UNIVERSIDAD DE GRANADA
Departamento de Ecología

Regeneración de la biodiversidad de especies leñosas en un marco de degradación de hábitats mediterráneos de montaña: combinación de interacciones ecológicas y manejo humano

TESIS DOCTORAL

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Memoria presentada por la Licenciada Irene Mendoza Sagrera para optar al Grado de Doctora por la Universidad de Granada

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¿Encontraría a la Maga? Tantas veces me había bastado asomarme, viniendo por la rue de Seine, al arco que da al Quai de Conti, y apenas la luz de ceniza y olivo que flota sobre el río me dejaba distinguir las formas, ya su silueta delgada se inscribía en el Pont des Arts, a veces andando de un lado a otro, a veces detenida en el petril de hierro, inclinada sobre el agua. Y era tan natural cruzar la calle, subir los peldaños del puente, entrar en su delgada cintura y acercarme a la Maga que sonreía sin sorpresa, convencida como yo que un encuentro casual era lo menos casual en nuestras vidas, y que la gente que se da citas precisas es la misma que necesita papel rayado para escribirse o que aprieta desde abajo el tubo del dentífrico.

Julio Cortázar.
Rayuela.

A todas las personas queridas
a las que esta tesis les robó mi presencia,

especialmente,

a mis padres, Ramón y Reyes

a mi abuelo Jorge,

a Jairo,

a Juan Peña Llopis

a Omar

y a mi abuela Antonia,
que se fue al cielo un poco antes de que la acabara.

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Gracias a la vida, que me ha dado tanto
Me ha dado el sonido y el abecedario
Con él las palabras que pienso y declaro:
Madre, amigo, hermano y luz alumbrando
La ruta del alma del que estoy amando.

Violeta Parra.
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INTRODUCCIÓN GENERAL

Interacciones planta-animal y regeneración

La diversidad de una comunidad depende tanto de la diversidad de sus componentes como de la diversidad de sus interacciones ecológicas (Thompson 2002). El ciclo de vida de una especie leñosa es un proceso complejo en el que se suceden secuencialmente diversos estadios (Herrera et al. 1994): semilla, plántula, juvenil y adulto. Cada una de estas fases se conecta con la siguiente por procesos tales como la dispersión del polen y las semillas, la germinación, emergencia y supervivencia de plántulas, y el establecimiento de los juveniles para llegar a adultos (Clark et al. 1999; Nathan & Muller-Landau 2000). Las interacciones planta-animal están afectando cada uno de los estadios de una planta bien mediante interacciones mutualistas positivas (polinización, dispersión de semillas) o bien mediante interacciones antagonistas negativas (depredación de semillas, herbivorismo), modificándose el balance final del proceso de regeneración (Schupp 1995; Schupp y Fuentes 1995). Si la probabilidad de transición entre cada una de estas etapas fuese cercana a cero, se podría llegar al colapso de todo el ciclo de regeneración de la especie (Houle 1995, Jordano & Herrera 1995). Pero además, desde el punto de vista de la comunidad, dispersando semillas o consumiendo plantas selectivamente, los animales pueden favorecer o perjudicar unas especies vegetales en detrimento de otras. El resultado de las interacciones mutualistas o antagónicas puede tener un papel clave en la regeneración de la vegetación, filtrando la composición específica de las comunidades de plantas y modulando la sucesión ecológica. Por lo tanto, el conocimiento de la abundancia, distribución y patrón de dichas interacciones es de sumo interés a la hora de comprender la dinámica demográfica de las plantas y el funcionamiento a largo plazo del sistema en el que se encuentran.

El hombre y su interacción con el entorno

Al igual que el resto de los animales, desde su aparición como especie el hombre (Homo sapiens) también interacciona con su entorno, comunidades vegetales incluidas. Este proceso de transformación del medio ambiente, que en un principio era moderado, se ha visto acelerado desde el surgimiento de la Revolución Industrial, que trajo consigo una nueva escala de actividad humana (Pullin 2002). Una de las consecuencias más graves del impacto humano ha sido la destrucción y consiguiente fragmentación del medio natural en toda la Tierra. De hecho, según diversos autores (Vitousek et al. 1997; Sala 2000; Primack 2002; Foley et al. 2005), la amenaza más directa a la biodiversidad proviene de la degradación del hábitat por causas antrópicas. En la actualidad quedan pocas zonas vírgenes en el planeta (Sanderson et al. 2002), ya que la mayor parte de los sistemas naturales han sido destruidos, quemados, urbanizados, transformados en campos de cultivo, empleados para pastos de animales, atravesados por carreteras u otras vías de comunicación, explotados para fines silvícolas, desecados… Unido a esto está la modificación del clima como consecuencia de las actividades humanas, que ya ha sido ampliamente aceptada por la comunidad científica e incluso por la mayor parte de los ciudadanos (sirva de ejemplo el informe IPCC 2007 a escala mundial y el informe de la FCI 2006 a nivel andaluz). El cambio climático impone una amenaza global para todos los ecosistemas, pero en el caso de la cuenca Mediterránea, las previsiones son especialmente desesperanzadoras, ya que se prevé una mayor aridez (menor precipitación y lluvias más irregulares), así como un aumento de las temperaturas. Por lo tanto, la tendencia es hacia un mayor estrés para las plantas, que ya de por si tienen que hacer frente a la sequía estival que caracteriza este clima.

En la cuenca Mediterránea, el proceso de destrucción del hábitat ha sido especialmente intenso, ya que la presencia del hombre es milenaria (Blondel y

Aronson xx). De hecho, el ser humano forma parte de los sistemas mediterráneos de una forma tan estrecha que no tiene sentido hablar de zonas “naturales”, ya que en todas ellas existe algún tipo de impacto humano, por mínimo que sea. Más bien encontramos distintos niveles de intensidad de degradación de hábitats, que abarcan desde zonas más conservadas hasta otras donde prácticamente no queda ningún resto de los sistemas originales. A pesar de esto, muchos estudios ecológicos realizados en ecosistemas mediterráneos excluyen la consideración explícita de la interacción del hombre con los sistemas biológicos, centrándose en áreas bien conservadas donde el impacto antrópico es mínimo (p. ej. Jordano y Herrera 1995; Hampe y Arroyo 2002; Rey et al. 2006). Aunque esta aproximación es más sencilla, adquiere un carácter más alejado de la realidad al no tener en cuenta los distintos tipos de manejo humano. Una de las principales aportaciones de esta tesis doctoral al estudio de los sistemas ecológicos en ambientes mediterráneos es que incluye explícitamente al ser humano como un componente más del sistema, y analiza su impacto mediante distintos tipos de manejo de los hábitats.

El cambio de paradigma en la degradación y fragmentación del paisaje

Inherente al proceso de degradación, se produce el de fragmentación de hábitats o ecosistemas, definido como un cambio en la estructura del paisaje por el cual una superficie grande y continua queda dividida en dos o más fragmentos (Lovejoy et al. 1986; Reed et al. 1996). La base teórica sobre la que se fundamenta el estudio de la fragmentación de hábitats viene dada por el modelo de biogeografía insular que MacArthur y Wilson propusieron en 1967 en su obra The Theory of Island Biogeography. Dicha teoría está centrada en las comunidades que habitan las islas oceánicas y postula que la diversidad de una isla responde a un equilibrio dinámico entre dos tasas opuestas de inmigración y extinción, resultando en un número de especies constante.

Debido a que el modelo biogeografía insular considera a todas las especies equivalentes, no permite predecir la identidad de las especies de una isla en concreto, ya que dependería del azar el que una especie colonizase una isla dada y no otra. Lo más interesante de este modelo es que relaciona el número de especies de una isla con su tamaño y grado de aislamiento. Cuanto más grande y cercana al continente está una isla, mayor es la probabilidad de un organismo de alcanzarla (tasa de inmigración). De la misma forma, la tasa de extinción estaría relacionada con el tamaño de la isla, ya que islas más pequeñas tendrán tamaños poblacionales menores y mayor interferencia entre especies. No obstante, Browson y Kodric-Browson introdujeron en 1977 el concepto de "efecto rescate", por el cual la tasa de extinción también estaría determinada por su grado de aislamiento. Las islas más cercanas a los continentes tendrían mayores probabilidades de recibir inmigrantes de especies ya presentes, que mejorarían el tamaño y eficacia biológica de las poblaciones insulares y reducirían su probabilidad de extinción.

A pesar de que MacArthur y Wilson mencionan esta posibilidad de una forma superficial y más bien metafórica (Haila 2002), el modelo de la teoría de biogeografía de islas y su refinamiento realizado por Brown y Kodric-Brown (1977) se ha tomado tradicionalmente como la herramienta teórica que permitiría explicar las consecuencias de la fragmentación del hábitat para las comunidades. Para ello, se parte del presupuesto de que un fragmento de hábitat equivale a una isla, y la matriz de hábitat degradado que bordea al fragmento funcionaría como una especie de océano hostil. A medida que el fragmento se vuelve más pequeño y aislado del resto, basándonos en la biogeografía insular, es predecible que contenga más especies de las que es capaz de mantener, con lo que algunas poblaciones de especies comenzarán a extinguirse y el equilibrio de especies descenderá (Saunders, 1991). Por el contrario, fragmentos mayores contendrán más especies.

Sin embargo, la utilización de la teoría de biogeografía de islas aplicada a la fragmentación de hábitats ha sido ampliamente criticada a partir de los años 80 (Williamson 1989; Fahrig 1993; Wiens 1995; Saunders 1991; Haila 2002; Fisher y Lindenmayer 2007). La discrepancia más importante proviene de la analogía entre una isla oceánica rodeada por mar y un fragmento de hábitat bordeado por una matriz degradada (Desouza et al. 2001; Haila 2002). En primer lugar, la diferencia más obvia entre los fragmentos de hábitats respecto a las islas es que en los primeros es posible la invasión de especies procedentes de los alrededores degradados, mientras que esto no ocurre con las islas oceánicas

(Desouza et al. 2001). Además, en las islas oceánicas creadas por primera vez, todas las especies provienen del exterior; por el contrario, en los fragmentos hay especies que provienen de la vegetación original. Otra característica que diferencia a las islas oceánicas de los fragmentos de hábitat es que la flora y fauna de las islas depende de las peculiaridades de su historia geológica y evolutiva, mientras que en los fragmentos no existe ningún tipo de historia evolutiva ya que tienen una vida demasiado efímera como para que en ellos pueda darse un proceso de especiación (Haila 2002). En ese sentido, según Haila (1999), en los fragmentos funcionaría una escala individual (en la que el criterio relevante es el patrón de movimiento de los individuos: un paisaje está fragmentado si un individuo no puede moverse de un parche a otro) y poblacional (el criterio es la dinámica poblacional y la diferenciación: en el paisaje fragmentado los parches son dinámicamente independientes unos de otros). Por el contrario, en el caso de las islas oceánicas, nos encontramos bajo una escala evolutiva: el criterio relevante en este caso es la especiación y los procesos de divergencia de la flora y fauna. Unido a todo esto está el hecho de que los fragmentos de hábitats se diferencian de las islas oceánicas en que existen en un paisaje complejo en forma de mosaico, en el cual, la dinámica de un fragmento se ve afectada por factores externos que varían en la medida en que lo hace la estructura del mosaico (Wiens, 1995).

Todas estas críticas a la biogeografía de islas han conducido a un cambio de paradigma a finales de los años 80 hacia la teoría de metapoblaciones (Hanski y Simberloff 1997). Levins acuñó en 1970 el término de metapoblación para referirse al hecho de que la población de una determinada especie que aparece en un fragmento interacciona con las poblaciones circundantes, intercambiando material genético por medio de la migración y emigración. Asimismo, la aparición de la nueva disciplina de la ecología del paisaje surge ante la necesidad de comprender cómo la estructura espacial de los fragmentos influencia a las comunidades que aparecen en ellos y sus procesos (Turner et al. 2001). Especialmente relevante es el concepto de paisaje en mosaico (Wiens 1995; Duelli 1997), el cual estipula que los paisajes no corresponden a una estructura continua de matriz degradada en la que se encuentran inmersos los fragmentos, sino que todo el paisaje está compuesto por parches con distintos grados de perturbación. Este concepto de paisaje en mosaico es muy apropiado para los ecosistemas mediterráneos, ya que en ellos, la larga e intensa presencia del ser humano durante miles de años ha provocado la destrucción casi completa del medio. En los sistemas mediterráneos no tiene sentido distinguir la matriz del fragmento, ya que el paisaje está compuesto por parches de hábitats que se diferencian en el tipo de manejo humano.

Manejos humanos en la montaña mediterránea

La montaña mediterránea es un paisaje en mosaico formado por algunos fragmentos remanentes de bosque autóctono, rodeados por parches con vegetación que proceden de la degradación del bosque, con dos tipos de manejo humano que son en cierta medida opuestos. Por una parte, aunque el fuego pueda ser un componente natural de estos sistemas (Ojeda 2001), las actividades humanas han acrecentado su periodicidad y extensión. Tras un incendio, la vegetación típica que se presenta es un matorral pionero, que en muchas ocasiones ve restringida su sucesión hasta estadios más maduros. Por tanto, la vegetación se queda estancada en una misma composición de especies (fenómeno designado como autosucesión por Hanes en 1971). Uno de los principales inconvenientes para la regeneración de estos matorrales pioneros es que la falta de sombra debida a la ausencia de árboles adultos incrementa la radiación en el sotobosque, ejerciéndose un importante estrés para las plantas debido al daño fotoquímico (Valladares 2003) y a la reducción de la humedad del suelo.

Por otro lado, las talas intensivas, el roturado de la tierra con fines agrícolas y el sobrepastoreo han provocado la deforestación de muchas zonas. En los años 50 se llevaron a cabo muchas repoblaciones con coníferas, auspiciadas por una política forestal que primaba la producción maderera en lugar de crear bosques diversos. Hoy en día, muchas de estas masas forestales aparecen como bosques homogéneos, con poquísimas especies que componen la copa y en muchas ocasiones compuestas de especies introducidas. Además, el dosel de las repoblaciones es tan denso que incluso se puede restringir la llegada de la luz al sotobosque, con el consiguiente detrimento que esto supone para el crecimiento y supervivencia de los individuos que componen los estratos inferiores.

Objetivo general de la tesis y estructura en capítulos

Esta tesis doctoral tiene como objetivo general el conocer las limitaciones para la regeneración que se producen como consecuencia de la degradación del hábitat en un paisaje en mosaico mediterráneo. Para responder a esta pregunta, se adopta una aproximación mecanicista que analiza secuencialmente las fases del ciclo de regeneración (semilla-plántula-juvenil) de cada una de las especies que componen la comunidad de leñosas. En cada fase se identifican los principales factores abióticos y bióticos (interacciones planta-animal e interacciones planta-planta) que pueden limitar el éxito de transición a la fase siguiente, así como la magnitud de su variabilidad espacio-temporal. En este trabajo se consideran dos tipos principales de limitación (Clark et al. 1999; Nathan y Muller-Landau 2000; figura 1): limitación a la dispersión, que ocurre cuando el reclutamiento está limitado por un fracaso de la dispersión a sitios potenciales para el reclutamiento; y limitación al establecimiento, cuando el reclutamiento está limitado por factores bióticos o abióticos postdispersivos que afectan al establecimiento de nuevos individuos, independiente del número de semillas que llegan a un sitio. Analizamos el balance entre ambas limitaciones desde una perspectiva observacional, basada en mediciones relativas de la lluvia de semillas, establecimiento de plántulas y daños por herbívoros, y mediante una aproximación experimental, sembrando de semillas de todas las especies consideradas. Con esta aproximación pretendemos determinar el papel de las especies animales mutualistas (dispersantes de semillas) y antagónicas (predadores de semillas y herbívoros), así como del escenario abiótico (hábitats, veranos con distinta cantidad de lluvia), en el mantenimiento, regeneración de la diversidad y posible trayectoria sucesional de las comunidades de plantas en los ecosistemas forestales de montaña mediterráneos (Fig. 2). La comparación entre bosque autóctono, repoblaciones y matorral sucesional nos permitirá evaluar también los efectos demográficos de las prácticas y actuaciones forestales que se llevan a cabo en los paisajes Mediterráneos.

La originalidad de esta tesis doctoral radica en que es un estudio de comunidad que incluye explícitamente el papel de las interacciones planta-animal en la regeneración e incluye un marco de degradación de hábitats, en el que el distinto tipo de manejo humano (repoblaciones, incendios) ha conducido a un paisaje en mosaico. Por el contrario, todos los estudios anteriores de regeneración en la misma zona de estudio se han hecho considerando sólo al hábitat mejor conservado, el bosques autóctono de Pinus sylvestris subsp. nevadensis de Sierra Nevada, y además, utilizando una aproximación poblacional (Castro 1999; Gómez-Aparicio 2004; Puerta-Piñero 2008). Desconocemos por el momento cómo condicionan los distintos factores ecológicos a la regeneración natural en las repoblaciones y en el matorral sucesional, así como falta un enfoque de comunidad que englobe todas las especies leñosas y su interacción con los animales.

Área de estudio

La zona de estudio de todos los capítulos de esta tesis es el Parque Nacional de Sierra Nevada, en los alrededores del pico del Trevenque (Granada; 37º5' N, 3º28' W), entre 1600-1800 m de altitud. Esta zona es un paisaje en mosaico formado por tres tipos distintos de unidades de paisaje: bosque autóctono, pinares de repoblación y matorral sucesional post-incendio. Estas dos últimas proceden de la degradación del bosque autóctono original que estaba presente en la zona.

• Bosque autóctono

El bosque autóctono de pino albar de Sierra Nevada corresponde a la distribución más meridional del planeta de Pinus sylvestris. Esta población está aislada del resto y tiene una identidad genética distintiva (Hódar et al. 2003), habiendo sobrevivido a sucesivos períodos glaciares e interglaciares acantonadas en las montañas. Presentan además un estado de conservación muy aceptable, y constituyen una de las escasas representaciones de pinares de alta montaña aún existentes en el sur peninsular (Blanca y Morales 1991; Molero et al. 1992). Este cúmulo de circunstancias históricas y ecológicas ha propiciado que estos pinares hayan sido uno de los objetivos prioritarios en los programas de conservación, estando de hecho la población de Sierra Nevada protegida bajo el amparo de la declaración de Parque Nacional.

El bosque autóctono de pino albar ocupa el piso oromediterráneo nevadense, en el sector calizo de Sierra Nevada, con ombroclima subhúmedo (Martínez-Parras y Peinado 1987; Molero et al. 1992). La cobertura de copas es de aproximadamente un 30-40% como promedio. Las especies arbóreas acompañantes son el arce (Acer opalus subsp. granatense), el tejo (Taxus baccata), la encina (Quercus ilex) y el mostajo (Sorbus aria). El estrato arbustivo es rico y diverso, siendo frecuentes las especies productoras de fruto carnoso dispersado por animales como el enebro (Juniperus communis), la sabina (J. sabina), y numerosas especies de espinar como el majuelo (Crataegus granatensis), el endrino (Prunus ramburii), cerezo rastrero (P. prostrata), agracejo (Berberis hispanica) y diversas especies de rosas (Rosa spp.; para una descripción detallada de la flora y vegetación consúltese Martínez-Parras y Peinado 1987, Martínez-Parras et al. 1987 y Molero et al. 1992).

A pesar de que el bosque autóctono de pino albar de los alrededores del Trevenque (Sierra Nevada) está actualmente protegido, su reducida área de distribución lo hace muy vulnerable frente a perturbaciones frecuentes en los ambientes mediterráneos, como el fuego o las plagas, por lo que se considera en peligro de extinción (Blanca et al. 1998, Hódar et al. 2003). La extensión de estos pinares ha sufrido además una regresión constatable en tiempos recientes, y tanto Willkomm (1882) como Voigt (1889) denunciaron ya el declive de las poblaciones del área del Trevenque debido a las cortas de árboles para el carboneo. Además, el pinar está fragmentado en rodales de pequeño tamaño, con la consiguiente pérdida de conectividad, aumento de la relación perímetro/superficie, y amenaza para su persistencia. Este bosque relicto presenta dos grandes fuentes de amenaza: el actual clima mediterráneo, que no corresponde al clima presente en la época en la que se formó el bosque y que es adverso para el mantenimiento y desarrollo de poblaciones de especies boreo-alpinas como el pino albar o el tejo, y el cambio climático, prediciéndose para la región mediterránea un aumento de las temperaturas, una disminución de las precipitaciones y un aumento de su variabilidad (IPCC 2001, Moreno et al. 2005). Por lo tanto, es necesario un conocimiento científico profundo de los factores que están modulando la regeneración del pinar autóctono para poder diseñar actuaciones que favorezcan su recuperación, conservando así uno de los bosques más diversos y complejos de toda la Península Ibérica.

- **Pinares de repoblación**

Las repoblaciones de Sierra Nevada se practicaron en la década de 1950, utilizando especies de coníferas alóctonas, en concreto, el Pinus sylvestris subsp. iberica (cuando la subespecie autóctona es la nevadensis) y el Pinus nigra, que está fuera de su distribución natural en la zona de estudio.

Dichas repoblaciones han sufrido tres tipos distintos de manejo. Por una parte, la gran mayoría de la masa forestal se ha mantenido intacta desde la plantación, con lo cual aparece una masa muy densa de adultos conespecíficos (a lo largo de esta tesis, se denominará repoblación densa). No obstante, en el 2000 se produjo el aclareo de algunos parches de repoblación, reduciéndose la densidad de adultos a la mitad (repoblaciones aclaradas). El tercer tipo de manejo fue la exclusión frente a los grandes herbívoros que se llevó a cabo en algunos parches en 1982.

- **Matorral sucesional post-incendio**

El matorral sucesional post-incendio tiene una estructura abierta dominada por matorrales como Crataegus monogyna Jacq., Prunus ramburii Boiss., Salvia lavandulifolia Vahl., y E. anthyllis. También hay algunos individuos adultos dispersos que sobrevivieron a un fuego en 1983.

Diseño espacial de muestreo

De cada uno de estos cinco tipos de unidades de paisaje (bosque autóctono, repoblaciones densas, aclaradas y cercadas y matorral post-incendio) se seleccionaron tres parcelas. El tamaño de las parcelas oscila en torno 0.16 a 0.93 ha, con un tamaño medio de parcela de 0.53 ha, y una distancia media entre las parcelas del mismo tipo de unidad de paisaje de 687.7 m (Fig. 3).

Este diseño espacial recoge la estructura en mosaico de la zona de estudio, que constituye un experimento natural de perturbación forestal, ya que se conocen perfectamente los diferentes tipos de impacto (fuegos y repoblaciones), su distribución espacial y la fecha exacta en la que ocurrieron.

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CAPÍTULO 1

TITLE:
Seed limitation vs. establishment limitation of the woody plant community in a degraded Mediterranean landscape: implications for conservation

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ABSTRACT

Question: How does habitat degradation affect recruitment limitation and its components (seed limitation vs. establishment limitation) of woody plant communities in a Mediterranean landscape?

Location: 1600-1900 m a.s.l., Sierra Nevada National Park, Southern Spain. The landscape was a mosaic composed of native forest and two degraded landscape units: reforestation stands and shrubland.

Methods: We evaluated fruit production, seed rain, soil seed bank, seedling emergence, and seedling survival in two consecutive years with contrasting rainfall patterns. Seed and seedling data were used to calculate values of seed and establishment limitation.

Results: In general the woody community was both severely seed and establishment limited. Species were less seed limited in the landscape units with higher adult density (i.e. shrub species in shrubland, *Pinus* spp. in reforestation stands). On the contrary, degradation did not exacerbate establishment limitation, which was severe in all landscape units. This general pattern was modulated by the biogeographical distribution, dispersal type, and life form of the species. Boreo-alpine species were more limited in establishment than species with a typical Mediterranean distribution. Zoochorous species were less seed-limited in the landscape units preferred by dispersers (i.e. native forest). Tree species were more establishment-limited than shrub species, irrespective of the landscape unit. Seed limitation and especially establishment limitation varied among years, with establishment being almost nil in very dry years.

Conclusion: Degradation from human impact implies changes in the adult abundance of the woody plant community (trees and shrubs), thereby affecting seed limitation although establishment limitation was high in all landscape units. Conservation and restoration strategies should take into account the lack of tree recruitment in very dry years, especially for boreo-alpine species, as more aridity is expected under a climatic-change scenario.

Keywords

Acer opalus; *Pinus sylvestris*; land use change; regeneration dynamics; seed dispersal; *Sorbus aria*; *Taxus baccata.*

Nomenclature

Castroviejo et al. 1986, Valdés et al. 1987, and Blanca et al. 2002.

Who robbed the woods,
The trusting woods?
The unsuspecting trees
Brought out their burrs and mosses
His fantasy to please.
He scanned their trinkets, curious,
He grasped, he bore away.
What will the solemn hemlock,
What will the fir-tree say?

Emily Dickinson

INTRODUCTION

Human impact is so widespread throughout the Earth's ecosystems that most habitats undergo some type of degradation (Sanderson et al. 2002). Habitat loss as consequence of land use/land cover changes is a major driver of global change (Vitousek 1997; IPCC 2007), and is projected to have the largest global impact on biodiversity by year 2100 (Sala et al. 2000). Under this general context of habitat degradation, it is crucial to understand the recruitment limitations hampering the natural capacity of plant populations to recover (Jordano et al. 2004).

Most previous studies addressing recruitment limitations have examined well-conserved habitats, i.e. tropical (Dalling et al. 2002; Muller-Landau et al. 2002; Svenning & Wright 2005), temperate (Schupp & Fuentes 1995; Clark et al. 1998; Caspersen & Saprunoff 2005), boreal (Eriksson & Ehrlén 1992) or, more rarely, Mediterranean (Jordano & Herrera 1995; Hampe & Arroyo 2002; Rey et al. 2006). While these studies provide a general understanding of recruitment limitations when human impact is relatively low, case-specific studies focusing on habitat degradation are needed, because most aspects of structure and functioning of ecosystems cannot be understood without considering human influence (Vitousek et al. 1997; Hobbs et al. 2006).

If plant recruitment has severe limitations under natural conditions (Hurtt & Pacala 1995; Clark et al. 1998; Jordano & Herrera 1995; Jordano et al. 2004), the situation becomes even more critical in degraded habitats (Traveset et al. 2003). The standard approach to analyse recruitment limitation differentiates two components (Eriksson & Ehrlén 1992; Clark et al. 1998, 1999; Nathan & Muller-Landau 2000; Muller-Landau et al. 2002): 1) seed limitation, defined as the failure of seeds to arrive at all suitable sites, and 2) establishment limitation, defined as the reduced suitability of microsites to successful seedling establishment. The first component, seed limitation, can result from low density of adults, reduced adult fertility, and limited seed dispersal (Clark et al. 1998). The second component, establishment limitation, may derive from low seed survival and germination, as well as the failure of seedlings to emerge and to survive (Clark et al. 1998). Habitat degradation might translate as seed limitation by lowering the density and fecundity of parent trees (Gazhoul et al. 1998) and by altering dispersal patterns of frugivores (Da Silva et al. 1996). Analogously, human impact could translate as establishment limitation by altering physical factors (e.g. lower amount of soil humidity, nutrients, or light availability) and biotic ones (e.g. higher number of post-dispersal seed and seedling predators, pathogens, or competitors) that reduce microsite suitability for seedling emergence and survival.

Mediterranean ecosystems provide compelling case studies to determine the components that limit recruitment in degraded habitats, given that millennia of human presence have disturbed the 99.8% of all natural areas (Blondel 2006). Native forests have almost disappeared due to massive timber cutting, fires, cultivation, or herbivore pressure (Conacher & Sala 1998). The result is a patch mosaic of native vegetation and degraded habitats such as reforestation stands and shrublands (Zamora et al. 2001; Gómez-Aparicio et al. 2005) where mixed communities vary in their biogeographical distribution (Boreal-Alpine, Mediterranean, or European-North African), dispersal systems (zoochorous vs. non-zoochorous), and life forms (trees vs. shrubs). Different types of habitat degradation, biogeographical distribution, dispersal types, and life forms may impose diverging constraints on plant recruitment, eventually determining different successional trajectories towards forest recovery.

