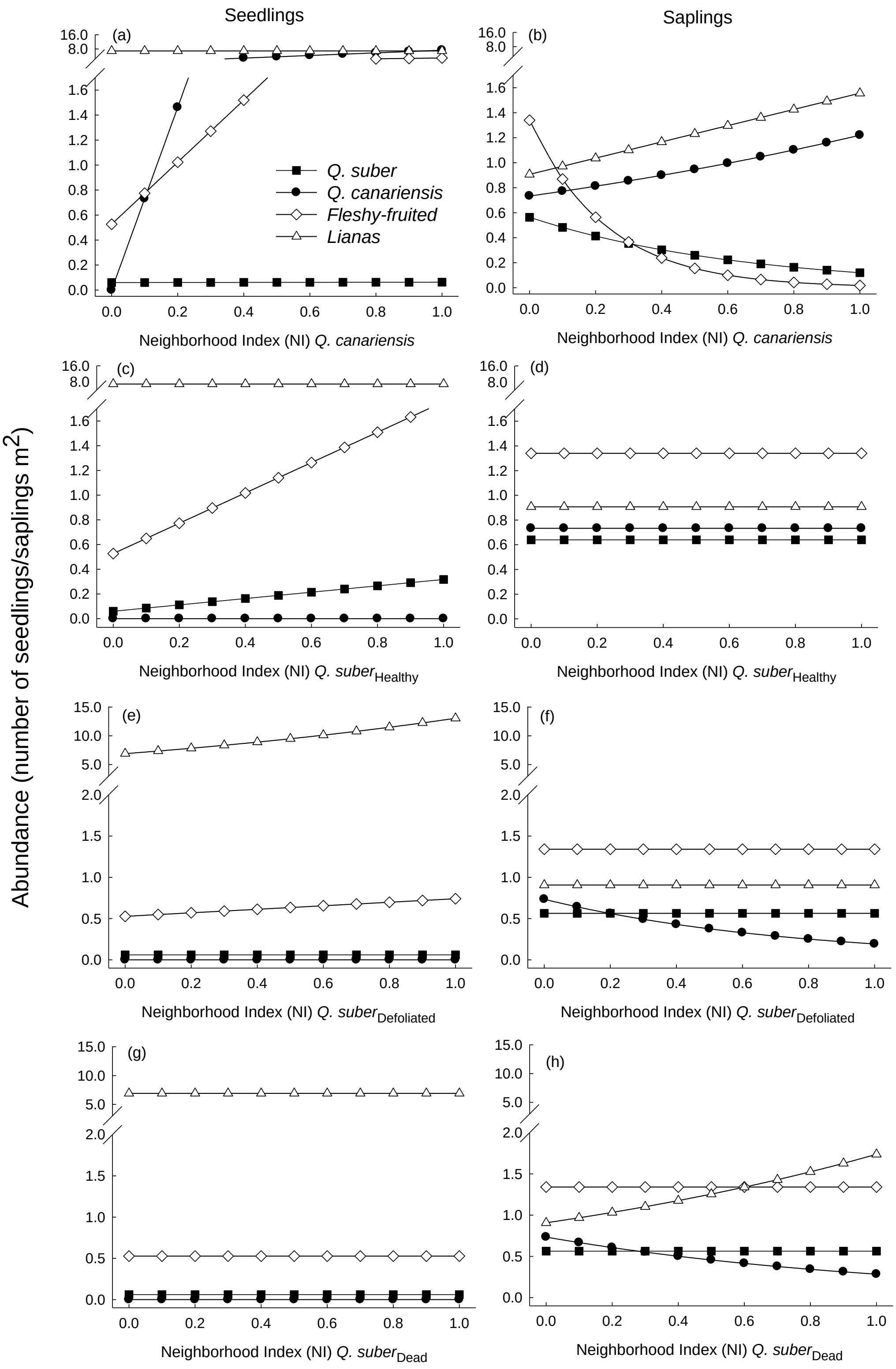

Figure 2 Predicted variation in the abundance of seedlings and saplings of different woody species (*Quercus suber*, *Quercus canariensis*, fleshly-fruited shrubs, and lianas) as a function of the neighborhood index (NI) calculated for four different neighbor types (*Q. canariensis* [a, b], healthy *Q. suber* [c,d], defoliated *Q. suber* [e, f] and dead *Q. suber* [g,h]) in closed forest sites. NI values of 0 represent neighborhoods in the data set without trees, whereas NI values of 1 represent, for each neighbor category, the neighborhoods with the highest observed value of NI (i.e. the highest influence of that neighbor type). Predicted abundance of seedlings and saplings was calculated using the values of the parameters *a*, *b* and λ in Eq. 1 or 2, given in Supporting Information Table S3 and S4.

and dead *Q. suber* trees (Table S6). In closed forests, the best model found effects of all factors tested. Thus, in this forest type richness varied among sites, was lower in *Q. canariensis* neighborhoods than in any *Q. suber* neighborhood (in all years but the dry 2012), and were positively affected by shrubs in the three study years (Table S6). Values of the α and β parameters in the Neighborhood Index of the two best richness models were roughly around 1, indicating that neighbor effects scaled with tree size (α) and declined as a simple inverse function of distance (β) (Table S6).

DISCUSSION

Our results indicate that the decline of *Q. suber* in Mediterranean forests has detectable effects on both new seedlings and older saplings of coexistent woody species belonging to very different functional groups (trees, shrubs and lianas). As a consequence, we found total and relative regeneration abundance (both within and among functional groups) to vary depending on the health status of the canopy cover. We recognize that our models produced small R^2 values, in part due to the low densities of seedlings and saplings characteristic of water-limited Mediterranean forests and the associated difficulty to fit models when spatial variability in regeneration abundance at fine scale is limited (see Pérez-Ramos & Marañón, 2012). Nevertheless, we consider that our neighborhood approach provides a useful framework that integrates the myriad ways that canopy and seedling species interact under natural conditions, improving our understanding of the net effects that changes in the health status or composition of the adult tree community could have on community dynamics of forests affected by problems of decline.

Patterns of natural regeneration in healthy tree neighborhoods

Healthy neighborhoods of the three dominant tree species in the study forests (*Q. suber*, *O. europaea*, and *Q. canariensis*) showed a tree seedling and sapling bank composed largely by conspecifics. It is interesting to note that the positive relationship found between abundance of conspecifics in the canopy and the recruit bank was stronger for new seedlings than for saplings (as indicated by much larger positive λ values; Tables S4 and S5). Stronger positive conspecific effects for seedlings than for saplings could indicate the existence of negative density-dependent processes from conspecifics acting at the seedling stage due to host-specialized antagonists (e.g. Janzen-Connell effects; Janzen, 1970; Connell, 1971), intense competition for resources, or to the generation of unfavorable abiotic conditions (e.g. Bonanomi *et al.*, 2008). Accordingly, we found negative effects of conspecific neighborhoods on seedling survival of the three tree species (negative λ values), in agreement with previous studies (Pérez-Ramos & Marañón, 2012, Ibáñez et al. submitted). Our results however suggest that the magnitude of these negative density-dependent processes was not strong enough to counteract the high number of seedlings emerged in conspecific neighborhoods. High emergence values under conspecific trees are likely the result of dispersal patterns, with most seeds not being biotically dispersed and arriving under mother trees in both *Olea* (Rey & Alcántara, 2000) and *Quercus* species (Pulido & Díaz, 2005). The existence of a conspecific sapling bank under healthy individuals of co-dominant tree species would serve as a guarantee of self-replacement suggesting that, in the absence of disturbances, positive canopy-sapling feedbacks could favor species coexistence and lead to a rather stable stand structure (Wilson & Agnew, 1992; Frelich & Reich, 1995; van Breemen & Finzi, 1998; Catovsky & Bazzaz, 2002). The process of *Q. suber* decline could however act as a destabilizing force of this structure through its impacts on the regeneration bank.

Effects of Quercus suber *decline on natural regeneration*

A clear consequence of *Q. suber* decline was a reduction in the absolute abundance of regeneration (both seedlings and saplings) in all tree species. The negative impact of *Q. suber* decline in tree species regeneration might explain the reduction of the local richness found in declining neighborhoods in the woodlands, as a consequence of a reduction in the probabilities of finding tree species in the seedling and sapling banks. However, the magnitude of this effect varied substantially among co-dominant tree species. In woodland sites, the decline of *Q. suber* had a stronger negative effect on conspecific regeneration than on *O. europaea* regeneration, causing a shift in sapling relative abundance towards the dominance of *O. europaea*. Such among-species difference in the magnitude of the negative effects of decline could be due to the high abundance of *Phythopthora cinnamomi* (a soil-borne pathogen with high preference for *Q. suber*) under declining trees in woodlands (Gómez-Aparicio *et al.*, 2012) or to the better capacity of drought-tolerant *O. europaea* seedlings to tolerate stressful abiotic conditions in gaps opened after tree death (e.g. high light levels and evaporation demand, Fetcher *et al.*, 1985; Royer *et al.*, 2011). In closed forests, on the contrary, the somewhat weaker negative effect that *Q. suber* decline had on conspecific regeneration compared to *Q. canariensis* regeneration caused a shift in sapling relative abundance towards a slight advantage in dominance for *Q. suber*. This result was quite unexpected since, in a parallel experimental study, we did not detect clear differences in the response of new seedlings and young saplings (2-3 years old) of the two oak species to neighborhoods of contrasting health (Ibáñez *et al. submitted*). Because the sapling bank in this study potentially included saplings much older than three years, it is possible that this result reflect the development of among-species differences with ontogeny, with older saplings of the shade-tolerant *Q. canariensis* being more impaired than those of *Q. suber* by the high light levels of the gaps open after tree death.

Whereas the decline of *Q. suber* had important negative effects on abundance and performance of tree seedlings and saplings, other functional groups such as fleshy-fruited shrubs and lianas were more independent of the decline process and even benefited from them in some situations. These finding could be related to the fact that seedling survival of both lianas and fleshy-fruited shrubs has been shown to benefit from high-light microsites in the forest understory (Pérez-Ramos & Marañón, 2012), and they are the dominant woody species recruiting in degraded forests (Mendoza *et al.*, 2009). Our results therefore suggest that the process of *Q. suber* decline could induce an increase in the relative abundance of functional forms other than trees in the woody community. This finding is in agreement with previous studies that have proposed a potential development of Mediterranean forests towards more open systems with lower tree cover and shrub dominance due to global environmental change (Acácio *et al.*, 2007; Matías *et al.*, 2012; Pérez-Ramos & Marañón, 2012).

Implications for successional dynamics in declining forests

The effects of tree dieback on regeneration dynamics is probably one of the less studied aspects of forest die-off, particularly when compared with the abundance of studies exploring the physiological mechanisms underlying tree dieback or its impacts on ecosystem processes (McDowell *et al.*, 2013). Among the scarce regeneration studies available, a large majority has focused on regeneration patterns after insect-decline mortality in mountain forests (Veblen *et al.*, 1991; Battles & Fahey, 2000; Nigh *et al.*, 2008; Vyse *et al.*, 2009; DeRose & Long, 2010; Collins *et al.*, 2011; Kayes & Tinker, 2012), and to a lesser extent after temperature- or drought-driven mortality in water-limited systems (Van Mantgem & Stephenson, 2007; Galiano *et al.*, 2013; Redmond & Barger, 2013). Here we show, for a complex system involving water-limited forests affected by aggressive exotic pathogens, that the decline of the dominant species (*Q. suber*) implies shifts in the ranking of seedling and sapling abundance among tree species, which could affect successional trajectories potentially leading to vegetation shifts (Suarez & Kitzberger, 2008; Kayes & Tinker, 2012; but see Redmond & Barger, 2013).

Yet, predicting trajectories of forest recovery after tree dieback is not an easy task. For tree dieback to induce compositional shifts, it is necessary that the die-off species has a disadvantage in terms of propagule input or that the new conditions created are relative more favorable for regeneration of coexisting species (Suarez & Kitzberger, 2008). Here we found that in some forest types, like open woodlands, the die-off species *Q. suber* met both requisites, showing much lower seedling and sapling abundance than the co-dominant *O. europaea* in all sites (Table S2) and a stronger negative response to declining neighborhoods. Everything being equal, we could therefore expect these oak woodlands to change towards *O. europaea*- dominated systems, in agreement with our initial hypothesis of study. In closed forests, on the contrary, we found *Q. suber* to have much lower regeneration abundance than the co-dominant *Q. canariensis* at the site-level (Table S2), but to be somewhat less negative affected by the process of adult decline. Therefore, the future dominance patterns in this forest type will likely depend on the extent to which the relative advantage of *Q. suber* over *Q. canariensis* saplings under defoliated and dead trees can compensate for the intrinsic lower regeneration capacity of the species and its increasing seed-limitation as the process of adult decline advances.

Understanding recruitment dynamics in *Q. suber* forests is of major ecological and social importance given the prominent role that this tree species plays in the configuration of the landscape and the economy of the Mediterranean basin, and the problems of regeneration and decline that *Q. suber* suffers throughout its distribution area (Urbieta *et al.*, 2008; Aronson *et al.*, 2009). Here we have shown that, based on current patterns of woody plant regeneration in declining mixed *Q. suber* forests, we could expect these systems to suffer from important changes in relative abundance among tree species as well as among functional groups (trees, shrubs, lianas) in the near future. Because most of these changes point towards a loss of cover and dominance of *Q. suber*, management strategies are urgently needed in order to either attenuate adult mortality (e.g. adequate phytosanitary measures) or promote its regeneration (e.g. enrichment plantings). Only by looking for stabilizing mechanisms that improve the balance between mortality and recruitment (Lloret *et al.*, 2012) we will be able to counteract the negative effects of global change drivers (exotic pathogens, climate change) on *Q. suber*, and preserve the many ecosystem services provided by these valuable forests.

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SUPPORTING INFORMATION

Table S1 Description of main characteristics of the six study sites located in the South, Center and North of the Alcornocales Natural Park. Values of tree basal area (m^2/ha) and shrub crown area (m^2/ha) represent median [P10 – P90, 10th and 90th percentiles] for the 49 sampled neighborhoods at each site. Neighborhoods are circles of 15-m (for trees) and 5-m (for shrubs) radius around each sample point. Shrub crown area is given for the most common species across the six study sites.

	Woodlands			Closed forests		
	South Site	Center Site	North Site	South Site	Center Site	North Site
Latitude (N)	36º 04′ 38″	36º 04′ 38″	36º 31′ 69″	36º 06′ 09″	36º 23′ 10″	36º 28′ 13″
Longitude (W)	05º 33′ 05″	05º 33′ 05″	05º 38′ 08″	05º 30′ 53″	05º 31′ 52″	05º 35′ 31″
Annual rainfall (mm)	948.9	726.4	973.1	1067.1	1022.6	1097.0
Mean annual T (ºC)	16.3	16.9	16.3	15.4	17.3	15.9
Tree basal area						
Olea/*Q. canariensis*	5.20	4.18	2.57	15.55	5.45	14.81
	[2.72-7.49]	[2.37-11.59]	[1.26-5.09]	[7.93-24.01]	[0-13.39]	[10.22-22.06]
Q. suber $_{\text{Healthy}}$	2.43	19.02	10.26	5.45	5.61	9.56
	[0-5.56]	[10.82-26.65]	[6.07-15.52]	[1.50-12.48]	[2.47-6.19]	[3.52-17.52]
Q. suber$_{\text{Defoliated}}$	5.33	3.91	19.44	7.18	7.61	0.26
	[2.47-8.04]	[1.48-7.28]	[12.68-28.7]	[4.72-9.00]	[2.18-10.47]	[0-3.52]
Q. suber $_{\text{Dead}}$	2.14	0.00	0.89	5.52	0.00	0.44
	[0-7.09]	[0-1.00]	[0-1.79]	[3.22-7.64]	[0-3.52]	[0-0.93]
Shrub crown area						
Pistacia lentiscus	198.6	1276.0	1975.0	------	0.00	------
	[0.00-599.7]	[0.00-2977.0]	[1442.0-3106.0]		[0-0.00]	
Erica spp.	0.00	0.00	------	648.1	3358.0	0.00
	[0-0.00]	[0-0.00]		[151.2-2472.0]	[2116.0-7810.0]	[0-126.4]
Phillyrea latifolia	0.00	0.00	112.7	0.00	0.00	112.7
	[0-0.00]	[0-0.00]	[0-1638.0]	[0-0.00]	[0-0.00]	[0-1638.0]
Crataegus monogyna	449.5	0.00	1013.0	------	0.00	0.00
	[150.2-714.3]	[0-0.00]	[611.2-1458.0]		[0-0.00]	[0-0.00]

Table S2 Mean density of seedlings/saplings (number m^{-2}) of the woody species sampled at the six study sites during the three years of study (average for 2010, 2011 and 2012). Species were gathered in four functional groups: trees, fleshy-fruited shrubs, dry-fruited shrubs, and lianas.

Functional group	Species	Woodlands			Closed forests		
		South Site	Center Site	North Site	South Site	Center Site	North Site
Trees	*Quercus suber*	0.10/0.22	0.18/0.61	0.35/0.33	0.02/0.04	0.29/1.16	0.08/0.16
	Olea europaea	0.29/0.41	1.98/1.08	0.29/0.55	-	-	-
	Quercus canariensis	-	-	-	1.16/0.61	1.20/1.14	0.41/0.55
Fleshy-fruited shrubs	*Arbutus unedo*	-	-	-	0.02/0.02	0.27/0.10	0.08/0.02
	Crataegus monogyna	0.06/0.02	0/0	0.02/0.04	0/0	0.02/0	0/0
	Ilex aquifolium	-	-	-	0.53/0.59	0/0	0/0
	Laurus nobilis	-	-	-	0.12/0.06	0/0	0/0
	Phillyrea latifolia	0.02/0	0.04/0	0.02/0.02	0.18/0.41	0.04/0.37	0.20/0.73
	Pistacia lentiscus	0.02/0.04	0/0.02	0.06/0.02	0/0	0.04/0.02	0/0
	Rhamnus alaternus	0.06/0	0/0	0/0	0.10/0.08	0.10/0.06	0/0
	Rubus ulmifolius	0.02/0	0/0	0/0	0.02/0	0/0.02	0/0
	Ruscus aculeatus	0.06/0	0/0	0/0	0.04/0.02	0.02/0	0/0
	Ruscus hypohyllum	-	-	-	0/0.04	0/0	0/0
	Viburnum tinus	-	-	-	0.04/0.16	0.04/0.10	0.04/0.02
Dry-fruited shrubs	*Erica spp.*	0/0	0/0	0/0	0/0	0/0.02	0/0
	Genista triacanthos	0/0	0/0	0/0	0/0	0.02/0	0.04/0
	Teucrium fruticans	0.02/0	0/0	0/0	0/0	0.02/0.02	0/0
	Ulex spp.	-	-	-	0/0	0.02/0	0/0
Lianas	*Smilax aspera*	0.88/0.08	0.02/0	0.04/0	1.84/0.43	0.12/0.06	0.16/1.24
	Hedera helix	-	-	-	18.76/1.27	0.04/0.06	0.10/0
	Lonicera spp.	-	-	-	0.06/0.04	0/0	0/0

Table S3 Parameter estimates and 2-unit support intervals for the best models of seedling abundance of *Q. suber*, *O. europaea*, *Q. canariensis*, fleshy-fruited shrubs, dry-fruited shrubs and lianas. See text for description of the parameters.

Forest type	Seedling species	a	b	c	λ				α	β	Size
					O. europaea/ Q. canariensis	Healthy *Q. suber*	Defoliated *Q. suber*	Dead *Q. suber*			
Woodland	*Q. suber*	0.00 [0,0.07]	0.83 [0.66,1.38]	-	**0.13 [0.01,0.76]**	**0.61 [0.17,1]**	**1.00 [0.36,1]**	0.06 [-0.03,0.49]	0.006 [0.0,1.68]	1.34 [0.77,1.57]	0.15 [0.09,0.25]
	O. europaea	0.27[0.17,0.39] 1.31[0.97,1.72] 0.31[0.20,0.45]	3.07 [1.81,4.22]	-	**0.57 [0.08,1]**	**0.93 [0.53,1]**	**-0.95 [-1.00,-0.38]**	-0.87 [-1,0.84]	2.86 [2.03,2.91]	1.67 [1.63,1.88]	0.43 [0.38,0.49]
	Fleshy-fruited	0.16[0.09,0.32] 0.04[0.01,0.08] 0.04[0.02,0.15]	3.20 [0.57,10]	-	**-0.99 [-0.98,-1.00]**	**0.52 [0.16,0.55]**	-0.84 [-0.86,0.05]	**0.85 [0.53,1.00]**	3.74 [3.70,4]	0.01 [0,0.40]	0.13 [0.06,0.13]
	Dry-fruited	0.03[0.02,0.07] 0[0,0.004] 0[0,0.004]	3.15 [1.38,4.47]	-	**0.69 [0.03,1]**	0.91 [-0.28,1]	0.38 [-0.63,1]	0.81 [-1,1]	2.66 [1.78,4.00]	0.22 0,1.53]	0.33 [0.07,0.43]
	Lianas	0.02[0.01,0.04] 0[0,0.01] 0.50[0.36,0.76]	2.57 [1.26,3.43]	-	**0.88 [0.39,1.00]**	**0.72 [0.41,1]**	**-0.61 [-0.90,-0.11]**	-0.60 [-1.00,0.74]	1.13 [0.53,2.52]	0.001 [0,0.79]	0.26 [0.17,0.45]
Closed forest	*Q. suber*	0[0,0.03] 0.18[0.11,0.35] 0[0,0.04]	0.26 [0.15,0.46]	-	**0.01 [0.00,0.14]**	**0.99 [0.37,1]**	0.29 [-0.001,1]	0.34 [-0.07,1]	3.33 [2.07,4]	0.32 [0,1.23]	0.43 [0.27,0.47]
	Q. canariensis	0 [0,0.06]	7.31 [5.36,8.68]	-	**1.00 [0.45,1]**	**0.002 [0.001,0.05]**	**0.01 [0,0.05]**	-0.002 [-0.003,0.06]	2.91 [2.70,3.23]	1.33 [1.08,1.65]	0.30 [0.22,0.40]
	Fleshy-fruited	1.14[0.49,1.44] 0.32[0.15,0.50] 0.12[0.05,0.28]	2.67 [0.96,4.55]	-	**0.93 [0.24,1.00]**	**0.46 [0.06,1.00]**	**0.08 [0.03,1.00]**	0.29 [-0.33,1]	3.89 [1.94,4]	2.64 [2.22,3.73]	0.23 [0.16,0.30]
	Lianas	20.21[15.56,26.79] 0.22[0.13,0.33] 0.26[0.15,0.37]	0.65 [0.08,1.17]	-	-0.74 [-1,0.28]	0.36 [-0.27,1]	**0.98 [0.72,1]**	0.83 [-0.45,1]	3.98 [2.98,4]	0.13 [0,1.63]	0.36 [0.30,0.41]

Table S4 Parameter estimates and 2-unit support intervals for the best models of sapling abundance of *Q. suber*, *O. europaea*, *Q. canariensis*, fleshy-fruited shrubs and lianas. See text for description of the parameters.

Forest type	Seedling species	a	b	c	λ				α	β	Size
					O. europaea/ Q. canariensis	Healthy *Q. suber*	Defoliated *Q. suber*	Dead *Q. suber*			
Woodland	*Q. suber*	0.71[0.43,1.21] 0.69[0.52,1.18] 1.44[1.08,3.36]	7.33 [4.71,8.9]	**-**	**-0.95** **[-1.00,-0.46]**	**0.06** **[0.01,0.20]**	**-0.11** **[-0.16,-0.05]**	**-0.99** **[-1.00,-0.80]**	1.45 [0.83,2.08]	0.25 [0.00,1.08]	0.26 [0.16,0.36]
	O. europaea	0.45[0.30,0.60] 1.21[0.95,1.63] 0.38[0.30,0.57]	1.06 [0.60,1.85]	**1.01** **[0.37,1.55]**	-0.38 [-1.00,0.38]	**-0.60** **[-0.83,-0.05]**	**0.99** **[0.74,1.00]**	**-0.99** **[-1.00,-0.20]**	0.47 [0.18,1.59]	0.00 [0,0.41]	0.56 [0.48,0.62]
	Fleshy-fruited	0.11[0.05,0.19] 0.004[0,0.06] 0.22[0.12,0.32]	1.00 [0.49,1.71]	-	**0.15** **[0.11,0.21]**	**-1.00** **[-1.00,-0.67]**	-0.11 [-0.47,0.17]	-0.58 [-1,0.28]	3.94 [3.71,4]	1.07 [0.10,1.98]	17.60 [1.58,20]
	Lianas	0[0,0.003] 0[0,0.003] 0.03[0.01,0.06]	3.68 [1.96,5.60]	-	**0.70** **[0.04,1.00]**	**-0.99** **[-1,-0.78]**	**1.00** **[0.68,1.00]**	0.90 [-1.00,1.00]	1.55 [0.32,2.85]	0.05 [0,0.70]	0.17 [0.03,0.31]
Closed Forest	*Q. suber*	0.04[0.01,0.10] 1.44[1.02,2.12] 0.21[0.10,0.31]	1.58 [0.58,3.18]	-	**-0.98** **[-1.00,-0.14]**	0.37 [-1.00,1.00]	-0.99 [-0.83,1.00]	0.99 [-1.00,1.00]	3.98 [2.71,4]	0.00 [0,0.16]	0.24 [0.19,0.29]
	Q. canariensis	0.69[0.52,1.22] 1.00[0.68,1.46] 0.51[0.35,0.82]	1.34 [0.25,1.91]	-	**0.38** **[0.31,1.00]**	0.14 [-0.07,0.93]	**-1.00** **[-1.00,-0.03]**	**-0.71** **[-1.00,-0.03]**	0.03 [0,0.68]	0.01 [0,1.42]	0.22 [0.190,0.31]
	Fleshy-fruited	1.34 [1.15,1.80]	4.37 [0.78,8.94]	**-**	**-0.99** **[1,0.09]**	-0.30 [-0.61,0.53]	-0.08 [-1,0.02]	-0.01 [-0.16,0.19]	0.83 [0,2.05]	3.93 [2.55,4]	0.37 [0.27,0.44]
	Lianas	1.52[1.19,2.25] 0.16[0.10,0.28] 1.04[0.78,1.54]	0.65 [0.34,1.00]	-	**1.00** **[0.73,1]**	-0.31 [-0.43,0.63]	-0.34 [-0.57,1]	**1.00** **[0.20,1.00**]	3.89 [2.87,4]	0 [0,0.88]	0.36 [0.26,0.55]

Table S5 Parameter estimates and 2-unit support intervals for the best models of seedlings and sapling survival of *Q. suber*, *O. europaea* and *Q. canariensis*. See text for description of the parameters.

						λ					
Recruit type	Forest type	Species	a	b	c	*O. europaea/ Q. canariensis*	Healthy *Q. suber*	Defoliated *Q. suber*	Dead *Q. suber*	α	β
Seedlings	Woodland	*Q. suber*	0.02 [0,0.71]	2.43[1.34,4.68] -10[-10,-2.91]	-	0.14 [-0.20,0.62]	-0.07 [-0.19,0.03]	**0.29** **[0.12,1]**	0.04 [-0.02,0.08]	0.007 [0,0.94]	1.73 [1.42,2.07]
		O. europaea	0[0,0.11]	6.76 [4.76,8.90]	-	**-0.15** **[-0.22,-0.10]**	**-0.11** **[-0.16,-0.08]**	**0.18** **[0.06,0.37]**	-0.50 [-0.98,0.14]	4 [3.32,4]	0.0003 [0,0.53]
	Closed Forest	*Q. suber*	0 [0,0.53]	6.53 [2.63,11.52]	-	**-0.99** **[-1,-0.07]**	**-0.20** **[-0.38,-0.00]**	**-0.02** **[-0.37,0.00]**	0.99 [-0.21,1]	1.40 [0,2.59]	2.93 [2.43,4]
		Q. canariensis	0 [0,0.36]	4.41 [3.37,5.18]	-	**-0.39** **[-0.70,-0.31]**	**-0.31** **[-0.47,-0.05]**	-1.00 [-1.00,0.75]	**0.84** **[0.39,1.00]**	1.65 [1.50,2.07]	1.11 [0.84,1.22]
Saplings	Woodland	*Q. suber*	0.83 [0.46,1.21]	0.27 [0.13,0.59]	-	0.59 [-0.63,1.00]	**-0.02** **[-0.03,-0.01]**	**0.011** **[0.06,0.18]**	0.80 [-0.13,1.00]	1.24 [0,1.83]	4 [3.28,4]
		O. europaea	1.83[1.08,2.54] 0.97[0.67,1.43] 2.24[1.48,3.01]	1.42[-0.34,4.12] -2.22[-3.21,-1.23]	-	**1.00** **[0.37,1.00]**	**0.31** **[0.03,0.89]**	0.00 [-0.26,0.66]	-0.36 [-1.00,1.00]	4 [3.08,4]	0.007 [0,1.21]
	Closed Forest	*Q. suber*	0.26 [0,0.89]	19.86[11.52,34.08] 8.98[6.05,11.80]	-	-0.49 [-0.58,0.06]	**0.53** **[0.41,1.00]**	**0.45** **[0.18,0.86]**	0.36 [-0.04,1.00]	1.30 [0.82,1.56]	1.30 [0.82,1.56]
		Q. canariensis	5.66[4.98,6.34] 2.85[2.40,3.24] 0[0,0.51]	5.45 [4.69,6.20]	-	**-0.21** **[-0.40,-0.14]**	0.04 [-0.14,0.15]	**-0.99** **[-1.00,-0.51]**	**-0.97** **[-1.00,-0.72]**	1.47 [1.21,1.69]	0 [0,0.25]

Table S6 Parameter estimates and 2-unit support intervals for the best models of woody species richness. See text for description of the parameters.

Forest type	a	b	c	λ				α	β
				O. europaea/ Q. canariensis	Healthy *Q. suber*	Defoliated *Q. suber*	Dead *Q. suber*		
Woodland	0.38 [0.29,0.44]	0.56 [0.70,0.37]	-	**0.98** **[0.42,1.00]**	**1** **[0.54,1.00]**	-0.08 [-0.45,0.32]	-0.18 [-0.37,0.09]	0.70 [0.57,1.09]	1.07 [1,1.30]
Closed Forest	2.09[1.82,2.28] 0.88[0.71,1.03] 0.42[0.33,0.52]	8.26[-0.87,14.94] 22.23[10.62,29.56] -10[-10,-2.28]	1.48[0.71,2.12] 1.06[0.41,1.83] 1.47[0.79,2.04]	**-1.00** **[-1,-0.40]**	-0.38 [-0.82,0.36]	-0.95 [-1,0.94]	0.10 [-1,1]	1.41 [1.40,2.20]	1.15 [1,1.14]

Capítulo 5

PATRONES ESPACIALES DE PATÓGENOS DEL SUELO EN BOSQUES EN DECAIMIENTO: IMPLICACIONES PARA LA REGENERACIÓN DE ESPECIES ARBÓREAS

Este capítulo reproduce el siguiente manuscrito:

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Patrones espaciales de patógenos del suelo en bosques en decaimiento: implicaciones para la regeneración de especies arbóreas

RESUMEN

Los organismos patógenos del suelo son un componente clave en las comunidades del suelo por el gran significado de sus impactos ecológicos y socio-económicos. A pesar de ello, se conoce muy poco sobre la complejidad de sus patrones de distribución en sistemas naturales.

En este estudio se exploran los patrones, las causas y las consecuencias ecológicas de la variabilidad espacial de la abundancia de patógenos en bosques mediterráneos afectados por el decaimiento del alcornoque. Se usan modelos de vecindad espacialmente explícitos para predecir la abundancia de especies de patógenos del suelo (*Phytophthora cinnamomi*, *Pythium spiculum* y *Pythium* spp.) en función de condiciones abióticas locales (textura del suelo) y de las características de las vecindades de árboles y matorrales (identidad, tamaño y estado de salud). Las implicaciones de la abundancia de patógenos en el comportamiento de plántulas fueron exploradas llevando a cabo experimentos de siembra en los mismos sitios donde se cuantificó la abundancia de patógenos.

La abundancia de patógenos no se encontró distribuida aleatoriamente sino que mostró patrones espaciales predecibles influenciados por los factores abióticos, y especialmente por los factores bióticos (especies de árboles y matorral). La abundancia de patógenos redujo la emergencia y supervivencia de plántulas, pero no en todos los sitios ni para todas las especies. Los resultados sugieren que la heterogeneidad espacial de los patrones de abundancia de patógenos puede ser importante para las dinámicas y la restauración de bosques mediterráneos en decaimiento.

Spatial patterns of soil pathogens in declining Mediterranean forests: implications for tree species regeneration

Lorena Gómez-Aparicio[a], Beatriz Ibáñez[a], María S. Serrano[b], Paolo De Vita[b], José M. Ávila[a], Ignacio M. Pérez-Ramos[a], Luis V. García[a], M. Esperanza Sánchez[b] & Teodoro Marañón[a]

a. *Instituto de Recursos Naturales y Agrobiología de Sevilla (IRNAS), CSIC, PO Box 1052, Sevilla E-41080, Spain*

b. *Dpto. Agronomía, ETSIAM, Universidad de Córdoba, PO Box 3048, Córdoba E-14080, Spain*

ABSTRACT

Soil-borne pathogens are a key component of the belowground community due to the significance of their ecological and socio-economic impacts. However, very little is known about the complexity of their distribution patterns in natural systems. Here we explored the patterns, causes and ecological consequences of spatial variability in pathogen abundance in Mediterranean forests affected by oak decline.

We used spatially-explicit neighborhood models to predict the abundance of soil-borne pathogen species (*Phytophthora cinnamomi*, *Pythium spiculum* and *Pythium* spp.) as a function of local abiotic conditions (soil texture) and the characteristics of the tree and shrub neighborhoods (species composition, size and health status). The implications of pathogen abundance for tree seedling performance were explored by conducting a sowing experiment in the same locations where pathogen abundance was quantified.

Pathogen abundance in the forest soil was not randomly distributed, but exhibited spatially predictable patterns influenced by both abiotic and particularly biotic factors (tree and shrub species). Pathogen abundance reduced seedling emergence and survival, but not in all sites or tree species.

Our findings suggest that heterogeneous spatial patterns of pathogen abundance at fine spatial scale can be important for the dynamics and restoration of declining Mediterranean forests.

Key words Forest decline, neighborhood models, *Quercus suber*, regeneration dynamics, soil-borne pathogens, soil texture, species coexistence

INTRODUCTION

Soil-borne pathogens are a key component of the belowground community due to the significance of their ecological and socio-economic impacts. For instance, several species of *Phytophthora* and *Pythium*, two well-known genera of soil-borne oomycete pathogens, are common causes of agricultural diseases (Erwin & Ribeiro, 1996; Martin & Loper, 1999) and are involved in the massive decline of *Quercus*, *Castanea*, *Eucalyptus* and other trees in forests worldwide (Brasier *et al*., 1993; Brasier, 1996; Rizzo *et al*., 2005; Romero *et al*., 2007; Cahill *et al*., 2008). Not surprisingly, understanding when and where soil-borne pathogens are more likely to cause destructive epidemics has long been an important topic of agricultural research. In natural systems, however, much less is known about the complexity of their distribution patterns, which remains as one of the most challenging aspects of studying belowground organisms (Ettema & Wardle, 2002; Reinhart & Clay, 2009).

The pathogen landscape can be affected by a variety of abiotic and biotic factors (Martin & Loper, 1999; Agrios, 2005). Among these factors, vegetation is a major determinant of the spatial distribution of soil pathogens both across and within plant species (Wardle, 2002). Plant species can affect soil-borne pathogen populations directly by providing living host tissue, or indirectly by generating environmental conditions that affect their reproductive activity (Augspurger, 1990). In forest ecosystems, for example, pathogen populations can benefit from the wetter microclimatic conditions found in the shaded understory compared to open environments (Gómez, 2004; Matías *et al*., 2011). On the other hand, understory environments tend to have more fertile soils than gaps and sustain a larger microbial community, which could negatively affect soil-borne pathogens through competition for resources and colonization space (Weste *&* Marks, 1987; Aponte *et al*., 2010). Depending on the relative importance of the different mechanisms, the net effect of a given woody species on soil pathogen abundance might range from highly positive to largely negative. However, species-specific effects could be obscured by intra-specific variation in plant traits such as size or tolerance to infection (Packer & Clay, 2000, 2003; Reinhart & Clay, 2009). Clearly, further research is needed in order to determine whether and how the mosaic of plant species and gaps in the forest canopy translate into a mosaic of soil pathogen abundance and composition.

Just as adult plants can drive the abundance and activity of soil-borne pathogens in forests, pathogens can in turn shape regeneration dynamics of the plant community (Packer & Clay, 2003; O'Hanlon-Manners & Kotanen, 2006). Seedlings are particularly vulnerable to pathogens because their roots are structurally simple and poorly lignified (Augspurger 1984, 1990; Romero *et al.*, 2007). Moreover, because pathogens vary in pathogenicity of different tree species (Augspurger & Wilkinson, 2007; Moralejo *et al*., 2009; Reinhart *et al.*, 2010), they can affect the composition of the seedling bank. For example, it has been proposed that shade-intolerance tree species are more susceptible to soil-borne diseases than shade-tolerant species, and that such susceptibility might be a key mechanism excluding them from the forest understory (O'Hanlon-Manners & Kotanen, 2004; McCarthy-Neumann & Kobe, 2008). If differential responses to soil pathogens exist, then interactions with soil-borne pathogens may contribute to species coexistence across heterogeneous forests.

The objective of this paper was twofold. First, we aimed to advance the understanding of the pathogen landscape by developing spatially-explicit neighborhood models that explain the importance of abiotic (soil texture) and biotic (tree and shrub community) drivers of soil-borne pathogen abundance in Mediterranean forests affected by cork oak (*Quercus suber*) decline. We built upon established methods for characterizing neighborhood processes (Canham & Uriarte, 2006), and applied these methods for the first time on soil organisms in close association with plants. A main advantage of the neighborhood approach is that it allows linking soil pathogen abundance with the distribution of neighboring individuals of the whole woody community. It therefore captures the complexity of natural plant communities, where a particular volume of soil is not necessarily occupied by just one host species. The second objective of our study was to explore the consequences of soil-borne pathogen abundance on seedling emergence and survival of dominant tree species with varying shade-tolerance (*Quercus canariensis* > *Q. suber* > *Olea europaea* var. *sylvestris*). For this, we conducted an *in-situ* field experiment where seeds of the three tree species were sown and monitored in the same locations where pathogen abundance was quantified. To the best of our knowledge, this is the first study that simultaneously analyzes the spatial relationship among abiotic soil properties, adult plants (trees and shrubs), and the pathogen and seedling community in a multi-species natural context.

MATERIAL AND METHODS

Study site and species

The study was conducted in Los Alcornocales Natural Park, a hotspot of biodiversity in southern Spain (Médail & Quézel, 1999). The climate is sub-humid Mediterranean, with most rainfall (95%) occurring from October to May. Soils are generally sandy, acidic and nutrient poor, derived from a bedrock dominated by Oligo-Miocene sandstones, but appeared interspersed with soils richer in clay derived from layers of marl sediments. The Alcornocales Natural Park contains the largest and best conserved *Q. suber* forests of Europe (Anonymous, 2005). In the drier lowlands of the park, *Q. suber* forms mixed open woodlands with the evergreen and shade-intolerant *Olea europaea* var. *sylvestris*, whereas in wetter areas *Q. suber* coexists with the deciduous shade-tolerant *Quercus canariensis* forming closed forests. The shrubby understory is diverse and rich in endemic taxa (Ojeda *et al.*, 2000).

A severe decline affecting *Quercus* species (especially evergreen oaks *Q. ilex* and *Q. suber*) has been reported since the early 1990s in the park and throughout the Mediterranean Basin (Brasier, 1992, 1996). Several abiotic (e.g. drought) and biotic (e.g. insects and pathogens) factors are potentially involved in this decline (Tuset & Sánchez, 2004). However, in the study area, two main oomycete soil-borne pathogens (*Phytophthora cinnamomi* and *Pythium spiculum*) have been isolated from symptomatic *Q. suber* trees and are suggested to be the main drivers of the decline of the species (Brasier, 1996; Sánchez *et al.*, 2002, 2006; Romero *et al.*, 2007).

Field sampling of soils and plants

We selected six study sites, three in open woodlands of *Q. suber* and *O. europaea* var. *sylvestris* (hereafter woodland sites) and three in closed forests of *Q. suber* and *Q. canariensis* (hereafter closed forest sites), distributed across the whole Natural Park (see sites description in Table S1). At each site, we established a 60 x 50 m permanent plot in a topographically uniform area. Topography was kept constant in order to avoid confounding effects for the analysis of impacts of soil texture and plants on pathogens. Each plot was subdivided in 30 10 × 10 m subplots. During the spring of 2010 (April-May), we took two soil samples (0-20 cm) at the center of each subplot, one for texture and another for pathogen analysis. Soil samples were taken within 1 m of where seeds were planted for the sowing experiment (see *Seed sowing experiment* below), rapidly put in a cooler, and transported to the lab for assessment of texture and pathogen abundance (see *Lab methods* below).

To characterize local neighborhoods, we identified and mapped all live and standing dead trees (including stumps) with a diameter at breast height (d.b.h.) > 2 cm and all shrubs in the 60 x 50 m permanent plots, as well as in a buffer zone 15-m (for trees) or 5-m (for shrubs) wide around each plot. Tree neighborhoods of similar size have been shown to capture the most important aspects of neighborhood interactions in temperate forests (Gómez-Aparicio *et al.*, 2008a; Coates *et al.*, 2009). Although we did not have any reference to choose the maximum shrub neighborhood, we considered a size of 5 m to be big enough based on the small size of most shrubs in these forests (height usually < 3 m). We measured the d.b.h. of each of the trees mapped (n = 1341 trees). Due to its multi-stem growth form, shrub size was characterized measuring the two diameters of the elliptical projection of its crown (n = 3005 shrubs). In addition, we evaluated the health status of *Q. suber* individuals by a visual estimation of crown defoliation on a standardized semi-quantitative scale widely used in the region for monitoring purposes of oak decline (e.g. García *et al.*, 2011): (1) healthy reference trees, (2) slightly defoliated trees (< 50 % crown defoliation), (3) highly defoliated trees (> 50% defoliation), and (4) dead trees (including stumps). No other tree or shrub species in the study area showed symptoms of decline.

Laboratory methods

Soil texture - Soil samples were air dried and sieved through a 2-mm mesh sieve to remove root material and stones. Particle size analysis was undertaken using the Bouyoucos hydrometer method (Gee & Bauder, 1986). Total sand (i.e. fine + coarse sand, 0.05-2 mm) was used as a representative measurement of the soil texture (see a similar approach in Gómez-Aparicio *et al.*, 2008b).

Pathogen abundance - Aliquots of 10 g from each soil sample were processed as described in Romero *et al.* (2007), preparing soil suspensions in 100 ml Water-Agar 0.2%. Aliquots of 1 ml taken from the soil suspensions were plated on NARPH Petri dishes (20 dishes per sample, Romero *et al.*, 2007). Colonies growing on the plates were morphologically identified and counted. As soil samples were previously dried, it was assumed that each colony obtained resulted from the germination of, at least, one resistant spore (oospore or chlamydospore). Results were expressed as colony forming units per gram of dry soil (cfu/g).

The identification of the isolated colonies was conducted by microscope observations after incubation on carrot-agar medium (Dhingra & Sinclair, 1995) at 24º C in the dark for 4-6 days and staining with acid fuchsine in lactophenol. Colonies were classified in three groups: *Phytophthora cinnamomi*, characterized by clustered hyphal swellings and smooth cell walled chlamydospores (Erwin & Ribeiro, 1996; Romero *et al*., 2007); *Pythium spiculum,* which has characteristic ornamented oospores (Paul *et al*., 2006; Romero *et al*., 2007); and *Pythium* spp., characterized by the absence of septa in narrow branched hyphae (less than 4 µm thickness). *Phytophthora cinnamomi* and *Py. spiculum* are the main soil-borne pathogens involved in the decline of *Quercus* species in southern Spain (Sánchez *et al.*, 2006; Romero *et al*., 2007; Jiménez *et al*., 2008). The *Pythium* spp. group represents a mix of *Pythium* species of unknown pathogenicity, and therefore it can include both virulent and avirulent (i.e. saprophytic) species (see a similar approach in Reinhart & Clay, 2009 and Reinhart *et al*., 2010). Although this group does not necessarily have to cause any pathogenic effect on trees, we will refer to the three different oomycete categories considered as "pathogen species" for simplicity.

Seed sowing experiment

During winter 2009-2010 (December-January), we conducted a sowing experiment in the six study sites. Surface sterilized seeds of the two dominant tree species were sown at the center of each of the 30 subplots. Seeds were sown at 2 cm depth in two adjacent 30 × 30 cm quadrats per subplot. Each quadrat contained three lines of seeds separated 7.5 cm from each other and from the border of the quadrat. Each line was randomly assigned for sowing either three *Quercus* or six *Olea* seeds. The larger number of *Olea* seeds was chosen based on their lower probability of germination (Goyiatzis & Porlingis, 1987; Rey *et al*., 2004). Sowing quadrats were protected with 1-cm mesh hardware to exclude seed predators. As a whole, we sowed 1620 seeds of *Q. suber*, 1620 seeds of *O. europaea*, and 810 seeds of *Q. canariensis*. Seedling emergence was monitored in early June 2010 to ensure that most seedlings had emerged (Pérez-Ramos & Marañón, 2011). Seedlings were revisited in early October 2010 to record survival after the first summer in the field, the main period of seedling mortality in Mediterranean systems (Gómez-Aparicio, 2008; Pérez-Ramos *et al*., 2011). Unfortunately, emergence of *O. europaea* was virtually nil in all sites (data not shown), which precluded us from testing the effect of pathogen abundance on emergence and survival of this tree species.

Statistical analysis

Neighborhood models of soil pathogen abundance.- We used likelihood methods and model selection for analysis of our data (Johnson & Omland, 2004; Canham & Uriarte, 2006). Following the principles of likelihood estimation, we estimated model parameters that maximized the likelihood of observing the pathogen abundance measured in the field given a suite of alternate neighborhood models.

We fit separate models for each combination of forest type (woodland and closed forest) and pathogen species (*P. cinnamomi*, *Py. spiculum* and *Pythium* spp.). Our analyses of soil-borne pathogen abundance estimated four terms: 1) average potential pathogen abundance (PPA, in cfu/g) at each of the three sites, and three multipliers that quantified the effects on average potential pathogen abundance of 2) local abiotic conditions (expressed in terms of soil texture), 3) the characteristics of the tree neighborhood (expressed in terms of the size, spatial distribution, species and health status of the trees), and 4) the characteristics of the shrub neighborhood (expressed in terms of shrub size). Our *full model* had the following form:

$$\text{Pathogen abundance} = \text{PPA}_{\text{Site}} \times \text{Abiotic effect} \times \text{Tree effect} \times \text{Shrub effect} \qquad \text{Eqn 1}$$

We also tried a linear model framework where the different effects were summed (see Baribault & Kobe, 2011, for a similar approach), but it showed in general poorer performance than the multiplicative model framework (data not shown). PPA_{Site} is an estimated parameter that represents the expected pathogen abundance at each site in the absence of sand in the soil texture and of trees and shrubs in the neighborhood (i.e. the abiotic, tree and shrub effects = 1). The three effects in Eqn 1 were modeled using Weibull functions:

$$\text{Abiotic effect} = \exp\,(b\ \text{Sand}) \qquad \text{Eqn 2}$$

$$\text{Tree effect} = \exp\,(c\ \text{NI}_{\text{Tree}}) \qquad \text{Eqn 3}$$

$$\text{Shrub effect} = \exp\,(d\ \text{NI}_{\text{Shrub}}) \qquad \text{Eqn 4}$$

where b, c and d are parameters estimated by the analyses determining the sign and magnitude of the abiotic, tree, and shrub effects, respectively.

The *abiotic effect* was modeled as a function of soil texture quantified as the proportion of sand content. Texture was chosen to represent the abiotic drivers of pathogen abundance because it is a relatively stable soil property that influences key environmental variables for pathogens (e.g. water availability) and it is not easily modified by plants, being therefore independent of the biotic effects in the equation.

The *tree effect* was modeled as a function of a tree neighborhood index (NI_{Tree}). This index quantifies the net effect of $j=1,...,n$ neighboring trees of $i=1,...,s$ species on pathogen abundance, and was assumed to vary as a direct function of the size (d.b.h.) and an inverse function of the distance to neighbors following the form:

$$\text{NI}_{\text{Tree}} = \sum_{i=1}^{s} \sum_{j=1}^{n} \lambda_i\ \text{dbh}_{ij}^{\alpha}\ \exp\left(-\gamma\ \text{distance}_{ij}^{\beta}\right) \qquad \text{Eqn 5}$$

where α, β and γ are estimated parameters that determine the shape of the effect of the d.b.h.

(α) and the distance to neighbors (β and γ) on pathogen abundance. Instead of setting α, β and γ arbitrarily, we tested two different versions of Eqn 5, fixing α to values 0 or 1 and letting β and γ to vary. A value of $\alpha = 1$ implies that the effect of a neighbor is proportional to its d.b.h., whereas a value of $\alpha = 0$ means that the tree influence on soil pathogen varies as a function of tree density, regardless of size.

We were particularly interested in exploring whether tree effects varied between individuals of different species or health status. For this purpose, we multiplied the net effect of an individual tree by a *per-capita* coefficient (λ) that ranged from -1 to 1 and allowed for differences between neighbors in their effects (negative or positive) on a target pathogen. We tested four different groupings of neighbor species in Eqn 5 with increasing complexity: 1) a model in which all trees were considered equivalent (i.e. fixing $\lambda = 1$); 2) a species-specific model that calculated two separate λ, one for *Q. suber* and another for the coexisting tree species (either *O. europaea* or *Q. canariensis*); 3) a model that also took into account the health status of *Q. suber* trees, and therefore calculated four separate λ (healthy *Q. suber*, slightly defoliated *Q. suber*, highly defoliated *Q. suber*, and the coexisting tree species); and 4) a model that not only considered alive trees of different species and health status, but also the legacy effect of dead *Q. suber* trees, calculating five separate λ.

The *shrub effect* was modeled as a function of a shrub neighborhood index (NI_{Shrub}). This index is a simplified version of the tree neighborhood index, and quantifies the net effect of $j=1,...,n$ neighboring shrubs of $i=1,...,s$ species on pathogen abundance following the form:

$$NI_{Shrub} = \sum_{i=1}^{s}\sum_{j=1}^{n} area_{ij} \qquad \text{Eqn 6}$$

The NI_{Shrub} was assumed to vary just as a direct function of the size (crown area) of neighbor shrubs in a 5-m radius neighborhood. We decided not to include distance in the calculation of the index given the already restricted area over which shrubs were mapped and to keep the number of parameters in the models manageable.

Finally, in order to test whether any of the three effects studied (i.e. texture, trees and shrubs) varied among sites of a given forest type, we tried variations of the full model in which the slopes of each effect (i.e. parameters *b, c* or *d*) were allowed to vary among sites.

Effect of soil-borne pathogens on seedling emergence and survival.- We fit models that estimated seedling emergence or survival at each subplot as a direct function of the pathogen abundance in the soil. We tried both a multiplicative and a linear model framework, this last offering a better fit to the data. Thus, for each combination of forest type, tree species, and pathogen species, seedling emergence and survival were predicted as:

$$\text{Seedling emergence} = PSE_{Site} + b \text{ Pathogen abundance} \qquad \text{Eqn 7}$$

$$\text{Seedling survival} = PSS_{Site} + c \text{ Pathogen abundance} \qquad \text{Eqn 8}$$

where PSE_{Site} and PSS_{Site} are the potential seedling emergence and survival, respectively, at each site in the absence of pathogens, and *b* and *c* are the slopes of the regressions determining the pathogen effect. We explored the existence of site-dependent pathogen effects by fitting models that allowed the parameters *b* and *c* to vary among sites of a given forest type.

Parameter estimation and model selection - Following the principle of parsimony, we followed the strategy of systematically reducing the number of parameters in the full model to the simplest model that is not a significantly worse fit than any more complicated model. We used the Akaike Information Criterion corrected for small sample sizes (AIC_c) to select the best model, with lower AIC_c values indicating stronger empirical support for a model (Burnham & Anderson, 2002). Pathogen abundance values were modeled using a Poisson error distribution, and seedling emergence and survival using a binomial error distribution. We used simulated annealing, a global optimization procedure, to determine the most likely parameters (i.e., the parameters that maximize the log-likelihood) given our observed data (Goffe *et al.*, 1994). The slope of the regression (with a zero intercept) of observed on predicted pathogen abundance was used to measure bias (with an unbiased model having a slope of 1) and the R^2 of the regression was used as a measure of goodness-of-it. We used asymptotic two-unit support intervals to assess the strength of evidence for individual parameter estimates (Edwards, 1992). All analyses were performed using software written specifically for this study using Java (Java SE Runtime Environment v6, Sun Microsystems Inc., California, USA, 2010).