In Mediterranean ecosystems, contrary to temperate and tropical ones, empirical evidence supports the hypothesis that summer drought is the major limiting factor for seedling establishment among a wide diversity of habitats such as lowland forests (Traveset et al. 2003; Pulido & Díaz 2005), mountain forests (Herrera et al. 1994; Castro et al. 2005; Arrieta & Suárez 2006), shrublands (García 1999; Rey & Alcántara 2000), and semiarid systems (García-Fayos & Gasque 2006). The paradigm resulting from this ample data set assumes that the main limitation for establishment is recruitment, despite that early studies described seed-dispersing animals as “habitat shapers” in Mediterranean systems (Herrera 1985).

The objective of this study is to determine whether the magnitude of recruitment limitation in the entire woody plant community of a Mediterranean mountain is affected by habitat degradation. For this purpose, we evaluated adult density, fruit production, seed rain, soil seed bank, and seedling establishment of the woody community in three types of landscape units: native forest, reforestation stands, and shrubland. The first represents low degradation and thus is used as control, while the reforestation stands and the shrubland constitute two contrasting types of degraded habitats. Our general hypothesis is that recruitment would be more limited in degraded landscape units than in the native forest. Previous studies analyzing recruitment limitation along a gradient of habitat degradation focused on only one species, namely *Rhamnus ludovici-salvatoris* (Traveset et al. 2003), *Quercus ilex* (Pulido & Díaz 2005), or *Quercus suber* (Acácio et al. 2007). To date, no other study compares the relative importance of the two components of recruitment limitation (seed limitation vs. establishment limitation) using the entire woody-plant community, composed of trees and shrubs, except for tropical forests (see Dalling et al. 2002 and Muller-Landau et al. 2002).

Specifically, we seek to determine whether the relative importance of the two components of recruitment limitation (seed vs. establishment limitation) depends on 1) the type of degradation of the landscape unit, 2) the biogeographical distribution of the woody species (Boreal-Alpine, Mediterranean, or European-North African 3) the dispersal system (zoochorous vs. non-zoochorous) and/or, 4) the life form (tree vs. shrub). Results from this study will improve our understanding of the influence of habitat degradation on the magnitude and components of recruitment limitation at the community level, which in turn will serve in the design of conservation and restoration planning of native vegetation in Mediterranean ecosystems.

MATERIAL AND METHODS

Study area

The study was conducted from 2003 to 2005 at the locality of Trevenque, in Sierra Nevada National Park (37°05′ N, 3°28′ W, Granada, SE Spain). The bedrock is calcareous, with regosols and cambisols as predominant soil types (Delgado et al 1989, see also Castro et al 2005 for more information about the area). This mountain area has a continental Mediterranean climate, with cold winters and hot dry summers. The high inter-annual variability in rainfall of Mediterranean ecosystems (Rodó & Comín 2001) encouraged us to repeat this study in two consecutive years: 2004 and 2005. The first study year (2004) was considered as a normal year in terms of annual rainfall (750 mm yr^{1}), because it was included in the second quartile of a series 1958-2005 obtained from a meteorological station close to the study area; contrarily, 2005 (394 mm yr^{1}) was the driest year of that a 46-year series.

The study area is a patch mosaic composed of three different landscape units located from 1600 to 1900 m a.s.l.: 1) native forest (mixed pine forest); 2) reforestation stands; and 3) post-fire shrublands. Native forest is dominated by *Pinus sylvestri*s var. *nevadensis* Christ. mixed with other tree species such as *Taxus baccata* L., and the deciduous *Acer opalus* subsp. *granatense* Boiss. (hereafter *A. granatense*). The understory is composed of fleshy-fruited shrub species, principally *Berberis vulgaris* subsp. *australis* Boiss., *Crataegus monogyna* Jacq., *Juniperus communis* L., and *Lonicera arborea* Boiss. This native forest has an important conservation value because here the boreo-alpine species *T. baccata* and *P. sylvestris* subsp. *nevadensis* reach their southern distributional limit (Boratynski 1991, García et al. 2000). Both the reforestation stands and the shrubland came from the degradation of the native forest. Reforestation stands, planted in the 1950s, were dominated by *Pinus sylvestris* L., and *Pinus nigra* Arnold subsp. *salzmannii* (Dunal) Franco, mixed with scattered *Quercus ilex* subsp. *ballota* (Desf.) Samp., and the deciduous *Sorbus aria* (L.) Crantz. Reforestations have undergone three management types after plantation: 1) unmanaged (without any intervention after planting and therefore with a high density of trees); 2) cleared (where 50% of the trees were harvested in 2000); and 3) fenced (protected against ungulates since 1982 and with the similar tree density as in the unmanaged plots). Shrubland is an area where a fire in 1983 destroyed the existing forest. Currently, the shrubland has an open structure dominated by shrub species such as *Crataegus monogyna*, *Prunus ramburii* Boiss., *Salvia lavandulifolia* Vahl., and *Erinacea anthyllis* Link, plus some scattered trees that survived the fire.

Sampling design

We selected three plots per landscape unit. In the case of reforestation stands, the three plots were replicated for each kind of management (unmanaged, cleared, and fenced; n = 15 plots in total for all landscape units). Plot sizes were determined with a centimetre-precision GPS (Leica SR 500, Leica Geosystems, Switzerland) and sizes varied from 0.16 to 0.93 ha, with a mean size of 0.53 ha. The average distance between the three plots of the same landscape unit was 687.7 m. In native forest, we selected four microhabitats that represented the dominant vegetation: under the canopy of the two species of fleshy-fruited shrubs more abundant in each plot, under the canopy of *P. sylvestris*, and in open spaces without woody vegetation. In shrubland, we also selected four microhabitats: under the canopy of the three dominant shrub species (two had fleshy fruits and the other one dry fruits), and in open spaces. In reforestation stands, due to its homogeneous vegetation structure, we selected only one microhabitat: under pine trees (*P. nigra* and *P. sylvestris*). In all landscape units, we measured seed rain, soil seed bank, and seedling monitoring at 15 points per microhabitat and plot combination, called hereafter *sampling stations*. The total number of sampling stations in the study was 495 (180 in native forest, 135 in reforestation stands, and 180 in shrubland).

- **Composition and abundance of tree and shrub adults**

In each of the 15 plots, we determined the diversity and abundance of tree and shrub adults (i.e. reproductive individuals). In the case of tree species, we counted all the individuals present in each plot. To facilitate tree census, we split the plot surface in several sectors and we exhaustively count all the trees appearing in each sector. Due to the high shrub density, shrub adults were sampled using 10 transects of 25 x 2 m (n= 150) haphazardly distributed in each plot, sampling in total 7500 m^2.

- **Fruit production**

Fruit production, which normally starts in September and finishes in February of the following year, was estimated for tree species and the most abundant fleshy-fruited shrubs: *B. vulgaris*, *C. monogyna*, *J. communis*, *P. ramburii*, *Lonicera xylosteum*, and *Rosa* spp. We sampled 15 individuals per plot. Fruit production was visually estimated both study years throughout the fruiting season using the fruit abundance index (FAI). The FAI followed a logarithmic scale: 0= no fruits, 1=1-10 fruits, 2=11–100 fruits, 3=101–1,000 fruits, 4=1,001–10,000 fruits, and 5= > 10,001–100,000 fruits (see Saracco et al. 2004 for similar methods).

- **Seed rain**

We quantified seed rain using seed traps from October 2003 to April 2005 (two complete dispersal seasons). A pair of seed traps was located at each sampling station (n = 990 seeds traps). Because wild boars intensively root the ground under pine trees, we used two different models of seed traps: under pine trees, we used pots nailed to trees at 160 cm (and therefore out of reach of wild boars), and for the rest of microhabitats, we used aluminium trays nailed to the ground. Sampling surfaces of both types of traps were roughly similar (0.04 m^2). Both kinds of traps were protected against post-dispersal seed predation by a wire mesh of 1 cm grid size. We considered the seed rain sampled by the two seed-trap models to be roughly similar based on three arguments. First, in the case of wind-dispersed seeds (i.e. *Pinus* seeds), we assumed that the pine canopy was high enough to create a similar seed rain at 160-cm height as at ground level. Second, in the case of ornithochorous dispersal, as pot traps were nailed below the lower branch of the pines, birds would normally be above the seed trap. Last, none of the two models of seed traps collected seeds dispersed by mammals, because their faeces were larger than the grid size of the wire mesh. Traps were emptied three times per year and all the seeds, fruits, and seed-bearing fruit fragments collected were identified to the species level. For each species, the number of mature fruits was multiplied by the average number of seeds per fruit (when the total number of fallen fruits was higher than 30 within a species) or fruits were opened and the number of seeds counted (less than 30 fallen fruits).

- **Soil seed bank**

In July 2003, we took 495 soil cores (8 cm in diameter by 16 cm in depth) at each sampling station using a bucket auger. Each soil core was mixed with vermiculite (to maintain sample wetness), spread 1.5 cm deep in a tray, and exposed to light in a field nursery placed in the study area. Samples were kept moist with automatic daily watering. Seed contamination from adjacent woody plants was avoided by the use of a white net (1 mm mesh) that allowed the light passage but excluded external seed input. Seedling emergence was monitored regularly during the growing season from July 2003 to November 2004 (five months after the last recorded seedling emergence). After 16 months of soil exposure, only 8 seedlings of woody species were found in the trays, all *Crataegus monogyna*. Therefore, we assumed that woody species in our study area do not have a permanent soil seed bank, emerged seedlings coming from a transient seed bank that belonged to the seed production of the season. Despite that species of *Fagaceae* and a few other families found in the soil seed bank produce innately dormant seeds which can be germinated following heat shock treatments which simulate the effects of fire (Bell et al. 1993), we performed none of these treatments because such methods were beyond the aim of the study. Due to the lack of data, the soil seed bank was not included in any statistical analyses.

- **Seedling emergence and survival**

Seedling emergence and survival were monitored using two 1-m^2 quadrats per sampling station, located close to each pair of seed traps. Seedling emergence was registered once per year at the beginning of the spring (May-June). That date was chosen to ensure that most seedlings were emerged. Emerged seedlings were individually tagged and their survival was monitored once per year at the end of the summer (one week after the first rainfall of the autumn was registered, happening in September-October). In the case of seedlings that emerged in 2004 and remained alive at the end of the summer, we monitored their survival until autumn 2005.

Data analyses

- **Density of adults, seeds and seedlings**

We calculated density values using summed data (seeds, emerged seedlings, or seedlings that survived the first and second summer) per plot in each landscape unit and year. In the case of adults, we divided the number of individuals in each plot to the area plot. For seeds and seedlings, we divided data to the summed area of seed traps or seedling quadrats. Density values were compared between landscape units for each species and year using Generalized Linear Models, with a Poisson distribution for the response variable and a logit link.

- **Fruit production**

The variation in fruit production between years and landscape units was compared using Generalized Models, with an ordinal multinomial distribution for the response variable (FAI) and a logit link.

- **Components of recruitment limitation**

The two components of recruitment limitation (seed and establishment limitation) were calculated separately for each study year, landscape unit, and species. First, they were calculated separately for each of the three types of reforestation stands (unmanaged, cleared, and fenced). However, since values were similar between management types, we decided to pool the data for the calculation of recruitment limitations in reforestation stands (i.e. considering the 9 plots). Limitations were also calculated separately for each tree species. The genus *Quercus* (5% of adult abundance) was excluded from all analyses because our seed traps were not suitable for sampling its seed rain (wire mesh was not wide enough to allow acorn pass, and jay, the main disperser of the species, buries acorns in ground; see Gómez 2003 for further details). For shrubs, we considered that the dispersal mode was more relevant to the community structure than species identity; therefore, we performed separate analyses for summed data of fleshy-fruited (zoochorous dispersal) or dry-fruited (non-zoochorous) species. The values of the components of recruitment limitation ranged from 0 (no limitation) to 1 (maximum limitation). Taking into account the results of previous studies using the same methodology (Dalling et al. 2002; Muller-Landau et al. 2002; Gómez-

Aparicio et al. 2007), we have considered seed and establishment limitation to be high for values > 0.8, intermediate for 0.2 – 0.8, and low < 0.2.

- **Seed limitation**

For each combination of landscape unit, tree species, dispersal mode of shrubs, and year, seed limitation was calculated as the proportion of sampling stations not receiving seeds (Nathan & Muller-Landau 2000; Muller-Landau et al. 2002) at the 0.08-m^2 (pair of seed traps per sampling station). Seed limitation calculated in this way refers to “fundamental” limitation and assumes optimal conditions for seedling establishment, i.e. conditions under which an adult establishes at every site receiving one or more seeds irrespective of the environment (Nathan & Muller-Landau 2000; Muller-Landau et al. 2002). Seed limitation was calculated in every landscape unit, even if adults of a given species were absent, because this information is relevant to identify whether long-distance dispersal events happened in our mosaic landscape.

- **Establishment limitation and its components: emergence and survival limitation**

For each combination of landscape unit, tree species, dispersal mode of shrubs, and year, establishment limitation (defined as the proportion of sampling stations receiving seeds where seedlings do not establish; Nathan & Muller-Landau 2000; Muller-Landau et al. 2002) was calculated at the 2-m^2 scale. Establishment limitation was calculated based on the number of surviving seedlings in the quadrats at the end of the first summer because seed traps and seedling quadrats were adjacent and we assumed that seed rain in quadrats was equivalent to traps (see Muller-Landau et al. 2002; García et al. 2005 for the same methods). To understand further whether establishment limitation was due to limitations in spring emergence or limitations in first summer survival, we split establishment limitation into two components: 1) emergence limitation, defined as the proportion of sampling stations receiving seeds where seedling emergence in spring does not occur, and 2) survival limitation, defined as the proportion of sampling stations where seedlings are emerged and they do not survive the first summer. Our calculations of establishment limitation and its components assume that if establishment does not occur, it is because other factors than seed arrival constrained seedling emergence and/or survival, such factors being “realized” limitations (Nathan & Muller-Landau 2000; Muller-Landau et al. 2002). Data for seed rain October 2003-April 2004 and seedlings in autumn 2004 were used to calculate the establishment limitation and its components in 2004, whereas data for seed rain in October 2004-April 2005 and seedlings in autumn 2005 were combined to calculate the establishment limitation and its components in 2005.

We sampled seed and seedling data at different spatial scales due to the inherent difficulties of sampling seed density at the large scale needed to get representative seedling data (i.e. 2 m^2). As a result, seed limitation was calculated at a smaller spatial scale than establishment limitation, which could involve an underestimation of seed limitation values. To explore the magnitude of the underestimation, we calculated the proportion of seeds that produced established seedlings at the plot level (for each combination of landscape unit, tree species, dispersal mode of shrubs, and year), a quantitative approach defined as the establishment fraction by Clark et al. (1998).

$$\text{Establishment fraction} = \frac{1}{\text{number of plots}} \sum \left(\frac{\text{density of established seedlings}}{\text{density of seeds}} \right)$$

Analogously, the establishment fraction was divided in two components: 1) the emergence fraction, estimated as the average proportion of seeds that produced emerged seedlings at the plot level, and 2) the survival fraction, calculated as the average proportion of emerged seedlings that survived the first summer at the plot level. Since the establishment fraction and its components are based on densities, these indexes control the differential size of the seed and seedling data.

Values are given throughout this paper with mean ± standard deviation. All analyses were done using specific codes written for R 2.4.1 software (R Development Core Team 2006), or using STATISTICA 7.1 (StatSoft Inc. 2005).

RESULTS

Composition and abundance of tree and shrub adults

Sampled adults belonged to 36 species: 5 trees, 20 fleshy-fruited shrubs dispersed by animals, and 9 dry-fruited shrubs with ballistic dispersal (see Appendix 1 for the full list of species). Among landscape units, native forest showed intermediate densities of trees and shrubs, reforestation stands showed the highest density of trees and the lowest of shrubs, and shrubland the lowest density of trees and the highest of shrubs (Table 1).

The canopy of the three types of landscape units was dominated by *P. sylvestris*, but each type significantly differed in the adult density of this species (LRχ^2 = 1488.681; df= 2; $P < 0.001$): density was intermediate in native forest, very high in reforestation stands, and very low in shrubland (Table 1). The second most common species of the canopy, *P. nigra*, also showed higher density in reforestation stands than in shrubland (LRχ^2 = 199.1308; df= 1; $P < 0.001$), whereas it was absent in native forest. The other tree species had low densities and were confined to one type of landscape unit (*T. baccata* and *A. granatense* in native forest; *S. aria* in reforestation stands).

Shrub density significantly differed among landscape units, being highest in shrubland landscape unit for both functional type of shrubs (LRχ^2 = 906.23; df= 2; $P < 0.001$ for fleshy-fruited shrubs and LRχ^2 = 1411.35; df= 1; $P < 0.001$ for dry-fruited shrubs; Table 1). The understory in native forest and reforestation stands was dominated by fleshy-fruited shrubs, whereas the shrubland understory was composed mainly of dry-fruited shrubs.

Fruit production

Fruit production was significantly higher in 2004 than in 2005 (LRχ^2 = 42.33; df= 1; $P < 0.001$; all species pooled). All species had an average fruit abundance index (FAI) greater than 1 both study years, except *B. hispanica* and *P. ramburii* in 2005 and *P. nigra* both years. *P. sylvestris* (LRχ^2 = 93.09; df= 1; $P < 0.001$), *B. hispanica* (LRχ^2 = 116.15; df= 1; $P < 0.001$), *Crataegus* spp. (LRχ^2 = 6.32; df= 1; $P < 0.05$), L. xylosteum (LRχ^2 = 17.84; df= 1; $P < 0.001$),

Table 1. Density values (mean ± standard deviation) of adults, dispersed seeds, emerged seedlings, and established seedlings of all studied species or functional groups. *None* means that density was 0. Different letters indicate significant differences among landscape units for each species and year combination (lack of letter indicates insufficient data for analyses).

			TREE SPECIES					FUNCTIONAL GROUPS OF SHRUBS			
Density values	Year	landscape unit	*P. sylvestris*	*T. baccata*	*P. nigra*	*A. granatense*	*S. aria*	Fleshy-fruited shrubs	Dry-fruited shrubs	All trees	All shrubs
Adults (indiv/ha)											
		Native forest	83.25 ± 9.03^{a}	16.85 ± 27.94	none	10.90 ± 17.64	none	350.27 ± 268.65^{a}	19.00 ± 12.73^{a}	100.10 ± 19.08^{a}	362.93 ± 278.73^{a}
		Reforestation	593.32 ± 264.59^{b}	none	188.35 ± 196.75^{a}	none	0.27 ± 0.81	94.91 ± 69.67^{b}	none	781.95 ± 289.87^{b}	94.91 ± 69.97^{b}
		Shrubland	23.59 ± 14.78^{c}	none	12.04 ± 12.94^{b}	none	none	1141.47 ± 495.35^{c}	2260.27 ± 967.39^{b}	35.63 ± 26.29^{c}	3401.73 ± 562.45^{c}
Seeds (seeds/m^{2})											
	2004	Native forest	55.37 ± 38.34^{a}	3.70 ± 6.42^{a}	none	3.09 ± 5.19^{a}	0.19 ± 0.19^{a}	76.07 ± 34.11^{a}	4.44 ± 4.19^{a}	62.35 ± 33.9^{a}	78.21 ± 33.47^{a}
		Reforestation	177.61 ± 112.82^{b}	none	7.24 ± 4.14^{a}	0.08 ± 0.25^{b}	0.33 ± 0.39^{a}	8.54 ± 6.46^{b}	2.55 ± 4.48^{b}	185.27 ± 110.53^{b}	10.85 ± 7.01^{b}
		Shrubland	1.11 ± 0.49^{c}	0.06 ± 0.11^{b}	4.94 ± 8.23^{b}	0.37 ± 0.49^{c}	none	66.48 ± 39.73^{c}	122.78 ± 47.73^{c}	6.48 ± 7.54^{c}	179.2 ± 21.74^{c}
	2005	Native forest	30.43 ± 25.03^{a}	3.64 ± 6.31	none	41.54 ± 71.95^{a}	0.06 ± 0.11	86.42 ± 80.28^{a}	0.43 ± 0.6^{a}	75.68 ± 96.94^{a}	86.85 ± 79.92^{a}
		Reforestation	81.4 ± 66.07^{b}	none	2.8 ± 4.67^{a}	none	none	6.37 ± 8.57^{b}	0.08 ± 0.25^{b}	84.2 ± 65.12^{b}	6.45 ± 8.52^{b}
		Shrubland	2.96 ± 2.96^{c}	none	0.43 ± 0.39^{a}	0.49 ± 0.39^{b}	none	147.09 ± 97.9^{c}	33.52 ± 18^{c}	3.89 ± 2.96^{c}	180.61 ± 88.43^{c}
Emerged seedlings (seedlings/m^{2})	2004	Native forest	0.09 ± 0.02^{a}	none	none	0.06 ± 0.10^{a}	0 ± 0.01^{a}	0.65 ± 0.13^{a}	0.12 ± 0.18^{a}	0.15 ± 0.11^{a}	0.78 ± 0.05^{a}
		Reforestation	3.32 ± 3.51^{b}	none	none	0 ± 0.01^{b}	0.01 ± 0.02^{a}	0.31 ± 0.24^{b}	0.10 ± 0.21^{b}	3.33 ± 3.53^{b}	0.42 ± 0.29^{b}
		Shrubland	none	none	none	0.01 ± 0.01^{b}	none	1.70 ± 0.08^{c}	0.06 ± 0.04^{c}	0.01 ± 0.01^{c}	1.76 ± 0.10^{c}
	2005	Native forest	none	none	none	none	0 ± 0.01	0.01 ± 0.01^{a}	none	none	0.01 ± 0.01^{a}
		Reforestation	0 ± 0.01	none	none	none	none	0.02 ± 0.04^{a}	0 ± 0.01^{a}	0.00 ± 0.01	0.03 ± 0.04^{a}
		Shrubland	none	none	none	none	none	0.17 ± 0.30^{b}	0.01 ± 0.01^{a}	none	0.18 ± 0.31^{b}
Seedlings established after the first summer (seedlings/m^{2})	2004	Native forest	0 ± 0.04^{a}	none	none	0.03 ± 0.05	none	0.22 ± 0.13^{a}	0.04 ± 0.04^{a}	0.03 ± 0.05^{a}	0.25 ± 0.09^{a}
		Reforestation	0.03 ± 0.05^{a}	none	none	none	0.01 ± 0.01	0.18 ± 0.45^{b}	0.05 ± 0.12^{b}	0.03 ± 0.05^{b}	0.23 ± 0.22^{b}
		Shrubland	none	none	none	none	none	1.09 ± 0.05^{c}	0.03 ± 0.02^{ab}	none	1.11 ± 0.07^{c}
	2005	Native forest	none	none	none	none	none	none	none	none	none
		Reforestation	none	none	none	none	none	0.00 ± 0.01	none	none	0.00 ± 0.01
		Shrubland	none	none	none	none	none	0.05 ± 0.09	none	none	0.05 ± 0.09
Seedlings established after the second summer (seedlings/m^{2})		Native forest	none	none	none	0.01 ± 0.02^{a}	none	0.03 ± 0.02^{a}	0.03 ± 0.03^{a}	0.01 ± 0.02^{a}	0.06 ± 0.03^{a}
		Reforestation	0 ± 0.01	none	none	none	0 ± 0.01	0.07 ± 0.03^{ab}	0.05 ± 0.08^{a}	0.01 ± 0.02^{a}	0.11 ± 0.09^{b}
		Shrubland	none	none	none	0.01 ± 0.02^{a}	none	0.29 ± 0.31^{c}	0.01 ± 0.01^{a}	0.01 ± 0.02^{a}	0.30 ± 0.30^{c}
dispersion type			anemochory	zoochory	anemochory	anemochory	zoochory	zoochory	ballistic	—	—

and *P. ramburii* (LRχ^2 = 93.03; df= 1; P < 0.001) significantly differed in fruit production between the two study years, with higher estimates in 2004 than in 2005. Differences in FAI were not significant for *P. nigra*, *J. communis* or *Rosa* spp. Fruit production significantly differed among landscape units, following the same pattern both study years (LRχ^2 = 56.40; df= 2; P < 0.0001 in 2004; LRχ^2 = 178.73; df= 2; P < 0.0001 in 2005; all species pooled): shrubland > native > reforestation stands.

Seed limitation

A total of 14,300 seeds were collected during the two study years: 5700 seeds of trees, 6000 of fleshy-fruited shrubs, and 2600 of dry-fruited shrubs. With all tree species pooled, seed limitation was intermediate in native forest (0.2 – 0.6; Fig. 1), low in reforestation stands (< 0.2), and high in shrubland (> 0.8) in both study years. Seed density of tree species was inversely correlated with seed limitation and it significantly differed between landscape units in both study years (LRχ^2 = 917.60 in 2004; LRχ^2 = 1516.40 in 2005; df= 2; P < 0.001; Table 1). For shrub species, seed limitation was also intermediate in native forest (0.3 – 0.6), but it was higher in reforestation stands (0.6 – 0.8) and lower in shrubland (< 0.3), the opposite pattern of trees in the degraded landscape units. Seed density of shrub species was inversely correlated with seed limitation and significantly differed between landscape units in both study years (LRχ^2 = 7257.64 in 2004; LRχ^2 = 7777.102 in 2005; df= 2; P < 0.001).

Seed limitation of the dominant species of the canopy, *P. sylvestris*, was intermediate in native forest (0.25 – 0.75), low in reforestation stands (< 0.2), and high in shrubland (> 0.85) in both study years. For the rest of tree species, seed limitation was very high in all landscape units (> 0.75; Fig. 1), with the only exception of *P. nigra* in reforestation stands in 2004 (0.61 ± 0.21). Fleshy-fruited shrubs showed intermediate values of seed limitation in all landscape units and years (0.25 – 0.75), except in reforestation stands in 2005, when the limitation was high (0.81 ± 0.12). Dry-fruited shrubs had higher values of seed limitation in reforestation stands and native forest (> 0.75) than in shrubland (0.6 – 0.7).

Table 2. Values of emergence and survival limitation (mean ± standard deviation) for each studied species or functional group. *None* means that no seed was collected in the seed traps and therefore we could not calculate limitation values. When mean values are shown without standard deviation, it indicates that seeds were collected only in one of the plots of the landscape unit.

			TREE SPECIES				**FUNCTIONAL GROUPS OF SHRUBS**			
	landscape unit	*P. sylvestris*	*T. baccata*	*P. nigra*	*A. granatense*	*S. aria*	Fleshy-fruited shrubs	Dry-fruited shrubs	All trees	All shrubs
Emergence limitation										
2004										
	Native forest	0.86 ± 0.06	1	none	0.69 ± 0.44	0.75 ± 0.35	0.43 ± 0.11	0.37 ± 0.55	0.76 ± 0.14	0.36 ± 0.05
	Reforestation	0.35 ± 0.35	none	1 ± 0	0	0.25 ± 0.5	0.26 ± 0.21	0.25 ± 0.5	0.35 ± 0.35	0.23 ± 0.21
	Shrubland	1 ± 0	1	1 ± 0	0.83 ± 0.24	none	0.25 ± 0.14	0.8 ± 0.14	0.96 ± 0.07	0.42 ± 0.13
2005										
	Native forest	1 ± 0	1	none	1	0	0.97 ± 0.05	1 ± 0	0.98 ± 0.03	0.97 ± 0.05
	Reforestation	0.98 ± 0.05	none	1 ± 0	none	none	0.87 ± 0.23	0.97 ± 0.05	0.99 ± 0.04	0.82 ± 0.26
	Shrubland	1 ± 0	none	1 ± 0	1 ± 0	none	0.97 ± 0.05	1 ± 0	1 ± 0	0.91 ± 0.15
Survival limitation										
2004										
	Native forest	0.94 ± 0.10	none	none	0.38	1	0.47 ± 0.3	0.57 ± 0.1	0.77 ± 0.27	0.45 ± 0.28
	Reforestation	0.96 ± 0.10	none	none	1	0.33 ± 0.58	0.14 ± 0.03	0.39 ± 0.35	0.94 ± 0.09	0.41 ± 0.4
	Shrubland	none	none	none	0	none	0.47 ± 0.3	0.57 ± 0.1	0	0.19 ± 0.1
2005										
	Native forest	none	none	none	none	1	1	none	1	1
	Reforestation	1	none	none	none	none	0.36	1	1	1
	Shrubland	none	none	none	none	none	1	none	none	0.42

Establishment limitation

A total of 2050 emerged seedlings were sampled during the two study years: 950 were seedlings of trees, 1000 of fleshy-fruited shrubs, and 100 of dry-fruited shrubs. With all tree species pooled, establishment limitation was above 0.8 (Fig. 1) in all landscape units in 2004 (normal year), whereas it was complete in 2005 (very dry year). Accordingly, the density of tree seedlings established after the first summer was very low in all landscape units in 2004 and nil in 2005 (Table 1). Shrub species showed intermediate values of establishment limitation in all landscape units in 2004 (0.55 – 0.65; Fig. 1), but they were very high in 2005 (> 0.9). Density of shrub seedlings that were established after the first summer was much higher in 2004 than in 2005 (Table 1). Also, more shrub than tree seedlings survived the second summer (Table 1).

When the two components of establishment limitation (emergence and survival limitation) were compared, we found different patterns depending on the year and the life form. In 2004, tree and shrub species showed similar values of emergence and survival limitation in native forest (0.35-0.77), but these two components differed in the degraded landscape units (reforestations and shrublands). Recruitment was more limited in survival than emergence in reforestation stands, whereas the opposite pattern appeared in shrubland (Table 2). In 2005, emergence and survival limitation were very high (1 or close to 1) in all cases except for survival limitation of shrub species in shrubland (0.42).

The main component of the tree canopy, *P. sylvestris*, showed strong establishment limitation in all landscape units and years. Such limitation was due to survival more than to emergence (values of survival limitation close to 1, Table 2). *P. nigra* and *T. baccata* were completely collapsed in recruitment, as no emerged seedlings were found in any of the two study years. Despite that *S. aria* and *A. granatense* showed strong establishment limitation in both study years, these two species were the least limited of trees in 2004 (particularly *S. aria* in reforestation stands, and *A. granatense* in native forest and shrubland; Fig. 1). Recruitment of *S. aria* was more limited in survival than in emergence in 2004, whereas the opposite pattern was found for *A. granatense* in native forest (Table 2).

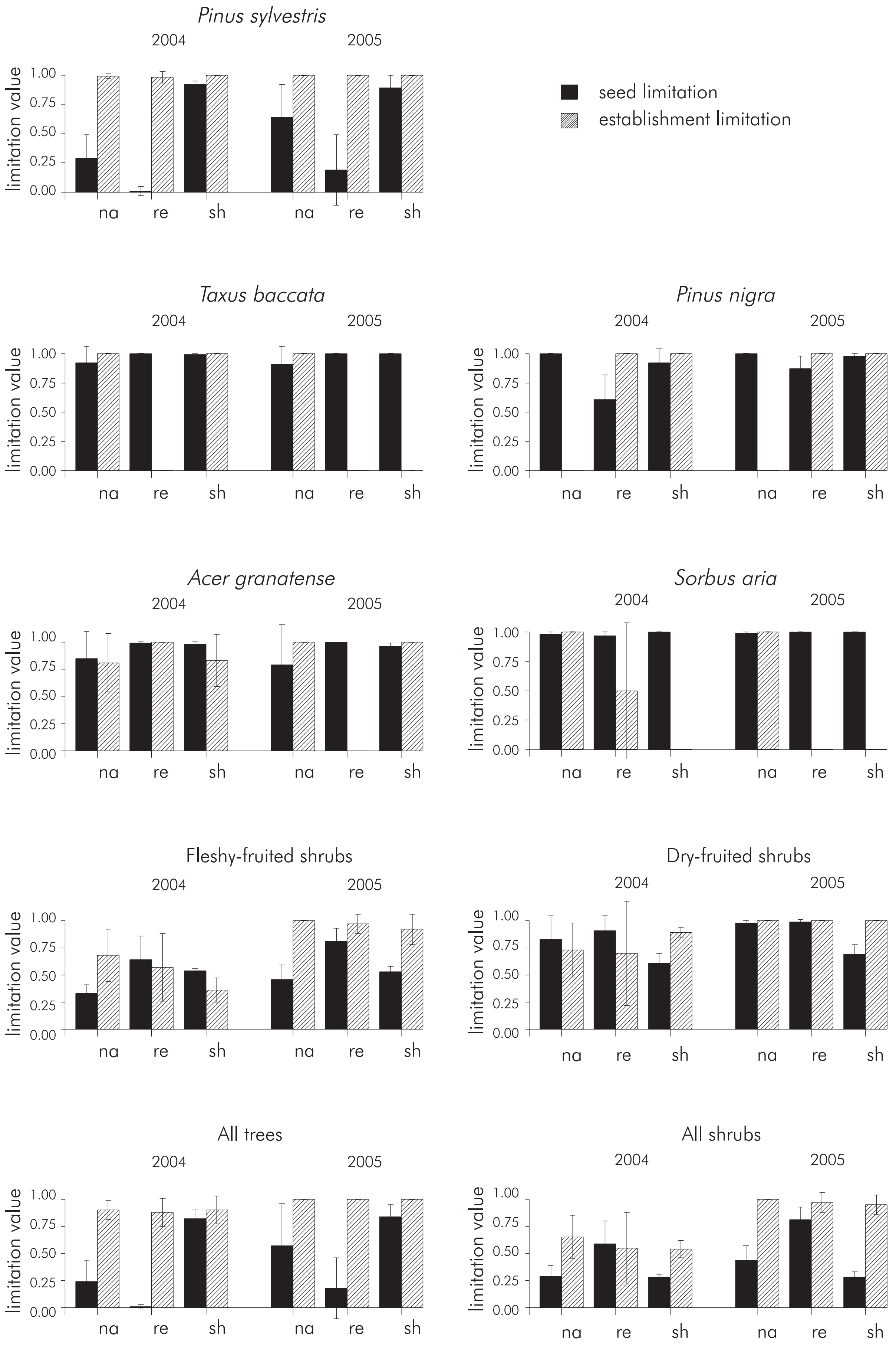

Figure 1. Seed and establishment limitation for each studied species or functional group in each landscape unit (na, native; re, reforestation stands; sh, shrubland). The first 3 groups of columns in each graph represent limitation values in 2004 (normal year) and the last three ones in 2005 (dry year).

Fleshy-fruited shrub species showed in all landscape units intermediate values of establishment limitation (0.35-0.75) in 2004 (normal year), while values were close to 1 in the very dry 2005 year (Fig. 1). Fleshy-fruited shrubs were the only species that recruited some seedlings in 2005, most of them appearing in shrubland. When the two components of establishment limitation were compared for fleshy-fruited shrubs, we found that survival limitation was stronger than emergence limitation in native forest and reforestation stands, whereas emergence limitation prevailed in shrubland (Table 2). Dry-fruited shrubs showed patterns similar to those of fleshy-fruited shrubs, but with higher limitation values in most cases.

Establishment fraction and its two components (emergence and survival fraction) had values of 0 or close to 0 for all species and landscapes units (Appendix 2). These results indicate that the density of collected seeds was much higher than the density of emerged or surviving seedlings in all cases, despite that sampling surface was smaller for seeds than for seedlings. Therefore, our estimates of seed limitation can be considered conservative, and we are confident that the main conclusions of our study are not affected by differences in sample size for seeds and seedlings.

DISCUSSION

In the context of worldwide human impact (Vitousek et al. 1997; Sanderson et al. 2002), we asked whether the magnitude of recruitment limitation was affected by habitat degradation. We found that the entire woody community under study, including the least degraded landscape unit (native forest), undergoes substantial recruitment limitation. When the relative importance of seed vs. establishment limitation was compared among landscape units, we found that seed arrival depended on the type of habitat degradation, whereas establishment limitation was high in all landscape units. Species-specific characteristics (such as the biogeographical distribution, the dispersal type, and/or the life form) also modified the relative importance of seed vs. establishment limitation. However, these spatial and species-specific patterns were detected only in the normal year, whereas in the dry year establishment completely collapsed in all landscape units and for all species. Here we discuss each of the different factors that influence the relative importance of seed vs. establishment limitation. Finally, the implications for the conservation of native forests in Mediterranean mountains are developed.

Influence of the type of degradation in the relative importance of seed vs. establishment limitation

The type of habitat degradation determined the composition and abundance of the tree and shrub community, thereby varying the relative importance of seed vs. establishment limitation. When human management increased densities of tree and/or shrub adults (i.e. *Pinus* spp. in reforestation stands; shrub species in shrubland), seed arrival was not a main limitation but rather the existence of suitable microsites for seedling establishment. Contrarily, when degradation implied a reduction in the number of adults as the consequence of fires or logging (i.e. all tree species in shrubland; shrub species in reforestation stands), recruitment was limited in seed arrival as well as in establishment. For example, in native forest, the most abundant species (i.e. *P. sylvestris*) had the main limitation for the recruitment in establishment instead of in seed arrival (Table 1, Fig. 1). Contrarily, rare species in the canopy of the native forest such as *A. granatense* and dry-fruited shrubs were both seed and establishment limited. Therefore, we found a consistent spatial pattern for the seed limitation inversely related to adult density, whereas establishment limitation was high in all landscape units.

However, the above-mentioned general pattern of spatial variation in recruitment depended on species-specific characteristics such as biogeographical distribution, dispersal type, and life form of each species, and was subjected to strong inter-annual variability.

Species-specific variability of seed vs. establishment limitation

- **Biogeographical distribution**

The woody community in the study area was biogeographically diverse, including boreo-alpine species being at the southern limit of their distribution

(*T. baccata* and *P. sylvestris*), sub-Mediterranean species with European-North African (*S. aria*) or Iberian-North African (*A. granatense*) distributions, and species with a typical Mediterranean distribution and requirements (*P. nigra* and all shrub species; Blanca et al. 2002). The relative importance of establishment limitation (compared to seed limitation) was much higher for boreo-alpine species than for the rest of the tree and shrub species. This result was presumably influenced by the fact that boreo-alpine species under Mediterranean climate undergo suboptimal climatic conditions that limit seedling emergence and survival (García et al. 2000; Hódar et al. 2003; Castro et al. 2004a, 2005). *T. baccata* represented an extreme case of establishment limitation, since no seedling emerged in either of the two study years. In fact, the results from an irrigation experiment conducted in the same study area indicated that seedlings of *T. baccata* required high soil-water content to emerge (Chapter 3), a condition not met in either of the two study years. Surprisingly, we failed to find any emerged seedling of *P. nigra*, despite its Mediterranean distribution. This result might be influenced by the fact that this species is out of its natural distribution range, as it appears in the study area only in reforestation stands. Establishment limitation of *A. granatense*, *S. aria*, and shrubs (species with Mediterranean or sub-Mediterranean ecological requirements) was also high, but at least it was not completely precluded as for the rest of species.

- **Dispersal type**

The dispersal type influenced the spatial variation of seed vs. establishment limitation and uncoupled it from adult abundance. Species with wind and ballistic dispersal followed the general spatial pattern of higher seed limitation at lower adult densities, because dispersal distances are shorter (mainly for ballistic dispersal) and therefore seed arrival depends on the proximity of parents, as in *P. sylvestris* (Castro et al. 2004a) and *A. granatense* (Gómez-Aparicio et al. 2007). Nevertheless, in both study years we found dispersed *A. granatense* seeds in the shrubland, where parents were absent, indicating the existence of long-distance dispersal patterns for this species. Taking into account the overall seed limitation of *A. granatense*, such long-distance dispersal events are vital for forest expansion (Nathan 2006).

For species with zoochorous dispersal, seed limitation was not necessarily lower in landscape units with higher adult density. For example, fleshy-fruited shrubs had the lowest seed limitation in the native forest, despite that adult density was relatively low (especially when compared with shrubland). The native forest offers food and shelter to bird dispersers thanks to its high degree of structural heterogeneity (García et al. 2000). In addition, birds are important long-distance dispersers and their movements may also reduce differences in seed deposition among landscape units (García et al. 2005; Jordano et al. 2007). For this reason, we found seeds of zoochorous species in all landscape units, even when parents were absent or scarce (i.e., *S. aria* in the native forest). In this respect, reforestation stands act as a sink for the seeds of many fleshy-fruited shrubs and trees prone to dispersal by animal vectors from nearby native forest and shrublands.

- **Life form**

The relative importance of the two components of recruitment limitation (seed vs. establishment limitation) was consistent among life-form groups. Both the trees and the shrubs were in general more establishment- than seed-limited (Fig. 1). However, establishment limitation was stronger for trees than for shrubs, which recruited more seedlings in all landscape units. Despite that dry-fruited shrubs are normally considered pioneer species (Blanca et al. 2002), they were less successful in recruitment than were fleshy-fruited shrubs, which are normally assumed to be the dominant vegetation in intermediate successional stages. In addition, seedlings surviving the second year were mainly fleshy-fruited shrubs (81.6%).

Stronger establishment limitation for trees than shrubs indicates that the two contrasting strategies suggested for maintenance of populations (regeneration and persistence; Bond & Midgley 2001; García & Zamora 2003) may be operating in our communities. On the one hand, populations of fleshy-fruited shrub species seem to be maintained every year by regeneration (adults are replaced by seedlings), irrespective to climatic conditions, as they were able to recruit in very dry years. On the other hand, persistence by longevity is the maintenance strategy that is presumably operating in tree populations, particularly the more long-lived, mesic ones such as *T. baccata* and *P. sylvestris* (García & Zamora 2003). Tree failure to recruit seedlings in two years might not mean the local extinction of the species, thanks to their ability to survive for long periods under unfavourable recruitment conditions. This potential for persistence has been reported for some relict species in Mediterranean ecosystems (see García et al. 1999 for *J. communis* and Lázaro et al. 2006 for *Buxus balearica*), and this appears to be the survival strategy of our tree species. For example, *T. baccata* is one of the longest-lived trees in Europe, and thus the failure to find any seedling establishment in two years is inconsequential. Mature yews may live for thousands of years, and thus are perfectly capable of surviving in a system, even if they recruit only in exceptionally wet years that may occur only every ten (or even every hundred) years.

Temporal variability of seed vs. establishment limitation

We found that the temporal variability in rainfall overshadowed the spatial pattern of seedling establishment. In 2004, a year of normal rainfall, establishment limitation was high in all landscape units but not complete, as some species even showed intermediate limitation (i.e. fleshy-fruited shrubs in shrubland). In the very dry year (2005), recruitment almost completely collapsed: emergence was low and very few of the emerged seedlings survived. As a result, the only species that were able to recruit some seedlings in the dry year were fleshy-fruited shrubs. Moreover, since a soil seed bank of woody species is almost non-existent at our study area (see Marañón 2001 for similar results), seeds dispersed in the dry year did not have the possibility of germinating in following years under more favourable conditions (Jiménez & Armesto 1992).

Another source of temporal variability for recruitment is asynchronous fruit-production dynamics (Kelly & Sork 2002). Masting is a common pattern in Mediterranean plants (Herrera et al. 1998) and our results also show inter-annual variability in fruit production, with lower fruit production in general terms for the dry year. A decrease in fruit production related to drier conditions has been reported in tropical systems (Wright et al. 2005). However, our results indicate that all species produced fruits both study years (although pine-cone production was extremely low for *P. nigra*), so a lack of recruitment in very dry years is mainly a consequence of lack of suitability of microsites for establishment rather than reduced fruit production.

Because the current global-change scenario predicts harsher environmental conditions in the Mediterranean Basin (increased frequency of extreme droughts, greater irregularity of precipitation, and fire events for Mediterranean-climate regions; IPCC 2007; Moreno 2005), native forests are seriously threatened by a lack of recruitment. In this climatic scenario, a rainy summer, the only suitable "window of regeneration" for the more mesic species, will become even rarer than today. As fleshy-fruited shrub species were the only ones that recruited in very dry years, our results imply that all landscape units, irrespective of the degree of degradation, have a potential successional trend towards shrub dominance and arrested succession (Acácio et al. 2007).

Implications for the conservation and restoration of native forests

According to our results, degradation from human impact implies changes in the adult abundance of the woody plant community (trees and shrubs), thereby affecting seed limitation although establishment limitation was high in all landscape units. Recruitment in both "normal" and "very dry" years was more successful for species with Mediterranean distribution, zoochorous dispersal, and shrubby life form, with fleshy-fruited shrubs being the only species that recruited in very dry years. Furthermore, seedlings of fleshy-fruited shrubs are especially dominant in the two degraded landscape units: reforestation stands and shrubland. All these results signal a trend towards more abundance of fleshy-fruited shrubs in the overall mountain landscape.

As climatic change implies more aridity, the increased limitation for tree recruitment in dry years demonstrated in the present work should be taken into account in conservation strategies, because it signifies further threats for tree poplations, especially for boreo-alpine ones, which have a trend towards less abundance and more restricted distribution. These results have strong conservation implications, and even more so given that *T. baccata*, *P. sylvestris*, *A. granatense*, and *S. aria* are listed as "Vulnerable" in the IUCN (1994) and appear in the Red List of Threatened Vascular Plants of Andalusia (Blanca et al., 1998).

Where the existing type of degradation implies more severe seed limitation of a tree species through reduced adult abundance (i.e. *A. granatense* and *S. aria* in all landscape units; *Pinus* spp. in shrubland; *T. baccata* in reforestation stands and shrubland), management measures should prioritize the increase of seed availability. Foresters have long understood the need for an adequate seed supply for stand regeneration at logged sites (Clark et al. 1999 and references therein), the most successful techniques being seed-tree retention (Godman & Mattson 1976), soil scarification (Zaczek 2002), seed addition (Turnbull et al. 2000), or clear-cutting to increase light availability and consequently, fruit production (Greene et al. 2002). Also, management measures should be directed to enhance the attractiveness of landscape units for avian dispersers, as birds are the main dispersers of *T. baccata* and *S. aria*. These practices include logging to reduce the density of pine trees, or the planting of shrubs to increase food availability. To reduce establishment limitation of tree species (especially boreo-alpine species such as *T. baccata* and *P. sylvestris*), management measures should use or create appropriate microhabitats for seedling survival and growth. Many shrub species with fleshy fruits (*B. hispanica*, *Crataegus* spp.) or dry fruits (*S. lavandulifolia*, *Cytisus scoparius*) serve a nurse effect in Mediterranean mountains, boosting survival and overall performance of woody seedlings planted beneath in comparison with open interspaces (Gómez-Aparicio et al. 2004; Castro et al. 2004b). Therefore, the dominance in recruitment of shrubs could also benefit the establishment of many other tree and shrub species such as *P. sylvestris*, *T. baccata*, *A. granatense*, *Q. ilex*, *Q. pyrenaica*, *S. aria*, or *C. monogyna* (García et al. 2000; Gómez-Aparicio et al. 2004; Castro et al. 2006), which in turn would promote global diversity of the woody community, especially in the most degraded landscape units.

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Appendix 1. Complete list of all sampled species grouped according to their functional type. The first column provides the complete scientific name of the species following the taxonomy of Castroviejo (1986) when possible, or Valdés (1987) or Blanca (2002) for the rest of the species. The second column lists the dispersal system of each species: anemochorous, ballistic (autochorous) and zoochorous.

SPECIES	DISPERSAL TYPE
Trees	
Acer opalus subsp. granatense (Boiss.) Font Quer & Rothm.	Anemochorous
Pinus nigra subsp. *salzmannii* (Dunal) Franco	Anemochorous
Pinus sylvestris var. *nevadensis* Christ.	Anemochorous
Sorbus aria (L.) Crantz	Zoochorous
Taxus baccata L.	Zoochorous
Fleshy-fruited shrubs	
Amelanchier ovalis Medik.	Zoochorous
Berberis vulgaris subsp. *australis* (Boiss.) Heywood	Zoochorous
Cotoneaster granatensis Boiss.	Zoochorous
Crataegus granatensis Boiss.	Zoochorous
Crataegus monogyna Jacq.	Zoochorous
Hedera helix L.	Zoochorous
Juniperus communis L.	Zoochorous
Juniperus sabina L.	Zoochorous
Lonicera arborea Boiss.	Zoochorous
Lonicera xylosteum L.	Zoochorous
Prunus avium L.	Zoochorous
Prunus domestica L.	Zoochorous
Prunus ramburii Boiss.	Zoochorous
Pyrus communis L.	Zoochorous
Rhamnus alaternus L.	Zoochorous
Rosa canina L.	Zoochorous
Rosa pimpinellifolia L.	Zoochorous
Rosa sicula Tratt.	Zoochorous
Rosa stylosa Desv.	Zoochorous
Rubus ulmifolius Schott.	Zoochorous
Dry-fruited shrubs	
Adenocarpus decorticans Boiss.	Autochorous
Astragalus granatensis Lam.	Autochorous
Cytisus scoparius (L.) Link	Autochorous
Echinospartium boissieri (Spach) Rothm.	Autochorous
Erinacea anthyllis Link	Autochorous
Genista cinerea (Vill.) DC.	Autochorous
Ononis aragonensis Asso	Autochorous
Retama sphaerocarpa (L.) Boiss.	Autochorous
Salvia lavandulifolia Vahl.	Autochorous

Appendix 2. Values of emergence, survival, and establishment fraction (mean ± standard deviation) for each studied species or functional group. None means that no seed was collected in the seed traps and therefore we could not calculate fraction values. When mean values are shown without standard deviation, it indicates that seeds were collected only in one of the plots of the landscape unit.

		TREE SPECIES					FUNCTIONAL GROUPS OF SHRUBS			
	landscape unit	*T. baccata*	*P. sylvestris*	*P. nigra*	*A. granatense*	*S. aria*	Fleshy-fruited shrubs	Dry-fruited shrubs	All trees	All shrubs
Emergence fraction										
2004										
	Native forest	0	0 ± 0	none	0.01 ± 0.01	0.01 ± 0.01	0.01 ± 0.01	0.02 ± 0.02	0 ± 0	0.01 ± 0
	Reforestation	none	0.01 ± 0.01	0 ± 0	0.04	0.03 ± 0.02	0.03 ± 0.01	0.03 ± 0.02	0.01 ± 0.01	0.03 ± 0.01
	Shrubland	0	0 ± 0	0 ± 0	0.01 ± 0.01	none	0.03 ± 0.01	0 ± 0	0 ± 0	0.01 ± 0
2005										
	Native forest	0	0 ± 0	none	0	0.04	0 ± 0	0 ± 0	0 ± 0	0 ± 0
	Reforestation	none	0 ± 0	0 ± 0	none	none	0 ± 0.01	0.04	0 ± 0	0.01 ± 0.01
	Shrubland	none	0 ± 0	0 ± 0	0 ± 0	none	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Survival fraction										
2004										
	Native forest	none	0 ± 0	none	0.02	0	0.01 ± 0.01	0.02 ± 0.01	0.01 ± 0.01	0.01 ± 0.01
	Reforestation	none	0 ± 0	none	0	0.03 ± 0.02	0.02 ± 0.01	0.01 ± 0.02	0 ± 0	0.02 ± 0.01
	Shrubland	none	none	none	0.02	none	0.03 ± 0	0.02 ± 0.02	0.02	0.03 ± 0
2005										
	Native forest	none	none	none	none	0	0	none	0	0
	Reforestation	none	0	none	none	none	0.01± 0.01	0	0	0 ± 0.01
	Shrubland	none	none	none	none	none	0.01	0	none	0.01
Establishment fraction										
2004										
	Native forest	0	0 ± 0	none	0 ± 0.01	0 ± 0	0 ± 0	0.01 ± 0.01	0 ± 0	0 ± 0
	Reforestation	none	0 ± 0	0 ± 0	0	0.02 ± 0.02	0.01 ± 0.01	0.01 ± 0.01	0 ± 0	0.01 ± 0.01
	Shrubland	0	0 ± 0	0 ± 0	0 ± 0.01	none	0.02 ± 0.01	0 ± 0	0.01 ± 0.01	0.01 ± 0
2005										
	Native forest	0	0 ± 0	none	0	1	0 ± 0	0 ± 0	0 ± 0	0 ± 0
	Reforestation	none	0 ± 0	0 ± 0	none	none	0 ± 0	0	0 ± 0	0 ± 0
	Shrubland	none	0 ± 0	0 ± 0	0 ± 0	none	0 ± 0	0 ± 0	0 ± 0	0 ± 0

CAPÍTULO 2

TITLE:
Consistent pattern of habitat and species selection by post-dispersal seed predators in a Mediterranean mosaic landscape

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ABSTRACT

There is still little information on spatial-scale effects on post-dispersal seed predation, especially in mosaic landscapes. The aim of this study was to determine whether post-dispersal seed predation varied at the landscape scale depending on the type of habitat degradation and/or seed traits. Experimental seed removal was investigated in six Mediterranean woody plant species, four trees (*Pinus sylvestris*, *Quercus ilex*, *Acer opalus* subsp. *granatense*, and *Sorbus aria*) and two shrubs (*Berberis vulgaris* and *Crataegus monogyna*), in an extensively used mosaic landscape on the Sierra Nevada massif (SE Spain). Seed depots were distributed over two years in five differently degraded landscape units, each one with three plots: native forest, shrubland, and dense, cleared, and fenced reforestation stands. Predation was highest in fenced reforestation, native forest and shrubland, and lowest in dense and cleared reforestation stands due in part to a positive correlation between shrub cover and post-dispersal seed predation. However, the main factors driving post-dispersal seed predation were intrinsic to seeds, as species preference explained the most of the variance in our model for predation. Plant species ranking was *Quercus* > *Pinus* > *Sorbus* > *Berberis* > *Acer* > *Crataegus*. Both species- and spatial-selection patterns remained consistent through time. These findings are novel because they demonstrate for the first time that post-dispersal seed predation is temporally consistent in all habitats that comprise a mosaic landscape, whether native forest, reforestation stands, or successional shrubland.

Keywords

degraded habitats; field experiment; land use change; logistic regression; predator preference; Sierra Nevada.

INTRODUCTION

Post-dispersal seed predation is a limiting factor for natural regeneration of many forest ecosystems worldwide (Crawley 1992; Davidson 1993; Hulme 1993). In terms of plant populations, seed predators limit the abundance of seed banks and determine their spatial distribution, thereby having demographic consequences such as local extinction of species (Crawley 1992; Hulme 1996). From a community perspective, preferences of post-dispersal seed predators can modify composition and abundance of species inhabiting forests and shrublands (Hulme 1996; García et al. 2005).

There are two main sources of variability on post-dispersal seed predation: intrinsic to seeds, such as size, nutrient content, coat thickness, or toxic defences (Vander Wall 1994; Hulme 1994; Hulme & Hunt 1999; García et al. 2005); or extrinsic, such as the structure of the habitat where seeds are dispersed (Myster & Pickett 1993; Manson & Stiles 1998; Hulme 1997; Rey et al. 2002). In relation to these latter factors, most studies have analysed the variability of predation rates between microhabitats of the same landscape unit (Schupp & Fuentes 1995; Rey et al. 2002; Fedriani & Manzaneda 2005; García-Castaño et al. 2006). These field studies have provided strong evidence of a patchy structure of seed predation at a microsite scale within a given landscape unit. However, information on spatial-scale effects on post-dispersal seed predation at the landscape scale is still scarce (but see García et al. 2005).