RESULTS

Neighborhood models of soil pathogen abundance

All of the models produced unbiased estimates of soil-borne pathogen abundance (i.e. slopes of predicted vs. observed abundance were all very close to 1.0) and explained a percentage of the variation in the data that ranged from 0.07 to 0.43 (Table 1). The full model (i.e. including the effect of texture, trees and shrubs) was the best fit in 5 of the 6 forest type-pathogen species combinations. The only exception was *Py. spiculum* in closed forests, for which a simpler alternate model that ignored the effect of texture and shrubs ("No Texture + Shrub model" in Table 1) had a much lower AIC_c score (i.e. was much better supported statistically) than the full model. Site-dependent models were never a better fit to the data than more simple site-independent models (results not shown for simplicity), which implies that soil and plant effects on pathogen abundance can be considered consistent across sites of the same forest type.

The proportion of sand in the soil always had a negative effect on pathogen abundance (i.e. negative *b* parameter, Table S2). The magnitude of the texture effect (indicated by the magnitude of the *b* parameter) was larger in woodlands than in closed forests for all three pathogen species (Fig. 1). Within forest types, the texture effect also varied among pathogen groups (i.e. support intervals for the *b* parameter did not overlap), being larger for *Pythium* spp. > *P. cinnamomi* > *Py. spiculum* (Fig. 1).

Table 1 Comparison of the alternate models for the three pathogen species in the two forest types using AIC$_c$. The full model includes the effect of texture, tree neighbors and shrub neighbors on each pathogen species. The “No Texture”, "No Tree", "No Shrub" and “No Texture+Shrub” models ignore the effect of these factors, respectively. The "Type of tree effect" column indicates whether the best model considered all tree species as equivalent ("Equiv."), differentiated among species ("Sp") and health status ("H"), or considered the legacy effect of dead trees ("D"). The most parsimonious model (indicated in bold) is the one with the lowest AIC$_c$. *NP* is the total number of parameters in the best model, and *n* the sample size. The slope and R^2 for the relationship between predicted and observed pathogen abundance is also given.

		AIC$_c$										
Forest type	Pathogen species	Full	No Texture	No Tree	No Shrub	No Texture + Shrub	Null	Type of tree effect	NP	n	Slope	R^2
Woodlands	*P. cinnamomi*	**16597**	17576	18910	17735	17758	18914	Sp+H+D	12	90	1.00	0.35
	Py. spiculum	**614**	639	650	619	642	654	Equiv.	7	60	1.00	0.07
	Pythium spp.	**2035**	2472	2510	2194	2486	2565	Sp+H+D	11	60	0.96	0.43
Closed forests	*P. cinnamomi*	**4241**	4476	6020	5813	5911	6038	Sp+H+D	11	90	1.08	0.36
	Py. spiculum	128	126	131	121	**118**	129	Equiv.	5	60	1.07	0.18
	Pythium spp.	**1789**	2237	2270	2070	2253	2298	Sp+H+D	11	60	1.01	0.28

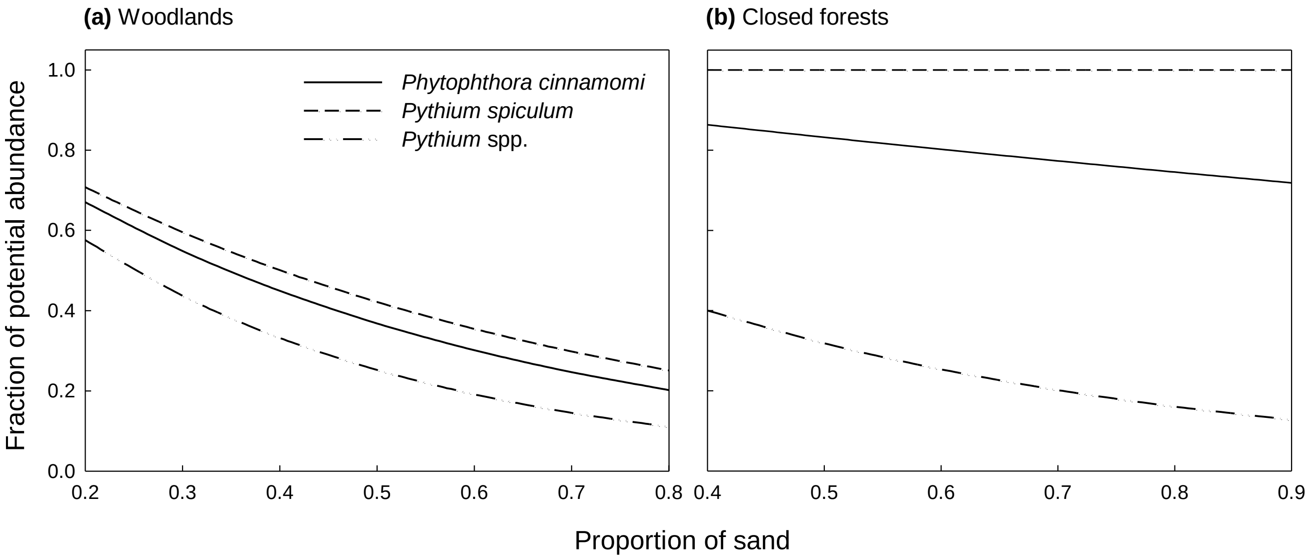

Figure 1 Predicted effect of soil texture (proportion of sand) on potential abundance of *Phytophthora cinnamomi*, *Pythium spiculum*, and *Pythium* spp. in a) woodlands and b) closed forests. The texture effect on potential abundance is calculated using Eqn 2 and values of the *b* parameter reported in Table S2. Y-values < 1 indicate a negative effect of sand proportion on potential pathogen abundance.

Much of the variation in soil-borne pathogen abundance was explained by the tree neighborhood from which the soil was sampled. Thus, excluding the tree effect from the full model ("No Tree" model in Table 1) always caused a much larger increase in AIC$_c$ than excluding either the texture or shrub effect (Table 1). In all models, $\alpha = 1$ offered a better fit to the data than $\alpha = 0$, indicating that the tree influence on pathogen abundance was proportional to its size. The effect of distance to neighbors on pathogen abundance (controlled by parameters β and γ in Eqn 5, Table S2) was however not consistent among pathogen species. The decline in distance varied from very steep in *P. cinnamomi* to virtually null in *Pythium* spp., for which abundance was only proportional to host density (Fig. 2).

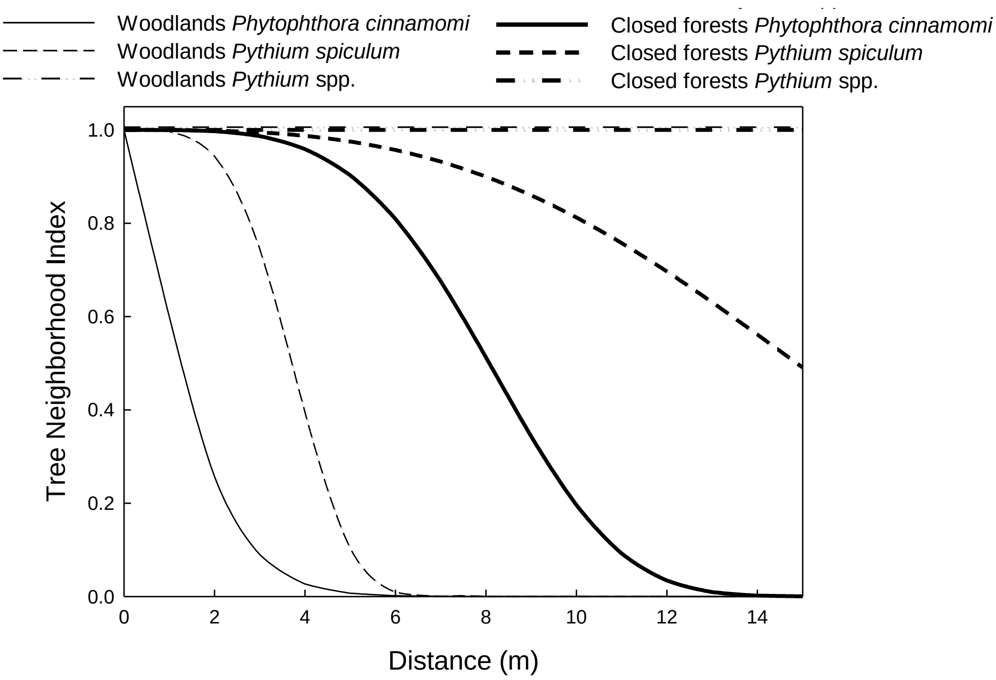

Figure 2 Predicted change in the tree Neighborhood Index (NI_{Tree}) as a function of distance to a neighbor for the three studied pathogen species in woodlands and closed forests. The NI_{Tree} is calculated using Eqn 5 and values of the γ and β parameters given in Table S2 (λ=1 and α=0 for simplicity of presentation of results). To facilitate comparison among pathogen species, NI_{Tree} values are shown standardized (i.e. divided by the maximum value for the species).

For *P. cinnamomi* and *Pythium* spp. in both forest types, models that discriminated among living trees of different species and health status and included the legacy effect of dead trees (i.e. calculated 5 different λ values) provided a much better fit to the data (i.e. had lower AIC_C) than simpler models that ignored species or health differences (Table 1). In woodlands, λ values varied from very positive in highly defoliated *Q. suber* trees to largely negative in *O. europea* (Table S2). This is because neighborhoods dominated by healthy *Q. suber* trees had lower abundance of *P. cinnamomi* and *Pythium* spp. than those dominated by symptomatic *Q. suber* trees, but higher abundance than neighborhoods dominated by dead *Q. suber* and *O. europaea* trees (Fig. 3). Similarly, in closed forests, neighborhoods dominated by healthy *Q. suber* trees had lower *P. cinnamomi* and *Pythium* spp. abundance than those dominated by symptomatic *Q. suber* trees. In this forest type, on the contrary, healthy *Q. suber* neighborhoods also had lower pathogen abundance than neighborhoods of the coexisting species *Q. canariensis* (Table S2, Fig. 3). Finally, for *Py. spiculum*, models that grouped all tree species as equivalent always had the largest empirical support (i.e. lower AIC_C, Table 1). It is likely that the substantial lower abundance of *Py. spiculum* compared to the other two pathogen groups limited the capacity of the models to detect complex spatial patterns for this species. In both forest types, the abundance of *Py. spiculum* varied positively with tree abundance in its neighborhood (Table S2, Fig. 3).

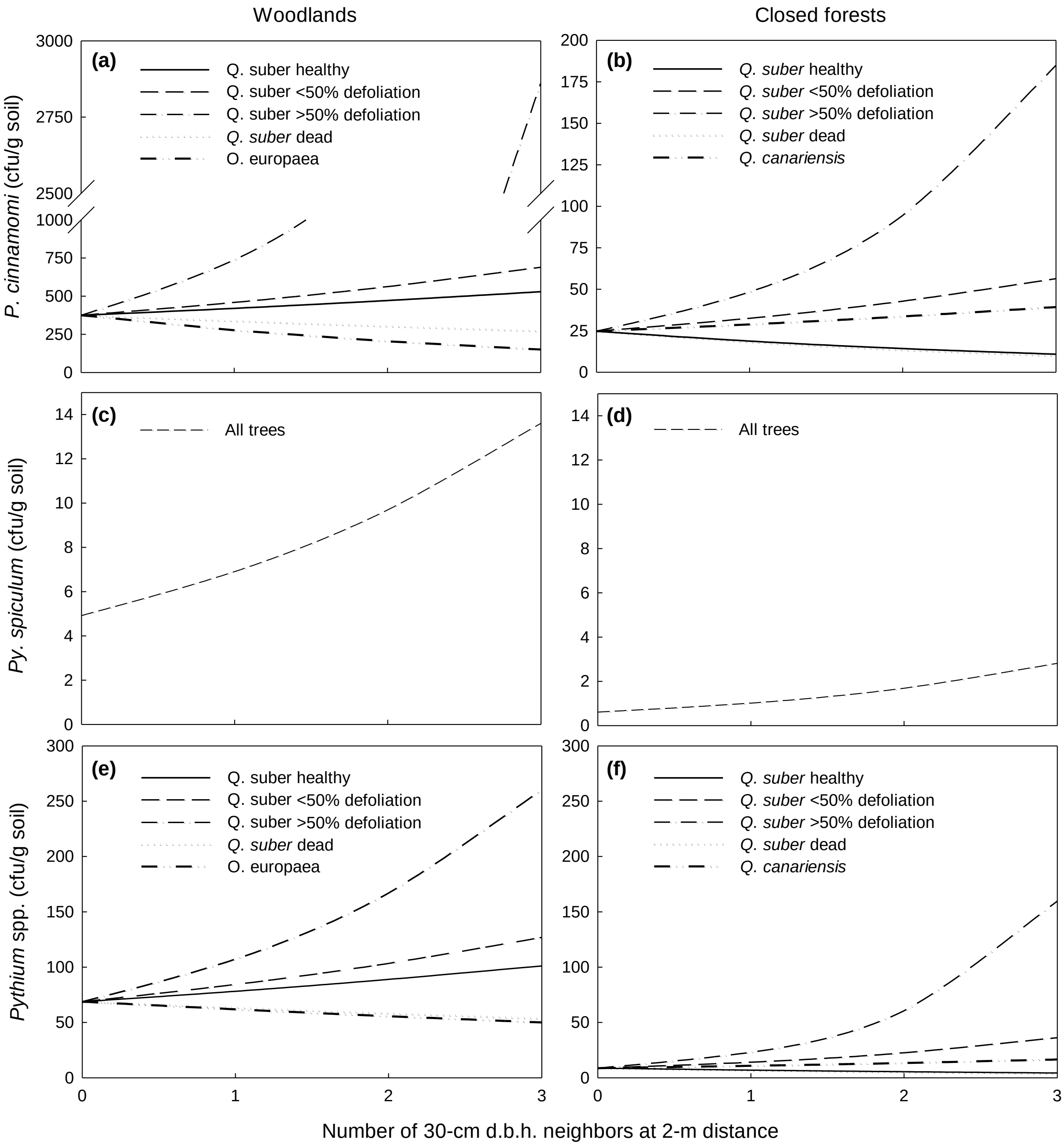

Figure 3 Predicted effects of variation in neighbor identity and quantity on abundance (measured in colony forming units per gram of dry soil) of a) *Phytophthora cinnamomi* in woodlands, b) *P. cinnamomi* in closed forests, c) *Pythium spiculum* in woodlands, d) *Py. spiculum* in closed forests, e) *Pythium* spp. in woodlands, and f) *Pythium* spp. in closed forests. Neighbor types are given by the best model for each pathogen species (Table 1). For *Py. spiculum,* the best model considered all trees as a single group. Pathogen abundance is calculated using Eqn 1-6 and optimum texture values, standard 30-cm tree neighbors (the average tree size across study sites) at 2-m distance from target soils, and no shrubs. For each combination of pathogen species and forest type, only the site with the largest potential pathogen abundance ($\mathrm{PPA}_{\mathrm{Site}}$ in Table S2) is represented.

The effect of shrubs on pathogen abundance varied strongly among forest types, being negative in woodlands but positive (*P. cinnamomi* and *Pythium* spp.) or neutral (*Py. spiculum*) in closed forests (Fig. 4). The magnitude of the effect did not vary among pathogen species in most cases, as indicated by the overlapping values of the *d* parameter (Table S2).

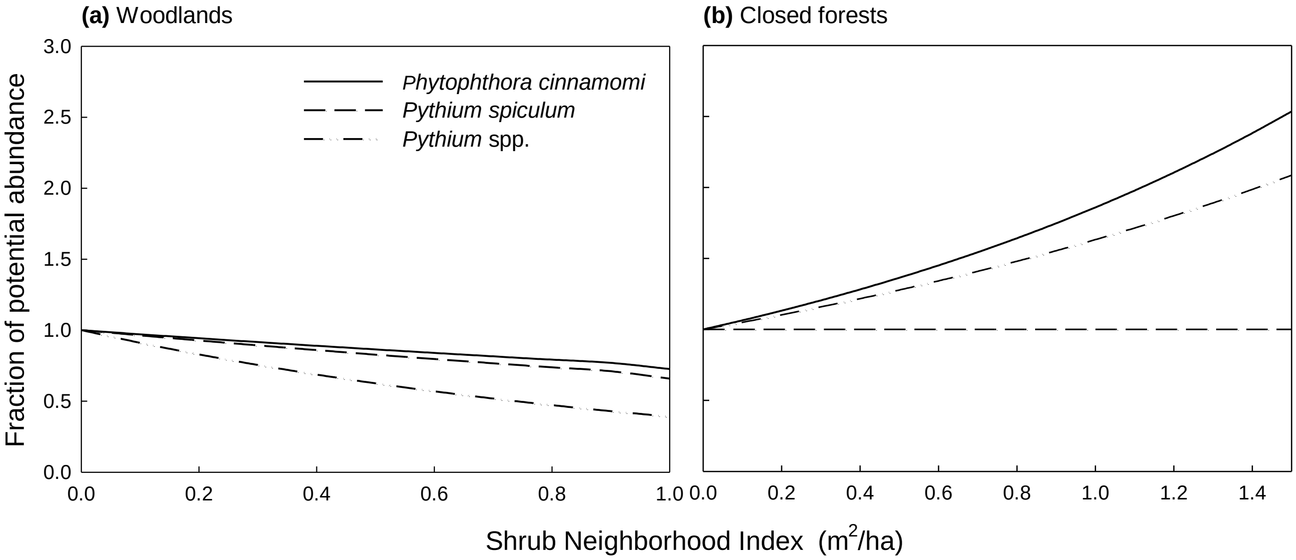

Figure 4 Predicted effect of variation in the shrub Neighborhood Index (NI_{Shrub}) on potential abundance of *Phytophthora cinnamomi*, *Pythium spiculum*, and *Pythium* spp. in a) woodlands and b) closed forests. The shrub effect on potential abundance is calculated using Eqn 4 and values of the *d* parameter reported in Table S2. Y-values < 1 indicate a negative effect of shrubs on potential pathogen abundance, whereas values > 1 indicate a positive effect.

Effect of soil-borne pathogens on seedling emergence and survival

Among the nine combinations of forest type-seedling species-pathogen species tested, we only found support for an effect of *P. cinnamomi* on the emergence of *Q. suber* seedlings in woodlands (Table 2). This effect varied among sites, as indicated by the fact that a site-specific model was a better fit to the data than a simpler linear model (Table 2). Thus, *P. cinnamomi* had a large negative effect on *Q. suber* emergence in two sites (Cinchao and Picacho) and a neutral effect (i.e. support interval for the *b* parameter overlaps zero, Table S3) in one site (Ahumada, Fig. 5).

We found support for an effect of *P. cinnamomi* on survival of *Q. suber* seedlings in woodlands, but not in closed forests (Table 2). The model that incorporated site-effects had a lower AIC_c than a simpler model omitting those effects. Thus, *P. cinnamomi* had a negative effect on *Q. suber* survival in just one of the three woodland sites (Ahumada), which happened to be the only site where *P. cinnamomi* effects on seedling emergence were not found (Table S3, Fig. 5). Although models incorporating pathogen effects were the most parsimonious fit in two other situations - effects of *P. cinnamomi* and *Pythium* spp. on *Q. canariensis* survival- the differences in AIC_c with the null model were < 2 units (Table 2), and therefore do not provide strong support for a pathogen effect on survival of this species.

Table 2 Comparison of alternate models analyzing the effect of pathogens on seedling emergence and survival. The most parsimonious model (indicated in bold) is the one with the lowest AIC$_c$. The Site-specific model considers differential pathogen effects among sites, the Linear model a homogeneous pathogen effect among sites, and the Null model the absence of pathogen effects. *NP* is the total number of parameters in the best model, and *n* the sample size. The slope and R^2 for the relationship between predicted and observed emergence/survival are given for best models other than the null.

Forest type	Seedling species	Pathogen species	AIC$_c$ Site-specific	Linear	Null	NP	n	Slope	R^2
Emergence									
Woodlands	*Q. suber*	*P. cinnamomi*	**363.01**	368.56	369.13	6	90	1.00	0.12
		Py. spiculum	244.34	242.65	**240.65**	3	60		
		Pythium spp.	259.53	256.24	**255.72**	3	60		
Closed forests	*Q. suber*	*P. cinnamomi*	392.02	388.01	**386.19**	3	88		
		Py. spiculum	258.01	255.47	**251.97**	2	58		
		Pythium spp.	296.66	292.25	**290.25**	2	58		
	Q. canariensis	*P. cinnamomi*	423.27	416.38	**414.48**	3	88		
		Py. spiculum	293.34	291.79	**289.88**	2	58		
		Pythium spp.	277.07	275.80	**273.84**	2	58		
Survival									
Woodlands	*Q. suber*	*P. cinnamomi*	**190.68**	194.81	195.33	6	86	1.04	0.16
		Py. spiculum	145.89	142.23	**140.60**	2	57		
		Pythium spp.	121.55	119.29	**117.31**	2	56		
Closed forests	*Q. suber*	*P. cinnamomi*	230.42	226.33	**224.60**	3	81		
		Py. spiculum	143.98	141.00	**139.06**	2	51		
		Pythium spp.	159.03	156.00	**154.02**	2	56		
	Q. canariensis	*P. cinnamomi*	282.49	**278.44**	279.27	3	82	0.98	0.14
		Py. spiculum	181.08	178.67	**176.69**	2	52		
		Pythium spp.	192.79	**190.59**	191.77	3	56	0.97	0.04

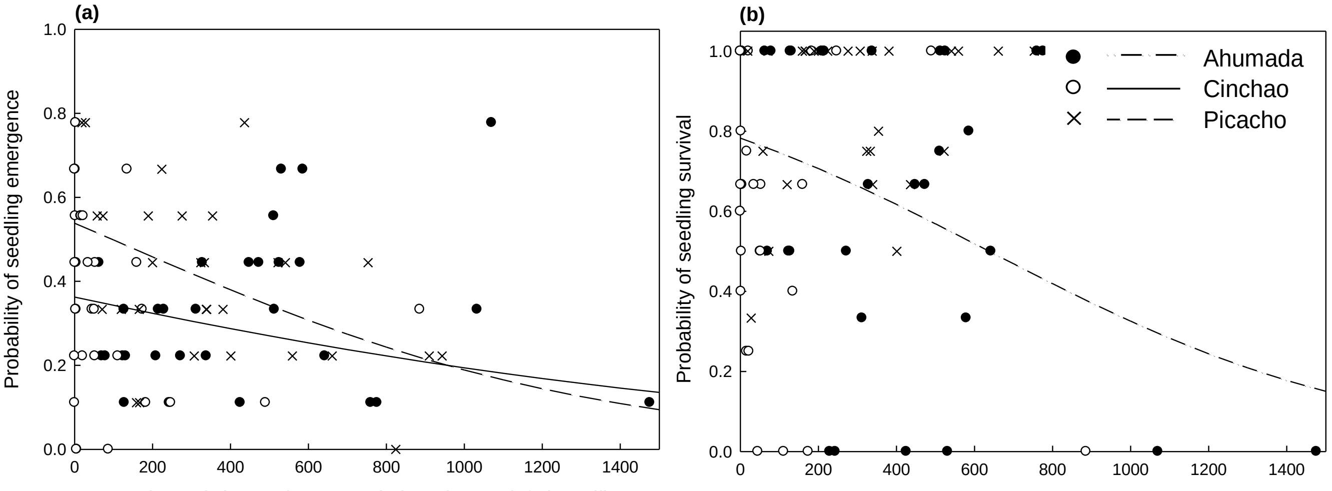

Figure 5 Probability of a) emergence and b) survival of *Quercus suber* seedlings in the three woodland sites as a function of the abundance (colony forming units per gram of dry soil) of *Phytophthora cinnamomi* in the soil.

DISCUSSION

Our results indicate that pathogen abundance in the forest soil is not randomly distributed, but exhibits spatially predictable patterns influenced by both abiotic (soil texture) and particularly biotic factors (tree and shrub species). The relative importance of each factor on soil-borne pathogen abundance varied among forest types and/or pathogen species, revealing the complexity of the pathogen landscape. We also found that the spatial variability in the pathogen community had significant ecological consequences by affecting the performance of tree seedlings under natural field conditions, but only for particular combinations of species and sites. Our findings suggest that heterogeneous spatial patterns of pathogen abundance at fine spatial scale can have important implications for the dynamics and restoration of declining Mediterranean oak forests.

Drivers of soil-borne pathogen abundance: the role of soil texture

Our models showed a consistent negative effect of soil sand content on pathogen abundance, presumably due to the direct influence of texture on water availability. Sandy soils have lower water-holding capacity and higher percolation rates than do clayish soils (Brady & Weil, 2008). Therefore, they are less prone to suffer temporal waterlogging conditions that strongly benefit pathogen abundance and disease development (Hendrix & Campbell, 1973; Weste & Marks, 1987). The texture effect was much larger in woodlands than in closed forests for the three pathogen species, probably because the closed forest soils were all very sandy (Table S1). In fact, the sandier soils of closed forests could also explain why they showed lower loads of all pathogen species than woodlands (Fig. 3). Our results therefore suggest that texture is an important abiotic driver of soil-borne pathogen variation at both the local and landscape scale.

Drivers of soil-borne pathogen abundance: the role of the tree community

A main finding of this paper is the strong empirical support found for a spatial concordance among the distribution and health status of trees of different species and the abundance of soil-borne pathogens in the soil. *P. cinnamomi* and *Pythium* spp. were much more abundant under declining *Q. suber* trees, particularly those already showing a high defoliation level (>50%), than under healthy *Q. suber* trees. Although our observational approach does not allow separating cause and effect in the tree-pathogen interaction, the finding of a concomitant increase in the abundance of pathogens in the soil and defoliation in the canopy is consistent with the predictions of the *hypothesis of decline development* in oak forests, which propose a tree-pathogen feedback process (Brasier, 1996). According to this hypothesis, the loss of fine roots by soil-borne pathogens may translate into a loss of leaf area aboveground. The opening of the canopy trigger a series of environmental changes (e.g. higher soil temperature, reduced organic matter content and microbial activity) that might in turn favor pathogen development, giving rise to a feedback loop where pathogens under the trees produce changes at the canopy level that favor the build-up of larger pathogen loads, eventually killing the tree. However, the fact that our models supported a negative effect of dead trees on soil pathogen abundance (negative λ, Table S2) suggests that once a tree dies, its legacy is a gap with lower pathogen abundance than the surrounding forest matrix. These gaps could play a role of refuge for the establishment of susceptible species as reported for canopy gaps in tropical and cool temperate forests (Augspurger, 1984; O'Hanlon-Manners & Kotanen, 2004, 2006; Reinhart *et al*., 2010).