Most predation studies at the landscape scale have been conducted under the habitat-fragmentation paradigm. The size reduction of the fragment and the edge effect have been related to predation pressure, which proved to be increased (Santos & Tellería 1994, 1997; Kollmann & Buschor 2003; Fleury & Galetti 2006; García & Chacoff 2007) or reduced (through changes in seed-predator abundances; Wyatt & Silamn 2004; Hanson et al. 2006) with fragment size. This conceptual approach of intact forest fragments immersed in a degraded matrix is based on the classical biogeographical island theory of MacArthur & Wilson (1967). However, it may be valid for recently fragmented areas in tropical and temperate systems, but not for landscapes where human impact is ancient and widespread, such as almost all Mediterranean ones. In these, disturbance by long and intense human presence has resulted in several phases of habitat degradation (Terradas 2001; Valladares et al. 2004). Therefore, Mediterranean landscapes do not correspond to a "fragment-matrix" structure of suitable habitats surrounded by inhospitable matrices, but rather they are mosaics composed of adjacent patches with different degrees of degradation and suitability for species (Wiens 1995; Duelli 1997). Despite the commonness of mosaic landscapes around the world as result of human impact (Turner et al. 2001), there are no explicit studies addressing the variability in post-dispersal seed predation in the overall landscape units of a mosaic landscape.

The aim of the present study was to determine whether post-dispersal seed predation varied at the landscape scale depending on the type of habitat degradation and/or seed traits. For this purpose, we experimentally evaluated seed removal in the different landscape units composing the mosaic landscape in Mediterranean mountains: native forest (the least degraded landscape unit), pine reforestation stands, and post-fire successional shrublands (these two latter coming from the degradation of the former). Our working hypothesis was that the composition and structure of the landscape unit (the spatial pattern) will affect the post-dispersal seed predation rate (the process, *sensu* Turner 1989). Different plant-species composition and structure of landscape units may impose diverging abundance and/or activity of predators, eventually determining different post-dispersal seed-predation rates. In particular, we sought to determine: 1) whether post-dispersal seed predation varied more depending on seed traits or the type of landscape unit, and 2) whether there was consistency in the two criteria (species *versus* landscape-unit selection) over time. The identification of landscape unit- and species-selection patterns, and their consistency through time, would provide a fuller understanding of the consequences of post-dispersal seed predation for the regeneration of the woody community in different landscape units comprising the mosaic landscape.

METHODS

Study area

The present study was conducted at Sierra Nevada National Park, surrounding the Trevenque Peak area (37° 5´N, 3° 28´W, Granada Province, SE Spain), in 2004 and 2005. The climate is Mediterranean mountain type, with hot dry summers and cold, snowy winters, and rainfall (818.1 mm year^{-1}, average 1990-2006) heaviest in autumn and spring. The bedrock is calcareous and the predominating soils are regosols and cambisols (Delgado et al. 1989). The study area is a mosaic landscape composed of five different landscape units located between 1600-1900 m a.s.l.: native forest, dense, cleared, and fenced reforestation stands, and shrubland. The first represents low degradation, while the reforestation stands and the shrubland constitute two contrasting types of degraded habitats. The native forest is mainly composed of *Pinus sylvestris* var. *nevadensis* Christ. mixed with other trees such as *Taxus baccata* L. or *Acer opalus* subsp. *granatense* Boiss. (mean tree density 114 trees ha^{-1}), and a dense shrubby understory composed of different fleshy-fruited shrub species (*Berberis vulgaris* subsp. *australis* Boiss., *Crataegus monogyna* Jacq., *Juniperus communis* L., and *Lonicera xylosteum* L.). Dense reforestation stands contain *Pinus sylvestris* L. and *Pinus nigra* Arnold subsp. *salzmannii* (Dunal) Franco with mean densities of 1041 individuals ha^{-1}. Fenced stands are reforestations with herbivore exclosure since 1982 and the same tree density as dense stands. In cleared reforestation stands timber was harvested in 2000, reducing tree densities to 521 individuals ha^{-1}. Shrubland is a post-fire area dominated by *Crataegus monogyna* Jacq., *Prunus ramburii* Boiss., *Salvia lavandulifolia* Vahl., and *Erinacea anthyllis* Link, with widely scattered trees (21 individuals ha^{-1}). Each landscape unit was represented by three plots of similar size (mean 0.53 ha), and an average distance between the three plots of the same landscape unit of 688 m. Plot areas were calculated by GIS using GPS

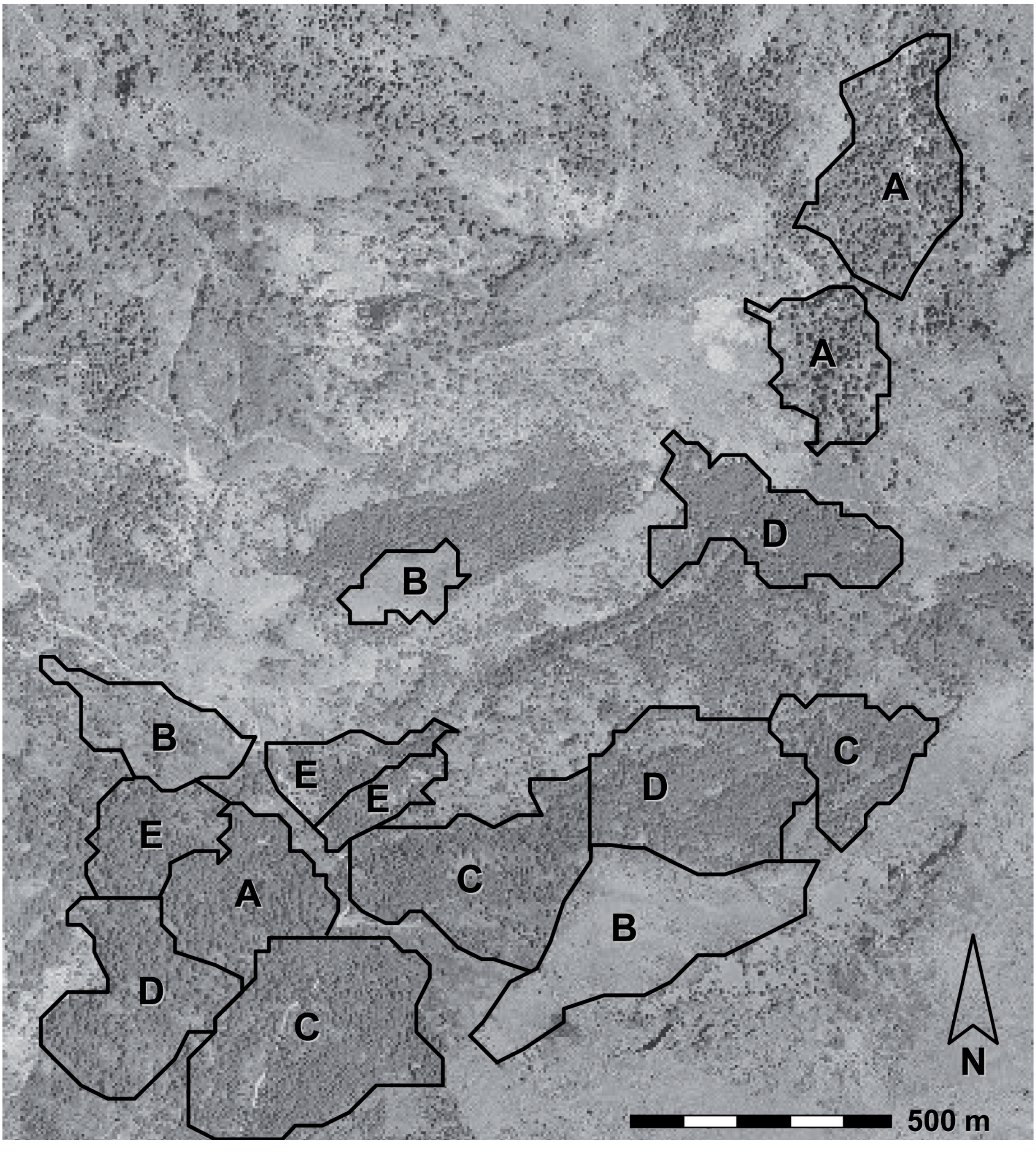

Figure 1. Map of the study area representing a mosaic landscape with adjacent patches comprised of habitats with different degrees of degradation. Each letter represents a different habitat type: A = native forest, B = shrubland, C = cleared reforestation stands, D = dense reforestation stands and E = fenced reforestation stands.

data (Leica SR 500; Leyca Geosystems, Switzerland). The five different landscape units were mixed, occupying an area of about 3 km^2 and were representative of the study area (Fig.1).

Study species

To quantify the predation rate, we used seeds of six woody species based on two arguments. First, these species were representative of the woody community appearing in the native forest of the study area, including four trees (*Pinus sylvestris* var. *nevadensis* Christ., *Quercus ilex* L., *Acer opalus* subsp. *granatense* Boiss, and *Sorbus aria* L.) and two shrubs (*Berberis vulgaris* subsp. *australis* Boiss. and *Crataegus monogyna* Jacq; hereafter all them will be called by their genus name). *Pinus* and *Quercus* are the dominant tree species, whereas *Berberis* and *Crataegus* are the dominant shrubs. *Quercus*, *Sorbus*, *Berberis*, and *Crataegus* are dispersed by vertebrates, whereas *Pinus* and *Acer* are wind-dispersed, and thus the sample included both anemochorous and zoochorous species, in addition to a broad array of different mechanical or toxic defences (Kollmann et al. 1998; García-Castaño 2001; García et al. 2005). Second, the size range of the seeds of the selected species (Mean ± SD; n = 100: *Quercus*, 5.078 ± 1.554 g; *Crataegus*, 0.742 ± 0.017 g; *Acer*, 0.042 ± 0.006 g; *Sorbus*, 0.022 ± 0.009 g; *Berberis*, 0.019 ± 0.004 g; *Pinus*, 0.012 ± 0.001 g) was representative of the size range of the whole community available for seed predators. All fruits were collected in the same study area in the previous autumn of each experiment trial, and seeds were extracted and stored at 4 °C until the field exposure.

Previous studies in the same study area (Castro et al. 1999, García et al. 2000, Gómez 2004a, 2004b) have reported by field observation and trapping that the community of seed predators is composed of *Apodemus sylvaticus* (woodmouse), small sized, and *Sus scrofa* (wild boar), large sized. *S. scrofa* only consume acorns of *Quercus* spp, whereas *A. sylvaticus* predates seeds of the six species used in our experiment. Consumption of seeds by birds on the ground is rare in our study area (no data recorded after bird censuses and focal observations for three years; *unpublished data*). Ants were not considered seed predators because during the experiment performance they were inactive.

Experimental design

Seed predation was quantified by recording removal of seeds of the six species offered simultaneously to predators in the field. Each experimental unit, a seed depot, was composed of two squares (20 x 20 cm) of plastic mesh pegged to the soil at 2 m one from each other. To each square of plastic mesh, two seeds of five species (*Acer*, *Pinus*, *Sorbus*, *Crataegus*, and *Berberis*) were glued with a low-odour thermoplastic adhesive (wind and rain resistant). Also, one *Quercus* acorn was placed next to the mesh (see Herrera et al. 1994, Alcántara et al. 2000, and García et al. 2005 for a similar procedure). This procedure was intended to mimic natural seed dispersal; *Quercus* acorns were partially buried, imitating activity of *Garrulus glandarius* (blue jay), while the rest of seeds were mixed with litter, simulating dispersal by wind or birds.

Seed depots were included in sampling stations. In reforestation stands, the only kind of microhabitat present was "under pine canopy", due to the high density and uniform distribution of planted pines. Therefore, we considered the sampling stations to be composed of the two meshes of each seed depot. By contrast, the native forest and shrubland had greater horizontal structural heterogeneity. Because it has been demonstrated that the predation rate changes between microhabitats of the same landscape unit (Hulme 1994; Manson & Stiles 1998; Russell & Schupp 1998), we considered this source of heterogeneity in forest and shrub habitats. Thus, in each landscape unit, sampling stations were composed of four seed depots, each one in the four dominant microhabitats. In the native forest, these were: under pine trees, under the two most abundant fleshy-fruited shrubs, and open areas. In shrubland, these were: under the canopy of *Crataegus*, *Prunus* and *Salvia*, and open areas. The overall design was: five landscape units (native forest; dense, cleared, and fenced reforestation stands; and shrubland), three plots per landscape unit, and 15 sampling stations per plot, making a total of 45 sampling stations per landscape unit. Seeds were exposed during winters 2004 and 2005 (March), after natural seed dispersal by wind and by zoochorous animals, and seed removal was monitored after 30 days.

For the overall 15 plots, the mean density of the exposed seeds was 0.013 ± 0.006 seeds m^{-2} for *Quercus*, and 0.025 ± 0.013 seeds m^{-2} for each one of the rest of species. This value was consistently lower than the natural seed rain for the studied species in the same areas (3-180 seeds m^{-2} depending on the species and the landscape unit; Mendoza et al. *in review;* Chapter 1), thereby avoiding attraction of predators due to increased seed density (García et al. 2007 and references therein).

We considered a seed to be depredated in two cases: when it was missing from the plastic mesh, or when it remained on the mesh but was gnawed and empty (García et al. 2005). During monitoring sessions, we identified predator when possible (rodent *versus* wild boar): gnaw marks on the seed coat and the presence of typical faeces were attributed to rodents, whereas visible damage to the soil due to rooting around the seed and characteristic faeces were assigned to *S. scrofa*.

A defining characteristic of each type of habitat degradation was the shrub cover within each landscape unit. In order to test its influence on seed predation, we measured shrub cover at each seed depot, using a 2-m radius circle centred in the seed depot and recording the percentage of the surface area covered by shrubs.

Data analysis

In the case of reforestation stands, we used the predation rate from the 15 sampling stations per plot, while in the case of native forest and shrubland, the 15 sampling stations were composed of four seed depots each, and we used the mean value of the seed depots per sampling station. Data were analysed with a logistic model using predation rate (proportion of the number of predated seeds to the total number of exposed seeds) as the response variable, binomial probability distribution (as each individual seed had a binary probability to be predated), and logit link function. The categorical predictors were species, year, and landscape unit and the continuous predictor was shrub cover. Interactions of shrub cover with the other predictors were not included in the model because they had not biological sense (as shrub cover was sampled only once for each seed depot where seeds of six species were exposed). We used the R_L^2 measure of explained variance (Menard 2000; Quinn & Keough 2002). Explained variance was calculated using the rate of the Wald χ^2 of each factor to the whole model G^2 variance (Zar 1999). JMP v. 7.0 (SAS Institute Inc. 2007) was used for data analysis.

RESULTS

From the total of cases when the predator was identified, 98.5 % of the predation was by rodents, and only the 1.5 % by wild boars (consistently acorn consumption), identifying rodents as the principal seed predators in our study system.

All the main effects considered (species, landscape unit, year, and shrub cover) were strongly significant separately (Table 1). The interactions between such main effects were significant in all cases except for the interaction between landscape unit and year. However, the explained variance of the triple interaction and of the interaction between species and year was very low (Table 1); therefore the effect was negligible.

Table 1. Results of the generalized linear model examining the significance of habitat, species identity, year, and the interactions among main factors on the seed predation rate. Binomial was the probability distribution, and logit the link function. Explained variance is calculated as the proportion of whole model variance (G^2) fitted by each factor (Wald χ^2).

Model effects	DF	Wald χ^2	*P*	Explained variance (%)
Species	5	4040.18	<0.0001	68.62
Year	1	127.91	<0.0001	2.17
Landscape unit	4	95.93	<0.0001	1.63
Shrub cover	1	26.25	<0.0001	0.44
Landscape unit × Species	20	214.36	<0.0001	3.64
Species × Year	5	43.55	<0.0001	0.74
Landscape unit × Year	4	8.31	0.08	0.14
Landscape unit × Species × Year	20	62.67	<0.0001	1.07

Whole model test: $G^2 = 5887.77$; $R_L^2 = 0.447$; d.f.= 60; $P < 0.0001$

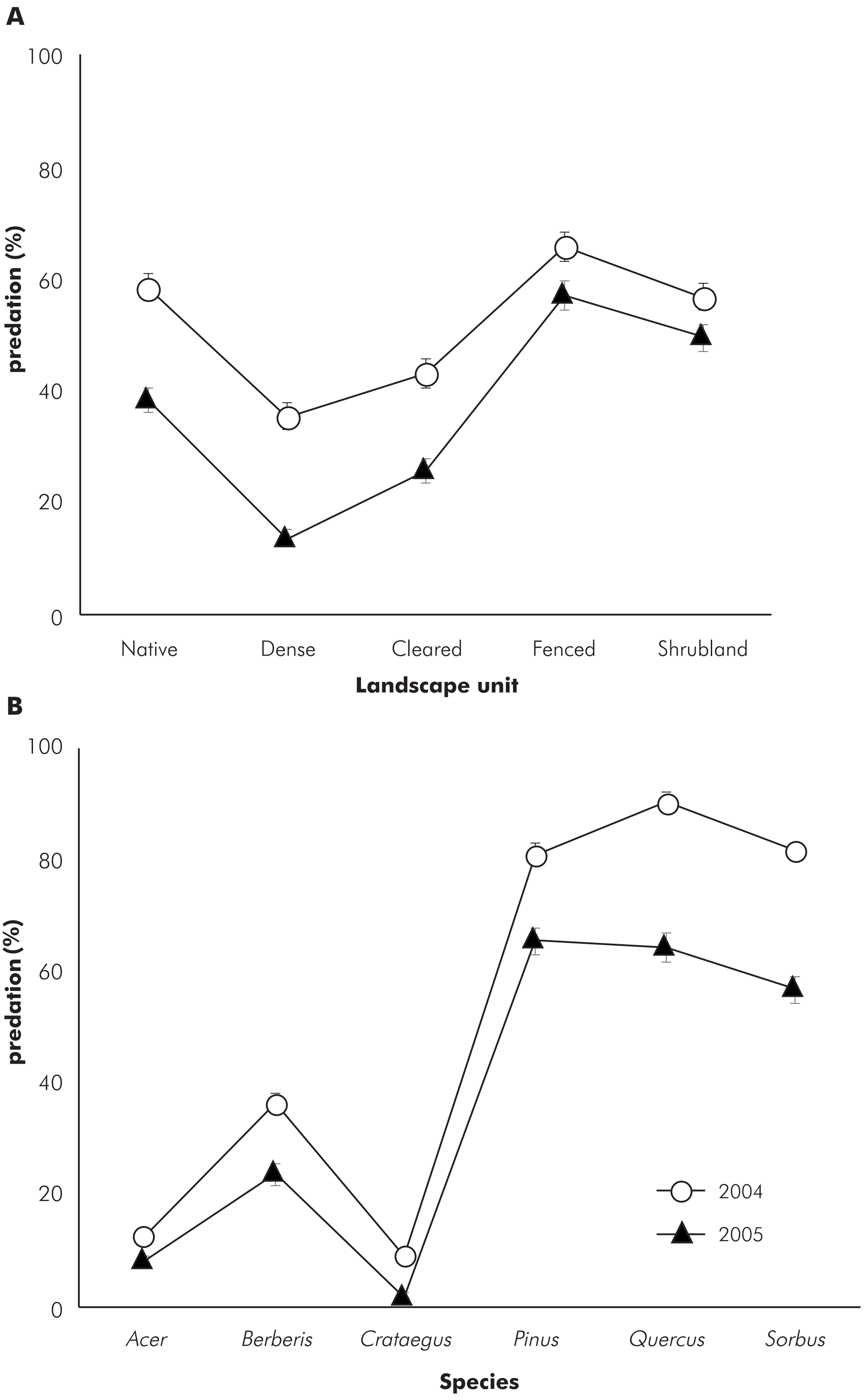

Figure 2. Mean predation percentage among landscape units (A) and species (B), differing between the two study years. Bars show ± 1 SE. Each point represents the mean predation percentage for the five landscape units or the six study species respectively.

The fenced reforestation stand was the landscape unit with the highest predation pressure (61.2 % ± 42.6 SD), followed by the shrubland (53 % ± 41.4 SD) and the native forest (48.3 % ± 38.7 SD), the lowest being in cleared (34.16 % ± 39.8 SD) and dense reforestation stands (24.4 % ± 36.1 SD; Fig. 2). The lack of significance between the interaction of landscape unit and year showed that this spatial pattern of seed predation was consistent through time (Fig. 2). Shrub cover had a significant effect over predation rate, although the variance explained by this effect was low (Table 1). Habitats with higher percentages of shrub cover -i.e. shrubland (36.6 % ± 3.6 SD of shrub cover), native forest (32.9 % ± 5.3 SD), and fenced reforestation stands (25.5 % ± 4.1 SD)– had higher predation rates compared than in landscape units where the shrub cover was scant, as in cleared reforestation stands (13.5 % ± 2.8 SD) and, particularly, dense reforestation stands (1.9 % ± 0.9 SD).

In terms of species, the most depredated was *Quercus* (77.4 % ± 35.6 SD), followed by *Pinus* (73.3 % ± 34.1 SD), and *Sorbus* (69.2 % ± 35.5 SD; Fig. 2). *Berberis* (30.1 % ± 30.7 SD) showed medium predation values, whereas *Acer* (10.4 % ± 16.9 SD), and *Crataegus* (5.5 % ± 14.2 SD) registered very low predation rates. Again, this pattern of species preferences was in general terms consistent through time, even if predation rates between years for *Acer* and *Crataegus* hardly differed (reflected in the significant interaction between species and year). The predation rate differed significantly between years, being higher in 2004 than in 2005 for all cases (Fig. 2).

DISCUSSION

Landscape unit selection

Classical approaches to landscape degradation based on a “fragment-matrix” concept assumed that intact fragments were surrounded by an unattractive matrix, differences in predation being determined by fragment size or edge effect (Burkey 1993; Orrock et al. 2003; Tallmon et al. 2003). On the contrary, in a mosaic-landscape approach there is no place for an unattractive matrix, because the landscape is composed of adjacent patches diverging in their degradation type (Wiens 1995). In fact, within our mosaic landscape, we found a consistent pattern that related landscape units to post-dispersal seed predation over time, indicating that the predation process was directly affected by the type of degradation in part through the abundance of shrubs. Presumably, shrubs offer shelter and food to rodents, the main predators, thereby increasing their abundance and activity (Simonetti 1989; Fedriani & Manzaneda 2005; Muñoz 2005; Mortelliti & Biotani 2006). Following this trend, the native forest (the least-degraded landscape unit) as well as shrubland showed heavy predation pressure (Fig. 2). We explain these results because in these landscape units the shrub cover was more dense, as well as there was higher heterogeneity of microhabitats. On the contrary, dense and cleared reforestation stands had the lowest values of seed predation. The low shrub cover in these landscape units resulted in less availability of safe sites for rodents (Muñoz 2005), and therefore these landscape units were unattractive for seed predators. Fencing dramatically boosted predation rates in reforestation stands due to an increase of the shrub understory and the reduction of natural predators of rodents and wild boars (Smit et al. 2001; Muñoz & Bonal 2007).

Species selection

In our predation model, species identity explained most of the variability in the predation rate (Table 1). This agrees with other many studies showing that the predation risk depends more on structural and biochemical characteristics of species than on the place where a seed is dispersed (Crawley 1992; Barnea et al. 1993; Hulme 1997; García-Castaño 2001). Our predation experiment revealed that rodents selected certain species, establishing a strong preference ranking: *Quercus* > *Pinus* > *Sorbus* > *Berberis* > *Acer* > *Crataegus* (Fig. 2). Species preference may be determined by intrinsic seed factors, such as the presence of toxins, nutrient contents or a thick coat (Kollmann et al. 1998; Rey et al. 2002), as well as seed size (Martínez et al. 2007; Mendoza & Dirzo 2007). In the case of *Berberis*, the relatively low predation rate found can be influenced by the presence of several toxins such as oxyacanthine, chelidonic acid, and isoquinoline alkaloid (Kollmann et al. 1998). The lowest predation rate of *Crataegus* is presumably because of the very thick seed coat of this species (García-Castaño 2001; García et al. 2005). That is, for similar sizes, seeds with a proportionally thicker coat are better defended, so they are less profitable for predators (in terms of higher seed-husking cost, Hulme 1993) than those with an embryo plus endosperm fraction surrounded by a thinner coat. Therefore, the absence of either a thick coat or toxins in *Pinus* and *Sorbus* may be one reason for their high predation values. *Quercus* was the most depredated species, presumably because it was also the heaviest seed of the six species and contained a high percentage of lipids, therefore representing a valuable resource for predators (Gómez 2004b). Also, this species was depredated by all the predators in the area (wild boar as well as rodents) so the predation risk was increased.

Spatial and temporal consistency of species-specific selection criteria

Strong post-dispersal predation pressure (average for all species and landscape units both years = 44 %) was found in the landscape mosaic of Sierra Nevada, similar to values found in other Mediterranean mountains such as Sierra de Cazorla (48 %; Herrera et al. 1994), Sierra Sur de Jaén (47 %; Alcántara et al. 2000), or temperate woodlands (51 %; García et al. 2005). However, this pressure of post-dispersal seed predation did not have the same magnitude between adjacent landscape units in a landscape mosaic. According to our results, predation pressure was higher in some landscape units (shrubland, native forest, and fenced reforestation stands) than in others (dense and cleared reforestation stands). Although differences between landscape units were significant, there was no significant interaction between year and landscape unit (Table 1), reflecting that the landscape unit pattern was consistent over time. Despite this, the total intensity of predation rates shifted among years, potentially opening windows for forest recruitment (Eriksson & Fröborg 1996), especially for the preferred species (*Pinus* and *Quercus*). The year 2005 was more favourable for seed survival than 2004, when predation intensity was very high and only a few seeds were available to create a seed bank. In the case of species-selection pattern, it was consistent over space and time in general terms; that is, in most cases, the same ranking of seed predation was maintained in each landscape unit every year except for *Quercus*, the most depredated species in all landscape units except in fenced reforestation stands (Fig. 3). This predation rate of *Quercus* undoubtedly decreased because of the exclusion (by fencing) of wild boar, one of the main acorn predators (Gómez et al. 2008). Similar consistent spatio-temporal patterns on species

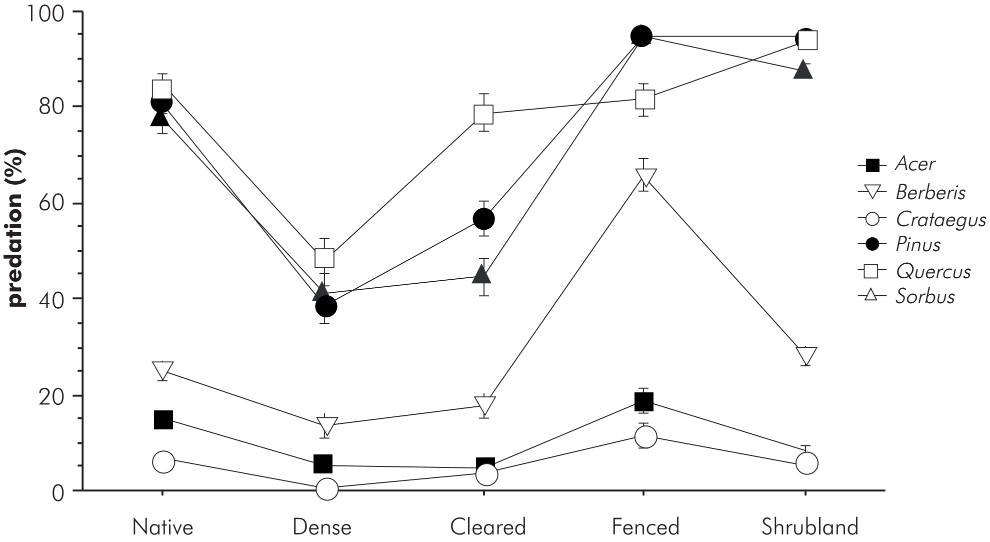

Figure 3. Differences in seed predation among habitats of the six study species. Bars show ± 1 SE. Each point represents the mean predation percentage of the three patches of each habitat.

preference can be found in other systems (Hulme 1997; Kollmann et al. 1998; Hulme & Borelli 1999; Rey et al. 2002).