Our results indicate that tree species can play very different roles in the pathogen landscape. Thus, among the species co-existing with the susceptible *Q. suber* in our study sites, *O. europaea* neighborhoods seem to suppress pathogens (pathogen abundance was lower under *O. europaea* than in neighborhoods without trees), whereas *Q. canariensis* seem to act as a reservoir without showing any apparent disease symptom (Fig. 3). These results help us to understand the nature of plant-plant interactions mediated by pathogens in these forests. Specifically, they suggest that whereas *O. europaea* trees could indirectly benefit *Q. suber* by acting as refuges for its recruitment, the presence of *Q. canariensis* could result in apparent competition (Cobb *et al*., 2010) by promoting pathogens that harm *Q. suber* more strongly than itself. These complex indirect effects, although largely ignored in the literature, show the need to use a community approach when trying to explain patterns of spatial variation in disease dynamics for particular tree species (e.g. Janzen-Connell effects; Mordecai, 2011).

Our neighborhood approach allowed valuable insights into the role of tree size and distance as determinants of pathogen abundance. This type of information is extremely rare in the literature on plant-pathogen interactions, since most studies do not quantify pathogen abundance but measure disease expression directly, which can be affected by additional factors such as host susceptibility or environmental conditions (e.g. Augspurger & Kelly, 1984; Gilbert *et al*., 1994; Packer & Clay, 2000, 2003; but see Reinhart & Clay, 2009). First, our models indicate that the tree effect on pathogen abundance is not independent of its size, with larger trees hosting larger pathogen communities. This result provides empirical support for the hypothesis of the importance of dbh as a source of intra-specific variation in plant-pathogen interactions (Reinhart & Clay, 2009), and calls for the inclusion of this plant trait as a covariable in experimental and observational studies of pathogen abundance and disease. Second, our models showed that the decline of the net effect of a neighbor tree within the 15-m neighborhood vary strongly among pathogen species, from rather sharp for *P. cinnamomi* (tending to zero within 5-6 m) to virtually null for *Pythium* spp. (Fig. 2). This result suggests that pathogen species can vary strongly in their scale of spatial variation, with some of them showing heterogeneous patterns at smaller scales than others.

Drivers of soil-borne pathogen abundance: the role of the shrub community

We found that not only the tree community, but also the shrub community had a strong effect on soil-borne pathogen abundance, supporting previous studies that have emphasized the relevance of the understory as a driver of the soil microbial community (Nilsson & Wardle, 2005; Wu *et al*., 2011). However, the sign of the shrub effect was not consistent among forest types, being negative in woodlands but positive in closed forests. A likely explanation for this difference would be that the net effect of the understory was driven by the identity of the dominant shrub species, which differed among forest types. Thus, despite their similar species composition, species relative abundance changed from dominance of *Pistacia lentiscus* in woodlands to dominance of *Erica* spp. in closed forests. These two species vary strongly in their litter quality and effects on soil fertility: *P. lentiscus* forms islands of fertility rich in organic matter (Armas & Pugnaire, 2009), whereas *Erica* spp. produces low-quality litter and is indicative of acidic nutrient-poor soils (Van Vuuren & Berendse, 1993; Zas & Alonso, 2002). Because an acidic pH, low nutrient content and low organic matter favor soil-borne pathogen growth and disease expression (Weste & Marks, 1987; Jönsson *et al*., 2003; Serrano *et al*., 2011), soils under *Erica* spp. could be expected to provide more favorable conditions for pathogen build-up than soils under *P. lentiscus*. Although this hypothesis remained to be tested, our results highlight the strong variability in the understory effects on pathogen populations that can be expected even in forests with similar shrub species composition.

Pathogen effects on seedling emergence and survival: implications for regeneration dynamics

Our models of seedling emergence and survival indicate that, under natural field conditions, the spatial variability of soil-borne pathogen abundance translates into spatial variation in seedling performance, but not for all species or forest types. Indeed, we only found support for a negative effect of *P. cinnamomi* on emergence and survival of *Q. suber* seedlings in woodlands. The fact that we detected negative effects of *P. cinnamomi* but not of *Py. spiculum* or *Pythium* spp., on seedling performance is probably influenced by its much larger abundance in the studied forests, but could also be indicative of the larger aggressiveness of this species (Romero *et al*., 2007). Differences in *P. cinnamomi* abundance, much greater in woodlands than in closed forests, could also explain its stronger effects in the former forests. These findings therefore suggest that certain thresholds in pathogen abundance need to be overcome before they translate into measurable effects on seedling performance in the field. Interestingly, these thresholds seem to be higher than those expected based on pathogenicity trials, where much lower *P. cinnamomi* abundances (<500 cfu/g) are lethal for Mediterranean *Quercus* seedlings (Sánchez *et al.*, 2002; Serrano *et al.*, 2011).

Our results do not support the hypothesis of lower susceptibility to pathogens in shade-tolerant than shade-intolerant species (Augspurger 1990, McCarthy-Neumann & Kobe, 2008). Unfortunately, the lack of emergence of *O. europaea* precluded the exploration of interspecific differences in pathogen susceptibility in woodlands. However, in closed forests, neither *Q. suber* nor *Q. canariensis* seedlings were negatively affected by pathogens, despite their differences in shade-tolerance. A question that remained to be answered is whether differences among the two *Quercus* species would emerge at larger pathogen abundances such as those found in woodlands, where *Q. suber* emergence and survival was severely impaired by *P. cinnamomi* (Fig. 5). To date, our findings do not support a significant role of pathogens as promoters of species coexistence through species-specific effects at the seedling level. On the contrary, because adults of *Q. suber* are much more susceptible to pathogen attack than adults of *Q. canariensis*, soil-borne pathogens seem more likely to play a role for species exclusion than for coexistence in the studied forests.

Although our results indicate important net impacts of pathogens on tree seedlings under natural conditions, the rather low explanatory power of the emergence and survival models should be taken as evidence that pathogens are just one of many other relevant abiotic and biotic drivers of natural patterns of recruitment. These drivers could interact with each other, a given abundance of soil-borne pathogens having implications for seedling performance only under specific environmental situations such as low light availability or low mycorrhizal abundance (Hood *et al.*, 2004; Morris *et al.*, 2007). Further studies that explore the simultaneous effect of multiple abiotic and biotic drivers of seedling performance are clearly needed to advance our understanding of the factors affecting the expression of disease in forest ecosystems.

Concluding remarks

This study provides new insights into the highly complex spatial distribution of soil-borne pathogens and reveals the degree to which soil characteristics and the woody plant community can explain pathogen abundance in forest soils. Because we have shown that the spatial variation in pathogen abundance can affect the recruitment of susceptible tree species, such as *Q. suber*, these findings might be useful in the restoration of forests affected by pathogen-driven decline, which frequently involves planting of seeds or seedlings of susceptible species to replace dead trees in the future (Tuset & Sánchez, 2004). Specifically, our results could help to choose those planting microsites in which seedling emergence and survival would have lower probability of being impaired by soil-borne pathogens, hence maximizing the economic and ecological benefits of restoration efforts.

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SUPPORTING INFORMATION

Table S1 Description of main characteristics of the six study sites located in the South (S), Center (C) and North (N) of the Alcornocales Natural Park. Values of texture (proportion of sand), tree basal area (m^2/ha) and shrub crown area (m^2/ha) represent median [P10 – P90, 10th and 90th percentiles] for the 30 sampled neighborhoods at each site. Neighborhoods are circles of 15-m (for trees) and 5-m (for shrubs) radius around each sample point. Shrub crown area is given for the most common species across the six study sites.

	Woodlands			Closed forests		
	Ahumada (S)	Cinchao (C)	Picacho (N)	Comares (S)	Jimena (C)	Tala (N)
Latitude (N)	36º 04′ 38″	36º 04′ 38″	36º 31′ 69″	36º 06′ 09″	36º 23′ 10″	36º 28′ 13″
Longitude (W)	05º 33′ 05″	05º 33′ 05″	05º 38′ 08″	05º 30′ 53″	05º 31′ 52″	05º 35′ 31″
Annual rainfall (mm)	948.9	726.4	973.1	1067.1	1022.6	1097.0
Mean annual T (ºC)	16.3	16.9	16.3	15.4	17.3	15.9
Texture	0.47	0.67	0.54	0.72	0.66	0.75
	[0.24-0.61]	[0.56-0.77]	[0.36-0.63]	[0.65-0.79]	[0.55-0.76]	[0.69-0.82]
Tree basal area						
Olea/*Q. canariensis*	3.49	4.09	3.73	16.99	10.21	11.34
	[0.10-7.47]	[0-23.41]	[0.34-17.49]	[6.14-32.14]	[0-21.19]	[3.31-23.03]
Q. suber $_{\text{Healthy}}$	0.82	14.08	0.82	2.22	2.06	5.37
	[0-10.98]	[3.88-25.37]	[0-10.98]	[0-16.27]	[0-9.97]	[0-14.77]
Q. suber $_{\text{<50\% defoliation}}$	3.29	2.37	15.74	3.09	2.18	0.09
	[0-4.92]	[0-9.91]	[3.76-35.69]	[0.21-4.48]	[0-12.32]	[0-5.76]
Q. suber $_{\text{>50\% defoliation}}$	1.76	------	2.54	1.92	0.00	0.00
	[0-6.59]		[0-5.53]	[0.23-4.85]	[0-2.43]	[0-0.00]
Q. suber $_{\text{Dead}}$	3.76	0.00	0.00	3.46	0.00	0.44
	[0-17.75]	[0-0.64]	[0-3.64]	[1.68-8.50]	[0-3.90]	[0-2.54]
Shrub crown area						
Pistacia lentiscus	0.00	845.3	0.14	------	0.00	------
	[0-600]	[0-0.47]	[0-0.25]		[0-0.00]	
Erica spp.	0.00	------	------	0.02	3600	0.00
	[0-0.00]			[0-0.21]	[800-1080]	[0-300]
Phillyrea latifolia	0.00	0.00	200	0.00	0.00	100
	[0-0.00]	[0-0.00]	[0-900]	[0-0.09]	[0-0.04]	[0-2900]
Crataegus monogyna	300	0.00	500	------	0.00	------
	[0-1300]	[0-0.00]	[0-1600]		[0-0.00]	

Table S2 Parameter estimates and 2-unit support intervals (in brackets) for the best model selected for each combination of soil pathogen species and forest type. See text for a description of the parameters.

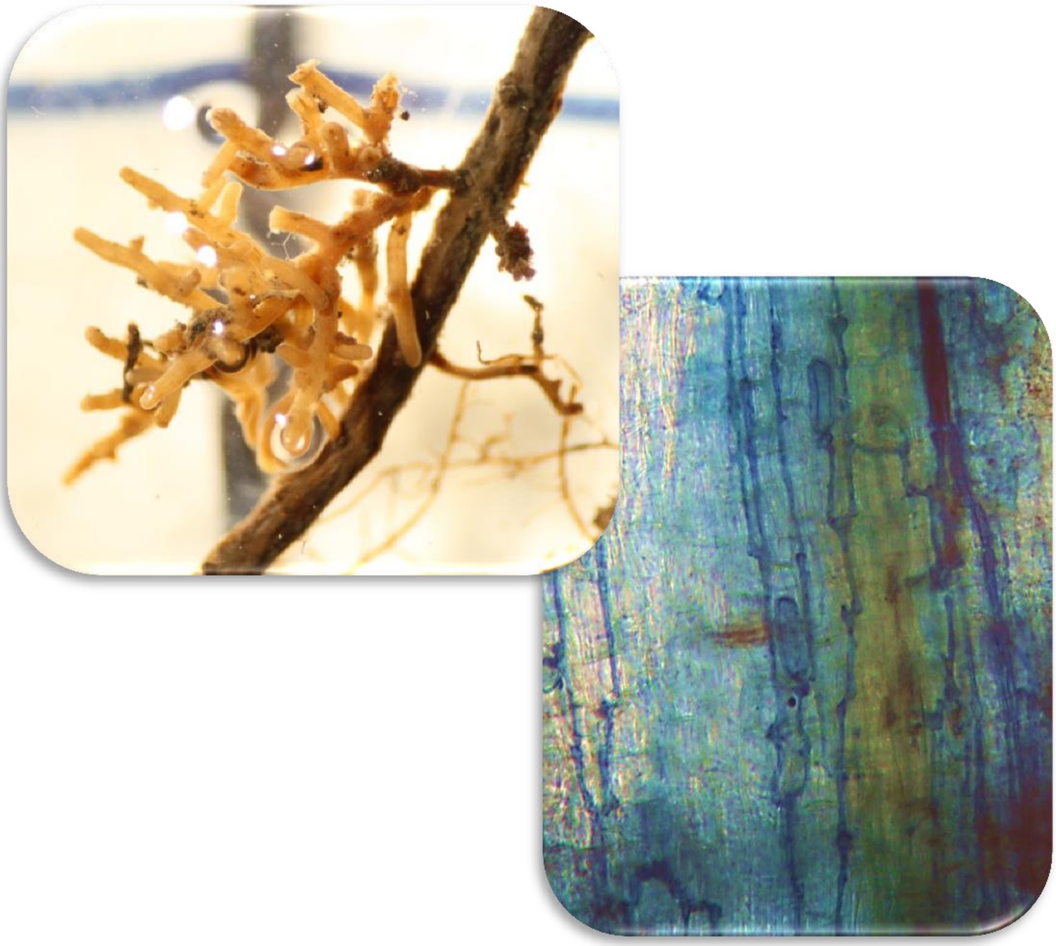
	Woodlands			Closed forests		
Parameter	*Phytophthora cinnamomi*	*Pythium spiculum*	*Pythium* spp.	*Phytophthora cinnamomi*	*Pythium spiculum*	*Pythium* spp.
PPA_{South}	1133.24	8.17	-----	5.35	-----	44.35
	[1133.23-1133.25]	[8.16-8.18]		[4.19-6.01]		[41.76-47.27]
PPA_{Center}	383.74	12.52	89.51	31.87	0.61	3.61
	[383.73-383.75]	[12.51-12.53]	[89.43-89.89]	[30.23-32.90]	[0.60-0.62]	[2.58-4.84]
PPA_{North}	1002.35	-----	305.11	4.20	0.40	-----
	[1002.34-1002.36]		[305.10 -305.12]	[3.63-5.15]	[0.39-0.41]	
b (texture)	-2.05	-1.73	-2.76	-0.37	-----	-2.29
	[-2.17 to -1.96]	[-1.91 to -1.56]	[-2.77 to -2.75]	[-0.38 to -0.36]		[-2.30 to -2.28]
c (tree)	0.72	1.22	2.78	2.23	3.98	3.23
	[0.71-0.73]	[1.21-1.23]	[2.77-2.79]	[2.22-2.24]	[3.99-3.97]	[3.22-3.24]
d (shrub)	-0.29	-0.38	-0.94	0.62	-----	0.49
	[-0.45 to -0.12]	[-0.58 to -0.21]	[-1.09 to -0.79]	[0.54-0.71]		[0.33-0.63]
α	1	1	1	1	1	1
γ (x 10^{-3})	510.62	3.63	0.00	0.21	0.17	0.00
	[470.71-550.73]	[0.45-13.63]	[0-10]	[0.12-5.22]	[0.05-6.13]	[0-10]
β	1.41	3.99	1.60	3.99	3.03	3.67
	[1.35-1.46]	[3.72-4]	[0.50-4]	[3.76-4]	[2.75-3.11]	[0.50-4]
$\lambda_{\textit{Olea/Q. canariensis}}$	-0.45		-0.24	0.23		0.22
	[-0.46 to -0.44]		[-0.25 to -0.23]	[0.22-0.24]		[0.22-0.24]
$\lambda_{\textit{Q. suber}\text{ Healthy}}$	0.17		0.29	-0.41		-0.28
	[0.16-0.18]		[0.28-0.30]	[-0.42 to -0.40]		[-0.29 to -0.30]
$\lambda_{\textit{Q. suber} <50\%}$	0.30		0.46	0.41		0.49
	[0.29-0.31]		[0.45-0.47]	[0.40-0.42]		[0.48-0.50]
$\lambda_{\textit{Q. suber} >50\%}$	1		1	1		1
	[0.99-1]		[0.99-1]	[0.99-1]		[0.99-1]
$\lambda_{\textit{Q. suber}\text{ Dead}}$	-0.16		-0.19	-0.46		-0.24
	[-0.17 to -0.15]		[-0.12 to -0.17]	[-0.47 to -0.45]		[-0.25 to -0.23]

Table S3 Parameter estimates and 2-unit support intervals (in brackets) for the best models of *Phytophthora cinnamomi* effects on emergence and survival of *Quercus suber* and *Quercus canariensis* seedlings. Because emergence and survival were modeled with a binomial distribution, parameter values predict the logit(emergence) and logit(survival). See text for a description of the parameters.

		Woodlands	Closed forests	
Variable	Parameter	*Q. suber*	*Q. suber*	*Q. canariensis*
Emergence	PSE_{South}	-0.83 [-1.12 to -0.59]	0.27 [0.02-0.52]	-0.22 [-0.46 to 0.04]
	PSE_{Center}	-0.56 [-0.80 to -0.27]	-0.01 [-0.25 to 0.25]	-0.31 [-0.55 to -0.05]
	PSE_{North}	0.15 [-0.12 to 0.40]	-0.67 [-0.93 to -0.41]	-1.07 [-1.36 to -0.79]
	b_{South}	0.03 [-0.02 to 0.08]		
	b_{Center}	-0.09 [-0.27 to -0.01]		
	b_{North}	-0.16 [-0.23 to -0.09]		
Survival	PSS_{South}	1.28 [0.84-1.85]	1.20 [0.83-1.66]	1.08 [0.73-1.46]
	PSS_{Center}	0.35 [0.84-1.85]	1.36 [0.92-1.83]	1.31 [0.91-1.73]
	PSS_{North}	0.93 [0.84-1.85]	0.36 [-0.05 to 0.82]	0.15 [-0.20 to 0.52]
	c_{South}	-0.20 [-0.29 to -0.11]		
	c_{Center}	-0.19 [-0.68 to 0.06]		
	c_{North}	0.12 [-0.02 to 0.27]		

Capítulo 6

IMPACTO DEL DECAIMIENTO ARBÓREO EN LOS PATRONES ESPACIALES DE LA INTERACCIÓN PLÁNTULA-MICORRIZA: IMPLICACIONES PARA LAS DINÁMICAS DE REGENERACIÓN EN BOSQUES MEDITERRÁNEOS



Este capítulo reproduce el siguiente manuscrito:

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Impacto del decaimiento arbóreo en los patrones espaciales de la interacción plántula-micorriza: implicaciones para las dinámicas de regeneración en bosques mediterráneos

RESUMEN

La distribución espacial de las micorrizas en los bosques está determinada en gran medida por la identidad y la situación de los individuos adultos de árboles y matorrales. En bosques afectados por decaimiento, el estado de salud de los árboles puede ser un factor adicional que defina la abundancia de micorrizas. Sin embargo, aún es poco conocido como el decaimiento de una especie puede afectar a las micorrizas en bosques mixtos, lo cual a su vez puede influir en el establecimiento de las plántulas, en un proceso de retroalimentación.

En este estudio se usó una aproximación Bayesiana para analizar el impacto del decaimiento de *Quercus suber* en los patrones espaciales de la asociación plántula-micorriza en bosques mixtos mediterráneos, y se evaluó la importancia relativa de esta asociación en el establecimiento de plántulas.

Los resultados obtenidos indicaron que la variación espacial de la intensidad de colonización de las raíces de las plántulas por micorrizas está parcialmente ligada al proceso de decaimiento de *Q. suber*, aunque con diferencias entre tipo de micorriza (endo y ecto) y tipo de bosque (bosque abierto y bosque cerrado).

La supervivencia de plántulas de un año fue más afectada por endomicorrizas que por ectomicorrizas. Además, los efectos fueron neutros o negativos, pero nunca positivos, probablemente relacionado con que plántulas de un año tienen aún reservas en la semilla por lo que cualquier posible beneficio de la asociación con micorrizas quedó amortiguado.

Al responder la distribución espacial de la asociación plántula-micorriza a la identidad y estado de salud de los árboles, y al afectar esta asociación a las plántulas, se concluye que el decaimiento arbóreo puede afectar a la dinámica forestal a través de procesos bióticos de retroalimentación. Aunque la magnitud del efecto fue baja, se propone un posible incremento con la edad, ya que a medida que se desarrolla la plántula tendrá una demanda mayor de recursos que dejará de ser cubierta por la semilla.

Impact of tree decline on spatial patterns of seedling-mycorrhiza interactions: implications for regeneration dynamics in Mediterranean forests

Beatriz Ibáñea[a], Lorena Gómez-Aparicio[a], José M. Ávila[a], Ignacio M. Pérez-Ramos[a], Luis V. García[a], Teodoro Marañón[a]

a. *Instituto de Recursos Naturales y Agrobiología (IRNAS, CSIC), PO Box 1052, Sevilla 41080, Spain.*

ABSTRACT

In forest ecosystems, the spatial distribution of mycorrhizal fungi is largely driven by the identity and location of adult trees and shrubs. Moreover, in forests affected by problems of tree dieback, the health status of canopy trees can be an additional factor shaping mycorrhizal abundance. However, it is poorly known how species-specific tree decline may affect the spatial distribution of mycorrhizal fungi in mixed forests, which in turn could alter the probability of seedling establishment in a feedback process.

In this study we used a Bayesian framework to analyze the impact of *Quercus suber* decline on spatial patterns of seedling-mycorrhiza interactions in mixed Mediterranean forests, and evaluate the relative importance of this symbiosis as a driver of seedling establishment in the understory.

Our models indicated that the spatial variability found in the intensity of seedling mycorrhizal colonization was partially linked to the process of *Q. suber* decline. However, the influence of tree health status varied among mycorrhiza (endo vs. ecto) and forest types (woodlands vs. closed forests), showing how context-dependent the effects of tree decline can be on forest function.

Survival of 1-year old oak seedlings was affected to a larger extent by endo- than by ecto-mycorrhizal colonization. Moreover, these effects were negative or neutral, but never positive. We hypothesized that seed reserves could be buffering any potential benefit of mycorrhizal infection at these early stages of development.

We conclude that because the spatial distribution of the seedling-mycorrhiza association responded to the identity and health status of individual trees, and mycorrhizal infection did in turn affect seedling performance, tree decline might affect forest dynamics through plant-soil biota feedbacks. Although the magnitude of this effect was relatively low, we propose that it could increase and even change in sign in the long-term, as saplings become older and have a higher resource demand not covered by seed reserves.

Key-words Ectomycorrhiza, endomicorrhiza, neighborhood processes, *Olea europaea* var. *sylvestris, Quercus suber, Quercus canariensis,* seedling survival, spatially-explicit models, plant-soil feedbacks, tree dieback

INTRODUCTION

The plant-mycorrhiza association is one of the most common symbiosis among organisms in forest ecosystems (Smith & Read, 2010). Mycorrhiza help plant roots uptake water and nutrients in exchange for C, which may improve plants' growth or their resistance to biotic and abiotic stresses (Augé, 2001; van der Heijden *et al.*, 2008; Smith & Read, 2010). By altering plant performance, plant-mycorrhiza association plays an important role in community development and ecosystem processes (see van der Heijden *et al.*, 2008 and cites therein). For example, it has been shown that the success of seedling establishment, one of the most critical processes determining ecosystem structure (Grubb, 1977), can be greatly improved by seedling-mycorrhiza associations (Amaranthus & Perry, 1987; Perry *et al.*, 1989; Alexander *et al.*, 1992; Horton *et al.*, 1999; Dickie *et al.*, 2002; Onguene & Kuyper, 2002; Nara & Hogetsu, 2004). The likelihood of this interaction, and consequently its implications for forest stand dynamics, will be strongly dependent on the spatial relationship between the mycorrhiza and the tree seedling community at fine spatial scales (Wolfe *et al.*, 2009). However, so far relatively few spatially-explicit studies have attempted to disentangle the main factors determining the probability and functional significance of seedling mycorrhizal infection in forest communities (Dickie *et al.*, 2002; Dickie & Reich, 2005).

The spatial distribution of mycorrhiza in forest soils can be shaped by several biotic and abiotic variables (Smith & Read, 2010). Specifically, the density and composition of the canopy cover are major factors that influence the assemblage of mycorrhizal communities both directly and indirectly. Tree species act as direct sources of fungal inoculum and determine the dominant mycorrhizal type (e.g. ecto [ECM], vesicular-arbuscular [VAM] or ericoid) or species due to the strong host-specificity of some fungus species (Molina *et al.*, 1992; Dickie *et al.*, 2001; Dickie *et al.*, 2002; Cline *et al.*, 2005; Morris *et al.*, 2008). Canopy trees also indirectly influence mycorrhizal presence or abundance acting as modulators of key abiotic conditions such as soil moisture (Worley & Hacskaylo, 1959; Allen & Kitajima, 2013) or nutrient availability (Dickie *et al.*, 2006; Aponte *et al.*, 2010). The strong response of mycorrhiza to canopy composition implies that any disturbance occurring aboveground at the overstory level could translate into important changes in belowground mycorrhizal communities, which in turn could affect the probability of seedling establishment in the forest understory in a feedback process (Bever *et al.*, 2010).

In the last decades, an increasing number of forest decline events and widespread tree mortality have been reported worldwide as a consequence of one or more Global Change drivers (Van Mantgem *et al.*, 2009; Allen *et al.*, 2010; Carnicer *et al.*, 2011). Such a general decrease in tree health and cover has an almost unexplored potential to impact mycorrhiza communities. The few studies that have assessed the effect of tree dieback on mycorrhiza have shown that mycorrhizal communities in the roots of declining trees can differ in type, abundance and/or composition compared with those found in healthy trees (Perrin & Estivalet, 1989; Causin *et al.*, 1996; Montecchio *et al.*, 2004; Ishaq *et al.*, 2013; Lancellotti & Franceschini, 2013). Defoliation might negatively affect mycorrhiza fungi through C allocation to roots, since the progressive loss of photosynthetic area in declining trees could translate into a reduction of the amount of soluble carbohydrates delivered to the symbiotic fungal partners (Gehring & Whitham, 2003). Additionally, mycorrhiza communities could be indirectly affected by changes in abiotic conditions associated with the process of decline and gap opening after tree death, such as higher light availability (Royer *et al.*, 2011) or changes in soil fertility (Orwig *et al.*, 2008; Cobb *et al.*, 2013). However, because most studies to date have been conducted comparing affected vs. not affected trees in monospecific stands, we still lack a clear picture of the implications of species-specific tree decline for the spatial distribution of mycorrhiza in mixed forests. Moreover, it is unknown how these decline-induced changes in the mycorrhizal community could impact tree regeneration dynamics.

In this study we aim to analyze the impact of tree decline on spatial patterns of seedling-mycorrhiza interactions in Mediterranean oak forests, and evaluate the relative importance of this symbiosis as a driver of seedling establishment in the forest understory. We focused our work on mixed forests of the southwestern Iberian Peninsula undergoing severe problems of adult mortality and recruitment limitation of one of their dominant species, *Quercus suber* (Brasier, 1992; Brasier, 1996; Ibáñez *et al.*, 2014). Using a Bayesian framework, we combined spatially-explicit data on mycorrhizal colonization in experimental seedlings, the distribution of the woody plant community, and the abiotic environment to answer the following questions: (1) Does canopy composition and health status directly influence mycorrhizal infection of seedling roots?; (2) Does the abiotic environment (i.e. soil nutrients, soil moisture, soil texture, light) influence fungal colonization of seedlings?; (3) What is the relative importance of mycorrhizal associations and abiotic factors as determinants of seedling survival?

MATERIAL AND METHODS

Study sites and species

The experiment was carried out in Los Alcornocales Natural Park, a region considered to be a *hot spot* of biodiversity in the Mediterranean Basin (Médail & Quézel, 1997). The climate is Mediterranean type with warm, dry summers and cool, humid winters. Vegetation in the overstory is dominated by the evergreen, shade semi-tolerant *Quercus suber*. In the drier lowlands of the park, characterized by clayish soils, *Q. suber* coexists with the evergreen, shade-intolerant *Olea europaea* var. *sylvestris* forming open woodlands. The understory in these woodlands is usually very dense and dominated by shrub species such as *Pistacia lentiscus* L. (Table S1). In wetter areas and sandier soils *Q. suber* coexists with the winter deciduous, shade-tolerant *Quercus canariensis* Willd., forming closed forests. These closed forests are characterized by a rich understory dominated by tall shrub species, such as *Arbutus unedo* L., *Phillyrea latifolia* L., *Erica arborea* L., and *Erica scoparia* L (Table S1). Both *Quercus* species typically associate with ectomycorrhizas, while the other coexistent tree and shrub species (e.g. *O. europaea*, *P. lentiscus*, *A. unedo* or *Erica* spp.) are typical arbuscular or ericoid mycorrhizal species (Molina *et al.*, 1992).

We selected six sites within the park to conduct our experiment, three located in open woodlands of *Q. suber* and *O. europaea* var. *sylvestris* (hereafter woodland sites) and three in closed forests of *Q. suber* and *Q. canariensis* (hereafter closed forest sites). In the six sites *Q. suber* showed symptoms of decline associated to the attack of exotic soil-borne pathogens (mainly *Phytophthora cinnamomi*) and its interaction with other global change factors such as global warming (Brasier, 1996; Carnicer *et al.*, 2011). No other tree or shrub species in the study area showed evident symptoms of decline. Topography was kept constant to avoid confounding effects of this variable on mycorrhizal communities. At each of the six sites we established 49 plots regularly distributed in a 10 x 10 m grid (n = 294 plots).

Seed sowing experiment

Seeds of *Q. suber*, *O. europaea* and *Q. canariensis* were collected from different trees within the park and sowed in winter 2010 (cohort 1) and 2011 (cohort 2). Sterilized and weighed seeds were sown in each site in two adjacent 30 x 30 cm^2 squares at the center of each of the 49 subplots. In each square we sowed seeds of *Quercus* and *Olea* in three lines 7.5 cm apart from each other and from the border of the square. In the woodland sites we alternatively sowed each line with three seeds of *Q. suber* or six seeds of *Olea*. In the closed forest sites we alternatively sowed each line with three seeds of *Q. suber* or three seeds of *Q. canariensis*. A larger number of *Olea* seeds was chosen based on their lower probability of germination (Voyiatzis & Porlingis, 1987). Seedlings that emerged during the spring were measured in early June (initial height) and revisited in early October (October 2011 for cohort 1, October 2012 for cohort 2) to record survival after the first summer, the main period of seedling mortality in Mediterranean systems (Gómez-Aparicio *et al.*, 2008; Pérez-Ramos *et al.*, 2012).

At the end of the spring 2010, we collected one healthy-looking seedling per plot and species when available (total of 27 seedlings per site and species on average). Unfortunately, emergence of *O. europaea* was virtually nil in all sites (data not shown), which precluded us from including this species in the analyses. The samples were kept moist and in cold temperatures in sealed plastic bags until taken to the laboratory, and stored at 4°C for one or two days while processing. We separated the aerial from the root part and preserved the roots in ethanol. One root fraction was retained to quantify the percent of root colonization by ectomycorrhizal fungi (ECM), as *Quercus* spp. are typical ectomycorrhizal species. Under a binocular microscope we counted colonized and non-colonized root tips and calculated the percentage of colonization following the gridline intersect method (Giovannetti & Mosse, 1980). Additionally, as arbuscular mycorrhizal infection (VAM) has also been found in trees and seedling of *Quercus* spp (e.g. Dickie *et al.*, 2001; Egerton-Warburton & Allen, 2001), a subsample of fine roots was examined for VAM infection. We cleared roots 50 minutes in 10% KOH at 100°C, rinsed them in water, acidified them for 15 minutes in 0.1 N HCl, stained them for 15 minutes in 0.05% trypan blue in lactic acid at 100°C, and rinsed and preserved them in lactic acid (modified of Phillips & Hayman, 1970). Stained roots were inspected at 200 x magnification in samples of 30 1-cm sections. The presence/absence of VAM structures was recorded.

Characterization of the biotic and abiotic environment

In each site we mapped all trees with diameter at breast height (dbh) > 2 cm using a total station Leica TC 407. We measured dbh for trees and crown projection for shrubs (1341 trees and 3005 shrubs mapped). We then identified all live and dead trees and shrubs to species level, and we divided *Q. suber* trees into three different health categories (healthy, defoliated, and dead trees) following a scale widely used in the region to monitor oak decline (García *et al.*, 2011). Local neighborhoods in each of the 49 plots were quantified using a neighborhood index (NI_j) calculated as the sum of the size (basal area for trees and crown projection for shrubs) of individual trees and shrubs (neighbor *i*) included in a 15 and 5 m radius circle, respectively, around plot *j*, divided by the distance of each neighbor *i* to the center of the plot *j*:

$$NI_j = \sum_{i}^{n} \frac{size_{ij}}{distance_{ij}}$$

NI values were separately calculated for five categories of neighbors: healthy *Q. suber* trees, defoliated *Q. suber* trees, dead *Q. suber* trees, the main tree species coexisting with *Q. suber* (i.e. *O. europaea* or *Q. canariensis* depending on the forest type), and shrubs.

For each of the 294 sampling plots, we took measurements of soil nutrients, soil texture, soil moisture, and light availability (Table S1). A first set of superficial soil samples (0-10 cm) was collected in spring 2010 from each plot with a cylindrical auger. Soil samples were air dried at 30°C in a forced air oven and sieved (mesh width: 2 mm). Soil total C and N were estimated using an Autoanalyzer LECO. Available P in HCl-NH_4F extracts was measured using the Bray Kurtz method (Bray & Kurtz, 1945). Available Ca and K were extracted using neutral 1 M ammonium acetate and were then assessed using atomic absorption spectroscopy. Particle size analysis was undertaken using the Bouyoucos hydrometer method (Gee *et al.*, 1986). Total sand (i.e. fine + coarse sand, 0.05-2 mm) was used as a representative measurement of soil texture. A second set of soil samples (0-10 cm) was collected from each plot in spring 2010 and 2011 to determine soil gravimetric water content on dry-weight basis after drying the soil during 24h at 105ºC. We chose to carry out those measurements in the first 10 cm of soil because the fine roots of seedlings used for mycorrhiza estimation were located at this depth. Light availability at the seedling level was estimated by means of hemispherical photographs taken in the center of each plot at 20 cm height, using a horizontally leveled digital camera with fish-eye lens of 180° field of view (Quilchano *et al.*, 2008). We estimated the global site factor (GSF) as an index of light availability by analyzing the digital images with Hemiview software (Hemiview Canopy Analysis; Delta-T Devices Ltd., 1999, v.2.1). The set of abiotic variables measured was poorly correlated among them, but for soil total C and N, which showed a very high correlation (r > 0.85, Table S2). Therefore, soil C was not included in the models to avoid problems of collinearity and parameter instability.

Data analysis

We developed an integrated model compound by two submodels for the analysis of our data. First, we fitted a submodel to estimate mycorhizal colonization (endo and ecto) in seedlings as a function of two sets of biotic and abiotic variables. Biotic variables included the abundance and spatial distribution of each of the five neighbor categories quantified using the Neighborhood Index, whereas abiotic variables included soil nutrients, soil texture, soil moisture, and light. The first set of biotic variables was intended to capture the direct effects of the different neighbor categories on the spatial distribution of mycorrhizal fungi, whereas the second set of abiotic variables would capture the non-direct effects of woody neighbors on mycorrhiza. These non-direct effects include indirect effects of tree canopies on the environment (e.g. soil modification, shading) as well as other uncontrolled sources of abiotic variability (e.g. substrate differences, herbaceous vegetation).

Second, we fitted a submodel that quantified the effect that mycorrhizal colonization and abiotic factors had on seedling survival. Seed weight and initial seedling height for each cohort were also included in the survival submodel as covariables to control for their broadly recognized effects on seedling performance in stressful environments (e.g. Lloret *et al.*, 1999; Pérez-Ramos *et al.*, 2010; Pérez-Ramos *et al.*, 2012). Models were run separately for each tree species (i.e. *Q. suber* and *Q. canariensis*), mycorrhizal type (i.e. endo and ectomycorrhiza), and forest type (i.e. woodland and closed forest). We analyzed seedlings from the first and second cohort together, since preliminary analyses showed that seedlings from both cohorts had similar responses to the different factors considered (results not shown for simplicity).

First submodel: Mycorrhizal fungal colonization

The presence/absence of arbuscular-mycorrhizal infection, VAM_j in plot(j), was estimated from a Bernoulli likelihood with probability π and process model:

$$\pi_j = \Phi\,(\mu 1_{\text{Site(j)}} + \mu 2{*}NI_{\textit{Q. suber}\text{ healthy(j)}} + \mu 3{*}NI_{\textit{Q. suber}\text{ defoliated(j)}} + \mu 4{*}NI_{\textit{Q. suber}\text{ dead(j)}} + \mu 5{*}NI_{\text{heterospecific(j)}} + \mu 6{*}NI_{\text{Shrub(j)}} + \mu 7{*}N_{(j)} + \mu 8{*}P_{(j)} + \mu 9{*}Ca_{(j)} + \mu 10{*}K_{(j)} + \mu 11{*}\text{soil texture}_{(j)} + \mu 12{*}\text{soil moisture}_{(j)} + \mu 13{*}GSF_{(j)} + \varepsilon)$$

Φ is the normal cumulative distribution function, that is, a normal distribution for the latent errors ε with mean 0 and standard deviation 1 (Gelman & Hill, 2007). We included random effects for each site, μ_{Site}, with mean and variance μ_m~*Normal*(0,10000) and $1/\sigma_\mu^2$~ *Gamma*(0.01,0.01). The fixed effects associated with soil and neighborhood variables were estimated as μ~*Normal*(0,10000).

The percent of ECM colonization , ECM_j in plot(j), was estimated from a Poisson likelihood with mean ψ and process model:

$$\log(\psi_j) = \alpha 1_{Site(j)} + \alpha 2{*}NI_{\textit{Q. suber}\ healthy(j)} + \alpha 3{*}NI_{\textit{Q. suber}\ defoliated(j)} + \alpha 4{*}NI_{\textit{Q. suber}\ dead(j)} + \alpha 5{*}NI_{heterospecific(j)} + \alpha 6{*}NI_{Shrub(j)} + \alpha 7{*}N_{(j)} + \alpha 8{*}P_{(j)} + \alpha 9{*}Ca_{(j)} + \alpha 10{*}K_{(j)} + \alpha 11{*}\text{soils texture}_{(j)} + \alpha 12{*}\text{soil moisture}_{(j)} + \alpha 13{*}GSF_{(j)}$$

We included random effects for each site, α_{Site}~*Normal*(α_m, σ_α^2) with α_m ~*Normal*(0,10000) and 1/ σ_α^2 ~ *Gamma*(0.01,0.01). The fixed effects associated with neighborhood and soil variables were estimated as α~*Normal*(0,10000).

Because mycorrhizal colonization (both endo and ecto) was only measured in the first seedling cohort, these variables were considered as latent variables for the second cohort and were estimated as part of the model. We estimated plot level predicted percentage of mycorrhizal colonization for each plot and year by using parameter values from the mycorrhizae models and the biotic and abiotic conditions in each plot. In the model, both cohorts shared the same woody neighbors, soil nutrients, soil texture, and light environment, since these predictor variables are unlike to change substantially among two consecutive years. However, the two cohorts differed in the spring soil moisture data, which was measured in both years in order to capture its strong inter-annual variability in these systems.

Second submodel: Seedling survival

Survival of seedling *i* after the first summer in the field was analyzed at the seedling level using Bernoulli likelihood with probability Þ and process model:

$$\text{logit}(Þ_i) = \beta 1_{Site(i)} + \beta 2{*}\text{height}_i + \beta 3{*}\text{weight}_i + \beta 4{*}N_{plot(j)i} + \beta 5{*}P_{plot(j)i} + \beta 6{*}Ca_{plot(j)i} + \beta 7{*}K_{plot(j)i} + \beta 8{*}\text{soil moisture}_{plot(j)i} + \beta 9{*}GSF_{plot(j)i} + \beta 10{*}VAM_{plot(j)i} + \beta 11{*}ECM_{plot(j)i}$$

We included random effects for each site, β_{Site}~*Normal*(β_m, σ_β^2) with β_m~*Normal*(0,10000) and 1/σ_β^2~ *Gamma*(0.01,0.01). The fixed effects associated with seed weight, seedling height, soil nutrients, soil moisture, light, and mycorrhizal colonization were estimated as β~*Normal*(0,10000). Because the effect of mycorrhizal colonization on plants can vary strongly depending on the environmental conditions (Zhou & Sharik, 1997; Smith *et al.*, 2010; Smith & Read, 2010), we first run the model including the interactions among VAM $_{plot(j)i}$ and ECM $_{plot(j)i}$ and the different abiotic variables. However, since none of the interactions was significant, they were excluded from the final model for simplicity.

Parameter estimation

We followed a Bayesian approach to estimate the parameters and random effects. Parameters were estimated from non-informative prior distributions. Models were run until convergence of the parameter was reached (~200000 iterations). Two chains were monitored for convergence, and parameters and their confidence intervals were estimated after the burn-in period was discarded (~20000). To evaluate the fit of the model for ECM colonization, plots of predicted versus observed values were used (unbiased model having a slope of unity) and the R^2 was used as a measure of goodness-of-fit. Submodels using Bernoulli distributions (i.e. VAM colonization and survival) were validated using the area under the receiver operated characteristics (ROC) curve, with ROC > 0.7 considered as acceptable fits (Hosmer & Lemeshow, 2000). Fixed effects coefficients whose 95% credible intervals did not include zero were considered statistically significant. To improve model runs and to be able to make direct comparisons among parameter values, previous to the analysis, we standardized each variable by subtracting the mean and dividing by the standard deviation.

RESULTS

Mycorrhizal fungal colonization

The two *Quercus* species were colonized by both VAM and ECM types. Nevertheless, the number of roots infected by VAM was only relevant in seedlings growing in woodland sites, so this mycorrhizal type was not considered for statistical analyses in the closed forest sites. All of the models produced unbiased estimates of mycorrhizal colonization (i.e. ROC for VAM colonization > 0.7, slopes of predicted vs. observed for ECM colonization ~1.0, Table S3). In woodland sites, the probability of VAM colonization was negatively affected by the presence of dead *Q. suber* trees in the neighborhood (Table S3, Fig. 1). VAM colonization did not respond to any of the abiotic factors considered.

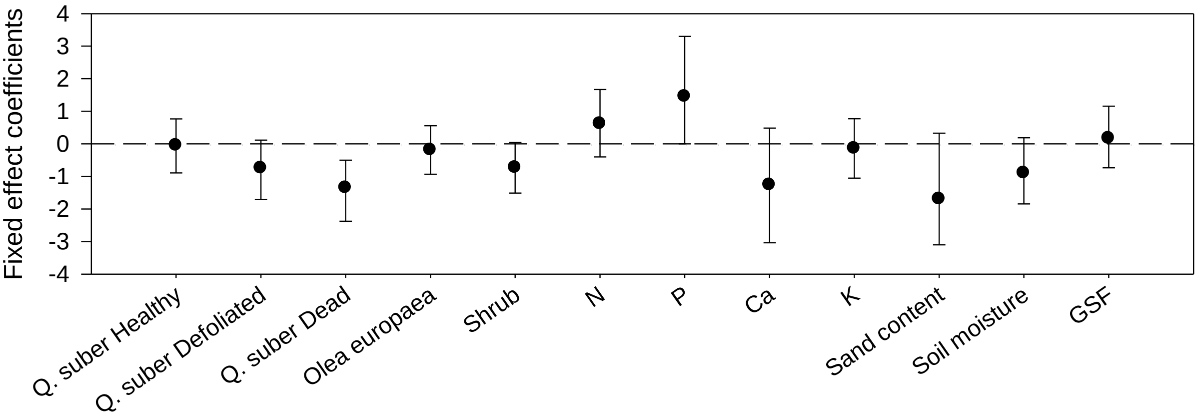

Figure 1 Fixed effects coefficients of μ parameters of the biotic and abiotic variables included in VAM analysis. Results for *Q. suber* seedlings in the woodlands. Coefficients that do not include zero in their credible intervals are considered statistically significant.

At both forest types, the percent of ECM infection of seedling root tips was influenced by the identity and health status of canopy trees (described by parameters α_{2-5}, Table S3). However, the sign of the influence differed among forest types (Fig. 2). In the woodland sites, ECM colonization was higher in neighborhoods dominated by defoliated and dead *Q. suber* trees than in healthy neighborhoods (particularly in those dominated by *Olea* trees) (Table 1, Fig. 2a). In closed forests, on the contrary, the highest ECM colonization for the two seedling species was found in *Q. canariensis* neighborhoods, followed by healthy *Q. suber* neighborhoods, whereas the lowest colonization rates occurred in neighborhoods of dead *Q. suber* trees (Table 1, Fig. 2b,c). The shrub community only had a (positive) effect on ECM colonization at woodland sites (Fig. 2a, b, c). ECM colonization was also affected by all the abiotic factors considered. At both forest types and for both seedling species, ECM colonization was positively affected by Ca and negatively by P. ECM colonization was also affected by soil K and N but in a less consistent pattern (i.e. only *Q. suber* seedlings in closed forests for K, only *Q. suber* seedlings in woodlands for N). Spring soil moisture and light availability had consistent effects (positive and negative, respectively) on mycorrhizal colonization, although they were generally of lower magnitude than that of soil nutrients (Fig. 2, Table S3). Soil texture (measured in term of sand content) was the only abiotic variable that had contrasting effects on mycorrhizal colonization among forest types. Thus, a higher sand percentage had a strong positive effect on ECM colonization in woodland sites but a neutral or negative effect in closed forest sites (Fig. 2, Table S3).

Table 1 Percentage of root seedling colonization by ECM in neighborhoods dominated by healthy, defoliated and dead *Q. suber* trees, and the coexistent species (*O. europaea* and *Q. canariensis* depending on the forest type). Percentages calculated using the parameters of the models (Table S3) for the maximum neighborhood index (NI=1) in each category. It shows the predicted mean for the three sites.

	Quercus suber			
	Healthy	Defoliated	Dead	*O. europaea/ Q. canariensis*
Woodlands				
Q. suber seedlings	17.6	24.8	25.0	15.18
Closed Forest				
Q. suber seedlings	38.1	32.8	27.7	55.70
Q. canariensis seedlings	30.4	32.9	21.6	36.72

Seedling survival

All models produced unbiased estimates of seedling survival (i.e. ROC > 0.7, Table S4). In woodland sites, VAM colonization decreased *Q. suber* seedling survival (β_{10} = -3.44), whereas ECM colonization had neutral effects (Fig. 3, Table S4). In closed forest sites, ECM associations had negative effects on survival of both seedling species, although these effects were of small magnitude ($0 > \beta_{11} > -0.12$, Table S4). Seedling survival was also influenced by the abiotic environment in closed forests, but not in woodlands. Survival of *Q. suber* in closed forests was strongly influenced by base cations, mainly Ca (β_6 = 1.37, Table S4), whereas the most important abiotic factor driving *Q. canariensis* survival was light availability (β_9 = -2.17, Table S4). Both species were also negatively affected by soil P content, whereas N did not affect survival in any case. Seedling survival was in all cases positively affected by the intrinsic factors seed weight and/or seedling height. In closed forests, however, the magnitude of their effect was generally lower than that of the abiotic environment (lower β values in Table S4).

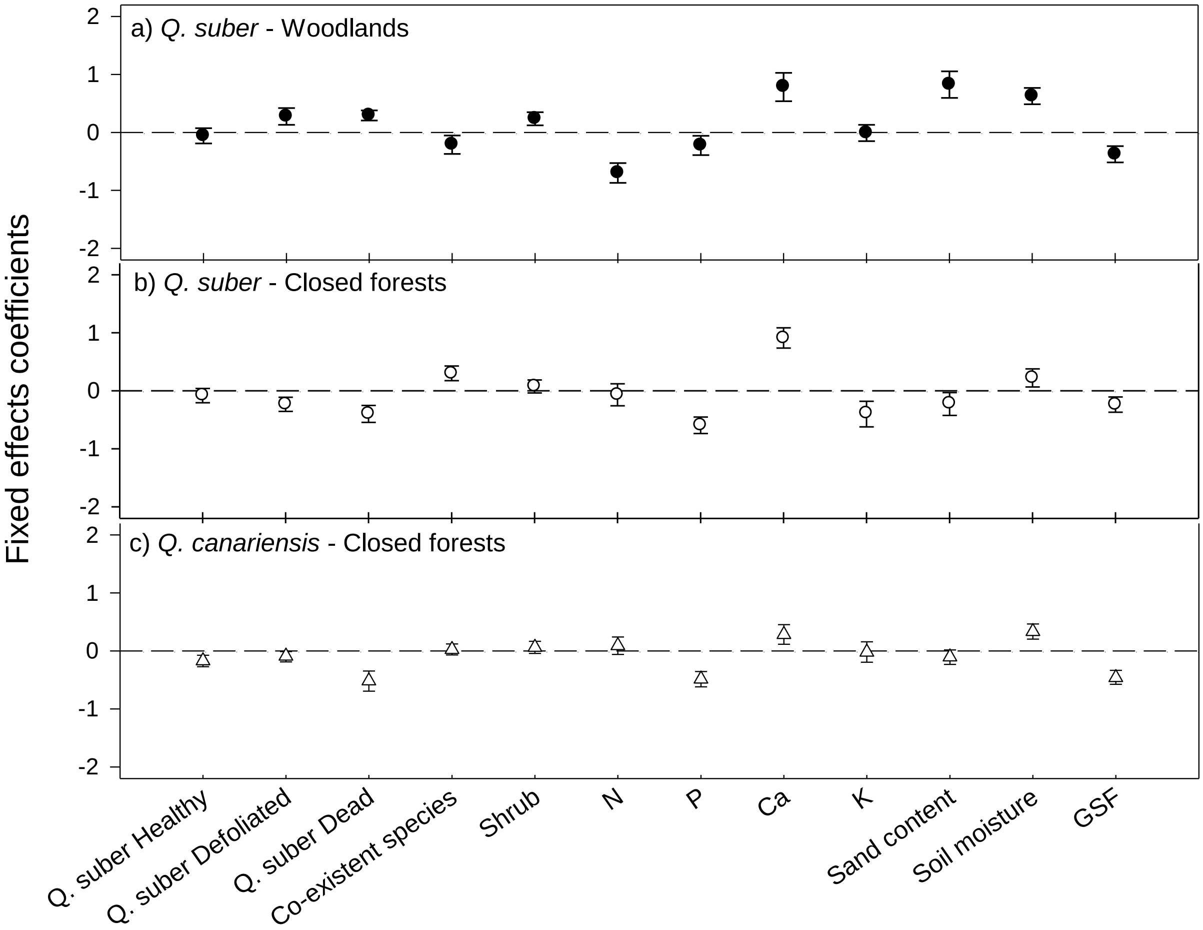

Figure 2 Fixed effects coefficients of α parameters of the biotic and abiotic variables included in ECM analysis. Panel *a* shows the results for *Q. suber* seedlings in the woodlands, panel *b* for *Q. suber* seedlings in the closed forests and panel *c Q. canariensis* seedlings. Coefficients that do not include zero in their credible intervals are considered statistically significant.

DISCUSSION

We found that the spatial pattern of the seedling-mycorrhiza association in Mediterranean mixed forests greatly responded to the spatial distribution of both biotic (i.e. tree identity and health condition, shrub abundance) and abiotic (i.e. soil resources, texture and light) factors. The spatial distribution of mycorrhiza abundance did in turn influence spatial patterns of seedling survival. Altogether, these results suggest that the process of *Q. suber* decline in Mediterranean forests implies a modification of the mycorrhiza landscape with implications for recruitment dynamics.