Consequences for regeneration

Our results show that seed predation differed between adjacent landscape units of similar size, and that the intensity of predation depended more on seed characteristics than on the shrub coverage conforming in each landscape unit. More importantly, species- as well as spatial-selection patterns were consistent through time. Thus, our experimental results strongly support the contention that differences in the composition and structure of this Mediterranean mosaic landscape (the pattern) do affect the post-dispersal seed-predation rate (the process) in a predictable way at the landscape scale.

Consistent patterns of species selection by seed predators can have demographic effects, as species that are systematically more consumed (i.e. *Quercus* and *Pinus*) suffer a significantly higher reduction in the number of propagules available for recruitment than the less consumed species (Janzen 1971; Louda 1989; Davidson 1993; Hulme 1996; Rey & Alcántara 2000; García et al. 2005).

As a consequence of this selection criteria, seed predators can affect the coexistence of different tree species (Hulme 1996; Wright 2002) by drastically reducing the seed survival of the two dominant tree species, (*Pinus* and *Quercus*), in favour of the rarest tree species (*Acer*; see Paine & Beck 2007 for a similar abundance-dependent pattern). The impact of seed predators on both dominant tree species is exacerbated by the fact that neither *Pinus* nor *Quercus* have a seed bank and they have less supra-annual variability in seed production in comparison with other Mediterranean species (Herrera et al. 1998), probably being unable to saturate rodents by crop overabundance.

Notably, seed predators favoured the shrub species (*Berberis* and *Crataegus*), which were less attacked than were tree species (*Quercus* and *Pinus*) in all landscape units. As shrub species are more abundant than tree species in terms of cover as well as number of individuals, this could potentially alter species composition and abundance of the woody community at the seedling stage. Consequently, post-dispersal seed predation can filter the species pool available for recruitment of the woody community in a similar way in all landscape units, irrespective of the degree of degradation, reducing the number of propagules of dominant tree species (*Pinus* and *Quercus*) and favouring a shrub-like landscape, which is the type of landscape unit where rodents can find both food and refuge. These findings are novel because they demonstrate for the first time that although seed predation pressure differs between adjacent landscape units, the selective filtering on the seed bank of woody species due to post-dispersal seed predators is consistent in all landscape units, whether native forest, reforestation stands, or successional shrubland.

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CAPÍTULO 3

TITLE:
Forest-diversity in a mosaic of Mediterranean habitats: a template where history and ecology meet

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ABSTRACT

1. As result of historical and ecological factors, current woody communities are composed of species with different biogeographic origins that presumably diverge in their ecological requirements. Therefore, each environmental scenario can filter out a different combination of species, with consequences for forest regeneration and species coexistence.

2. The goal of the present study is to analyse the spatio-temporal variability in habitat quality for seedling emergence and survival of the Mediterranean mountain forest. This understanding will allow predicting the capacity of forest to regenerate in relation to climatic events.

3. We experimentally sowed in field conditions a total of 16,650 seeds belonging to the six species that form the tree community: four of Mediterranean or Sub-Mediterranean origin (*Quercus ilex*, *Q. pyrenaica*, *Acer opalus* subsp. *granatense*, and *Sorbus aria*) and two boreo-alpine (*Pinus sylvestris* and *Taxus baccata*). We selected the three habitats more abundant where seeds can be naturally dispersed (open areas, shrubland, and woodland), and half of the sowing stations were irrigated simulating an eventual rainy summer in terms of Mediterranean ecosystems. The experiment was repeated twice, and each experimental trial was monitored for two growing seasons.

4. Simulation of a rainy summer had scant effect on emergence of five of the six species, likely because irrigation was applied on the onset of the emergence. By contrast, emergence of *T. baccata* occurred almost exclusively when watering was applied.

5. Seedling survival was increased with irrigation, although the effect depended on the species and habitat considered. For Mediterranean and Sub-Mediterranean species, seedling establishment was favoured in all habitats under eventual rainy summer, but in any case, it could also occur during typical dry summers. However, boreo-alpine species could have establishment pulses only during rainy summers.

6. **Synthesis:** Our results show that different climatic and successional scenarios filter out a different composition of species. Therefore, the predicted reduction of eventual rainy summers and the increase of aridity may cancel out the establishment of some species of the community and provoke a reduction of tree diversity.

INTRODUCTION

The diversity of species that comprise a plant community can be regulated by both historical and ecological factors (Archibold 1995; Davis & Scholtz 2001; Ricklefs 2004, 2006; Herzog & Kessler 2006; Qian et al. 2007). Historically, contemporary assemblages of woody species represent not only mixtures of taxa with disparate biogeographical origin but also they span in broad geological ages (Herrera 1992; Carrión et al. 2003; Ricklefs 2004; Thompson 2005). Ecologically, species composition is determined by dispersal mechanisms as well as by biophysical properties of environmental scenarios. Each scenario may filter out a different combination of species that in the end will determine species composition and abundance in local assemblages (Roughgarden & Diamond 1986; Morin 1999). Current theories of species coexistence (Hubbell 2001; Silvertown 2004; Gravel et al. 2006; Clark et al. 2007) accept that historical as well as ecological factors are needed to understand the current composition of a given community, although each theory places a different emphasis on the underlying mechanisms (interspecific competition for niche-partitioning theories or stochastic processes for neutral theory).

Due to its latitudinal position, the Mediterranean Basin has been a source and sink of species during glacial and inter-glacial periods of the Quaternary (Herrera 1992; Blondel & Aronson 1999; Carrión et al. 2003; Thompson 2005; de Heredia et al. 2007). Therefore, it is an excellent study system to analyze the ecology of communities composed of species with disparate historical origin (Raven 1971; Blondel & Aronson 1995). Species from temperate and boreal zones dominated the flora of the Mediterranean Basin during the glacial periods of the Pleistocene (Bennett 1997). At interglacial periods, when the climate was seasonally dry and the temperatures were higher, boreal taxa migrated northwards and altitudinally, and species with Mediterranean origin extended. Relict populations of boreal species remained in microclimatic islands in the Mediterranean Basin (mainly in high–mountain habitats; Hewitt 1999; Sinclair et al. 1999; Cox & Moore 2000; Castro et al. 2004). Particularly, Mediterranean mountain ranges in the South of the Iberian Peninsula acted as refuge for boreo-alpine species such as *Pinus sylvestris* var. *nevadensis* H. Christ. or *Taxus baccata* L. after the last glacial period (Tittensor 1980; Boratynski 1991; Sinclair et al. 1999; Blanca et al. 1998; López de Heredia et al. 2007). These populations represent the southern limit of the distribution area of each species and they are facing under a Mediterranean climate different environmental constrains than northwards (García et al. 2000; Castro et al. 2004; Hampe 2005).

Current Mediterranean landscapes are mosaics of patches with different size, degree of human management, and successional stages (Blondel & Aronson 1999; Thompson 2005). Each successional scenario has a characteristic habitat structure that directly influences light availability in the understory, soil moisture, nutrient availability, and ecological interactions. As each species may have a specific response to the environment, each current ecological scenario is able to filter out a different combination of species (Harper 1977; Pacala & Tilman 1994; George & Bazzaz 1999a, 1999b; Beckage & Clark 2003). Therefore, the diversity of woody species in a local successional mosaic will depend on different regeneration patterns of each species that conform the forest community, as well as on their complementarity, because some species give to others resources and/or protection that allow coexistence (Grubb 1977). While classical explanations regard interspecific competition as the source of species coexistence (Whittaker 1975; Grubb 1977), recent approaches argue for including facilitation as a mechanism for species diversity (Valiente-Banuet & Verdú 2007).

The goal of the present study is to analyse the spatio-temporal variability in habitat quality for seedling emergence and survival of the Mediterranean mountain forest. The knowledge of the magnitude of this variation has important implications, since high variability in the landscape mosaic faced by seedlings could translate into a forest community without a stable spatial distribution (Fowler 1988). Furthermore, the quality of different successional scenarios for recruitment can fluctuate inter-annually due to variation in climatic conditions (for a similar approach at the microhabitat level, see Greenlee & Callaway 1996; Tielbörger & Kadmon 2000; Ibañez & Schupp 2001; and Gómez Aparicio et al. 2005). Summer dryness dominates the Mediterranean climate and represents the main constraint for seedling establishment (Castro et al. 2005 and references therein; Giménez-Benavides et al. 2007). However, some scattered years have rainy summers, especially in mountain areas (Rodó & Comín 2001; Gómez-Aparicio et al. 2005), thus appearing two different climatic scenarios (the infrequent wet vs. the typical dry summers) that are supposed to influence seedling recruitment variably depending on the species. Wet summers are expected to be more crucial for the recruitment of boreo-alpine species, because normally they need such rare events of rainfall to have a window of opportunity for seedling recruitment (sensu Erikson). Contrarily, species with Mediterranean or Sub-Mediterranean origin appearing in Mediterranean mountains are supposed to be more adapted to drought stress (Rodà et al. 1999).

In order to reach the goal of this paper, we analysed seedling dynamics of six tree species at the habitat scale in three successional scenarios with different rainfall regimens (that represent variable climatic scenarios). We conducted a seed-sowing experiment in field conditions with all tree species composing a Mediterranean community. Seeds were sown under the three habitats most abundant where seeds are dispersed, equivalent to the most common successional scenarios, and that differ in radiation and soil moisture. We also irrigated seedlings simulating an eventual mild summer in terms of Mediterranean ecosystems (Rodó & Comín 2001), in order to represent the two climatic scenarios (wet summer vs. typical dry summer) that are potential to appear. To our knowledge, this is the first field experiment of seedling recruitment that includes all tree species of a Mediterranean community. Results of our study are necessary for the understanding of the regeneration dynamics under the strong spatio-temporal variability that characterize Mediterranean ecosystems.

MATERIAL AND METHODS

Study site and species

This field experiment was carried out from 2003 to 2005 in the Sierra Nevada National Park (S Spain) within La Cortijuela Botanical Garden (37°05’N and 3°28’W, 1600m a.s.l.), an area of 12.4 ha fenced against herbivores. The climate is Mediterranean with mountain properties: the precipitation is concentrated in late autumn and winter (usually snow) and there is a severe drought in summer (July-August). The mean precipitation in the 1991-2005 period was 840 mm yr-1 (data from a climatic station located in the study site). Rainfall in 2003 (975 mm yr-1; 14 mm yr-1 in summer) and 2004 (770 mm yr-1; 28 mm yr-1 in summer) was close to the average for the area, whereas 2005 (394 mm yr-1; 8 mm yr-1 in summer) was the driest of the 15-year series. The mean temperature of the coldest month (January) is 3.8 ± 0.4 °C and of the hottest month (August) is 21.3 ± 0.5 °C (series 1991-2005). The bedrock is calcareous with limestones and filite bloomings (see Castro et al. 2005a for more information about the study area).

The study species were *Quercus* ilex L., *Quercus* pyrenaica Willd., Acer opalus subsp. granatense (Boiss.) Font Quer & Rothm. (hereafter *A. granatense*), Sorbus aria L., *Pinus sylvestris* var. *nevadensis* Christ, and *Taxus baccata* L., which are the species that conform the tree canopy of natural stands in the study area. They diverge in their biogeographical origins (Castroviejo et al. 1986; Blanca et al. 2002): *T. baccata* and *P. sylvestris* have Euro-Siberian distribution; the two *Quercus* spp. have a typical Mediterranean distribution (Rodà et al. 1999); *A. granatense* appears in the South of the Iberian Peninsula, North of Africa, and Mallorca, normally in ravines and shady areas (Blanca et al. 2002); the distribution of *S. aria* ranges from Europe, Asia, Macaronesia, to North Africa, appearing in South Spain in shady ravines and north-sided slopes (Castroviejo et al. 1989). Taking into account their ecological requirements, *Quercus* spp. are Mediterranean, *A. granatense* and *S. aria* are Sub-Mediterranean, and *P. sylvestris* and *T. baccata* are boreo-alpine species (Blanco et al. 2005).

The vegetation in the study area is composed of small woodlets intermingled with early- and late-successional shrublands. The dominant tree species is

P. sylvestris, and secondly *Q. ilex*, while *A. granatense*, *Q. pyrenaica*, *S. aria*, and *T. baccata* are less abundant. The understory is composed of several shrubs, such as Genista cinerea (Vill.) DC., Crataegus monogyna Jacq., Prunus ramburii Boiss., Thymus mastichina L., and Salvia lavandulifolia Vahl. (see Molero-Mesa et al. 1992 and Rodríguez Hiraldo et al. 2001 for more information about the vegetation of the area). Pinus nigra subsp. salzmannii (Dunal) Franco is also a main component of the tree canopy, but all present individuals were planted in 1950s.

Field methods and experimental design

A sowing experiment with two levels of water addition was performed for the six study species. Fruits of each species were collected in the study site or in nearby areas. In the case of fleshy fruits, we removed the pulp and stored the seeds at 2-4°C until used. Acorns were stored on a moist substrate at 2-4°C until used. Before sowing, seed or fruit viability was tested by submerging acorns and selecting the non-floating ones in the case of *Quercus* spp., and by rejecting the clearly-aborted or depredated seeds by visual inspection in the case of the rest of species. For simplicity, we refer hereafter to all propagules as seeds.

Sowing was performed in the three habitats that cover the most part of the understory in the area, where seedling emergence occurs naturally (Castro et al. 2005a, 2005b), and that are representative of the successional scenarios in the area: 1) Open, areas of bare ground or covered by sparse herbaceous vegetation, separated to surrounding woody vegetation enough distance to avoid shading; 2) Shrublands, under the canopy of the most abundant shrubs in the study site; 3) Woodland, under the canopy of *P. sylvestris* or Pinus nigra. The sowing experiment was replicated in 2003 and 2004 (called hereafter 2003 trial and 2004 trial). In the 2003 trial we chose 60 sowing stations per habitat for each species; in 2004 trial, sowing was repeated in 30 of these sowing stations for all species except for *T. baccata*. The total number of sowing stations was 180 in 2003 trial and 90 in 2004 trial. A sowing station was composed of a set of randomly disposed wire cages (1.3 cm mesh size) with the sowed seeds of each species. We used wire cages in order to exclude seed predation. Sowing stations were randomly distributed and separated one to the others by at least 3 m. The number of seeds per sowing station was adjusted to seed size: 5 for *Quercus* species (sown in a cage of 0.042 m2 area), 10 for *T. baccata*, and 15 for *A. granatense*, *P. sylvestris*, and *S. aria* (all these five species sown in a cage of 0.0286 m2 area). For all species except for *Quercus* spp., seeds were sown 1 cm of depth and separated one to each other 2.5 cm. Seeds of *Quercus* spp. were sown 3 cm depth and the distance between them was 8-10 cm. All species were sown in January in 2003 and in 2004 except *T. baccata*, which was sown only in 2003 because of the lack of emergence of this species in 2003 discouraged us to repeat sowings in 2004. A total of 11,700 seeds were sown in 2003 trial and 4,950 in 2004 trial. Herbs were carefully removed in order to avoid interspecific competition. The study was monitored for 2 years for each sowing trial.

For each experiment trial, the half of the sowing stations was randomly assigned to an irrigation treatment and the other half to control. Water was applied only during the year of sowing (first-growing season), as eventual wet summers typically are followed by a dry summer (Gómez-Aparicio et al. 2005). The only exception was *T. baccata*, because watering was applied the year of sowing as well the following year, when the emergence of all seedlings was produced. Water was added with a dripping system at around 10-day intervals during the start of the drought until the first major rainfall was recorded (approximately from June to September). The surface irrigated (30 x 30 cm) was greater than the surface of the sown plot in order to avoid border effects. Irrigation consisted of adding ca. 2 l of water at each application time, this equivalent to approximately 22 mm (see Castro et al. 2005a for a similar procedure). This water addition simulated a rainy summer in terms of Mediterranean climate (Gómez-Aparicio et al. 2005; Castro et al. 2005a), because these rare summers typically consist on eventual strong-summer storms.

As the number of sown seeds was the same in each habitat, differences in recruitment were not produced by seed limitation but rather by species-specific variation in establishment limitation due to the environment. In order to analyse explicitly the effect of habitat and summer wetness conditions, we intentionally excluded herbivory in our experimental approach. Besides, herbivore effects on plant recruitment has been profusely analysed in previous studies in the same study area (Zamora et al. 2001; Baraza et al. 2006; Gómez-Aparicio et al. 2007; Mendoza et al. submitted).

Characterization of the abiotic environment

The spatial variability of light was explored with hemispherical photography (Rich 1990, Gómez-Aparicio et al. 2005). Pictures were taken in each of the 180 sowing stations using the standard procedure (see Puerta-Piñero et al. 2007 for a complete description of the methods). The images were analysed using Hemiview canopy analysis software version 2.1 (1999, delta-T Devices Ltd, Cambridge, United Kingdom), and we obtained a value of Global Site Factor (GSF) per image (Rich 1990). Values of GSF range from 1 (open sky) to 0 (complete obstruction).

The spatial variability of the percentage of volumetric soil water content (VWC%) of the top soil (12 cm depth) was monitored with a Theta-Probe sensor (Delta-T Devices Ltd, Cambridge, UK). Two measurements were taken in a half of the sowing stations every 14 days in 2003, and every 30 days in 2004. Measurements were conducted 3-5 days after irrigation.

Seedling monitoring

Seedling emergence (percentage of seeds emerged from the sown seeds), survival (percentage of seedlings surviving from the emerged seeds), and cause of mortality were monitored for two growing seasons; i.e. until September 2004 for seedlings emerged in 2003, and until September 2005 for seedlings emerged in 2004. Seedling monitoring was performed weekly in 2003 and fortnightly in 2004. Causes of mortality were assigned to: 1) “drought”, seedlings were turned brown and dried out without any visible damage, mortality occurring during periods of low soil moisture; 2) “winter death”, seedlings were found dead at the beginning of the following growing season, after winter time; 3) “fungi”, characterized by black and wet seedlings with necrosis in tissues; 4) “invertebrate herbivory”, seedlings severed by insects; and 5) “other”, with undetermined causes of mortality.

Data analysis

Differences in GSF between the three habitats were compared with one-way ANOVA. Volumetric soil water content was compared between habitat types and irrigation treatment using repeated measures ANOVA. Analyses of emergence

Table 1. Summary of the repeated measures analysis of variance for the Volumetric Water Content (%) under different habitats and irrigation levels. Habitats are Open, Shrubland, and Woodland. Irrigation levels are Control and Water supplementation. Significant P values are shown in bold.

	SS	d.f.	MS	F	P
Intercept	385325.8	1	385325.8	5632.328	< 0.0001
Habitat	561.0	2	280.5	4.100	0.02
Watering	3568.0	1	3568.0	52.154	< 0.0001
Habitat*Watering	56.2	2	28.1	0.411	0.67
Error	5062.6	74	68.4		
Time	69360.6	12	5780.1	354.593	< 0.0001
Time*Habitat	2116.4	24	88.2	5.410	< 0.0001
Time*Watering	3681.2	12	306.8	18.820	< 0.0001
Time*Habitat*Watering	227.7	24	9.5	0.582	0.95
Error	14474.9	888	16.3		

Table 2. Summary of the values of VWC (%) in each type of habitat and irrigation treatment. Water was added during summer in 2003 and 2004.

Habitat	Open		Shrubland		Woodland	
VWC (%)	Watered	Control	Watered	Control	Watered	Control
spring 2003	21.76 ± 0.59	22.36 ± 0.72	19.91±0.66	21.16±1.09	21.04±0.86	21.99±0.57
summer 2003	14.22 ± 0.34	7.64 ± 0.59	13.45 ± 0.67	7.20 ± 0.46	15.67 ± 1.10	9.98 ± 0.68
spring 2004	39.00 ± 0.22	37.75 ± 0.52	38.61 ± 0.48	37.10 ± 1.33	33.86 ± 2.25	35.12 ± 1.58
summer 2004	37.19 ± 2.92	23.73 ± 3.21	29.24 ± 2.72	19.71 ± 2.54	34.72 ± 2.86	28.27 ± 1.82

and survival were performed using a logistic model with emergence/survival rate (proportion of the number of emerged seedlings to the total number of sowed seeds or proportion of the number of surviving seedlings to the total number of emerged seedlings) as the response variable, binomial probability distribution (as each individual seedling had a binary probability to emerge/survive), and logit link function (Quinn & Keough 2002; Bravo-Oviedo et al. 2006). We used the type of habitat and the irrigation treatment as the main effects. Analyses were separated for each species and year of emergence, as our aim was to explore the influence of habitat type and irrigation treatment for each species. Furthermore, the inclusion of year, species, and their interactions in the models complicates interpretation of results. Values are given throughout this paper with mean ± standard error. All analyses were done using STATISTICA 7.1 (StatSoft Inc., 2005) or JMP v. 7.0 (SAS Institute Inc. 2007).

RESULTS

Abiotic environment

The GSF values significantly differed between habitat types (F2,179 = 326.99; P < 0.0001; R2 = 0.79). Open was the type of habitat with the highest radiation values (0.83 ± 0.01), followed by Shrubland (0.57 ± 0.03), and lastly by Woodland (0.23 ± 0.03).

The mean values of volumetric water content (% VWC) were significantly higher for watered sowing stations than for control ones in all the habitats (Table 1 and Table 2). % VWC in 2004 was higher than in 2003 for all habitats and watering treatments (Table 2), supporting that summer 2003 was drier than 2004.

First-year emergence

All species except *T. baccata* registered emergence the same year of sowing (Table 3). First-year emergence was of 3,094 seedlings for 2003 trial and 1,354 for 2004 trial (Table 3). The factor best explaining the emergence pattern for all species and years was the habitat type (Table 4), although the pattern was not

Table 3. Total number of emerged seedlings and percentage related to number of sown seeds in each combination (in brackets) for each year of sowing, year of emergence, habitat, and irrigation treatment. The total number of seeds sown in each year is also shown. Dash (–) means that seedlings did not emerge.

			EMERGED IN 2003						EMERGED IN 2004					
Year sowing	Species	Total sown	Open		Shrubland		Woodland		Open		Shrubland		Woodland	
			Control	Watered	Control	Watered	Control	Watered	Control	Watered	Control	Watered	Control	Watered
2003	*Q. ilex*	900	73 (48.7)	86 (57.3)	56 (37.3)	65 (43.3)	73 (48.6)	82 (54.6)	-	-	-	-	-	-
	Q. pyrenaica	900	62 (41.3)	59 (39.3)	60 (40.0)	65 (43.30)	61 (40.6)	39 (26.0)	-	-	-	-	-	-
	A. granatense	2700	45 (10.0)	35 (7.8)	36 (8.0)	40 (8.9)	41 (9.1)	48 (10.7)	13 (2.9)	9 (2.0)	18 (4.0)	19 (4.2)	19 (4.2)	23 (5.1)
	S. aria	2700	65 (14.4)	75 (16.6)	79 (17.5)	81 (18.0)	107 (23.7)	151 (33.5)	23 (5.1)	35 (7.8)	42 (9.3)	46 (10.2)	18 (4.0)	32 (7.1)
	P. sylvestris	2700	262 (58.2)	256 (56.9)	311 (69.1)	326 (72.4)	169 (37.6)	186 (41.3)	-	-	-	-	-	-
	T. baccata	1800	-	-	-	-	-	-	4 (1.3)	70 (23.3)	17 (5.6)	117 (39.0)	27 (9.0)	100 (33.3)

			EMERGED IN 2004						EMERGED IN 2005					
Year sowing	Species	Total sown	Open		Shrubland		Woodland		Open		Shrubland		Woodland	
			Control	Watered	Control	Watered	Control	Watered	Control	Watered	Control	Watered	Control	Watered
2004	*Q. ilex*	450	28 (37.3)	32 (42.3)	36 (48.0)	37 (49.3)	37 (49.3)	47 (62.6)	-	-	-	-	-	-
	Q. pyrenaica	450	39 (52.0)	33 (44.0)	32 (42.3)	44 (58.6)	48 (64.0)	49 (65.3)	-	-	-	-	-	-
	A. granatense	1350	7 (3.1)	6 (2.6)	11 (4.9)	9 (4.0)	22 (9.7)	15 (6.7)	11 (4.9)	3 (1.3)	17 (7.6)	9 (4.0)	0 (0)	0 (0)
	S. aria	1350	31 (13.8)	32 (14.2)	52 (23.1)	64 (28.4)	62 (27.5)	72 (32.0)	22 (9.8)	5 (2.2)	42 (18.7)	38 (16.9)	27 (12.0)	68 (32.2)
	P. sylvestris	1350	55 (24.4)	95 (42.2)	121 (53.7)	84 (37.3)	50 (22.2)	85 (37.7)	-	-	-	-	-	-

consistent among species and years (Table 3). Watering was significant in some cases, although less relevant than habitat (Table 4). Only seedlings of *Q. ilex* and *S. aria* sown in 2003, and of *P. sylvestris* sown in 2004 showed significantly higher emergence rates when watered (Table 3).

Second-year emergence

Seedlings of *A. granatense* and *S. aria* emerged the year of sowing as well as the following year. The emergence pattern of *T. baccata* was unique, because it emerged exclusively the year after sowing, i.e. in 2004 (Table 3). The total number of seeds sown in 2003 and emerged in 2004 was 694, and 247 seedlings emerged in 2005 from seeds sown in 2004 (Table 3). As in the case of first-year emergence, habitat was a common factor explaining second-year seedling emergence (Table 5). Watering was significant for one sowing year for *S. aria*, and in particular it had a strong effect for *T. baccata*, for which most part of seedlings emerged under irrigation (Tables 3 and 5). Some habitat x watering interactions appeared as a consequence of differences in the effect of watering depending on the habitat (Tables 3 and 5).

First-summer seedling survival

The total number of seedlings that survived the first summer was 1,573 (50.8%) for seedlings emerged in 2003 and 947 for seedlings emerged in 2004 (56.1%). Summer drought was the main mortality factor after the first summer, responsible of ca. 99 % of the deaths of all species pooled.

The type of habitat significantly affected seedling survival in all cases except for *P. sylvestris*. The most general pattern was an increase of survival in the Woodland habitat, and lower survival in Open, with intermediate values in Shrubland (Table 6; Figure 1). On the other hand, watering during first summer boosted survival for all species and study years compared to the control seedlings, although these differences were not significant for seedlings of *Q. ilex*, *A. granatense*, and *S. aria* emerged in 2004 (Table 6 and Fig. 1). The effect of watering was particularly relevant for boreo-alpine species. Watered seedlings of *P. sylvestris* survived 19 times more than control ones in 2003, and 3 times more

Table 4. Summary of the logistic model for first-year emergence under different habitats and irrigation levels. Habitats are Open, Shrubland, and Woodland. Irrigation levels are Control and Water supplementation. Emergence rate was calculated as the proportion of emerged seedlings to the total number of sowed seeds per cage. Significant P values are shown in bold.