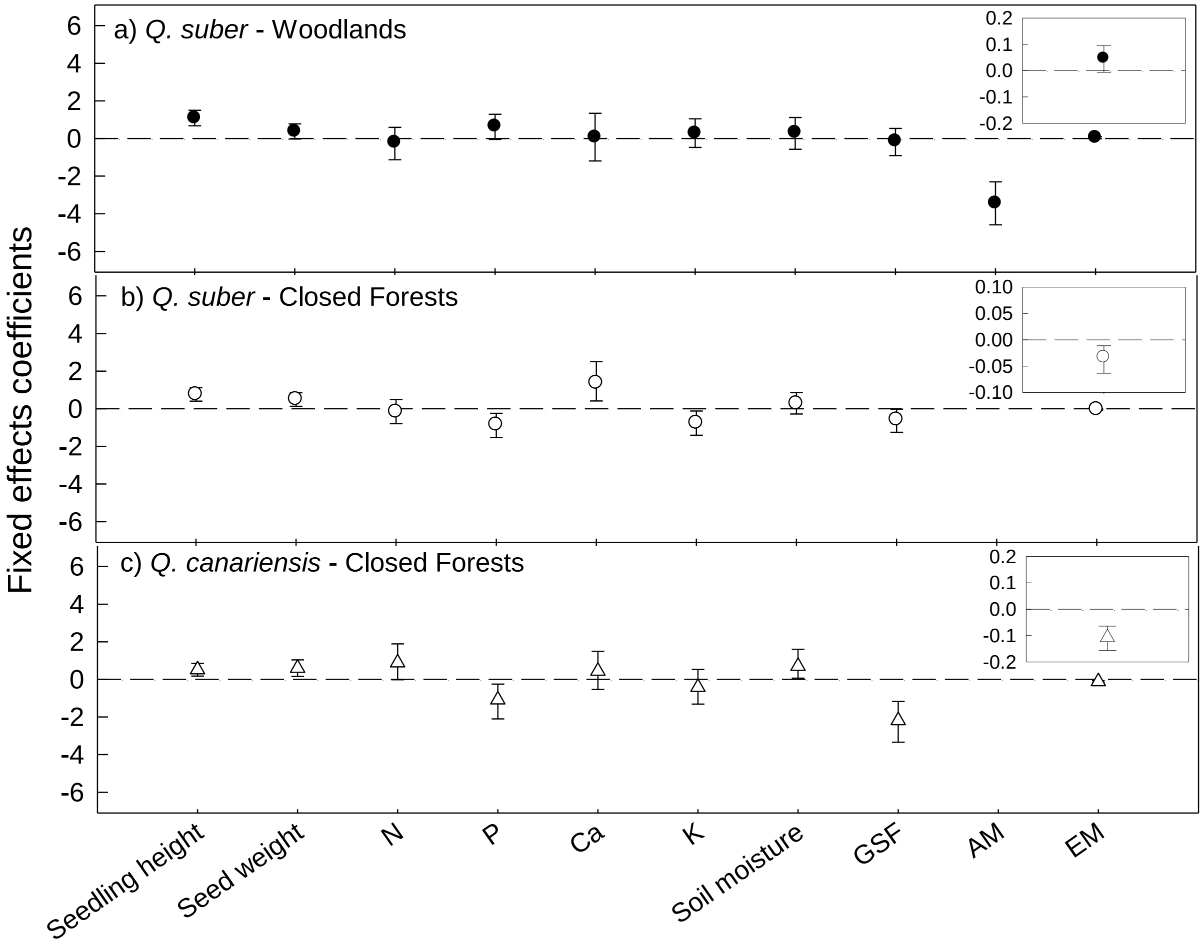

Figure 3 Fixed effects coefficients of β parameters of the biotic and abiotic variables included in the survival analysis. Panel *a* shows the results for *Q. suber* seedlings in the woodlands, panel *b* for *Q. suber* seedlings in the closed forests and panel *c Q. canariensis* seedlings. Coefficients that do not include zero in their credible intervals are considered statistically significant. Up-right in each panel, re-scaled, it is shown with more detail the effect of ectomycorrhiza in seedling survival.

The role of canopy composition and health status as direct drivers of seedling mycorrhizal colonization

It is widely accepted that mycorrhizal abundance and function depends on both the biotic (e.g. host plants) and abiotic context (Johnson *et al.*, 1997; Wolfe *et al.*, 2009; Hoeksema *et al.*, 2010). By including both types of variables in our models we demonstrated that the identity and health status of neighboring trees were major drivers of seedling mycorrhizal colonization in mixed Mediterranean forests, even after controlling for variation in the abiotic environment. The best example of the importance of the composition of the adult community as determinant of mycorrhizal infection is the fact that seedlings of a typically ECM oak species (*Q. suber*) established abundant and functionally relevant associations with VAM fungi in woodland sites, where the relative abundance of VAM adult trees and shrubs was high (e.g. *O. europaea*, *Pistacia lentiscus*), but not in closed forest sites with low relative abundance of VAM species. These results confirm the capacity of oak seedlings to associate with VAM in addition to ECM during early life stages (e.g. Egerton-Warburton & Allen, 2001), which is especially enhanced when the oaks co-exist with typically VAM species (e.g. Dickie *et al.*, 2001).

A main result of our study is that the spatial variability found in the mycorrhizal-seedling association was partially linked to the process of *Q. suber* decline. Interestingly, the influence of tree health status shaping mycorrhizal colonization varied among mycorrhiza and forest types. In woodland sites, seedlings in neighborhoods dominated by healthy *Q. suber* trees had higher VAM colonization but lower ECM colonization than seedlings in neighborhoods dominated by defoliated and dead trees (Table 1). This indicates that tree decline can have effects of contrasting sign on seedling colonization by different mycorrhizal types within the same sites. Among forest types, the effect of tree decline on ECM colonization was positive in woodlands but negative in closed forests (Table 1). We hypothesized that this result could be related to among-site differences in ECM colonization levels. It has been suggested that the positive effect of ECM colonization on seedling performance does not necessarily follow a linear relationship, but that it reaches an asymptote at low colonization levels (e.g. at 20% of root tips infected, Dickie *et al.*, 2002) or it is just a function of the presence/absence of the association (Karst *et al.*, 2008). We found that in woodland sites an important fraction of *Q. suber* seedlings did not show any ECM colonization (25% of the seedlings) or had low colonization values (37% of the seedlings had <20% of root tips infected). Therefore, in these sites a higher seedling investment in ECM associations in response to tree decline could be justified in terms of an expected gain in performance, particularly taking into account that seedlings established in defoliated and dead neighborhoods are severely impaired due to high soil-borne pathogen loads (Gómez-Aparicio *et al.*, 2012) and stressful microclimatic conditions (Ibáñez *et al.*, *submitted*). This result also agrees with the "intermediate host-plant stress hypothesis" (Swaty *et al.*, 2004), which postulates that stress can promote the establishment of mycorrhizal associations, at least until a certain threshold at which hosts can no longer support the C costs of the association. In close forests, on the contrary, all *Q. suber* seedlings were colonized by mycorrhizae and infection levels were generally much higher than in woodlands (35% vs. 19%). Under this more benign situation, an investment in higher mycorrhizae colonization might not be justified in terms of increased performance, so the lowest colonization found in the vicinity of defoliated and dead trees compared to healthy trees could be just a reflection of lower levels of ECM fungal inoculum in these soils (Swaty *et al.*, 2004). Overall, and despite site-specific particularities, our results highlight that the distribution of healthy and declining trees within a community could largely influence forest function through shaping plant-microbe interactions.

The role of the abiotic environment as a driver of seedling mycorrhizal colonization

One of the most widely tested hypotheses within the field of mycorrhizal ecology is that plant allocation of carbohydrates to mycorrhizal associations is strongly dependent on resource availability (Treseder, 2004; Hoeksema *et al.*, 2010; Smith & Read, 2010). Our results clearly supported this notion for ECM, but not for VAM. Whereas ECM colonization of seedling roots in woodland and closed forest sites was influenced by virtually all of the abiotic variables measured, the probability of VAM colonization in woodland sites was not influenced by any abiotic factor. This result could reflect differential sensibility of the two types of mycorrhizal associations to resource variability, with VAM colonization being mainly determined by direct effects of the biotic community.

The extent of seedling ECM infection was largely driven by soil nutrient availability at both forest types. Because mycorrhizal fungi contribute to nutrient uptake, it is generally assumed that plant mycorrhizal colonization is higher at low values of P and N (Smith & Read, 2010). Accordingly, we found seedling ECM colonization to be negatively influenced by soil P in the two oak species and forest types, whereas the negative effect of N availability was less consistent and detected only in woodlands. The consistency of P as a driver of mycorrhizal colonization in these forests could be due to the fact that P (instead of N) is the main limiting nutrient in Mediterranean forests and shrublands (Sardans *et al.*, 2004). Together with P, Ca was the soil nutrient with the largest impact on ECM colonization. Yet contrary to the other nutrients, its effect was strongly positive. Because our soils were fairly acidic (pH~4-6), and calcium levels are strongly correlated to soil pH in the study area (Aponte *et al.*, 2010), it is possible that the positive effect of soil Ca content on mycorrhizal infection were due to the known sensitivity of mycorrhizal fungi to soil pH. Thus, an increase in soil pH in acidic soils has been found to promote infection levels of different mycorrhizal fungi (Erland & Söderström, 1990; Bakker *et al.*, 2000) and to induce changes in the ECM community favoring ubiquist mycorrhizal species in detriment of more specific acidophilic ones (Aponte *et al.*, 2010; Rineau *et al.*, 2010).

Soil moisture and light did also consistently affect the extent of seedling ECM infection, although the magnitude of their effect was generally lower than that of nutrients. Mycorrhizal colonization increased with soil moisture, in agreement with previous studies showing how water limitation negatively affects colonization rates by constraining physiological performance of both symbionts (Dosskey *et al.*, 1991; Kennedy & Peay, 2007). Accordingly, the negative effect that sand content had on ECM infection in closed forest sites might be related to its negative effect on the low water-holding capacity of these sandy soils (Brady & Weil, 1996). In the clayish soils of woodland sites, however, our models detected a totally opposite effect of soil texture on ECM colonization, sand content promoting infection rates. This positive effect could be related to a lower compaction and higher aeration associated with increasing sand content, benefiting the development of ECM (Skinner & Bowen, 1974; Amaranthus *et al.*, 1996). Finally, whereas light has been shown to have a general positive effect on ECM colonization in cool temperate forests (Slankis, 1971; Smith & Read, 2010) we found the opposite pattern. This could be because in water-limited Mediterranean forests, where light often constitutes a stress factor more than a limiting resource, high light can lead to photoinhibition and reduced carbon assimilation (Valladares, 2004; Gómez-Aparicio *et al.*, 2006), limiting plant C investment in mycorrhizal associations.

Gradients of resource availability in the forest understory can be driven by different abiotic and biotic factors, such as topography, parent material or the own plant community (van Breemen *et al.*, 1997; García *et al.*, 2006; Gómez-Aparicio & Canham, 2008). Our modelling approach did not allow us to partition the variance found in the abiotic environment among the different potential drivers. However, recent studies in these forests suggest that adult trees of different species and health status are responsible to a large extent of this variability. For example, Aponte *et al.* (2013) found topsoil (0-25 cm) carbon and nutrient concentration and pH to be lower under *Q. suber* than under *Q. canariensis* trees. Because chemical and textural characteristics of the subsoil (25–50 cm, a proxy of the original soil conditions) did not differ among the two species but leaf and litter chemistry did, they concluded the existence of litter-mediated tree species effects on soil properties. Additionally, soil respiration rates and P availability have been found to be lower under declining *Q. suber* trees than under healthy adults (Ávila *et al*., unpublished). Based on this evidence, we propose that the process of *Q. suber* decline could not only directly affect the frequency and intensity of seedling-mycorrhizal interactions, but also play an important indirect role through the modification of the abiotic environment.

Relative importance of mycorrhizal associations and abiotic factors as determinants of seedling survival

Our models indicated that the spatial patterns of seedling mycorrhizal infection can influence seedling recruitment patterns. Surprisingly, we found a much stronger effect of VAM colonization than of ECM colonization on seedling survival, even though oaks are typical ECM species. In fact, VAM colonization was the most important factor driving patterns of *Q. suber* survival in woodland sites (i.e. largest β parameter value; Table S4). Moreover, the impact of both VAM and ECM colonization on seedling survival was negative, an unexpected result based on the general assumption that mycorrhizae favor forest regeneration (Amaranthus & Perry, 1987; Perry *et al.*, 1989; Dickie *et al.*, 2002), and more specifically on the works that have shown increased seedling performance due to ECM colonization in stressful Mediterranean-type ecosystems (Parke *et al.*, 1983; Querejeta *et al.*, 1998; Horton *et al.*, 1999; Sebastiana *et al.*, 2013). We are however unaware of any other studies that have evaluated the role of VAM infection for oak seedling performance under natural conditions in Mediterranean forests.

The strong negative VAM effect on survival of *Q. suber* seedlings could be explained by the fact that VAM fungi are rapid colonizers of the fine roots of recently established seedlings when inoculum is available in the soil (Chilvers *et al.*, 1987). This association could imply a high C demand, subsequently decreasing the C allocation to photosynthetic or defense structures that increase seedling survival probability (Johnson *et al.*, 1997). Moreover, colonization by both mycorrhizal types (endo and ecto) has been shown to imply a cost for oak seedlings (Egerton-Warburton & Allen, 2001), which could be particularly high in water-limited forests where drought imposes a severe constraint to C acquisition (Tenhunen *et al.*, 1990; Pereira *et al.*, 2007). Our findings therefore suggest that the possible short-term benefits from the symbiotic association might be overcome by the costs of allocating C to the developing fungi, negatively impacting survival of young seedlings. Seed reserves could also represent an additional factor buffering any potential benefit of mycorrhizal infection in the short-term, since it is well known that large-seeded oaks are strongly dependent on acorn reserves during the first year (Quero *et al.*, 2007; Pérez-Ramos *et al.*, 2010) and, accordingly, we found seed weight to be a much more important driver of survival than ECM infection. We could expect the role of mycorrhizal infection to increase with time, as seed reserves become exhausted and the benefits derived from the symbiosis outweigh the direct costs of establishing it (Johnson *et al.*, 1997).

Although ECM colonization significantly affected seedling survival of both oak species in closed forest sites, its effect was much lower than that of other abiotic and intrinsic (seed weight, seedling height) seedling factors (Table S4). Calcium and light availability were the abiotic factors with the largest effects on *Q. suber* and *Q. canariensis* survival, respectively. High calcium (and associated pH) levels have been related to increased photosynthetic rates and shade tolerance in seedlings (Kobe *et al.*, 1995; Kobe *et al.*, 2002), which could have contributed to favor survival of the shade semi-tolerant *Q. suber* in closed forests. On the other hand, the prominent role of light as a driver of *Q. canariensis* survival is explained by the fact that high light levels usually co-occur in open microhabitats with other unfavorable abiotic conditions that increase mortality risk, such as high waterlogging risk during the rainy season or high evapotranspiration demand during the dry summer (Gómez-Aparicio *et al.*, 2008; Urbieta *et al.*, 2008; Pérez-Ramos *et al.*, 2012). Not surprisingly, abiotic-driven facilitation by established "nurse" trees and shrubs have been consistently reported as a main process driving regeneration patterns in water-limited Mediterranean forests, particularly for late-successional shade-tolerant species such as *Q. canariensis* (Gómez-Aparicio, 2009). Altogether these results suggests that, at least during the first year of life of oak species, direct abiotic-driven facilitation by established vegetation might play a more important role that any indirect biotic effect through increased ECM infection (see also Richard *et al.*, 2009).

CONCLUSIONS

Our study allowed us to detect the degree to which the spatial patterns of the adult plant community can affect the distribution of seedling-mycorrhiza associations, providing new insights into the influence that a declining tree community could have on this important plant-microbe interaction, both directly and indirectly. The patterns found were far from simple, since the influence of tree health status shaping mycorrhizal colonization varied among mycorrhiza and forest types, showing how context-dependent the effects of tree decline can be on forest function. Yet, because the spatial distribution of seedling mycorrhizal infection responded to the identity and health status of the woody plant community, and mycorrhizal infection did in turn affect seedling performance, we suggest that tree decline might affect forest dynamics through plant-soil biota feedbacks. Our results however indicated that the magnitude of these effects could be relatively low, at least for 1-year old oak seedlings infected by ECM. Even more importantly, they showed that an investment in higher mycorrhization does not necessarily imply a gain in terms of increased performance in the short-term, but all the opposite. We hypothesize that it could do it in the long term, as saplings become older and have a higher resource demand not covered by seed reserves (Newton & Pigott, 1991; Egerton-Warburton & Allen, 2001). Further studies including later life-stages are needed in order to quantify the net effect that plant-mycorrhiza interactions might play on shaping the future structure and composition of changing declining forests.

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SUPPORTING INFORMATION

Table S1 Description of main characteristics of the six study sites located in the South (S), Center (C) and North (N) of the Alcornocales Natural Park. Values represent median [P10 – P90, 10th and 90th percentiles] for the 49 sampled neighborhoods at each site. Neighborhoods are circles of 15-m (for trees) and 5-m (for shrubs) radius around each sample point. Shrub crown area is given for the most common species across the six study sites.

	Woodlands			Closed forests		
	South Site	Center Site	North Site	South Site	Center Site	North Site
Latitude (N)	36º 04′ 38″	36º 04′ 38″	36º 31′ 69″	36º 06′ 09″	36º 23′ 10″	36º 28′ 13″
Longitude (W)	05º 33′ 05″	05º 33′ 05″	05º 38′ 08″	05º 30′ 53″	05º 31′ 52″	05º 35′ 31″
Annual rainfall (mm)	948.9	726.4	973.1	1067.1	1022.6	1097.0
Mean annual T (ºC)	16.3	16.9	16.3	15.4	17.3	15.9
Abiotic variables						
N (mm/g)	4.20	3.20	4.45	2.30	2.01	2.05
	[3.40,5.80]	[2.70-3.97]	[3.57-5.85]	[1.92,2.90]	[1.51,2.90]	[1.50,2.80]
C (mm/g)	69.90	46.90	70.00	45.15	39.54	36.75
	[51.90,88.60]	[36.36-55.33]	[51.33,87.88]	[35.17,55.70]	[31.34-58.57]	[26.32-53.42]
P (mm/Kg)	4.80	16.10	2.90	7.50	5.05	7.62
	[3.45-5.90]	[13.38-32.84]	[2.02-4.56]	[6.40-9.81]	[4.05-7.70]	[4.10-10.24]
Ca (mm/Kg)	3330	1315.3	5185	684.3	850.0	915.0
	[2690-3870]	[889.1-1954.1]	[3312-7119]	[467.4-865.4]	[607.0-1296.0]	[615.0-1135.0]
K (mm/Kg)	244.0	214.8	287.5	117.6	141.0	183.0
	[197.0-308.0]	[186.8-245.2]	[225.8-366.0]	[81.77-146.18]	[117.0-183.0]	[137.5-221.2]
Clay content (%)	29.62	15.17	29.62	12.84	12.59	9.19
	[25.01-35.57]	[11.76-18.21]	[22.99-41.97]	[10.03-16.71]	[10.01-15.59]	[7.72-11.73]
Sand content (%)	50.00	68.42	51.55	73.59	70.88	75.53
	[38.79,54.46]	[63.50-74.84]	[38.25-59.37]	[69.84-78.36]	[62.84-73.85]	[72.14-79.12]
Soil moisture (%)	40.58	26.32	40.37	28.00	18.77	23.00
	[34.72-49.00]	[18.79-32.55]	[32.56-49.35]	[19.79-34.91]	[13.79-15.59]	[19.64-29.22]
GSF	0.43	0.40	0.27	0.23	0.25	0.21
	[0.33,0.57]	[0.27-0.54]	[0.20-0.38]	[0.15-0.25]	[0.19-0.34]	[0.16-0.24]
Tree basal area (m^2/ha)						
O. europaea/*Q. canariensis*	5.20	4.18	2.57	15.55	5.45	14.81
	[2.72-7.49]	[2.37-11.59]	[1.26-5.09]	[7.93-24.01]	[0-13.39]	[10.22-22.06]
Q. suber $_{\text{Healthy}}$	2.43	19.02	10.26	5.45	5.61	9.56
	[0-5.56]	[10.82-26.65]	[6.07-15.52]	[1.50-12.48]	[2.47-6.19]	[3.52-17.52]
Q. suber$_{\text{Defoliated}}$	5.33	3.91	19.44	7.18	7.61	0.26
	[2.47-8.04]	[1.48-7.28]	[12.68-28.7]	[4.72-9.00]	[2.18-10.47]	[0-3.52]
Q. suber $_{\text{Dead}}$	2.14	0.00	0.89	5.52	0.00	0.44
	[0-7.09]	[0-1.00]	[0-1.79]	[3.22-7.64]	[0-3.52]	[0-0.93]
Shrub crown area (m^2/ha)						
Pistacia lentiscus	198.6	1276.0	1975.0	------	0.00	------
	[0.00-599.7]	[0.00-2977.0]	[1442.0-3106.0]		[0-0.00]	
Erica spp.	0.00	0.00	------	648.1	3358.0	0.00
	[0-0.00]	[0-0.00]		[151.2-2472.0]	[2116.0-7810.0]	[0-126.4]
Phillyrea latifolia	0.00	0.00	112.7	0.00	0.00	112.7
	[0-0.00]	[0-0.00]	[0-1638.0]	[0-0.00]	[0-0.00]	[0-1638.0]
Crataegus monogyna	449.5	0.00	1013.0	------	0.00	0.00
	[150.2-714.3]	[0-0.00]	[611.2-1458.0]		[0-0.00]	[0-0.00]
Mycorrhizal colonization						
ECM (%) *Q. suber*	6.00	21.50	17.00	38.00	21.00	40.00
	[3.00,29.00]	[0.00,36.50]	[7.00,33.00]	[24.75,61.25]	[6.50,39.00]	[37.5,42.50]
ECM (%) *Q. canariensis*	-	-	-	35.50	16.50	40.00
				[25.25,56.25]	[10.00,21.00]	[35.00,45.00]
VAM (% of mycorrhized seedlings)	54.17	69.56	47.62	-	-	-

Table S2 Correlation between the abiotic variables in the two forest types.

Forest type		N	C	P	Ca	K	Sand	Soil moisture	GSF
Woodlands	N	1.00							
	C	0.97	1.00						
	P	-0.08	-0.10	1.00					
	Ca	0.60	0.61	-0.43	1.00				
	K	0.46	0.49	-0.16	0.62	1.00			
	Sand	-0.53	-0.52	-0.52	-0.72	-0.51	1.00		
	Soil moisture	0.47	0.50	-0.41	0.56	0.40	-0.54	1.00	
	GSF	-027	-0.29	-0.01	-0.25	-0.27	0.10	-0.16	1.00
Closed Forests	N	1.00							
	C	0.85	1.00						
	P	0.39	0.36	1.00					
	Ca	0.39	0.26	0.34	1.00				
	K	0.36	0.27	0.28	0.49	1.00			
	Sand	-0.49	-0.46	0.02	-0.31	-0.34	1.00		
	Soil moisture	0.45	0.50	0.09	0.07	0.04	-0.28	1.00	
	GSF	-0.05	0.00	-0.14	-0.14	-0.02	-0.01	-0.18	1.00

Table S3 Results of parameter estimates, posterior means ±SD (95%credible intervals), for the two models assessing the effects of canopy cover and abiotic factors on mycorrhizal colonization. Fixed effects with statistically significant estimates (95% CI does not include zero) are in bold. ROC is the area under the receiver operated characteristics for the VAM analysis. R^2: the fit of predicted vs. observed for the ECM models. Slope: slope of predicted vs. observed.

Parameters	*Q. suber*	*Q. suber*	*Q. canariensis*
	Woodland	Closed Forest	Closed Forest
Endomycorrhiza-VAM			
ROC	0.70	-	-
p-value	0.004	-	-
Sites random-effects			
μ1 -Site1	0.43±0.42(-0.52,1.71)	-	-
Site2	**1.00±0.59(0.13,2.47)**	-	-
Site3	0.47±0.42(-0.48,1.17)	-	-
σ_μ^2-random effects	0.67±1.35(0.08,2.85)	-	-
Fixed effects			
μ2 - *Q. suber* $_{\text{Healthy}}$	-0.05±0.42(-0.89,0.76)	-	-
μ3 - *Q. suber* $_{\text{Defoliated}}$	-0.75±0.46(-1.71,0.11)	-	-
μ4 - *Q. suber* $_{\text{Dead}}$	**-1.35±0.48(-2.37,-0.50)**	-	-
μ5 - *O. europaea*/*Q. canariensis*	-0.19±0.38(-0.93,0.56)	-	-
μ6 - shrubs	-0.73±0.39(-1.51,0.04)	-	-
μ7 - N	0.61±0.52(-0.40,1.67)	-	-
μ8 - P	1.45±0.84(-0.001,3.30)	-	-
μ9 - Ca	-1.27±0.89(-3.04,0.48)	-	-
μ10- K	-0.35±0.56(-1.55,0.68)	-	-
μ11- sand content	-0.14±0.47(-1.05,0.77)	-	-
μ12- soil moisture	-0.90±0.52(-1.84,0.18)	-	-
μ13- GSF	0.17±0.48(-0.73,1.16)		
Ectomycorrhiza-ECM			
R^2	0.19	0.60	0.50
Slope	1.00	1.00	0.98
Sites random-effects			
α1 -Site1	**2.49±0.08(2.33,2.44)**	**4.07±0.13(3.81,4.36)**	**3.73±0.11(3.50,3.93)**
Site2	**3.22±0.11(3.01,3.44)**	**3.89±0.05(3.78,4.00)**	**3.96±0.06(3.85,4.07)**
Site3	**3.08±0.08(2.93,3.23)**	**3.20±0.06(3.08,3.32)**	**3.06±0.06(2.94,3.18)**
σ_α^2 -random effects	0.63±0.72(0.20,2.21)	0.83±1.026(0.27,2.80)	0.78±1.13(0.22,2.73)
Fixed effects			
α2 - *Q. suber* $_{\text{Healthy}}$	-0.06±0.07(-0.19,0.07)	-0.08±0.06(-0.20,0.04)	**-0.17±0.05(-0.27,-0.07)**
α3 - *Q. suber* $_{\text{Defoliated}}$	**0.28±0.07(0.13,0.42)**	**-0.23±0.07(-0.35,-0.11)**	**-0.09±0.05(-0.19,-0.01)**
α4 - *Q. suber* $_{\text{Dead}}$	**0.29±0.04(0.20,0.38)**	**-0.40±0.07(-0.54,-0.25)**	**-0.51±0.09(-0.69,-0.35)**
α5 - *O. europaea*/*Q. canariensis*	**-0.21±0.08(-0.37,-0.05)**	**0.30±0.06(0.17,0.43)**	0.02±0.05(-0.07,0.12)
α6 - shrubs	**0.24±0.06(0.12,0.35)**	0.08±0.06(-0.04,0.19)	0.06±0.05(-0.04,0.16)
α7 - N	**-0.70±0.09(-0.87,-0.52)**	-0.07±0.10(-0.26,0.12)	-0.09±0.08(-0.06,0.24)
α8 - P	**-0.22±0.08(-0.39,-0.06)**	**-0.59±0.07(-0.74,-0.55)**	**-0.48±0.07(-0.62,-0.35)**
α9 - Ca	**0.79±0.12(0.54,1.02)**	**0.91±0.09(0.74,1.09)**	**0.28±0.09(0.11,0.45)**
α10- K	-0.01±0.07(-0.15,0.13)	**-0.39±0.11(-0.62,-0.18)**	-0.02±0.09(-0.19,0.16)
α11- sand content	**0.82±0.12(0.59,1.05)**	**-0.22±0.10(-0.42,-0.03)**	-0.10±0.06(-0.23,0.02)
α12- soil moisture	**0.63±0.07(0.48,0.77)**	**0.22±0.08(0.06,0.38)**	**0.33±0.07(0.20,0.46)**
α13- GSF	**-0.38±0.07(-0.52,-0.24)**	**-0.24±0.07(-0.37,-0.10)**	**-0.46±0.06(-0.55,-0.33)**

Table S4 Results of parameter estimates, posterior means ±SD (95%credible intervals), from the model assessing the effects of canopy cover and abiotic factors on seedling survival. Fixed effects with statistically significant estimates (95% CI does not include zero) are in bold. ROC is the area under the receiver operated characteristics.