Species	Year of emergence	Effects	df	χ^2	P
Q.ilex	2003				
		Habitat	2	11.359	0.0034
		Watering	1	4.176	0.041
		Habitat x Watering	2	0.161	0.9228
		Model	5	15.660	0.0079
	2004				
		Habitat	2	7.489	0.0237
		Watering	1	2.170	0.1407
		Habitat x Watering	2	1.129	0.5687
		Model	5	10.733	0.0569
Q. pyrenaica	2003				
		Habitat	2	5.103	0.078
		Watering	1	2.137	0.1438
		Habitat x Watering	2	5.757	0.0562
		Model	5	12.245	0.0316
	2004				
		Habitat	2	10.017	0.0067
		Watering	1	0.388	0.5336
		Habitat x Watering	2	4.613	0.0996
		Model	5	15.075	0.01
A. granatense	2003				
		Habitat	2	1.177	0.5551
		Watering	1	0.001	0.9719
		Habitat x Watering	2	2.212	0.3308
		Model	5	3.402	0.6383
	2004				
		Habitat	2	12.051	0.0024
		Watering	1	1.131	0.2875
		Habitat x Watering	2	0.160	0.9232
		Model	5	14.574	0.0123
S. aria	2003				
		Habitat	2	50.039	<0.0001
		Watering	1	5.374	0.0204
		Habitat x Watering	2	4.197	0.1227
		Model	5	63.900	<0.0001
	2004				
		Habitat	2	37.594	<0.0001
		Watering	1	1.189	0.2756
		Habitat x Watering	2	0.286	0.8669
		Model	5	40.875	<0.0001
P. sylvestris	2003				
		Habitat	2	183.499	<0.0001
		Watering	1	1.203	0.2727
		Habitat x Watering	2	1.629	0.4429
		Model	5	185.979	<0.0001
	2004				
		Habitat	2	26.833	<0.0001
		Watering	1	6.576	0.0103
		Habitat x Watering	2	36.824	<0.0001
		Model	5	67.413	<0.0001

in 2004, while *T. baccata* increased its survival 3 times when irrigated (all habitats pooled; Fig. 1).

Significant or marginally significant habitat x watering interactions often appeared in many cases as consequence of the reduction of the beneficial effect of watering in Woodland in relation to the rest of habitats (Fig. 1; Table 6). In this sense, watered seedlings of *Q. ilex* in 2003 and *A. granatense*, as well as

Table 5. Summary of the logistic model for second-year emergence under different habitats and irrigation levels. Habitats are Open, Shrubland, and Woodland. Irrigation levels are Control and Water supplementation. Emergence rate was calculated as the proportion of seedlings emerged the second year after sowing to the total number of sowed seeds per cage. Significant P values are shown in bold.

Species	Year of sowing	Year of emergence	Effects	df	χ^2	P
A. granatense	2003	2004				
			Habitat	2	7.251	0.0266
			Watering	1	0.036	0.8505
			Habitat x Watering	2	1.168	0.5578
			Model	5	8.271	0.1419
	2004	2005				
			Habitat	2	34.314	<0.0001
			Watering	1	0.000	0.9994
			Habitat x Watering	2	0.928	0.6287
			Model	5	45.178	<0.0001
S. aria	2003	2004				
			Habitat	2	14.005	0.0009
			Watering	1	6.251	0.0124
			Habitat x Watering	2	2.083	0.3529
			Model	5	19.902	0.0013
	2004	2005				
			Habitat	2	46.172	<.0001
			Watering	1	2.494	0.1143
			Habitat x Watering	2	24.802	<.0001
			Model	5	69.046	<.0001
T. baccata	2003	2004				
			Habitat	2	29.881	<0.0001
			Watering	1	234.041	<0.0001
			Habitat x Watering	2	9.791	0.0075
			Model	5	266.177	<0.0001

Table 6. Summary of the logistic model for survival after first summer under different habitats and irrigation levels. Analyses were separated for each species and year of emergence. Habitats are Open, Shrubland, and Woodland. Irrigation levels are Control and Water supplementation. Survival rate was calculated as the proportion of seedlings that survived the first summer to the total number of emerged seedlings per cage. Significant P values are shown in bold.

Species	Year of emergence	Effects	df	χ^2	P
Q.ilex	2003				
		Habitat	2	10.111	0.0064
		Watering	1	29.827	<0.0001
		Habitat x Watering	2	18.116	0.0001
		Model	5	92.358	<0.0001
	2004				
		Habitat	2	7.257	0.0266
		Watering	1	1.453	0.2281
		Habitat x Watering	2	5.348	0.069
		Model	5	22.474	0.0004
Q. pyrenaica	2003				
		Habitat	2	7.296	0.026
		Watering	1	54.757	<0.0001
		Habitat x Watering	2	0.440	0.8027
		Model	5	100.297	<0.0001
	2004				
		Habitat	2	17.463	0.0002
		Watering	1	3.240	0.0719
		Habitat x Watering	2	4.992	0.0824
		Model	5	40.557	<0.0001
A. granatense	2003				
		Habitat	2	70.361	<0.0001
		Watering	1	20.108	<0.0001
		Habitat x Watering	2	7.511	0.023
		Model	5	110.040	<0.0001
	2004				
		Habitat	2	15.986	0.0003
		Watering	1	0.517	0.4719
		Habitat x Watering	2	0.691	0.7077
		Model	5	18.709	0.0022
S. aria	2003				
		Habitat	2	14.959	0.0006
		Watering	1	59.725	<0.0001
		Habitat x Watering	2	1.172	0.5566
		Model	5	79.777	<0.0001
	2004				
		Habitat	2	24.891	<0.0001
		Watering	1	1.604	0.2053
		Habitat x Watering	2	6.652	0.0359
		Model	5	39.691	<0.0001
P. sylvestris	2003				
		Habitat	2	5.884	0.0528
		Watering	1	460.756	<0.0001
		Habitat x Watering	2	7.917	0.0191
		Model	5	525.145	<0.0001
	2004				
		Habitat	2	1.125	0.5699
		Watering	1	43.112	<0.0001
		Habitat x Watering	2	8.248	0.0162
		Model	5	58.627	<0.0001
T. baccata	2003				
		Habitat	1	25.086	<0.0001
		Watering	1	19.639	<0.0001
		Habitat x Watering	1	0.929	0.3352
		Model	3	111.976	<0.0001

seedlings of *Q. ilex*, *Q. pyrenaica*, *S. aria*, and *P. sylvestris* in 2004 survived the same than control seedlings in Woodland. By contrast, drought alleviation boosted seedling survival in open areas for all species and study years (except for *A. granatense* in 2004). The case of *T. baccata* was the most extreme one, because all seedlings that emerged in open areas died after the summer, even if they underwent water addition. Finally, under a shrubby understory, watering had an intermediate effect as a general pattern across species (Fig. 1).

Second-summer seedling survival

A total of 1,339 seedlings emerged in 2003 survived the summer in 2004 (85.1% of the seedlings surviving the first summer) and 534 seedlings emerged in 2004 survived the second summer (56.4% of the seedlings surviving first summer). Summer drought was the main mortality factor after the second summer, responsible of 96 % of the deaths (all species pooled). The second cause of mortality was winter death, responsible of 2.8% of the deaths (all species pooled). Winter death was especially important in the case of *A. granatense* (cause of the 12% of the deaths of this species) and *Q. ilex* (10%).

The type of habitat influenced second-summer survival (Table 7). In general terms, seedling survival was higher in Woodland than in Open, with intermediate values in Shrubland (Fig. 2). The pattern of increased survival when seedlings were watered was maintained during the second summer, reinforcing the benefits for seedling survival of a single rainy summer (Table 7 and Fig. 2). Overall, watering was more important for survival in Open than in Shrubland and Woodland habitats. In fact, watering did not boost survival in Woodland and Shrubland for some species (e.g. *Q. ilex* emerged in 2003 and 2004, *S. aria* emerged in 2004), which resulted in significant habitat x watering interactions in some cases (Table 7). Again, boreal-alpine species were more dependent on the irrigation treatment for seedling survival after the second summer. The survival of *P. sylvestris* was practically zero for seedlings that were not irrigated, and irrigated seedlings of *T. baccata* in Woodland were practically the only ones that survived (Fig. 2).

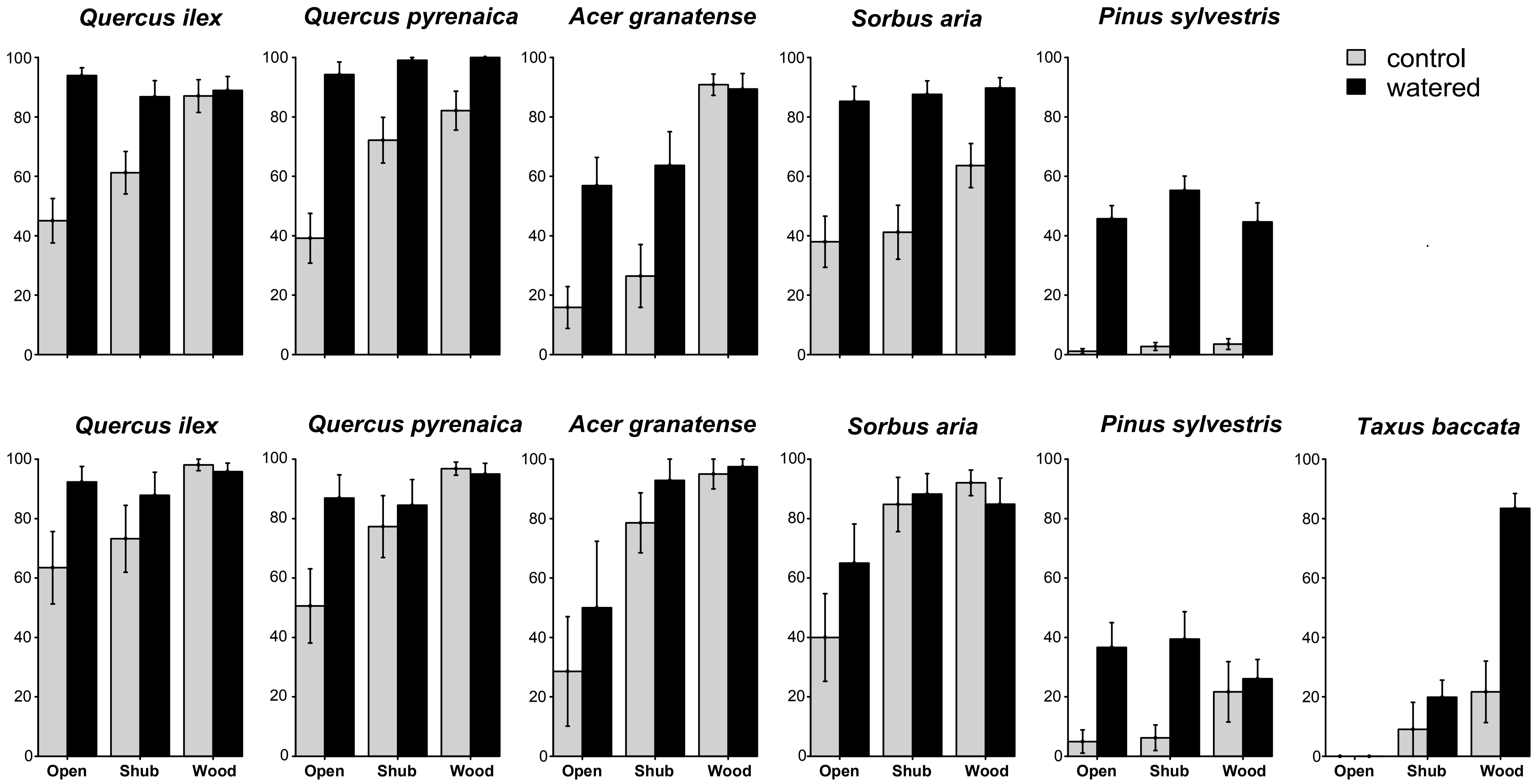

Fig 1. First-summer seedling survival (percentages) for the six studied species in different habitats and irrigation levels. Habitats are Open, Shrubland (Shrub) and Woodland (Wood). Irrigation levels are control (grey bars) and water (black bars) supplementation. First-summer survival is calculated as the number of seedlings surviving the first summer divided by the number of emerged seedlings.

Table 7. Summary of the logistic model for survival after the second summer under different habitats and irrigation levels. Analyses were separated for each species and year of emergence. Habitats are Open, Shrubland, and Woodland. Irrigation levels are Control and Water supplementation. Survival rate was calculated as the proportion of seedlings that survived the second summer to the total number of emerged seedlings per cage. Models for P. sylvestris emerged in 2004 and for T. baccata were not performed because the number of surviving seedlings was too low. Significant P values are shown in bold.

Species	Year of emergence	Effects	df	χ^2	P
Q.ilex	2003				
		Habitat	2	17.523	0.0002
		Watering	1	50.342	<0.0001
		Habitat x Watering	2	20.257	<0.0001
		Model	5	125.005	<0.0001
	2004				
		Habitat	2	54.774	<0.0001
		Watering	1	2.045	0.1527
		Habitat x Watering	2	3.262	0.1957
		Model	5	58.578	<0.0001
Q. pyrenaica	2003				
		Habitat	2	19.787	<0.0001
		Watering	1	43.913	<0.0001
		Habitat x Watering	2	4.012	0.1346
		Model	5	101.845	<0.0001
	2004				
		Habitat	2	59.104	0.011
		Watering	1	1.631	0.0963
		Habitat x Watering	2	14.038	0.6547
		Model	5	72.099	0.0075
A. granatense	2003				
		Habitat	2	66.668	<0.0001
		Watering	1	19.006	<0.0001
		Habitat x Watering	2	16.898	0.0002
		Model	5	91.249	<0.0001
	2004				
		Habitat	2	9.011	0.011
		Watering	1	2.766	0.0963
		Habitat x Watering	2	0.847	0.6547
		Model	5	15.781	0.0075
S. aria	2003				
		Habitat	2	18.686	<0.0001
		Watering	1	54.329	<0.0001
		Habitat x Watering	2	0.576	0.7497
		Model	5	76.764	<0.0001
	2004				
		Habitat	2	38.440	<0.0001
		Watering	1	9.960	0.0016
		Habitat x Watering	2	10.664	0.0048
		Model	5	42.781	<0.0001
P. sylvestris	2003				
		Habitat	2	6.669	0.0356
		Watering	1	465.923	<0.0001
		Habitat x Watering	2	3.990	0.136
		Model	5	528.413	<0.0001

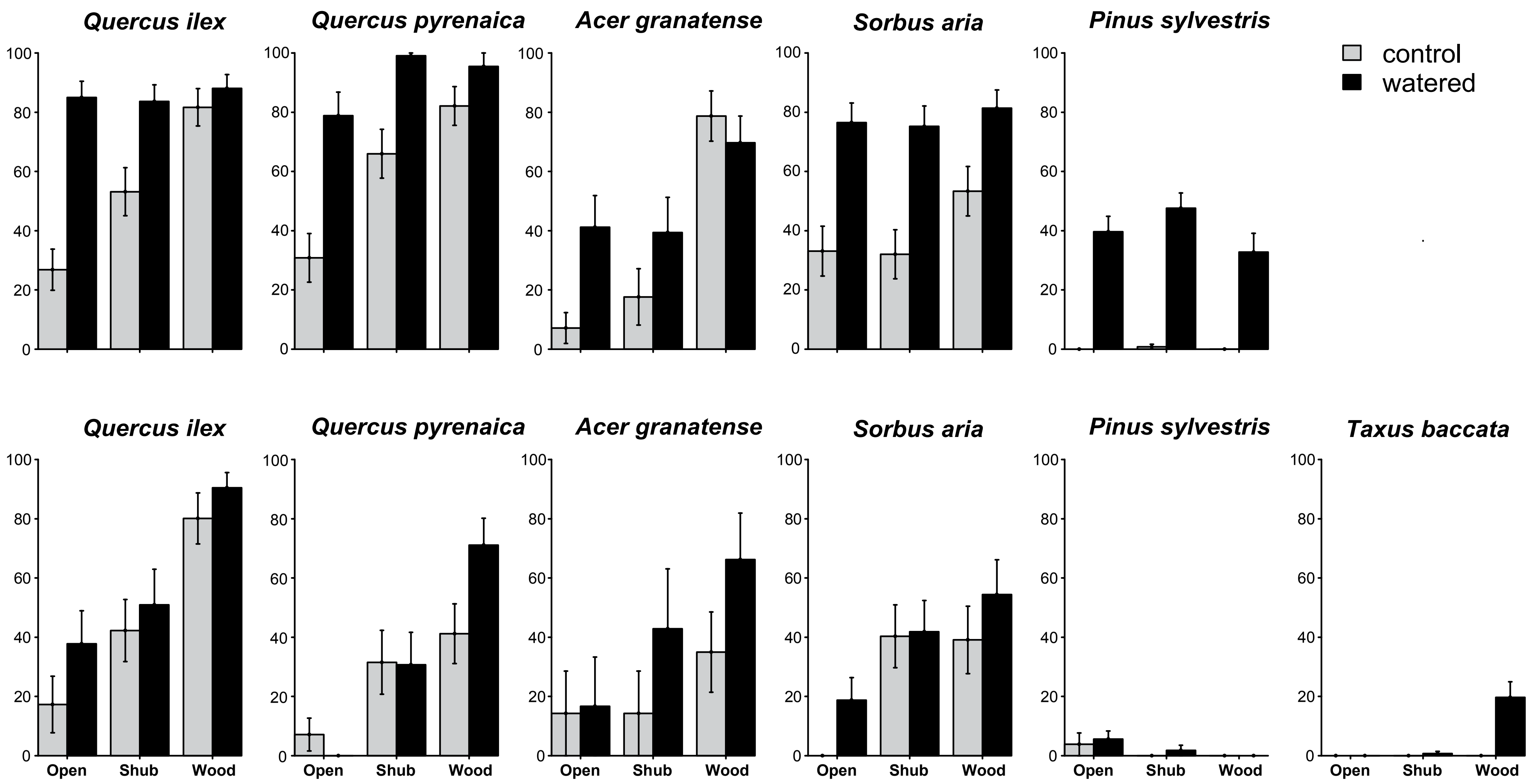

Fig 2. Second-summer seedling survival (percentages) for the six studied species in different habitats and irrigation levels. Habitats are Open, Shrubland (Shrub) and Woodland (Wood). Irrigation levels are control (grey bars) and water (black bars) supplementation. Second-summer survival is calculated as the number of seedlings surviving the second summer divided by the number of emerged seedlings.

DISCUSSION

Using an experimental approach in field conditions, we wanted to establish which combination of species was able to recruit under different habitat and rainfall regimens (that represent variable successional and climatic scenarios), with the final purpose to determine forest auto-regeneration and expansion in relation to climatic events. In general terms, we found that boreo-alpine species (*P. sylvestris* and *T. baccata*) were more dependent on summer rainfall for survival and even emergence (*T. baccata*) than the rest of species. Also, Open was the habitat type least favorable for seedling recruitment, while Shrubland and especially Woodland resulted more beneficial for early seedling survival.

• Seedling emergence

Rates of seedling emergence diverged depending on species, but we cannot guarantee that seed viability was similar between species at the sowing moment (e.g. *A. granatense* normally shows low rates of seed filling; Gómez-Aparicio 2004). Therefore, we do not intend to discuss among-species differences in emergence rates, but rather the effects that the different environmental scenario exerted on each species separately. For all species, seedling emergence was affected by habitat type. However, there was not a consistent pattern that related emergence with habitat across species and years. By contrast, only *P. sylvestris*, *Q. ilex*, and *S. aria* had increased first-year emergence thanks to watering, surely because irrigation treatment started after the emergence onset. Irrigation could result in a beneficial effect for seedlings that had delayed germination, mainly for *Q. ilex* because it had newly emerged seedlings even in August. Also, watering surely reduced the resistance to soil penetration for radicles and protrusion of hypocotyl, and hence diminishes the probability of fatal germinations (Hegarty & Royle 1978; Murdoch & Ellis 1992; Finch-Savage et al. 1998).

It is worth noting that *A. granatense* and *S. aria* showed a second peak of emergence that is related to physiological dormancy of seeds (Devillez 1978, 1979; Baskin & Baskin 1998). This strategy allows temporal dispersal, as not all seeds are germinating at the same time (Murdoch & Ellis 1993). The case of *T. baccata* was the most extreme one, because seedlings only emerged the year after sowing and the majority had been watered the year before. The strong dependence of *T. baccata* on wet summers for emergence indicates that this species undergoes a first limitation for recruitment on emergence, a requirement that did not appear for the rest of species.

- **Seedling survival**

Seedling survival was affected by the type of habitat and irrigation, although the relative importance of both factors varied depending on the species and the experimental year. Water addition increased first-summer survival mainly in 2003 (for all species except *A. granatense*), although it was less necessary in 2004 summer. This surely was due to 2004 was a milder year than 2003, as supported by the higher percentage of soil water content found in control plots in this year (Table 2). However, in both experimental trials the benefit of a wet summer was more critical for boreo-alpine species than for the rest. *P. sylvestris* strongly needed rainfall simulation for seedling recruitment (although some non-irrigated seedlings were able to survive), and only irrigated seedlings of *T. baccata* survived at the end of the experiment.

The benefit of a wet summer for seedling survival was also different depending on the habitat. In Open, where radiation is the highest, drought alleviation boosted survival of seedlings much more than in Shrubland and, especially, in Woodland, where radiation in the understory is the lowest. These results support previous studies that have emphasized the relevance of radiation as an environmental factor that defines the regeneration niche of Mediterranean tree species (Gómez-Aparicio et al. 2006, Puerta-Piñero et al. 2007 and references therein). Seedling survival decreased with habitat openness probably because high radiation exacerbates summer drought (Gómez-Aparicio et al. 2005; Castro-Díez et al. 2006), leading to desiccation and death of seedlings. In this sense, establishment in open areas was restricted to more drought-tolerant species (*Q. ilex*, *Q. pyrenaica*, and *S. aria*), even when a wet summer was simulated. *A. granatense* was also able to recruit in Open areas, but it had less surviving individuals in comparison with *Quercus* spp. and *S. aria*. Previous studies with *A. granatense* have already reported the reduced recruitment of this species in open areas, probably due to a dynamic and chronic photoinhibition in full sunlight, with severe implications for gas exchange and photosynthetic performance (Gómez-Aparicio et al. 2006; Quero et al. 2007). In Woodland, control seedlings had the same survival rate than irrigated ones for all species except for *T. baccata* (although not in all years). Presumably, shading reduces stress due to a combination of higher soil moisture, decreased photochemical damages such as photoinhibition or overheating, higher air-relative humidity, and lower soil temperature (Castro et al. 2002, 2004; Gómez-Aparicio et al. 2004).

- **Implications of summer rainfall for forest regeneration**

Our experimental approach tried to reproduce the three successional scenarios more common in Mediterranean ecosystems. Woodland, belonging to a late-successional stage, was the scenario that boosted the most seedling recruitment, because all species were able to recruit when the summer was wet, and only *T. baccata* failed in a typical dry summer. Shrubland, representing a mid-successional stage, boosted seedling emergence and survival in an intermediate way; in a normal summer, all species except boreo-alpine were able to recruit in Shrubland, but in a wet summer *P. sylvestris* also recruited. Lastly, Open represents the most pioneer habitat and it was the most adverse scenario for seedling recruitment, given that water stress precluded establishment, especially for boreo-alpine species. Therefore, results of this study allow us to determine that summer rainfall is critical for forest maintenance and expansion, as differences in summer rainfall can alter not only the magnitude of seedling survival, but also its spatial distribution between habitats. Only when the summer was wet, all species were able to recruit, and hence the woodland could be auto-regenerated (Fig. 3). Also, wet summers magnify colonization to more pioneer habitats such as shrubland and open areas, although *T. baccata* was the unique species that was not able to recruit in those habitats. When the summer was typically dry, forest maintenance in Woodland diminished and also it was not possible for *T. baccata*. In addition, forest expansion to more pioneer habitats in dry summers was possible only for species with Mediterranean or Sub-Mediterranean origin (mainly *Quercus* spp. and *S. aria*). Consequently, the landscape can change from being, during a typical dry summer, a low-quality matrix for recruitment with woodlands representing the last seedling refuges to become, when precipitation is high, a matrix of comparatively higher quality, where only open gaps have reduced quality.

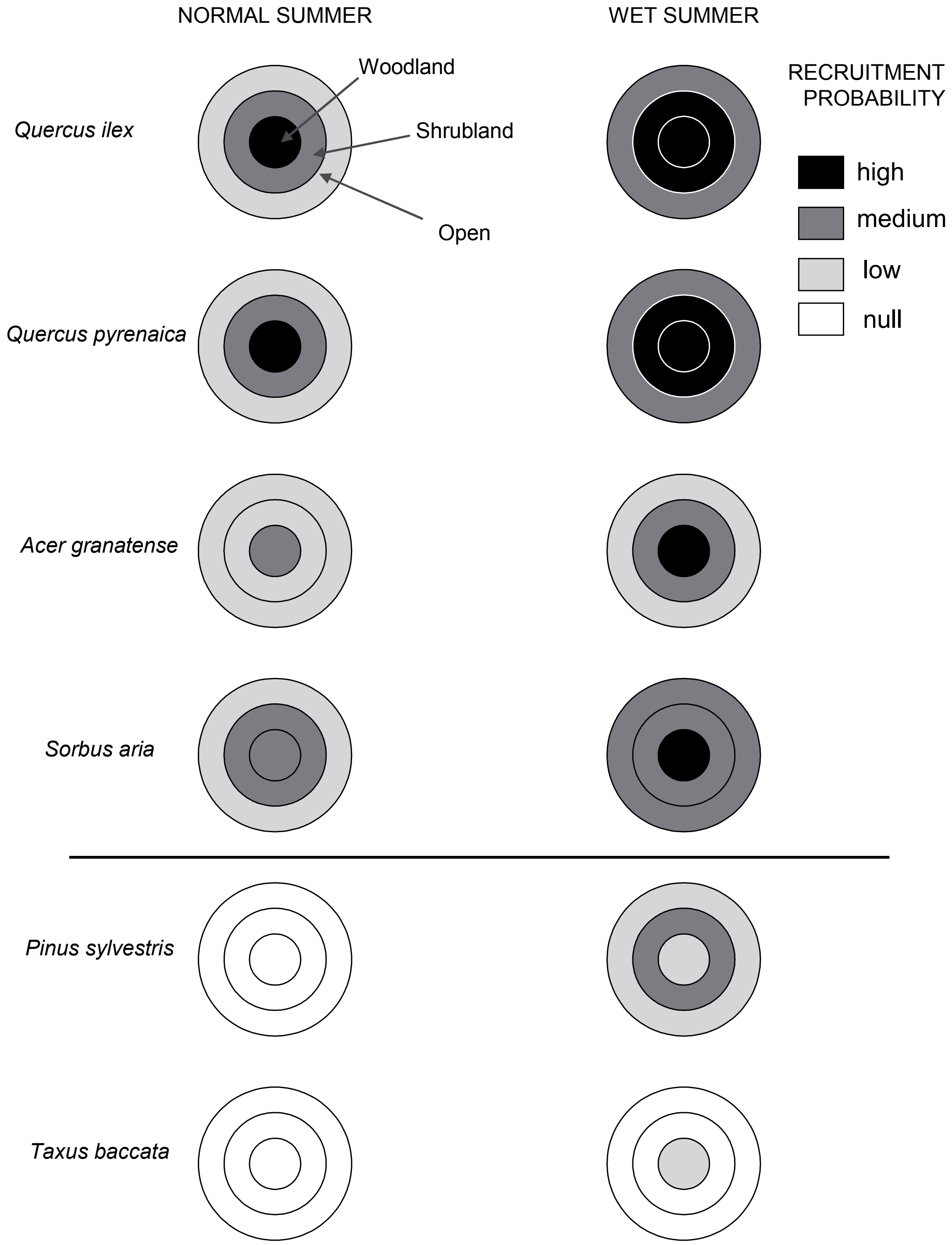

Fig. 3. Schematic diagram showing the recruitment probabilities under each different ecological scenario. Concentric circles represent a different successional scenario: the one inside is Woodland, the intermediate Shrubland, and the outer one shows Open. Circles are shadowed according to the probabilities of recruitment, the darker the circle, the higher the probability.