Parameters	*Q. suber* Woodland	*Q. suber* Closed Forest	*Q. canariensis* Closed Forest
ROC	0.88	0.79	0.87
p-value	0.000	0.000	0.000
Sites random-effects			
β1 -Site1	-0.46±0.53(-1.53,0.52)	**1.60±0.77(0.22,3.11)**	**3.87±1.02(1.98,5.91)**
Site2	-4.29±1.11(-6.32,1.63)	**1.97±0.69(0.86,3.42)**	**4.61±1.05(2.73,6.79)**
Site3	-2.66±0.85(-4.22,0.77)	**2.34±0.49(1.51,3.41)**	**4.24±0.79(2.84,5.91)**
σ_{β}^{2} -random effects	3.44±3.88(0.004,20.16)	0.61±1.30(0.001,8.04)	0.39±0.48(0.07,1.59)
Fixed effects			
β2 - height	**1.08±0.21(0.68,1.49)**	**0.76±0.18(0.419,1.12)**	**0.51±0.17(0.18,0.85)**
β3 - weight	0.37±0.20(-0.02,0.78)	**0.49±0.18(0.13,0.85)**	**0.60±0.22(0.16,1.04)**
β4 - N	-0.21±0.43(-1.13,0.49)	-0.17±0.33(-0.79,0.49)	0.88±0.49(-0.02,1.88)
β5 - P	0.65±0.34(-0.05,1.28)	**-0.85±0.33(-1.54,-0.24)**	**-1.08±0.46(-2.10,-0.25)**
β6 - Ca	0.06±0.64(-1.19,1.34)	**1.37±0.53(0.42,2.51)**	0.44±0.52(-0.54,1.49)
β7 - K	0.28±0.38(-0.47,1.05)	**-0.75±0.33(-1.41,-0.12)**	0.41±0.47(-1.31,0.52)
β8 - soil moisture	0.31±0.43(-0.57,1.12)	0.28±0.29(-0.28,0.86)	**0.71±0.41(0.06,1,70)**
β9 - GSF	-0.14±0.367(-0.91,0.54)	**-0.58±0.31(-1.25,-0.02)**	**-2,17±0.55(-3.34,-1.17)**
β10- AM	**-3.44±0.59(-4.58,-2.30)**	-	-
β11- EM	0.05±0.04(-0.01,0.09)	**-0.03±0.01(-0.06,-0.01)**	**-0.11±0.02(-0.16,-0.06)**

DISCUSIÓN GENERAL

Capítulo 7. Discusión General

La mortalidad extensiva de árboles adultos ha sido detectada en bosques de todo el mundo durante las últimas décadas, y su frecuencia podría verse incrementada en los próximos años (Allen *et al.*, 2010). Esta situación de cambio hace un llamamiento a la realización de estudios enfocados en evaluar cómo estos eventos de mortalidad podrían afectar a la composición futura de los bosques; estudios que, a pesar de su importancia, aún son escasos (Anderegg *et al.*, 2012). Para arrojar luz sobre el impacto del decaimiento en sistemas forestales, con esta Tesis Doctoral se ha tratado de entender la dinámica de bosques de *Q. suber* afectados por decaimiento. Los resultados obtenidos contribuyen a mejorar el conocimiento sobre el impacto del decaimiento en la dinámica forestal, lo que resulta fundamental para adaptar la gestión de los sistemas forestales a las actuales condiciones de cambio.

DINÁMICA REGIONAL DEL BOSQUE

Respuesta de árboles adultos y del regenerado a los gradientes climáticos

El estudio de los bosques de alcornoque en Andalucía analizando datos del Segundo y Tercer Inventario Forestal Nacional permitió detectar respuestas diferenciales entre individuos adultos y el regenerado a las variables climáticas. Los resultados obtenidos confirman el papel del clima como el factor principal que determina el comportamiento de las especies vegetales (Woodward, 1987), cuya importancia es clara tanto en fases tempranas del desarrollo de la planta como en su fase adulta. En este caso, se encontró que para el alcornoque los efectos del clima pueden ser variables según la edad del individuo (Figura 1). Por ejemplo, con temperaturas más elevadas la supervivencia de árboles adultos fue menor mientras que el número de plántulas aumentó, lo que podría implicar que ante situaciones de estrés ambos grupos pueden responder de forma distinta entre sí, con importantes implicaciones en la dinámica de la población (e.g. Cavender-Bares y Bazzaz, 2000; He *et al.*, 2005; Niinemets, 2010). Así, ante un aumento de temperatura, las poblaciones de árboles adultos de alcornoque verían disminuidas sus tasas de supervivencia, mientras que el número de plántulas aumentaría, y será el balance neto de las respuestas en cada fase lo que determinará la capacidad de respuesta de la especie al incremento de temperaturas. En cualquier caso, a pesar de la respuesta positiva de las plántulas, la escasez de plántulas y brinzales encontrados pone de manifiesto el cuello de botella existente en estas fases de la regeneración de esta especie (Plieninger *et al.*, 2010; Urbieta *et al.*, 2011), limitado por la escasez de agua en verano y por elevada herbivoría (Gómez-Aparicio, 2008; Pausas *et al.*, 2009; Pulido *et al.*, 2013). Estas limitaciones en la regeneración del alcornoque hacen que esta especie se encuentre ya de por sí en una situación delicada, a lo que se suman los efectos negativos del cambio climático (e.g. Benito-Garzon *et al.*, 2008; Carnicer *et al.*, 2011), comprometiendo la continuidad de la estructura y composición que estos bosques presentan actualmente.

El papel modulador del suelo en los efectos del clima sobre la vegetación

Además de las diferencias entre fases de vida de la planta, los resultados obtenidos en el **capítulo 2** ponen de relieve la importancia de considerar las interacciones entre el clima y el suelo a la hora de determinar la influencia del clima en las dinámicas de poblaciones vegetales (Piedallu *et al.*, 2012), especialmente en sistemas con escasez de agua (Fernandez-Illescas *et al.*, 2001). Aunque en este tipo de sistemas *a priori* se podría intuir que una mayor precipitación beneficiaría a las plantas, los resultados obtenidos en este trabajo ponen de manifiesto que esto no es siempre así, y que puede depender de la textura del suelo (Figura 1). En suelos arenosos y aireados un aumento en la precipitación de invierno puede suponer un aumento en la cantidad de agua almacenada en profundidad (Brady y Weil, 1996), que estaría disponible durante la época de sequía estival resultando, por tanto, beneficiosa. Sin embargo, en suelos pesados con elevados porcentajes de arcilla, el riesgo de encharcamiento aumenta y con ello la posible asfixia de las raíces, resultando perjudicial para la supervivencia de los árboles (Gaertig *et al.*, 2002). Estos resultados muestran la susceptibilidad potencial del alcornoque a los cambios que se predicen en el régimen de precipitación en la región mediterránea, en la que se espera una reducción de la precipitación anual, acompañada de un aumento de la precipitación durante los meses de invierno (Brunet *et al.*, 2007; Planton, 2012). Para relacionar adecuadamente los cambios en la precipitación con los cambios en la disponibilidad de agua para las plantas, que es lo que condiciona su comportamiento, es imprescindible considerar la capacidad de retención de humedad del suelo, la cual depende en gran medida de su textura.

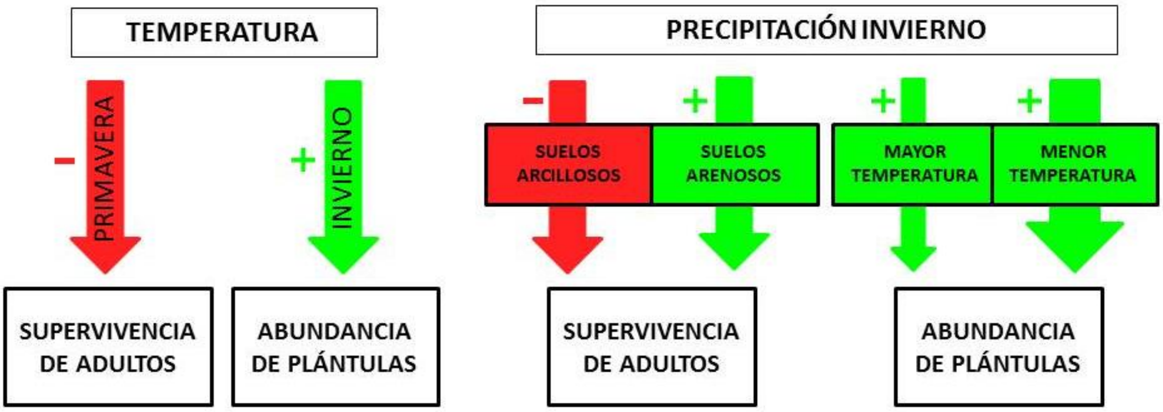

Figura 1. Síntesis de los efectos encontrados del clima (temperatura y precipitación) en la supervivencia de árboles adultos y la abundancia de plántulas de alcornoque. Flechas en rojo representan efectos negativos y en verde positivos. Diferencia en el ancho de la flecha dentro de la misma fase señala diferencias en la magnitud del efecto, mayor en la flecha de mayor tamaño. Destaca la diferencia entre estadios ontogenéticos de los efectos de la temperatura y los efectos de la precipitación, estos últimos influenciados a su vez por la textura del suelo (supervivencia de adultos) y por la temperatura (abundancia de plántulas).

Los resultados obtenidos en el **capítulo 2** sugieren, además, que en las dinámicas estudiadas de las dos fases de la vida del alcornoque la interacción entre el clima, la textura y los organismos patógenos del suelo podrían estar jugando un papel importante. Aunque en este capítulo no se estudia explícitamente la influencia de estos organismos en la supervivencia y la regeneración del alcornoque, a raíz de los resultados obtenidos se podría especular sobre su posible implicación en los procesos estudiados. Por ejemplo, el efecto negativo de la precipitación en la supervivencia de árboles adultos en suelos arcillosos podría estar también relacionado con que la mayor cantidad de agua retenida en estos suelos puede favorecer el desarrollo y acumulación de los organismos patógenos causantes de la podredumbre radical (e.g. Phytophthora cinnamomi, Sánchez *et al.*, 2005; ver capítulo 5), afectando negativamente a la supervivencia de los árboles. De forma similar, la respuesta encontrada en el caso de la regeneración, donde el efecto positivo de la precipitación se vio reducido en condiciones de mayor temperatura (Figura 1), podría estar relacionada con un efecto favorable del incremento de la temperatura sobre los oomicetos patógenos del suelo. Estos organismos se verían beneficiados en condiciones de mayor temperatura y humedad (Hendrix y Campbell, 1973; Sánchez *et al.*, 2002), llegando a afectar a las plántulas negativamente. Un análisis enfocado en las interacciones entre los organismos patógenos y el clima con las dinámicas de poblaciones del alcornoque, permitirán ahondar en la naturaleza de estas relaciones y predecir tendencias futuras.

DINÁMICA DEL BOSQUE A ESCALA RODAL

A escala local se han llevado a cabo distintos trabajos experimentales y observacionales. A través de estos estudios se evaluó cuál es el impacto del decaimiento en los procesos demográficos de las especies forestales y en las comunidades de organismos del suelo en los bosques mediterráneos estudiados. Estos trabajos, presentados en los capítulos 3 a 6 de esta Tesis, son pioneros en el uso de modelos de vecindad en bosques mediterráneos para el análisis del efecto de la vegetación establecida en las variables bióticas anteriormente indicadas. Y más concretamente, en su aplicación al análisis de los efectos del decaimiento en dinámicas forestales. El empleo de estos modelos ha permitido incorporar de forma espacialmente explícita las interacciones entre la dinámica de poblaciones de árboles, las tasas demográficas y las comunidades de organismos del suelo para detectar los cambios que pueden producirse a medida que se modifica la composición del dosel.

El papel de la vecindad en las dinámicas de regeneración del bosque

Para valorar la resiliencia de los bosques ante el cambio climático, es crucial conocer cuáles son los impactos que el decaimiento puede tener en las dinámicas de regeneración (Anderegg *et al.*, 2012). Hasta ahora, la mayor parte de los trabajos que han evaluado los efectos del decaimiento en el reclutamiento de plántulas han sido desarrollados en bosques templados (e.g. Suarez y Kitzberger, 2008; Axelson *et al.*, 2009; Collins *et al.*, 2011; Redmond y Barger, 2013), escasos en sistemas con limitación de agua (e.g. Galiano *et al.*, 2013). Los trabajos desarrollados en los capítulo 3-6 de esta Tesis han permitido determinar la capacidad de establecimiento de nuevas plántulas (capítulo 3), así como los patrones de regeneración en estos bosques (capítulo 4) en sistemas con estrés hídrico, tanto en una comunidad sana (i.e.

árboles no afectados por decaimiento) como en una comunidad afectada, donde las condiciones están cambiando a ritmo acelerado por perturbaciones en el dosel.

- Los efectos de la comunidad arbórea sana confieren estabilidad al sistema

Las tres especies de árboles se vieron favorecidas en vecindades de árboles sanos conespecíficos, los cuales favorecieron la abundancia de plántulas y brinzales de su propia especie. El hecho de que estas especies predominen en vecindades sanas conespecíficas frente a las otras especies con las que coexisten, muestra su capacidad de crear bancos de regeneración (bancos de plántulas y brinzales), indicando que en estas vecindades el aporte de semillas parece estar garantizando y se dan unas condiciones adecuadas para el desarrollo de sus propias plántulas. Este efecto positivo fue mayor para plántulas que para brinzales, especialmente notable en el caso del quejigo. El hecho de que los efectos conespecíficos positivos sean mayores para plántulas que para brinzales podría indicar la existencia de procesos negativos denso-dependientes. De hecho, el acebuche ejerce un efecto negativo en la supervivencia de sus propias plántulas (Rey y Alcántara, 2000), así como el quejigo (Pérez-Ramos y Marañón, 2012), cuya supervivencia aumentó al aumentar su distancia a árboles adultos de esta especie, tal y como predice el modelo teórico Janzen-Connell. Sin embargo, los efectos negativos no fueron lo suficientemente fuertes para contrarrestar el elevado número de plántulas producidas en las proximidades de los árboles adultos, y donde las densidades de brinzales se mantuvieron con abundancias competitivas en el sotobosque para las tres especies arbóreas. Este resultado pone de manifiesto la importancia del banco inicial de semillas y de plántulas en el cómputo global de efectos conespecíficos negativos (HilleRisLambers *et al.*, 2002). La capacidad de las dos especies de *Quercus* y el acebuche de formar un banco de brinzales en sus vecindades sanas indica el potencial que tienen estas especies de generar un banco de brinzales conespecíficos que contribuirían a favorecer su permanencia, sugiriendo que en estos bosques es esperable una estructura estable en ausencia de perturbaciones.

- El decaimiento del alcornoque perjudicó a la regeneración de las dos especies de *Quercus* y favoreció al acebuche y especies de matorral

Fue la presencia de las perturbaciones como consecuencia del decaimiento del alcornoque lo que modificó las dinámicas de regeneración en estos bosques, donde el alcornoque y quejigo se vieron especialmente perjudicados. El decaimiento y muerte de árboles de alcornoque puede conllevar la pérdida de producción de semillas (trabajo en desarrollo en los bosques de estudio), que sería el primer impedimento para esta especie para poder formar un banco de plántulas. A esto habría que añadir el efecto negativo que tuvieron los árboles muertos de alcornoque en la supervivencia de plántulas conespecíficas y de quejigo (ver capítulo 3), resultando en la disminución de la abundancia de plántulas y brinzales en vecindades de árboles en decaimiento (ver capítulo 4), llegando incluso a densidades nulas de brinzales de alcornoque cerca de árboles muertos. En los espacios abiertos tras la muerte del árbol se pierde la protección que confieren las copas. En sistemas como el mediterráneo las interacciones planta-planta son intensas y pueden jugar un papel fundamental en el establecimiento de plántulas, al suavizar las duras condiciones del verano (e.g. Gómez-Aparicio *et al.*, 2008; Rodríguez-García *et al.*, 2011; Ameztegui y Coll, 2013). La falta de protección existente en los espacios abiertos creados tras la defoliación o muerte del árbol, donde se puede producir un incremento en los niveles de luz y evapotranspiración (Gray *et al.*, 2002; Royer *et al.*, 2011), podría aumentar el riesgo de fotoinhibición (Valladares *et al.*, 2005) estresando a las plántulas e incrementando su mortalidad. Además, en vecindades de árboles defoliados existe una gran abundancia de oomicetos patógenos en el suelo (ver capítulo 5) que influyeron negativamente en la emergencia y supervivencia de plántulas de alcornoque en los bosques abiertos. A priori era esperable una respuesta contrastada al decaimiento entre plántulas de ambas especies de *Quercus*, dadas las diferencias fisiológicas y morfológicas entre las dos especies (Pérez-Ramos *et al.*, 2012), al tratarse por un lado de una especie perenne semi-tolerante a la sombra (i.e. alcornoque) y por otro lado de una especie caducifolia tolerante a la sombra (i.e. quejigo). En el trabajo experimental llevado a cabo (ver capítulo 3), sin embargo, plántulas de ambas especies respondieron de forma similar al decaimiento, mientras que en el análisis de los patrones de regeneración natural (ver capítulo 4) sí se encontraron pequeñas diferencias en la magnitud de la respuesta entre ambas especies. En concreto, aunque ambas fueron negativamente afectadas, el efecto negativo de vecindades afectadas por decaimiento fue ligeramente mayor en los brinzales de quejigo. Las diferencias entre ambos estudios pueden deberse a que en el análisis de regeneración natural se pudieron incluir potencialmente individuos mayores de 3 años, edad máxima de los individuos en el estudio experimental. Brinzales de mayor edad pueden estar mostrando una respuesta al estrés de los espacios abiertos que no es aún detectable en plántulas más jóvenes. Estos resultados sugieren una ligera ventaja del alcornoque frente al quejigo en estas vecindades, aunque es cuestionable si será suficiente para contrarrestar la limitación de producción de semillas esperable para esta especie tras la mortalidad de árboles adultos. Las consecuencias de estos efectos negativos, con la desaparición de nuevos individuos de alcornoque y quejigo en el sotobosque, hace que surja una oportunidad de colonización para otras especies arbóreas.

De hecho, en los boques abiertos el acebuche se vio especialmente beneficiado, ya que aunque la presencia de árboles muertos de alcornoque afectó negativamente a su abundancia de brinzales, el hecho de que esta especie formó un banco de plántulas con un elevado número de individuos le permitió garantizar su presencia aún en estos ambientes perjudiciales. La consecuencia fue un cambio en el ranking de abundancias relativas de individuos de las distintas especies, donde el acebuche pasó a dominar el banco de brinzales del sotobosque en vecindades en decaimiento. En cuanto a los matorrales, especialmente los de frutos carnosos, mantuvieron sus densidades a niveles similares a los mostrados en vecindades sanas. Su falta de respuesta negativa al decaimiento y la disminución de las densidades de plántulas de especies arbóreas, sobre todo del alcornoque, hicieron que su presencia relativa aumentase en el banco de plántulas, lo que muestra el potencial de estas especies leñosas de aumentar su presencia en estos bosques. El decaimiento del alcornoque podría traer consigo un cambio en la composición relativa del dosel leñoso, en el que pasaría a predominar el acebuche (en bosques abiertos) acompañado de algunas especies de matorral, y en el que el alcornoque y el quejigo quedarían relegados a una presencia secundaria. Así, las especies de lianas y matorrales de frutos carnosos, que bien no respondieron al decaimiento o bien mostraros respuestas positivas, confirman que el decaimiento del alcornoque puede inducir un cambio en la presencia relativa de otras especies leñosas, en concordancia con estudios previos que sugieren la transformación de bosques mediterráneos hacia formaciones con dominancia arbustiva como consecuencia del cambio climático (Acácio *et al.*, 2007; Pérez-Ramos y Marañón, 2012).

Se podría concluir, por tanto, que en los dos tipos de bosque el decaimiento del alcornoque puede producir un cambio en la composición relativa de estas masas. En los bosques abiertos sería esperable una dominancia del acebuche y la expansión del matorral, mientras que la presencia del alcornoque pasaría a ser secundaria. En los bosques cerrados, el alcornoque resultaría perjudicado por la desaparición de los árboles adultos y la falta de regeneración, y el quejigo, con problemas para establecerse en los espacios abiertos, podría mantener su presencia en parches poco afectados por la seca. Otras especies como lianas o matorrales de frutos carnosos verían incrementada su presencia relativa en estos bosques (Figura 2).

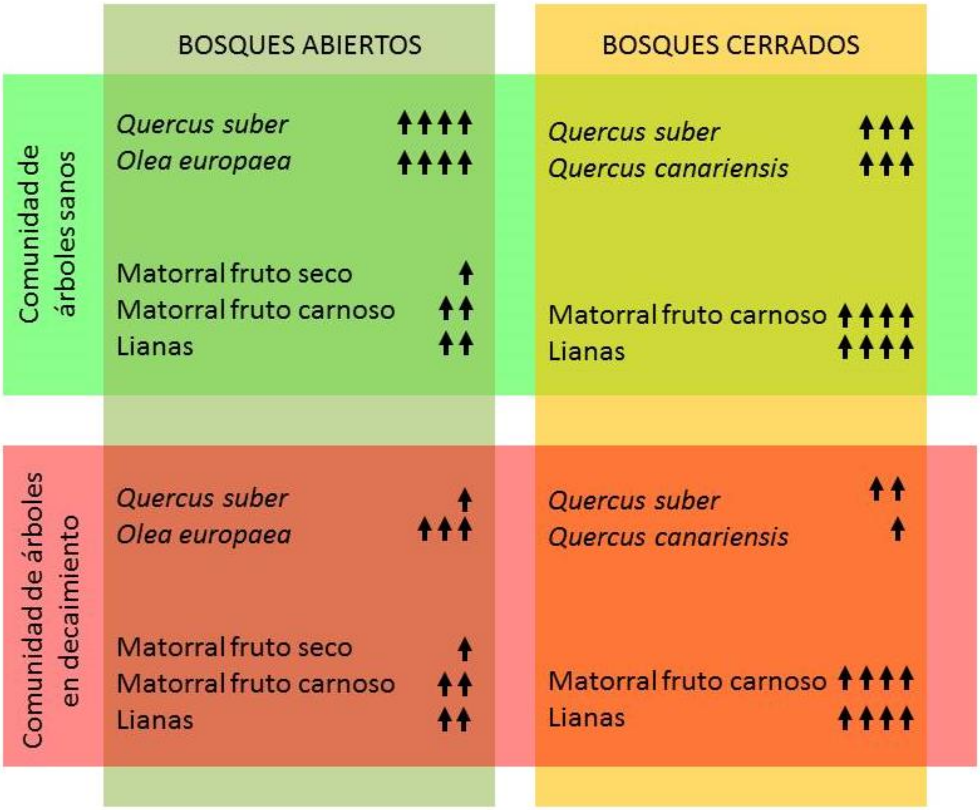

Figura 2. Esquema de las diferencias en la regeneración entre vecindades de árboles sanos y en decaimiento en los dos tipos de bosques, para cada uno de los grupos de especies estudiados (árboles, matorrales de fruto seco, matorrales de fruto carnoso y lianas). El número de flechas representa el éxito de establecimiento para cada grupo. Se puede apreciar como las especies de árboles son especialmente afectadas negativamente por el decaimiento, particularmente las dos especies de *Quercus*.

Los patrones de distribución de los organismos del suelo y su papel en las dinámicas de regeneración

Los componentes aéreo y subterráneo de los ecosistemas se encuentran en constante interacción, siendo motores de cambio el uno del otro, con retroalimentaciones tanto positivas como negativas (Wardle *et al.*, 2004). La vegetación, afectando bien directamente (i.e. identidad de la especie) o indirectamente (i.e. modificando las condiciones abióticas) puede determinar, entre otros factores, la composición y distribución de las comunidades de microorganismos del suelo. A su vez, el componente suelo juega un papel fundamental en los procesos demográficos de las plantas, ya que el conjunto de microorganismos que componen la fauna microbiana puede influenciar el establecimiento de plántulas (e.g. Packer y Clay, 2000; O'Brien *et al.*, 2011). Por lo tanto, parte de las interacciones planta-planta existentes en los bosques pueden estar mediadas por mecanismos relacionados con la comunidad biótica del suelo (Richard *et al.*, 2009). Explorando esta interacción, en los **capítulos 5 y 6** de esta tesis se ha mostrado cómo los patrones de distribución tanto de organismos antagonistas (oomicetos patógenos) como mutualistas (micorrizas) responden a factores abióticos no influenciados por las especies, como la textura, y a la composición y distribución de las especies leñosas de estos bosques. Es más, no solo la identidad de las especies sino también árboles con distintos grados de decaimiento mostraron estar relacionados con la distribución de estas comunidades de microorganismos. Además, tanto patógenos como micorrizas impactaron en las dinámicas de regeneración de las especies arbóreas, dando lugar a procesos de retroalimentación planta-suelo.