Despite that our results show that recruitment of *Quercus* spp. and *S. aria* is possible in Open areas, in normal conditions seed arrival would exert a primary limitation for recruitment. Spatial patterns of seed dispersal strongly depend on habitat characteristics and behaviour of zoochorous dispersers (Schupp & Fuentes 1995; Jordano & Schupp 2000; Russo & Augspurger 2004), and the probabilities of seed arrival are not the same for all the habitats. In fact, zoochorous vectors that disperse seeds of *Quercus* spp. (Garrulus glandarius) or *T. baccata* and *S. aria* (*Turdus* spp.) avoid open areas because they represent more risk of predation and less abundance of food (Gómez 2003; García et al. 2000 + references). Contrarily, birds prefer shrublands or woodlands because of their abundance of fleshy-fruited shrubs and safe sites against predators. Wind-dispersed species such as *A. granatense* and *P. sylvestris* have more probabilities to reach open habitats, but these species normally have short-dispersion distances (Gómez-Aparicio et al. 2007; Castro et al. 1999). As result, seed limitation in natural conditions may prevent forest expansion to open areas (Augspurger & Kitajima 1992; Schupp 1995).

- **How disparate species under a common ecological setting can coexist?**

The six studied species have different recruitment probabilities in each environmental scenario, supporting the existence of clear species-specific regeneration niches for the tree species composing the studied forest community (Grubb 1977). We found that species with a different historical origin also differed in their ecological requirements, in contrast with other studies (Clark et al. 2003, 2004; Baraloto & Goldberg 2004) and neutral theory (Hubbell 2001), which did not find that species differed in seedling survival due to habitat differentiation.

Boreo-alpine species were more constrained in seedling recruitment than were the Mediterranean or Sub-Mediterranean ones. The most dramatic case was *T. baccata*, because it depended in a double way on wet summers for seedling recruitment: for emergence and for survival. However, even within each group of species, each one differs not only in the degree of drought tolerance (*Q. ilex* > *Q. pyrenaica*; *S. aria* > *A. granatense*) but rather in the response to radiance. For instance, *P. sylvestris* and *T. baccata* share their need of a wet summer for recruitment, but they differ in their habitat preferences: *T. baccata*, a shade-tolerant species, mainly appears in woodlands (Tittensor 1980; Hulme 1996; García et al. 2000), whereas *P. sylvestris*, a shade-intolerant species, prefers shrublands (Richardson 1998; Castro et al. 2005).

Lastly, our experimental results also emphasize the role of positive-ecological interactions as an active mechanism for increasing ecological diversity in semi-arid ecosystems. Less drought-tolerant species are able recruit thanks to the amelioration of environmental conditions created by secondary successional shrublands (Valiente-Banuet & Ezcurra 1991; Callaway 1995; Gómez-Aparicio et al. 2004), and this at last allow the expansion of realized niches of tree species (Bruno et al. 2003; Baumeister & Callaway 2006; Valiente-Banuet & Verdú 2007).

- **Lessons for conservation under a global-change scenario**

The reduced potential for recruitment of boreo-alpine species in typical dry years has severe implications for forest diversity under a scenario of global change (Lloret et al. 2004). As the prediction is towards more aridity in Mediterranean ecosystems, rainy summers probably will be less frequent in the future (FCI 2006; Moreno et al. 2006; IPCC 2007). Therefore, woody taxa more dependent on summer rainfall are threatened to be less abundant or even to disappear, because they undergo severe limitations for emergence (i.e. *T. baccata*) and survival (*T. baccata* and *P. sylvestris*). This has a consequent implication for diversity in terms of species richness and taxonomic singularity (May 1980), as Taxus and Pinus are the only taxa that represent their corresponding family in the study area. Also, Mediterranean forests risk changing their composition from a Pinus-dominated vegetation towards another vegetation with more importance of Mediterranean species, especially *Quercus* spp. (due to their abundance in the current vegetation and their resistance to water stress). Even more, as temperatures are predicted to rise in a global change scenario (IPCC 2007), winter death of *Quercus* spp., one of the main constrains of this species in high mountain (Terradas & Savé XX) may be decreased, probably because winters will be warmer in the future. Lastly, the coexistence of species would be restricted to the most favorable scenarios for all species, i.e. woodlands. This reinforces the conservation value of woodlands, because they are the types of habitats where a diverse pool of seedlings can be maintained. Woodlands appear as good habitats for early stages of plants, but the scarcity of light may have negative consequences on sapling growth (Espelta et al. 1995; Castro et al. 2005a), thus hampering forest regeneration. Shrublands represent surrounding areas to which forests can be expanded, although a rainy summer is needed for the expansion.

In short, the frequency of wet vs. normal summers in the future will determine not only the number and identity of the species coexisting in a given community but also the capacity of the woodland to expand and to colonize surrounding degraded habitats, such as shrublands and open areas.

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CAPÍTULO 4

TITLE: Do wet summers offer delayed benefits for Mediterranean woody seedlings where climate is highly variable? A field experiment

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INTRODUCTION

Water is a critical resource limiting distribution, survival, and growth of plants (Kozlowski 1968; Archibold 1995; Grace 1997). Seedlings are the most vulnerable demographic stage to climatically haphazard events, and for this reason, many plant species fail to recruit in dry years (Zoladeski & Maycock 1990; Kitajima & Fener 2000; Ibáñez & Schupp 2001; Castro et al. 2005). In Mediterranean, semiarid, and arid ecosystems, unusual rainfall periods during the growing season represent a resource pulse that can offer recruitment opportunities, as this unusual boon of water encourages seedling establishment (Holmgren & Scheffer 2001; Yang et al. 2008). In the more specific case of Mediterranean ecosystems, dry summers are the rule (Henderson-Sellers & Robinson 1991), with exceptional rainy summers roughly every 7-40 years (Esteban-Parra et al. 1998; Rodó & Comín 2001). These rare wet summers are especially relevant for long-lived species, such as trees, in which recruitment is otherwise hampered by drought (Traveset et al. 2003, Gómez-Aparicio et al. 2005, Lázaro et al. 2006). Because most woody plants are iteroparous organisms, one successful reproductive event per individual over its lifetime can be, theoretically, enough to allow population maintenance (Harper 1977). The unpredictable conditions that allow this event to take place represent a window of opportunity for population persistence (Eriksson & Fröborg 1996).

Wet summers can provide an immediate benefit for plant recruitment, and short-term responses to increased rainfall have been reported (i.e. Dillon & Rundel 1990; Yakir et al. 1996; Gutiérrez et al. 1997; Polis et al. 1997; Holmgren et al. 2001; Schwinning & Sala 2004). Wet summer can also provide a delayed advantage for survival and growth, but few empirical data support this hypothesis (but see Benayas et al. 2004). As performance of organisms can be influenced by both current and previous environments (Bazzaz 1996; Reekie et al. 1997; Metcalfe & Monaghan 2001; Relyea 2002; Weinig & Delph 2001; Grether 2005), it is critical to determine if a favourable rainy period can only provide current benefits, or both current and delayed benefits. Another possibility is that the initial advantage of a wet summer would disappear over time depending on the functional traits of the species, and/or the climatic conditions of the coming years.

The aim of this study is to evaluate over time the delayed benefits of a wet summer for the survival and growth of six woody species coexisting in the Mediterranean-mountain forests with contrasting ecological characteristics. These species represent the entire tree community in our study area. Because of wet summers are rare events in Mediterranean ecosystems, it is often impracticable to discern the consequences for seedling recruitment with an observational approach. Thus, our experimental design included irrigation in order to simulate the summer storms characteristic of Mediterranean mountains. Our study focuses at the community level because different responses of species to wet summers have strong implications for forest dynamics and species coexistence (Silvertown et al. 2004). Given that Mediterranean forests are composed of plants with different ecological requirements and biogeographical origins (Herrera 1992; Blanca et al. 1999), species more sensitive to summer drought would be especially benefited from a wet summer. We expected that species more sensitive to water stress (i.e. boreo-alpine species) would need summer rainfall more for their recruitment than species with typical Mediterranean characteristics. We also selected the most abundant habitats where seeds are dispersed, ranging in habitat openness and soil properties. A rainy summer can produce two possible types of responses: inertia, i.e. plants retain the ability to respond favourably to natural environmental harshness after the rainy event; or reaction, i.e. plants were less capable of facing later environmental harshness. Our working hypothesis was that summer rainfall would increase growth and survival of tree species in the year of the event, as well as these positive benefits would be delayed over time (i.e. the response mechanism was inertia). After the third year of our experimental set up, an extreme dry year killed the most part of seedlings. Therefore, we were forced to end up our experiment. We take advantage of this unpredictable and extreme event to analyze to which extent an “infrequent” dry year can cancel out the potential benefits of a previous and “infrequent” wet year. Results of our study would help to clarify the regeneration dynamics of Mediterranean forests under current and future climatic scenarios, predicted to increase summer drought and to reduce the frequency of wet summers (Osborne et al. 2000; IPCC 2007).

MATERIAL AND METHODS

Study site and species

The field experiment was carried out from 2003 to 2005 in the Sierra Nevada National Park (S Spain). The study site, La Cortijuela Botanical Garden (37°05’N and 3°28’W, 1600m a.s.l.), is an area of 12.4 ha fenced against big mammals. The climate is Mediterranean with mountain properties: the precipitation is concentrated in late autumn and winter (usually snow) and there is a severe summer drought (June-August). The mean precipitation in the 1991-2005 period was 840 mm yr-1 (data from a climatic station located in the study site). Average cumulative rainfall in June, July, and August over the last century is 48 mm (1902-2001; data obtained from a meteorological station placed in Granada city and correlated with data of the meteorological station of the study area; $R^2=0.73$). In our long series, we found eight years when summer rainfall was above 95 mm, considered as wet summers in terms of Mediterranean climate. The study years showed contrasted rainfall patterns: rainfall in 2003 (975 mm yr-1; 14 mm yr-1 in summer) and 2004 (770 mm yr-1; 28 mm yr-1 in summer) was close to the average for the area, whereas 2005 (394 mm yr-1; 8 mm yr-1 in summer) was the driest year of the 15-year series. The dominant bedrock is limestone, giving rise to basic loamy soils.

The study species were *Quercus ilex* L., *Quercus pyrenaica* Willd., *Acer opalus* subsp. *granatense* (Boiss.) Font Quer & Rothm. (hereafter *A. granatense*), *Sorbus aria* L., *Pinus sylvestris* var. *nevadensis* Christ, and *Taxus baccata* L. These six tree species were selected because: 1) they were the components of the canopy; 2) they diverge in their biogeographical origins and therefore it is predicted that they differ in their ecological requirement (Castroviejo et al. 1986; Blanca et al. 2002); and 3) their seeds range in size (mean ± SE in g): *Q. pyrenaica* (5.04 ± 0.002) > *Q. ilex* (3.46 ± 0.002) > *T. baccata* (0.066 ± 4.8; García et al. 2005), *A. granatense* (0.042 ± 0.001) > *S. aria* (0.022 ± 0.002) > *P. sylvestris* (0.012 ± 0.0001; Castro et al. 2007)

The vegetation in the study area is composed of small woodlets intermingled with early- and late-successional shrublands. The dominant tree species is *P. sylvestris* and secondly *Q. ilex* (ca. 20% of tree cover; unpublished data), while *A. granatense*, *Q. pyrenaica*, *S. aria*, and *T. baccata* being less abundant. *Pinus nigra* subsp. *salzmannii* (Dunal) Franco is also another main component of the canopy, but the individuals in the study area were planted. The understory is composed of several shrubs such as *Genista cinerea* (Vill.) DC., *Crataegus monogyna* Jacq., *Prunus ramburii* Boiss., *Thymus mastichina* L., and *Salvia lavandulifolia* Vahl. (see Rodríguez Hiraldo et al. 2001 for more information about the vegetation of the area).

Field methods and experimental design

A sowing experiment with two levels of water addition was performed for the six study species. Fruits of each species were collected in the study area or in nearby areas in Andalusia. In the case of fleshy fruits, we removed the pulp and stored the seeds at 2-4°C until used. Acorns were stored on a moist substrate at 2-4°C until used. Before sowing, seed or fruit viability was tested by submerging acorns and selecting the non-floating ones in the case of Quercus spp, and by rejecting the clearly-aborted or depredated seeds by visual inspection in the case of the rest of species. For simplicity, we refer hereafter to all propagules as seeds.

Sowing was performed in the three habitats that cover the most part of the understory in the area, where seedling emergence occurs naturally (Castro et al. 2005a, 2005b), and that are representative of the successional scenarios in the area: 1) Open areas of bare ground or covered by sparse herbaceous vegetation, separated to surrounding vegetation enough distance to avoid shading; 2)

Shrublands, under the canopy of Salvia lavandulifolia, Crataegus monogyna, or Genista cinerea; 3) Woodland, under the canopy of *P. sylvestris* or P. nigra. For each kind of habitat, we selected three plots of similar area (0.2-0.3 ha) that were separated at least 100 m each other. Within each plot, seeds were sown in 20 sowing stations. A sowing station was composed of a set of randomly disposed wire cages (1.3 cm mesh size) with the sowed seeds of each species. Sowing stations were randomly distributed in each plot and separated one to the others by at least 3 m. The total number of sowing stations was 180. Seeds of each species were sown in a cage against seed predators and herbs were carefully removed in order to avoid interspecific competition. The number of seeds per sowing station was adjusted to seed size: 5 for Quercus species (sown in a cage of 0.042 m2 area), 10 for *T. baccata*, and 15 for *A. granatense*, *P. sylvestris*, and *S. aria* (all these five species sown in a cage of 0.0286 m2 area). For all species except for Quercus, seeds were sown 1 cm of depth and separated one to each other 2.5 cm. Acorns were sown 3 cm depth and the distance between them was 8-10 cm. We sowed a total of 11,700 seeds in January 2003.

In 2003, the half of the sowing stations was randomly assigned to an irrigation treatment and the other half to control. Water was applied with a drip-irrigation method at around 10-day intervals during the start of the drought until the first major rainfall was recorded (from June to September). Because the emergence of *T. baccata* was only produced the year after sowing (i.e., in 2004), only for this species we also irrigated seedlings in 2004. The surface irrigated (30 x 30 cm) was greater than the surface of the sown cage in order to avoid border effects. Irrigation consisted of adding ca. 2 l of water at each application time (equivalent to 22 mm). Irrigation simulated a rainy summer in terms of Mediterranean climate, because these rare summers typically consist on eventual strong-summer storms. Therefore, the addition of ca. 22 mm of water with an interval of around 10 days has biological sense and reproduces the natural conditions of the area (Gómez-Aparicio et al. 2005; Castro et al. 2005a)

Seedling monitoring

Each seedling that emerged in the cages during the spring of 2003 was individually tagged and its survival was monitored weekly in 2003 and fortnightly in 2004. In 2005, monitoring was done at the beginning (25th May) and at the end (20th September) of the growing season. The total number of seedlings tagged was: 245 for *A. granatense* (9% emergence), 1510 for *P. sylvestris* (39% emergence), 435 for *Q. ilex* (48% emergence), 346 for *Q. pyrenaica* (20.7 %) and 335 for *T. baccata* (19% emergence). Detailed analyses of seed germination and emergence patterns are the object of complementary studies (Mendoza et al. unpublished).

At the end of the experiment (2005), surviving seedlings were harvested in order to determine their final growth. Root was extracted until 20 cm depth. In the laboratory, fresh seedlings were separated into root, stem, and leaves. All parts were oven-dried at 80°C during 48 hours and weighted.

Data analysis

Seedling survival was assessed by means of survival analysis, an individual-based analysis, and also by a generalized model, based in the proportion that survived in each habitat and irrigation treatment at the end of the experiment. A Cox's Proportional Hazards semi-parametric model was used to estimate the survival function from the survival times in our data set. Survival time for each seedling was defined as the number of days from the emergence until the death. When seedling death did not occur before the end of the experiment (20th September 2005), we considered its survival time to be the last day of the experiment and we labelled the individual as right censored. We tested the effects of habitat type x irrigation treatment on species survival, using the maximum partial likelihood as the estimation method of the Cox's model (Fox 1993; Allison 1995). Analyses of final survival after three years of experiment were performed using a logistic model with final survival rate (proportion of the number of surviving seedling to the total number of emerged seedlings) as the response variable, binomial probability distribution (as each individual seedling had a binary probability to dead), and logit link function. We used the type of habitat and the irrigation treatment as the main effects. We removed *T. baccata* for these analyses because seedlings only survived at the end of the experiment in Woodland and when watered. Analyses of *A. granatense* were only performed for seedlings in Woodland and of *P. sylvestris* for watered seedlings.

Summed data of stem, root, and leaf biomass (this last for all species except for *A. granatense* and *S. aria*) were analyzed with a factorial ANOVA. Because many seedlings were dead after the three years of the experiment, we needed to adjust the models to the final sample size of each species: we removed from the analyses seedlings of Q pyrenaica and *S. aria* that grew up in Open; we compared control vs. watered seedlings that grew up in Woodland for *A. granatense*; and we compared biomass of watered seedlings emerged in Open vs. watered seedlings in Shrubland for *P. sylvestris*;

Analyses were separated for each species, as our aim was to explore the influence of habitat type and irrigation treatment for each species. Furthermore, the inclusion of species and their interactions with habitat and watering in the models complicates interpretation of results. Values are given throughout this paper with mean ± standard error. Analyses were done using STATISTICA 7.1 (StatSoft Inc., 2005), JMP v. 7.0 (SAS Institute Inc. 2007), or R 2.4.1 software (R Development Core Team 2006).

RESULTS

Final survival

From the 3429 seedlings that were emerged in 2003, 766 survived at the end of the experiment in 2005 (22 %). Species followed a rank of percentage for final survival (all individuals pooled): *Q. ilex* (48.87 ± 3.3 %) > *Q. pyrenaica* (44.13 ± 3.71 %) > *S. aria* (35.02 ± 3.36 %) > *A. granatense* (17.5 ± 3.37 %) > *P. sylvestris* (7.06 ± 1.38 %) > *T. baccata* (5.61 ± 1.67 %). Both habitat type and irrigation treatment influenced the probability of seedling survival for all species (Table 1). The general pattern (except for *P. sylvestris*) for the influence of habitat type on seedling survival was the following: survival was high in Woodland, intermediate in Shrubland, and low in Open (Table 2; Figure 1 and 2). However, seedlings of *P. sylvestris* had slightly higher survival in Shrubland than in the other two habitats.

In general terms, the irrigation treatment increased seedling survival the first summer of application (in all cases except for *T. baccata* in Open, as well as for *Q. ilex* and *A. granatense* in Woodland), and the effect was maintained the following summer (Fig. 1). However, this benefit was cancelled out the last year of the experiment (2005) for most species except for *Q. pyrenaica* and *S. aria*, because these two species had an increased survival for watering seedlings that

Table 1. Summary of the logistic model for second-year emergence under different habitats and irrigation levels. Habitats are Open, Shrubland, and Woodland. Irrigation levels are Control and Water supplementation. Emergence rate was calculated as the proportion of seedlings emerged the second year after sowing to the total number of sowed seeds per cage. Significant P values are shown in bold.

Species	Effects	df	χ^2	P
Q.ilex				
	Habitat	2	43.31	<0.0001
	Watering	1	17.14	<0.0001
	Habitat x Watering	2	7.06	0.0294
	Model	5	81.88	<0.0001
Q. pyrenaica				
	Habitat	2	29.20	<0.0001
	Watering	1	26.17	<0.0001
	Habitat x Watering	2	4.09	0.1292
	Model	5	63.37	<0.0001
S. aria				
	Habitat	2	63.99	<0.0001
	Watering	1	52.94	<0.0001
	Habitat x Watering	2	5.24	0.0729
	Model	5	117.38	<0.0001
A. granatense				
	Habitat	2	105.72	<0.0001
	Watering	1	8.08	0.0045
	Habitat x Watering	2	9.77	0.0076
	Model	5	119.57	<0.0001
P. sylvestris				
	Habitat	2	37.65	<0.0001
	Watering	1	343.14	<0.0001
	Habitat x Watering	2	10.25	0.006
	Model	5	417.69	<0.0001
T. baccata				
	Habitat	2	32.01	<0.0001
	Watering	1	12.42	0.0004
	Habitat x Watering	2	8.54	0.014
	Model	5	153.30	<0.0001

grew up in Woodland. *Q. pyrenaica* and of *A. granatense* did not show differences throughout the whole experiment between watered or control seedlings that grew up in Woodland. Compared with the rest of species, boreo-alpine species (i.e. *P. sylvestris* and *T. baccata*) were more dependent on wet summers for survival because only watered seedlings survived after three years of experiment (Figure 1 and 2).

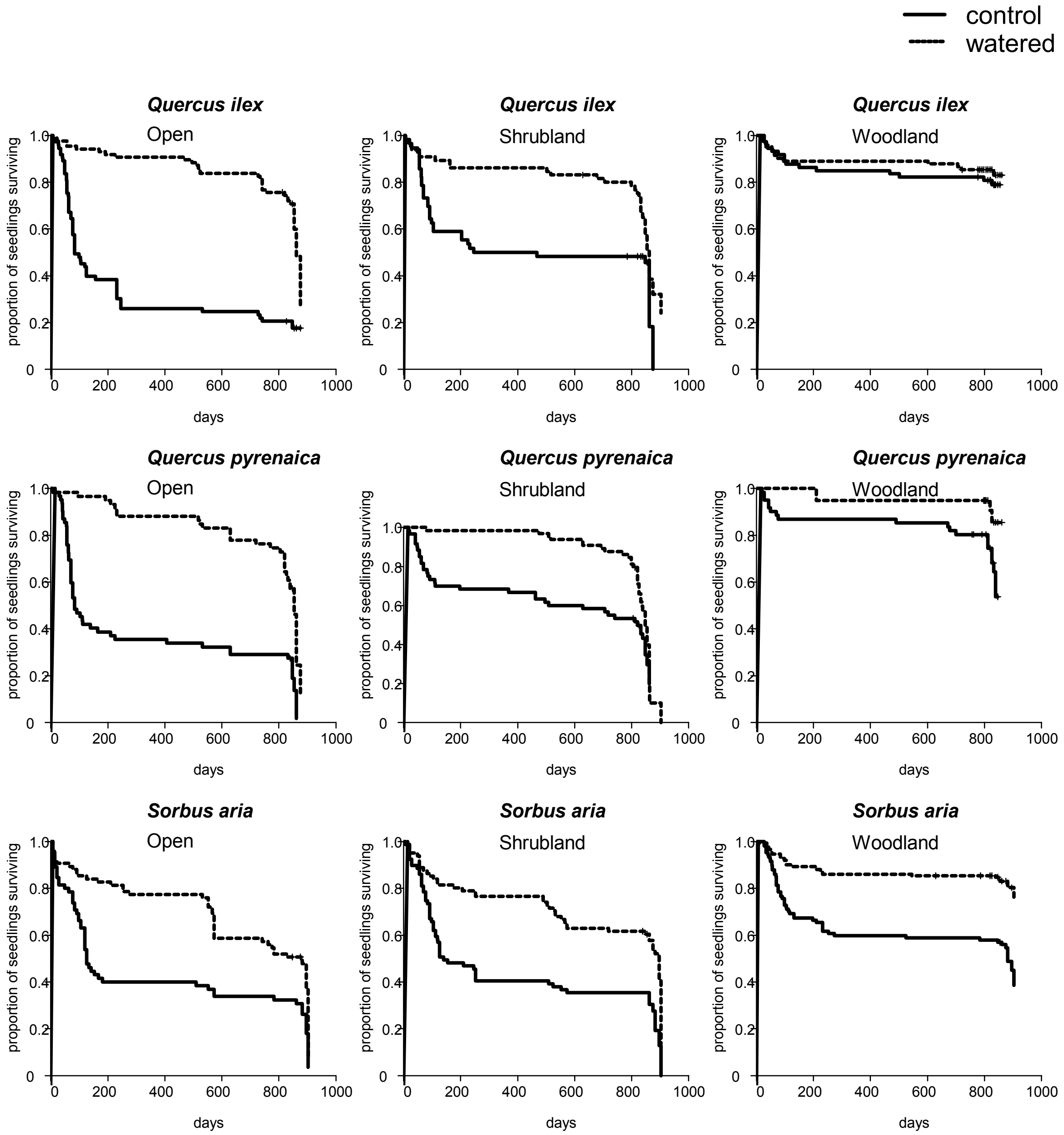

Fig 1a. Probability of seedling surviving of each species. Each graph shows survival for control (solid line) and watered (dashed line) seedlings of a species per habitat. Different letters show significantly different survival curves.

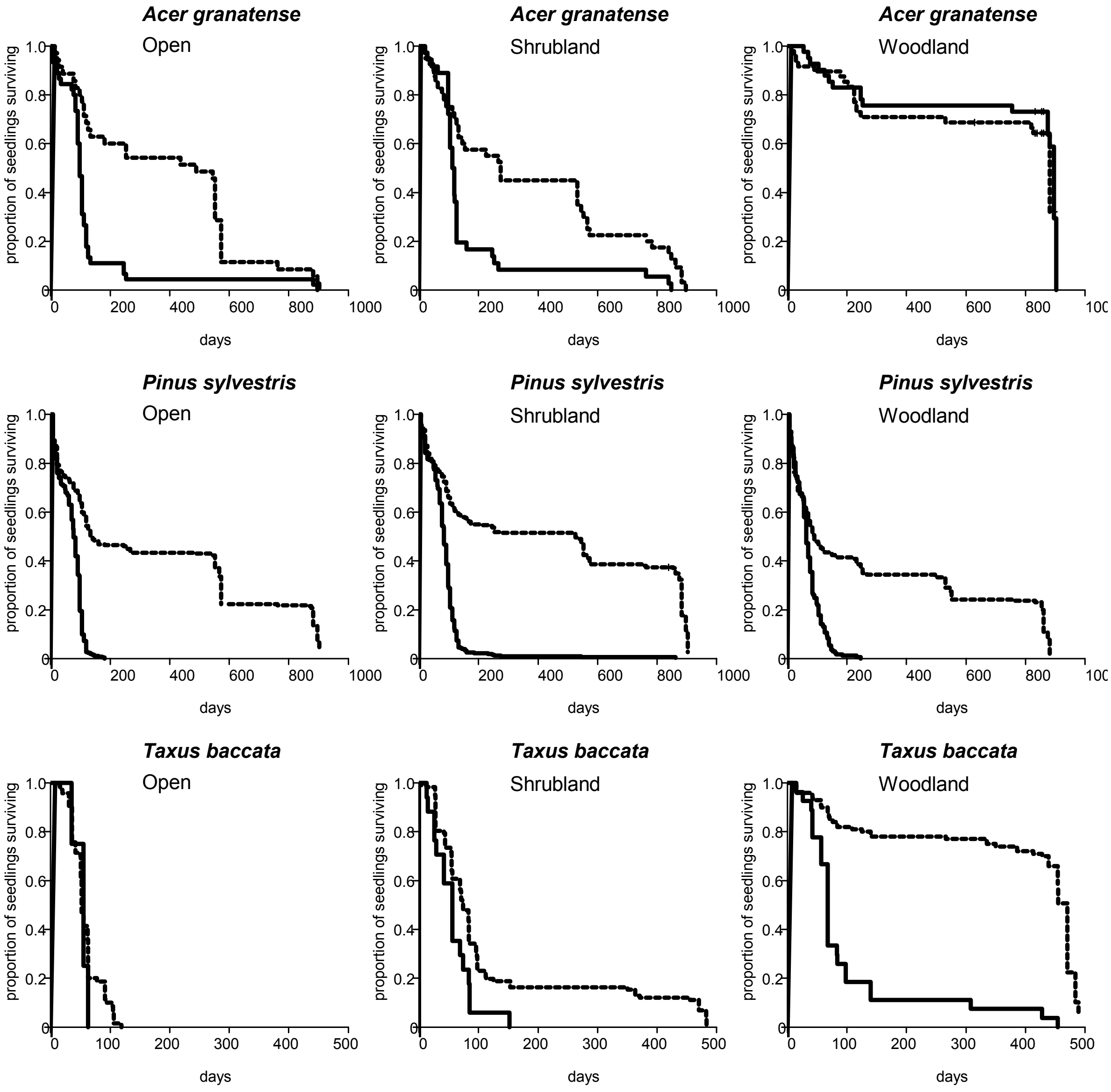

Fig 1b. Probability of seedling surviving of each species. Each graph shows survival for control (solid line) and watered (dashed line) seedlings of a species per habitat. Different letters show significantly different survival curves.