- La identidad de los individuos del dosel arbóreo-arbustivo definió los patrones de distribución de los organismos del suelo

La composición y distribución de las especies arbóreas y arbustivas determinaron en gran medida los patrones de distribución de antagonistas y mutualistas del suelo (Figura 3). La importancia de la especie vegetal definiendo las comunidades de microorganismos en suelos forestales ha sido ampliamente descrita tanto para patógenos (e.g. Packer y Clay, 2000; Augspurger y Wilkinson, 2007) como para micorrizas (e.g. Molina *et al.*, 1992; Dickie *et al.*, 2001) al proporcionar los tejidos donde oomicetos y hongos van a establecerse (Wardle *et al.*, 2004). Un resultado de especial interés fueron las diferencias en la abundancia de patógenos entre suelos en vecindades de acebuche y de quejigo. En vecindades de acebuche el contenido de patógenos en el suelo fue menor que en vecindades sin esta especie, mientras que el quejigo actuó como reservorio de estos organismos sin mostrar signos de decaimiento. Algunas de las implicaciones que se derivan de este resultado incluyen el efecto que las especies que coexisten con el alcornoque podrían estar teniendo en sus dinámicas poblacionales. Por ejemplo, el acebuche podría favorecer indirectamente al alcornoque al disminuir la abundancia del patógeno, mientras que el quejigo muestra una competencia aparente con el alcornoque al favorecer la presencia de patógenos que afectan al alcornoque pero no a sí mismo. Acorde con los efectos especie-específicos de los árboles en la abundancia de patógenos, se encontró que la identidad del matorral dominante en cada tipo de bosque también puede estar definiendo el contenido del oomiceto en el suelo. Los matorrales dominantes de los bosques abiertos (*Pistacia lentiscus*, lentisco) tuvieron efectos negativos en la abundancia de patógenos mientras que los matorrales dominantes de los bosques cerrados (*Erica* spp., brezos) favorecieron su abundancia. La mayor abundancia de patógenos en vecindades de *Erica* podría estar relacionada con las diferencias en los contenidos de materia orgánica (lentisco > brezo) y el pH del suelo (lentisco > brezo) bajo estas especies, ya que condiciones con poca materia orgánica y más ácidas favorecen a estos patógenos (Weste y Marks, 1987; Serrano *et al.*, 2012). En el caso de las micorrizas, también la identidad del matorral influyó en el tipo de micorrizas que colonizaron las plántulas de alcornoque y quejigo. Por ejemplo, las plántulas de los bosques abiertos mostraron una colonización por hongos endomicorrícicos mucho mayor que las plántulas de los bosques cerrados. La presencia de lentisco y de la especie arbórea acebuche, ambas típicamente endomicorrícicas, probablemente favoreció que las raíces de las plántulas de *Quercus* se asociaran con este tipo de micorrizas en esos bosques (e.g. Dickie *et al.*, 2001). En resumen, estos resultados son relevantes para entender la naturaleza de las interacciones planta-planta mediadas por organismos del suelo, mucho menos estudiadas que las mediadas por factores abióticos a pesar de su relevancia. Este tipo de interacción entre especies a través de su influencia en las comunidades de organismos del suelo es uno de los principales mecanismos de retroalimentación por los que se favorece la diversidad de las comunidades de plantas (Bever *et al.*, 1997; Wardle, 2006). También muestra la importancia de considerar toda la comunidad y la distribución de los individuos vegetales cuando se trata de comprender los procesos de retroalimentación entre las partes aérea y subterránea del bosque.

- Árboles de alcornoque con distintos estados de salud determinaron el mosaico espacial de organismos del suelo

Uno de los resultados más interesantes en este apartado de la Tesis fue la concordancia espacial existente entre el estado de salud del alcornoque y la abundancia de patógenos en el suelo y de micorrizas en las raíces de las plántulas (Figura 3). Aunque las interacciones entre una comunidad en decaimiento y los organismos del suelo han sido menos estudiadas que las interacciones especie-específicas, sus implicaciones en la dinámica de la comunidad de plantas podrían tener igualmente gran relevancia en estos sistemas afectados por decaimiento. Con respecto a los organismos patógenos, su abundancia en vecindades de árboles afectados aumentó a medida que aumentaba el grado de afección de los árboles, disminuyendo en vecindades de árboles sanos o muertos. Este resultado confirma el papel de las especies de oomiceto estudiadas (i.e. *Phytophthora cinnamomi* y *Pythium* spp.) en el decaimiento del alcornoque (Brasier, 1996; Sánchez *et al.*, 2006). Además, podría estar describiendo un proceso de retroalimentación negativa para la planta. Así, la afectación por patógenos produciría la muerte de raíces finas en el árbol, que se traduciría en la pérdida de hojas. Esto, a su vez, favorecería el paso de luz y con ello el aumento de la temperatura del suelo, lo que beneficiaría al patógeno y aceleraría el proceso de decaimiento hasta producir la muerte del árbol, tras la cual los niveles de patógenos en el suelo volverían a disminuir (al desaparecer las raíces con las que asociarse). El mosaico definido por árboles con distintos estados de salud se traslada por tanto a un mosaico en la densidad de organismos patógenos en el suelo que estaría definiendo espacialmente parches adversos (con abundante patógeno) o favorables (no patógeno). La existencia de espacios con y libre de patógenos actuaría como mecanismo impulsor de la coexistencia de especies ya que puede bien favorecer o bien perjudicar el establecimiento de las distintas especies.

Por otra parte, los patrones de distribución de la asociación plántula-micorriza también respondieron a la distribución de alcornoques con distintos estados de salud, aunque la respuesta varió en función del tipo de bosque. En los bosques abiertos, el aumento de la colonización por ectomicorrizas en vecindades en decaimiento pudo deberse a una inversión de las plántulas en esta relación simbiótica para resistir al estrés de las condiciones abióticas desfavorables en esas vecindades (Swaty *et al.*, 2004). El efecto fue detectable en estos bosques ya que las plántulas estaban de por sí poco colonizadas. Sin embargo, en los bosques cerrados, la diminución del porcentaje de micorrización de las plántulas en vecindades de árboles defoliados y muertos pudo deberse a las condiciones menos duras en estos bosques y a que la mayor parte de las plántulas ya se encontraban colonizadas por micorrizas, por lo que la respuesta negativa pudo deberse a una disminución en el inóculo disponible (Swaty *et al.*, 2004). Estos resultados suponen un avance en el entendimiento de los patrones espaciales de organismos antagonistas y mutualistas en relación a la distribución de individuos arbóreos en declive, que podrían ser parte de los mecanismos implicados en los efectos del decaimiento en las dinámicas de regeneración.

- La respuesta de patógenos y micorrizas a las condiciones abióticas

En la exploración de los factores abióticos que influyen en los patrones de distribución de oomicetos y micorrizas, hay que destacar el importante papel que jugó la textura del suelo. La importancia de la textura en las dinámicas de sistemas forestales ha sido ampliamente reconocida al influir en los ciclos de N y C (e.g. Borchers y Perry, 1992; Côté *et al.*, 2000; Silver *et al.*, 2000), capacidad de retención de agua (Brady y Weil, 1996), biomasa microbiana (Bauhus y Pare, 1998), o distribución de las especies al modificar la disponibilidad de nutrientes (van Breemen *et al.*, 1997) o de agua (Knoop y Walker, 1985). Ya en el **capítulo 2** se demostró que la textura del suelo puede ser determinante en la respuesta de la vegetación a otras variables ambientales. En los **capítulos 5 y 6** de esta Tesis se ha mostrado el papel de la textura como motor abiótico en la distribución de oomicetos patógenos y micorrizas, respectivamente, en sistemas mediterráneos. En general, mayores contenidos en arena resultaron perjudiciales para la abundancia de estos organismos. Presumiblemente esto se debe a que suelos con más contenido en arena retienen menos la humedad comparado con suelos arcillosos (Brady y Weil, 1996), y estos organismos son favorecidos por condiciones de mayor humedad (e.g. Hendrix y Campbell, 1973; Weste y Marks, 1987; Kennedy y Peay, 2007; Allen y Kitajima, 2013), particularmente los oomicetos que son organismos acuáticos que se dispersan por agua. La excepción se encontró para las micorrizas en los suelos predominantemente arcillosos de los bosques abiertos, donde en parches con mayor contenido de arena se favoreció el desarrollo de estos hongos, probablemente al reducir la compactación y favorecer la aireación de esos suelos en beneficio de las micorrizas (Skinner y Bowen, 1974; Amaranthus *et al.*, 1996). Estos resultados muestran cómo los cambios en la textura pueden modificar y definir los patrones de distribución de los organismos del suelo en sistemas forestales, proporcionando información de aquellas zonas donde la vegetación podría ser más proclive a sufrir un ataque por oomicetos patógenos y/o ser beneficiada por hongos mutualistas.

Aparte de la textura, los resultados obtenidos en el capítulo 6 mostraron que otras variables abióticas tales como nutrientes, humedad del suelo o luz, también son determinantes de los patrones de distribución de las micorrizas. La aproximación empleada permitió capturar por un lado el efecto directo de la vegetación en la asociación plántula-micorriza, previamente descrito, y por otro lado los efectos no directos de la vegetación en la asociación simbiótica, como la modificación de las condiciones ambientales. Así, en estos bosques, donde se ha mostrado la capacidad de los árboles de modular las condiciones ambientales, como por ejemplo los diferentes efectos de alcornoque y quejigo en la concentración de carbono, nutrientes y pH del suelo (Aponte *et al.*, 2013), o los cambios en las tasas de respiración y disponibilidad de P en suelos bajo árboles de alcornoque sanos y en decaimiento (Ávila *et al.*, no publicado), la amplia respuesta de las micorrizas a los factores abióticos (Figura 3), muestran el potencial que tiene el dosel arbóreo de influir en estos organismos a través de la modificación del medio abiótico.

- La implicación de los organismos del suelo en las dinámicas de regeneración

La distribución de organismos patógenos y micorrícicos influyó a su vez en la variación espacial del éxito de emergencia y supervivencia de plántulas (Figura 3). La implicación de estos organismos en procesos demográficos ha sido ampliamente estudiada en diversos sistemas forestales de todo el mundo. Por ejemplo, la presencia de patógenos cerca del árbol madre puede mermar la capacidad de plántulas conespecíficas para establecerse en sus proximidades (e.g. Packer y Clay, 2000; Reinhart y Clay, 2009). Por el contrario, establecerse cerca de un árbol de su misma especie podría ser beneficioso para la plántula al favorecerse la posible asociación con organismos mutualistas (e.g. Dickie *et al.*, 2002; O’Brien *et al.*, 2011). Los resultados obtenidos en los **capítulos 5 y 6** concuerdan parcialmente con estas ideas. Por ejemplo, sí se encontró que mayores abundancias de patógenos influyeron negativamente en la emergencia y supervivencia de plántulas, pero esto solo fue detectado en los bosques abiertos de alcornoque-acebuche. Este hecho puede estar relacionado con las elevadas cantidades de patógenos que se encontraron en estos bosques, mucho mayores que en los bosques cerrados, lo cual podría indicar que para que la plántula muestre signos de afección se requieran unos niveles mínimos en la abundancia de patógenos en el suelo. La presencia de estos oomicetos por tanto no siempre se traduciría en un efecto negativo para la plántula, como ya se ha encontrado en experimentos en situaciones controladas para esta especie (Rodriguez-Molina *et al.*, 2002). Este resultado sugiere que los efectos negativos de los árboles en declive en la supervivencia y abundancia de plántulas de alcornoque (ver capítulos 3 y 4) podrían estar más relacionados con las condiciones abióticas generadas en los huecos abiertos que con la presencia de organismos antagonistas en el suelo, al menos durante los primeros años de vida de la plántula y con abundancias no extremadamente elevadas del oomiceto. El estudio a largo plazo de la respuesta de brinzales

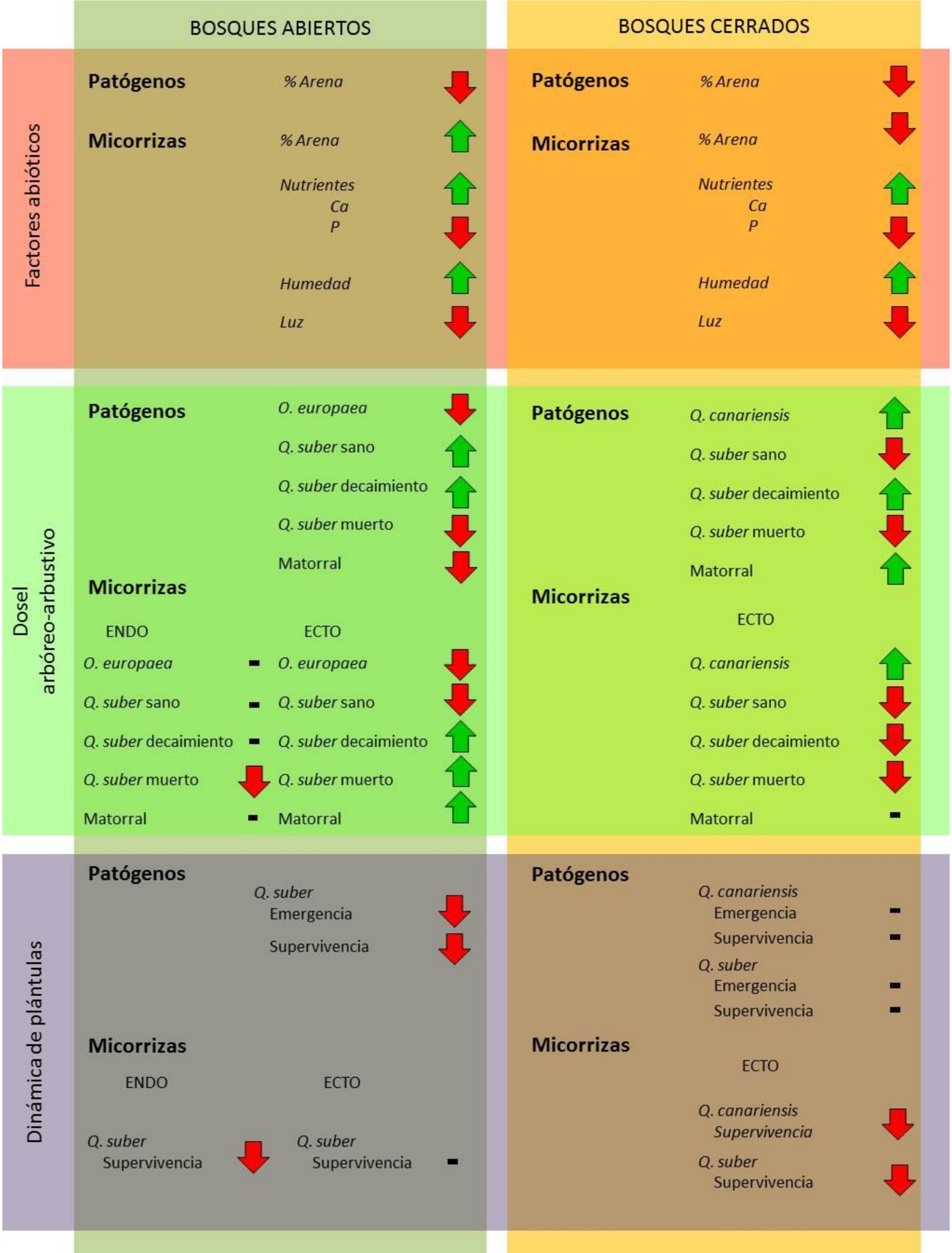

Figura 3. Síntesis de los efectos principales encontrados de los factores abióticos (panel superior) y del dosel arbóreo (panel central) en las abundancias de oomicetos patógenos del suelo y la asociación plántula-micorriza en los dos tipos de bosque de estudio. En el panel inferior se representa el efecto de estos dos tipos de organismos en la dinámica de plántulas. Flechas verdes indican efecto positivo, flechas rojas negativos, líneas negras efecto nulo.

y juveniles a la presencia y abundancia del patógeno permitiría conocer con mayor precisión el grado de implicación de estos organismos en el establecimiento del alcornoque en estos bosques.

En el caso de la asociación plántula-micorriza, los resultados obtenidos contrastan con los patrones más comunes encontrados en la literatura. Nuestra hipótesis de partida esperaba encontrar una relación mutualista entre plántula y micorriza, pero los resultados indicaron que se trató de una relación desde neutra a antagonista en la supervivencia de plántulas de un año de edad (Figura 3). Aunque las micorrizas son tradicionalmente consideradas como organismos mutualistas, en ocasiones esto no ocurre así existiendo una continuidad en la respuesta de la planta a la colonización por micorrizas que va desde el parasitismo al mutualismo (Johnson *et al.*, 1997). Las respuestas negativas son más frecuentes en plántulas jóvenes. Además, en sistemas con limitación de agua como los bosques de estudio, la síntesis de C se encuentra limitada como consecuencia del estrés hídrico (Tenhunen *et al.*, 1990; Pereira *et al.*, 2007). Una elevada demanda de C por parte del hongo micorrícico pudo resultar un compromiso para la plántula que, al no invertir en sus propios tejidos, le produjo la muerte (Johnson *et al.*, 1997). Asimismo, este fenómeno puede verse acrecentado cuando en las raíces de la plántula conviven dos tipos distintos de micorrizas. Así, cuando plantas típicamente ectomicorrícicas se asocian también con endomicorrizas, el balance neto de costes-beneficios puede ser negativo para la planta (Egerton-Warburton y Allen, 2001), en concordancia con lo obtenido en este trabajo. De estos resultados se deduce que los patrones de distribución de micorrizas podrían estar influyendo en los patrones de regeneración de plántulas jóvenes al influirlas negativamente. Sin embargo, en las siguientes etapas (ej. brinzales y juveniles) sería esperable un cambio de signo en el efecto de las micorrizas, donde las dinámicas de regeneración se verían beneficiadas por esta asociación (e.g. Chilvers *et al.*, 1987; Chen *et al.*, 2000; Egerton-Warburton y Allen, 2001; Wagg *et al.*, 2008). Este cambio de signo se produciría una vez que la plántula consume todas las reservas de las semillas. En ese momento la demanda de recursos de la plántula se vería incrementada ya que no podría adquirirlos de sus propias reservas, haciéndole más dependiente del contenido de nutrientes del suelo donde la asociación con micorrizas le facilitaría su obtención y donde los costes iniciales de establecimiento con el hongo mutualista ya habrían sido superados. En cualquier caso, en plántulas de un año de edad, factores abióticos y factores intrínsecos a la plántula (por ejemplo calcio, disponibilidad de luz o altura de la plántula) mostraron efectos de mayor magnitud sobre la supervivencia de las plántulas en comparación con los efectos de las micorrizas. Estos resultados sugieren que los efectos de árboles y matorrales en la supervivencia de plántulas están más relacionados con la modificación de las condiciones abióticas que con sus efectos en las comunidades micorrícicas del suelo, al menos en esta etapa temprana de la vida de las plántulas.

IMPLICACIONES PARA LA CONSERVACIÓN Y RESTAURACIÓN

Los resultados expuestos en esta Tesis permiten un mejor entendimiento de las dinámicas de regeneración de bosques mediterráneos en decaimiento. Se ha mostrado la importancia de considerar en los estudios demográficos de sistemas afectados tanto las dinámicas de árboles adultos como las del regenerado, así como la interacción de las variables climáticas con otros factores ambientales, particularmente con las características del suelo, que puede jugar un papel fundamental modulando los efectos del clima en la vegetación. Los resultados obtenidos ponen de manifiesto la gran influencia que el decaimiento del alcornoque puede tener en la regeneración de estos bosques así como en las comunidades de organismos patógenos y micorrícos del suelo.

En los sistemas de estudio, las dinámicas sucesionales son muy lentas debido a que los factores limitantes del clima (e.g. sequía en verano) o de la gestión (e.g. elevada herbivoría) producen una mortalidad alta de plántulas, limitando la regeneración. A esto se suma en las últimas décadas el decaimiento y muerte del alcornoque que están mermando las comunidades de esta especie, colocando a estos sistemas en una situación sin precedentes, donde la escasez de regeneración unida a la pérdida de árboles podría suponer un cambio de estructura y composición relativa del bosque a medio plazo. La creciente constatación de los problemas de continuidad de esta especie empuja cada vez con más fuerza a la necesidad de desarrollar políticas que permitan contrarrestar, al menos parcialmente, las tendencias negativas en las poblaciones de esta especie. Los resultados obtenidos muestran la importancia de que las medidas de actuación tomadas sean impulsadas considerando que se encuentran dentro de un marco de bosque afectado por decaimiento donde las interacciones con este fenómeno podrían marcar el éxito o fracaso de estas medidas.

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Capítulo 8

CONCLUSIONES

Capítulo 8. Conclusiones

1. Las predicciones de aumento de temperatura en la Cuenca Mediterránea podrían afectar negativamente a la supervivencia de árboles adultos de alcornoque y positivamente a su regeneración. En cualquier caso, la escasez de plántulas y brinzales de esta especie y la consecuente lentitud de los procesos de transición de estos bosques, hacen que el aumento predicho de mortalidad de árboles adultos constituya una amenaza para la persistencia de estos bosques.
2. El aumento de la precipitación predicho en los meses de invierno en la Cuenca Mediterránea podría tener efectos dispares en los patrones de supervivencia de alcornoque dependiendo de las características de los suelos. Ante este escenario, la persistencia de esta especie es más probable en suelos arenosos que en suelos arcillosos.
3. La composición y el estado de salud de la comunidad arbóreo-arbustiva influyó notablemente en el éxito de reclutamiento de estos bosques mediterráneos, debido a los efectos locales que individuos vecinos tuvieron sobre las plántulas, especialmente en su emergencia y supervivencia.
4. El decaimiento del alcornoque tuvo un efecto en general negativo en el establecimiento de plántulas de alcornoque y quejigo, al crearse condiciones desfavorables para las plántulas en vecindades de árboles defoliados y muertos. En sistemas con escasez de agua como el de este estudio, donde las interacciones positivas planta-planta son frecuentes, la apertura de claros en el dosel como consecuencia del decaimiento representan microhábitats que no parecen aptos para el reclutamiento de estas dos especies de *Quercus*.
5. El estudio de las dinámicas naturales de regeneración mostró la capacidad potencial que, en ausencia de perturbaciones, tienen alcornoque, acebuche y quejigo para mantener sus poblaciones, ya que fueron capaces de generar un banco de plántulas y brinzales que contribuiría a favorecer su permanencia en estos bosques, confiriendo una estructura estable al sistema durante generaciones.
6. Fue la presencia de perturbaciones en el dosel arbóreo como consecuencia del decaimiento del alcornoque lo que modificó las dinámicas de regeneración de estos bosques. En los bosques abiertos de alcornoque-acebuche fue el acebuche, acompañado por especies de matorral de fruto carnoso, el que mostró mayor capacidad de colonización de los espacios abiertos tras la muerte de los árboles. En los bosques cerrados de alcornoque-quejigo, ambas especies de *Quercus* fueron afectadas negativamente. Lianas y matorrales de frutos carnosos mostraron elevadas abundancias en los bancos de plántulas y brinzales en vecindades en decaimiento. Por tanto, en las zonas afectadas por el decaimiento del alcornoque, se podría producir un cambio en la composición relativa a medio plazo.
7. Los patrones de distribución de organismos patógenos del suelo mostraron una alta concordancia espacial con los factores abióticos (textura del suelo) y bióticos (composición del dosel arbóreo-arbustivo) estudiados. En zonas con mayor contenido

en arena disminuyó la abundancia de patógenos. En vecindades de árboles de acebuche se detectó una disminución en el contenido de estos organismos, mientras que aumentó en vecindades de quejigo. Las interacciones especie-específicas planta-planta podrían estar por tanto parcialmente mediadas por los efectos de las distintas especies en las comunidades de antagonistas del suelo.

8. El contenido de organismos patógenos en el suelo aumentó con el grado de decaimiento del alcornoque respecto a árboles sanos, desapareciendo en vecindades de árboles muertos. El mosaico definido por los árboles con distintos estados de salud y muertos se trasladó por tanto a un mosaico de organismos patógenos en el suelo.
9. La variabilidad espacial en el contenido de patógenos se tradujo parcialmente en una variación espacial del comportamiento de las plántulas, especialmente en zonas con elevado contenido en patógenos. El efecto de los patógenos no fue en cualquier caso determinante para la emergencia y supervivencia de las plántulas, sino tan solo uno más de los múltiples factores bióticos y abióticos que intervienen en las dinámicas de regeneración.
10. Los patrones espaciales de la asociación plántula-micorriza estuvieron considerablemente marcados por la distribución espacial de las distintas especies y factores abióticos. La presencia de especies endomicorrícicas favoreció la asociación de plántulas de alcornoque con endomicorrizas, confirmando la capacidad de esta especie de asociarse con este tipo de micorrizas. Todos los factores abióticos estudiados mostraron efectos en la colonización por micorrizas, sugiriendo que los árboles, a través de sus efectos en estos factores, podrían indirectamente definir la relación plántula-micorriza.
11. La variación espacial de la asociación plántula-micorriza respondió al proceso de decaimiento del alcornoque, con diferencias entre tipos de bosque. En los bosques abiertos de alcornoque-acebuche las plántulas se asociaron más con micorrizas en vecindades de árboles defoliados y muertos. En los boques de alcornoque-quejigo, las plántulas mostraron menor colonización en esas vecindades probablemente por limitación en la disponibilidad de inóculos. La distribución de árboles con distintos estados de salud puede por tanto influir en el funcionamiento del ecosistema a través de sus efectos en la interacción plántula-micorriza.
12. Las plántulas tuvieron una respuesta mucho mayor a la colonización por endomicorrizas que por ectomicorrizas, y la respuesta a ambos tipos de micorriza fue neutra o negativa. Esto se pudo deber a una elevada demanda de carbono en plantas jóvenes por parte de las micorrizas, lo que supuso una reducción en el carbono fijado en los tejidos de la plántula, disminuyendo su supervivencia. Factores abióticos e intrínsecos a la plántula mostraron mayores efectos en la supervivencia de plántulas que las micorrizas. Esto indica que la interacción planta-planta a través de mecanismos abióticos puede tener más importancia que a través de mecanismos bióticos en plántulas de un año.
13. Los resultados expuestos en esta Tesis muestran la importancia de conocer la interacción dosel arbóreo y regeneración a la hora de evaluar los impactos del

decaimiento en las dinámicas de bosques afectados. La creciente constatación de los problemas de continuidad de la especie de estudio empuja cada vez con más fuerza a la necesidad de desarrollar políticas que permitan contrarrestar, al menos parcialmente, las tendencias negativas en las poblaciones de esta especie. Los resultados obtenidos muestran la importancia de que las medidas de actuación tomadas sean impulsadas considerando que se encuentran dentro de un marco de bosque afectado por decaimiento donde las interacciones con este fenómeno podrían marcar el éxito o fracaso de estas medidas.