Final biomass

Species ranged enormously in their biomass (all individuals of the same species pooled): *Q. pyrenaica* (1.37 g) > *Q. ilex* (0.90 g) > *P. sylvestris* (0.26 g) > *S. aria* (0.18 g) > *A. granatense* (0.12 g) > *T. baccata* (0.02 g). Water addition significantly increased final biomass for *Q. ilex* (0.93 g for watered seedlings

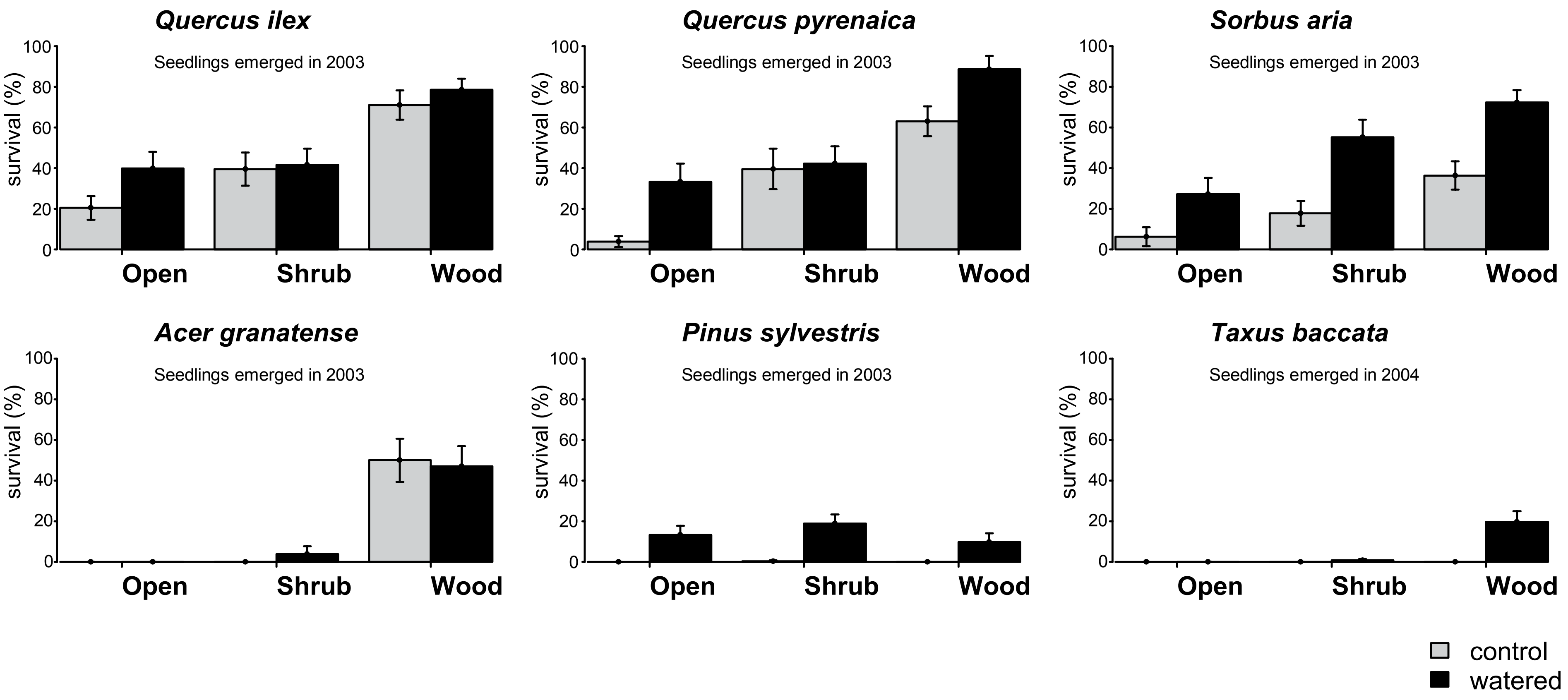

Fig 2. Probability of seedling surviving of each species. Each graph shows survival for control (solid line) and watered (dashed line) seedlings of a species per habitat. Different letters show significantly different survival curves.

vs. 0.79 g for control ones; all habitats pooled), *S. aria* (0.26 g vs. 0.18 g), and *A. granatense* (0.15 g vs. 0.09 g; Table 2 and Fig. 3). The type of habitat significantly affected the final biomass of all species (Table 2). In general terms, habitat openness increased final biomass (i.e., biomass in open > shrubland > woodland when data of all types of habitats were available). Seedlings of *Q. ilex* in Open (1.04 g; the two watering treatments pooled) were heavier than in Shrubland (0.84 g) and Woodland (0.71 g). The same pattern appeared for *Q. pyrenaica* (1.64 g in Shrubland vs. 1.56 g in Woodland), *S. aria* (0.25 g in Shrubland vs. 0.19 g in Woodland), and *P. sylvestris* (0.32 in Open vs. 0.19 in Shrubland). The interaction between water addition and habitat was significant only for seedlings of *Q. pyrenaica* and *S. aria* (Table 2), because biomass of watered and control seedlings differed only in one of the habitats.

Table 2. Summary of the logistic model for survival at the end of the experiment under different habitats and irrigation levels. Analyses were separated for each species and year of emergence. Habitats are Open, Shrubland, and Woodland. Irrigation levels are Control and Water supplementation. Survival rate was calculated as the proportion of seedlings that survived the second summer to the total number of emerged seedlings per cage. Model for *T. baccata* was not performed because the number of surviving seedlings was too low. Analyses of *A. granatense* were only performed for seedlings in Woodland and of *P. sylvestris* for watered seedlings.

Species	Effects	df	χ^2	P
Q.ilex				
	Habitat	2	27.268	<0.0001
	Watering	1	2.926	0.0872
	Habitat x Watering	2	1.042	0.5939
	Model	5	31.979	<0.0001
Q. pyrenaica				
	Habitat	2	44.206	<0.0001
	Watering	1	12.052	0.0005
	Habitat x Watering	2	7.323	0.0257
	Model	5	51.389	<0.0001
S. aria				
	Habitat	2	33.739	<0.0001
	Watering	1	20.818	<0.0001
	Habitat x Watering	2	0.434	0.8051
	Model	5	54.863	<0.0001
A. granatense				
	Watering	1	0.054	0.817
P. sylvestris				
	Habitat	2	3.473	0.176

Table 3. Results of the ANOVA with the total biomass as response variable and different effects (depending on the species) as predictors. Degrees of freedom, F statistic, percentage of explained variance (%), and P values are presented. Response variable is total biomass, including leaf mass for *P. sylvestris*, *Q.ilex*, and *Q. pyrenaica*.

Species	Effects	df	F	P
Q.ilex				
	Habitat	2	18.388	<0.0001
	Watering	1	8.961	0.003
	Habitat x Watering	2	1.560	0.213
	Model	5	12.287	<0.0001
Q. pyrenaica				
	Habitat	1	0.284	0.596
	Watering	1	0.781	0.380
	Habitat x Watering	1	6.783	0.011
	Model	3	2.772	0.047
S. aria				
	Habitat	1	4.080	0.045
	Watering	1	7.379	0.007
	Habitat x Watering	1	4.820	0.029
	Model	3	6.672	0.0003
A. granatense				
Woodland				
	Watering	1	4.427	0.046
P. sylvestris				
Watered				
	Habitat	1	19.276	<0.0001

DISCUSSION

Using an experimental approach in natural conditions, we wanted to determine whether the alleviation of summer drought (simulating a wet summer in terms of Mediterranean ecosystems) could offer delayed benefits for the survival and growth of six species of contrasting biogeographical origin that coexist in Mediterranean forests. The results of our experiment indicate three different advantages of wet summers: 1) watering increased survival for all species the year of occurrence, especially in Open and Shrubland habitats; 2) summer irrigation the first summer increased survival the following years; 3) water addition significantly increased final biomass of seedlings. Therefore, these results are concordant with our working hypothesis that the response mechanism was inertia, because the

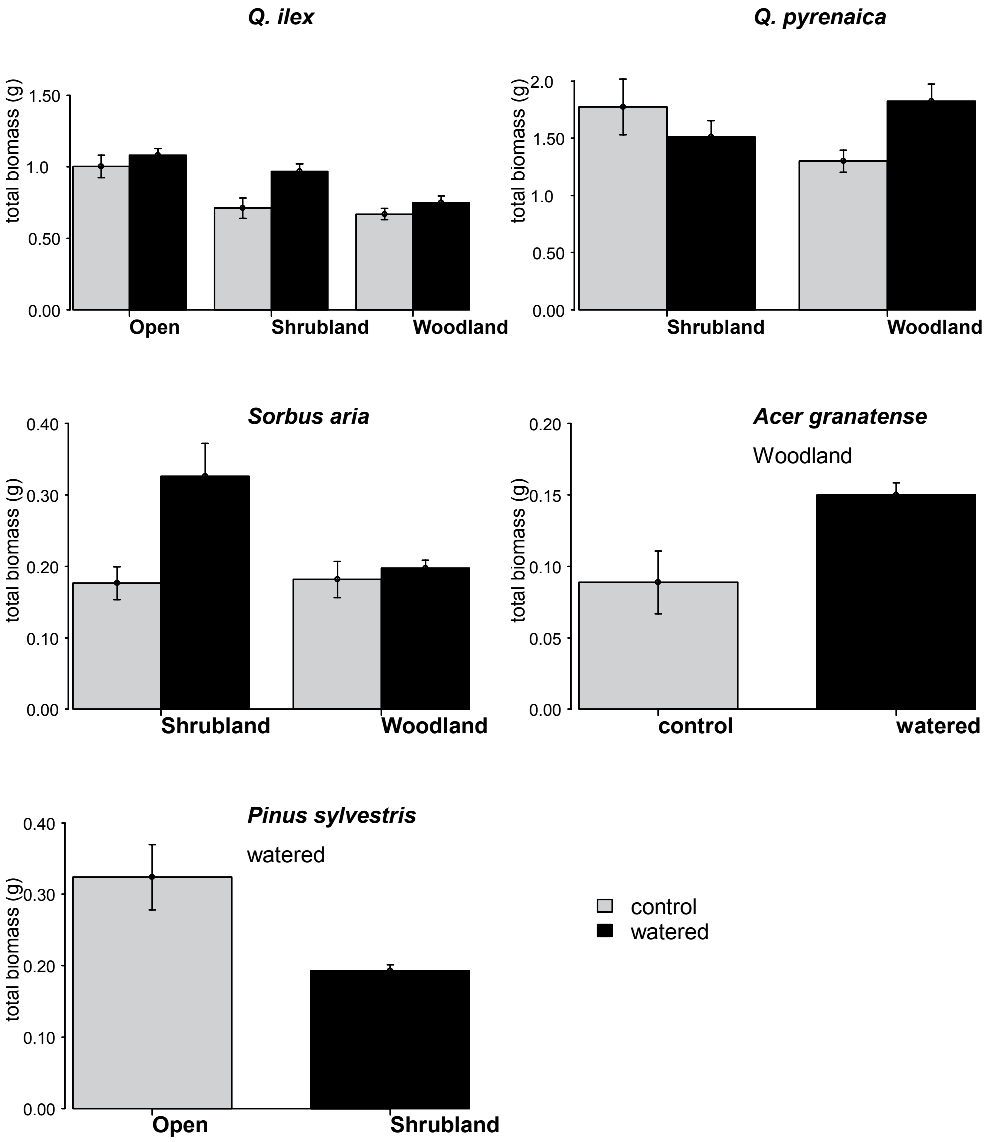

Fig. 3. Final biomass (g) for each combination of species, habitat, and irrigation treatment when data were available. Habitats are Open, Shrubland and Woodland. Irrigation levels are control (grey bars) and water supplementation (black bars). Seedlings growing up in Open lacked for *Q pyrenaica* and *S. aria*. *A. granatense* only had seedlings that grew up in Woodland and *P. sylvestris* only had watered seedlings emerged Open and Shrubland.

positive benefits of a wet summer were delayed over time. However, these benefits were cancelled out for four of the six species during a strong drought episode (2005 year) that provoked the mortality of many seedlings, irrespective to the previous conditions.

Many studies have demonstrated that the first year is critical for seedling establishment (Castro et al. 2004; Villar Salvador et al. 2004; Verdú & Traveset 2005; and references therein). Thus, mitigation of stress due to water addition in the first year resulted in lower mortality and higher growth rate during following years (see also Benayas 1998). Reduced post-establishment mortality may be due to the development of deep roots, which alleviated drought thanks to the access of deeper moist-soil layers (Padilla & Pugnaire 2007). Rooting depth determines the proportion of the soil profile from which plants can absorb water, and it varies among functional groups, plant species, and individuals of the same species (Jackson et al. 1996; Schenk & Jackson 2002; Padilla & Pugnaire 2007). Our irrigation treatment simulated a regimen of summer storms which was comparable to a pulse event of intermediate duration and size (Schwinning & Sala 2004), and probably water was able to saturate deeper soil layers. Therefore, seedlings with deep roots probably continued to take up water from the deeper soil after the rainy summer, in contrast with control seedlings (with presumably shallower roots), which only were able to access to shallow soil water (Schwinning & Sala 2004). Although water irrigation in 2003 summer resulted in a benefit for seedlings in 2004, the same trend was not maintained in 2005 for *Q. ilex*, *A. granatense*, P sylvestris, and *T. baccata*. Thus, most seedlings that had survived the first two years in sub-optimal microsites (i.e. high-radiation habitats) ultimately died because the third year was extremely dry. On the other contrary, watered seedlings of *Q. pyrenaica* (90% for watered seedlings vs. 70% for control) and *S. aria* (82% for watered seedlings vs. 50% for control) in Woodland significantly survived more than control seedlings throughout the whole study period. The delayed benefit of a wet summer was maintained when the year was extremely dry only for seedlings of *Q. ilex* and *S. aria* emerged in Woodland. This result highlights the relevance of woodlands for seedling survival, pointing out that the delayed benefits of a wet summer could be not only temporally dependent (Holmgren & Scheffer 2001; Holmgren et al. 2006), but rather show habitat specificity. Woodlands are the only habitat that could maintain a bank of seedlings of the most resistant species to drought even during periods of extreme dryness (Greene 1999; Catovsky & Bazzaz 2000)

However, dense canopy of Woodland resulted beneficial for survival but reduced seedling growth, indicating the existence of a trade-off between growth and survival. Similar survival-growth conflicts have been reported before for other Mediterranean tree species and systems (i.e. Zavala et al. 2000, Marañón et al. 2004, Castro et al. 2004, 2005). Biomass was augmented in more open habitats thanks to the increased carbon gain with radiation (Valladares 2003). Other studies have already reported the importance of irradiance for seedling growth and the limitations underwent by individuals growing up under dense canopies in Mediterranean ecosystems (Espelta et al. 1995; Castro et al. 2005). Our results also indicate the existence of a trade-off between growth and survival, because the habitats more appropriate for seedlings survival were not for seedling and sapling growth, an extension of the seed-seedling conflicts proposed by Schupp (1995, 2007).

Coexistent species differed in their response to summer drought, as boreo-alpine species (*P. sylvestris* and *T. baccata*) only were able to recruit seedlings in scattered years with an extended period of rainfall at the end of the spring (see also Rojo et al. 1994; Castro et al. 2005). However, Quercus spp., *A. granatense* and *S. aria* were less dependent on wet summers for their recruitment, especially under the densest canopies. Therefore, boreo-alpine species are more dependent on wet summers for having windows of opportunity for recruitment, although all species benefited from summer rainfall. This has been reported for some other relict, mesic species in Mediterranean ecosystems (see García et al. 1999 for Juniperus communis and Lázaro et al. 2006 for Buxus balearica) and is part of the strategy of persistence by longevity (García & Zamora 2003). These species fail to recruit seedlings in dry years, but this might not mean the local extinction of the species, thanks to their ability to survive for long periods under unfavourable recruitment conditions. When the extremely rare event of a rainy summer occurs, boreo-alpine species can recruit and therefore regenerate under current unfavourable climatic conditions (Castro et al. 2004; García et al. 2000).

Windows of opportunity in a context of global change

Under a global change scenario, aridity is expected to increase as well as summer rainfall to be more irregular in the Mediterranean region, and particularly in Southern Spain (Moreno 2005, IPCC 2007; FCI 2006). Current models predict more frequency of extreme events, which have already increased across the globe (Easterling et al. 2000). Therefore, on the one hand, strong summer storms would probably be more frequent, but recent models also suggest that global warming could augment evaporative demand. Therefore, average duration of storms in summers would become shorter, and soil moisture variation more extreme (Gregory et al. 1997; Daly et al. 2000). On the other hand, it is also highly expectable that extremely dry summers will be more common (Weltzin et al. 2003). As our results have proven, these years result dramatic for seedlings because they can cancel out the positive effects of previous wet years. This has important implications for forest biodiversity under future climatic conditions, because more mesic species are prone to become rarer or even to disappear. As consequence, the global change can result in a loss of forest diversity (Lloret et al. 2004), because species more adapted to summer drought are more probable to persist than species that are far away from their ecological optimum. Thus, climatic change will exert a double constrain, because the expected reduction in the average rainfall signifies more difficulties for recruitment (especially of boreo-alpine species) and also, the benefits of a sporadic wet summer will be diluted.

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CAPÍTULO 5

TITLE:
Sapling bank as a predictor of the future forest in a degraded Mediterranean landscape: consequences for forest dynamics

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ABSTRACT

Question: What are the consequences for forest dynamics of the degree of concordance between adult canopy and sapling bank in a Mediterranean degradation framework?

Location: 1600-1900 m a.s.l., Sierra Nevada National Park, Southern Spain. The landscape was a mosaic composed of native forest and four degraded landscape units: dense, cleared, and fenced reforestation stands, and post-fire stands.

Methods: In each plot (three replicates per landscape unit), all the adults were counted, and the composition and abundance of the sapling bank was estimated using 10 transects of 25 x 2 m. Age, height, and herbivore impact of each sapling individual were also recorded.

Results: Native forest, reforestation stands, and post-fire stands shared the same local pool of species in the sapling bank. However, canopy and sapling bank were discordant in all landscape units. In the native forest, adults and saplings were discordant in abundance rather than composition. By contrast, the discordance between adults and saplings in degraded landscape units was produced both in terms of composition and abundance. Fencing greatly increased the density and growth rate of saplings, signalling a negative impact of ungulates. Herbivores preferred sapling species following a range: *Sorbus aria* > *Acer opalus* subsp. *granatense* > *Quercus ilex* > *Pinus sylvestris*.

Conclusion: Discordances between adults and saplings suggest a general change from a forest dominated by *Pinus* spp towards a mixed forest with more abundance of *Q. ilex*, *A. opalus*, and *S. aria*. However, the definitive composition of the future forest will depend on whether the management practices are able to diminish the regeneration constraints imposed by light scarcity in dense reforestation stands, recruitment limitations in post-fire stands, and a high browsing pressure in nearly all stands.

Keywords

Adult canopy; herbivory; Sierra Nevada; remnant forests; pine reforestation stands; post-fire stands.

Nomenclature

Castroviejo et al. 1986, Valdés et al. 1987, and Blanca et al. 2002.

INTRODUCTION

Most ecosystems throughout the world are degraded by humans (Vitousek et al. 1997; Chapin et al. 2000; Sanderson et al. 2002), this impact being even more dramatic in Mediterranean Basin because native forests have almost disappeared today after several millennia of human pressure (Thirgood 1981; Pausas 1999; Blondel 2006). For the recovery of native forests through management, it is crucial to predict forest dynamics under different types of degradation. As forests are dominated by long-lived individuals, the current adult canopy may persist over hundreds of years, but the future forest will eventually result from the current sapling bank. In the specific case of Mediterranean ecosystems, saplings are the best predictors of future forests because they are the nearest demographic stage to adults. Furthermore, saplings have a reduced probability of death compared with seeds and seedlings (Benayas 1998; Zamora et al. 2001; Benayas & Camacho-Cruz 2004; Castro et al. 2006). The seed stage is frequently limited by reproduction failure (masting being common in Mediterranean forests; Herrera et al. 1998), seed-dispersal failure (Jordano & Herrera 1995; Reisman-Berman et al. 2006; Gómez-Aparicio et al. 2007a), pre-dispersal seed predation (Herrera 1991; García et al. 2000), and/or post-dispersal predation (Crawley 1992; Alcántara et al. 2000; Matías et al. *submitted*). In the case of seedlings, most die from typical Mediterranean summer drought (Castro et al. 2005 and references therein; Chapters 3 & 4).

Despite relatively low sapling mortality in comparison with other demographic stages, several ecological factors constrain sapling transition into adulthood. First, some forest-management practices change tree density and hence light availability in the understory. For example, reforestation stands produce a far denser canopy than do native forests, reducing recruitment of the most light-demanding tree species (Denslow et al. 1990; Canham et al. 1994). By contrast, radiation penetrating forest gaps, as in the case of post-fire stands, may photoinhibit saplings (Werner et al. 2002; Valladares et al. 2005; Gómez-Aparicio et al. 2006) or exacerbate drought (Quero et al. 2006). Second, the high herbivore pressure (of wild as well as domestic livestock), persisting over thousands of years in Mediterranean habitats (Le Houérou 1981; Papanastasis & Peter 1998), severely affects the regeneration ability of the most palatable tree species (Baraza et al. 2006). Herbivores can alter the development of the forest stand by selective browsing, with consequences for the composition and dynamics of the communities (Kienast et al. 1999; Weber et al. 2008). Therefore, the assumption that the sapling bank can be interpreted as a predictor of the composition of the future canopy in Mediterranean forests should take into account different forest-management practices and degrees of herbivore pressure, because they can constrain sapling transitions into adults.

The aim of this study is to evaluate the degree of concordance of the adult canopy and the sapling bank (i.e. between the “current forest” and the “future forest”) in a degradation framework at the landscape unit level (a similar approach at the individual level has already been used in temperate forests; Horn 1981). A study of this type is needed in anthropic habitats in order to improve our still scant knowledge on the dynamics of Mediterranean vegetation (Marrs & Bradshaw 1993; Bonet 2004). The Mediterranean landscape studied was a mosaic of native forest mixed with two kinds of degraded landscape units: pine reforestation stands and post-fire stands. Our working hypothesis was that the native forest would be in a later successional stage than degraded landscape units and therefore, the adult canopy and sapling bank would have a higher degree of concordance. To understand whether herbivore pressure was a cause for the discordance between adults and saplings, we also compared age and size categories of saplings (see García at al. 1999, Gómez-Aparicio et al. 2005 for a similar procedure) and we evaluated the herbivory risk in the sapling bank (following the same method as

Zamora et al. 2001). Results of this study will help to predict which future forest has potential to regenerate in a degradation framework. Forest managers of degraded habitats urgently need such understanding for their decision criteria, because recovery management should take into account the regeneration potential of the sapling bank, including herbivore constraints imposed on saplings (Rausher 1999; Bonet 2003).

MATERIALS AND METHODS

Study area

This study was carried out from 2003 to 2005 at the locality of Trevenque, in Sierra Nevada National Park (37°05′ N, 3°28′ W, Granada, SE Spain). The bedrock is calcareous, with regosols and cambisols as the predominant soil types (Delgado et al. 1989; see also Castro et al. 2005 for more information about the area). This mountain area presents a continental Mediterranean climate, with cold winters and hot summers. The rainfall (average from 1990 to 2005) is 840 mm yr^{-1}, being more intense in autumn and spring and showing a typical summer drought. The main herbivores of the area are *Capra pyrenaica* and extensive livestock during summer (domestic goats and sheep; Hódar et al. 1998, García et al. 2000). *Sus scrofa* also inflicts intensive damage on the vegetation by rooting.

The study area is a mosaic composed of five different landscape units located from 1600 to 1900 m a.s.l.: 1) fragments of native forest (mixed pine forest); 2) dense reforestation stands; 3) cleared reforestation stands; 4) fenced reforestation stands; and 5) post-fire stands. These last four landscapes units originated from the degradation of the native forest, which is currently reduced in extension to small remnant fragments (less than 5 ha in total). The canopy of the native forest is composed mainly of *Pinus sylvestris* var. *nevadensis* H. Christ., accompanied by other trees such as *Taxus baccata* L. and *Acer opalus* subsp. *granatense* Boiss. (hereafter *A. granatense*). The species composing the understory are fleshy-fruited shrubs (*Berberis vulgaris* subsp. *australis* Boiss., *Crataegus monogyna* Jacq., *Juniperus communis* L., and *Lonicera xylosteum* L.) and other dry-fruited shrubs such as *Erynacea anthyllis* Link or *Ononis aragonensis* Asso. Reforestation stands were planted in the 1950s using *Pinus sylvestris* var. *iberica* Svoboda and *Pinus nigra* Arnold subsp. *salzmannii* (Dunal) Franco, with the scattered appearance of individuals of *Quercus ilex* subsp. *ballota* (Desf.) Samp., *Q. pyrenaica* Willd., and *Sorbus aria* (L.) Crantz. The three types of reforestation stands differed in their management: dense reforestation stands did not have any intervention after tree planting, in cleared reforestation stands timber was harvested in 2000, and fenced reforestation stands had an exclosure against ungulates, built in 1982, and the same tree density as in the dense stands. Post-fire stands had an open structure dominated by shrubs such as *Crataegus monogyna* Jacq., *Prunus ramburii* Boiss., *Salvia lavandulifolia* Vahl., and *E. anthyllis*. There were also some scattered adult pine trees that survived a fire in 1983 and saplings. This mosaic landscape constitutes a natural experiment in forest perturbation, given that the different types of impact (reforestation and fire) occurred in patches separated by a maximum of 2 km, and the exact year of these processes is known.

Sampling design

We selected three plots per landscape unit (n = 15 plots in total for all landscape units). Plot size varied from 0.16 to 0.93 ha, with a mean size of 0.53 ha, and an average distance between the three plots of the same landscape unit of 687.7 m. Plot sizes were determined with a centimetre-precision GPS (Leica SR 500; Leica Geosystems, Switzerland). To sample the adult canopy, we counted all the individuals present in each plot. To facilitate tree census, we split the plot surface in several sectors and counted all the trees in each sector. For the saplings, we laid out 10 transects of 25 x 2 m (n= 150) haphazardly distributed in each plot, sampling a total of 7500 m^2. Transects were established using a metric tape fixed at both ends and all sapling individuals were searched. We defined saplings as trees older than one year, less than 2-m tall, without flowers or fruits, and clearly differentiated from old resprouts. Throughout the sampling area, we found saplings of seven tree species: *A. granatense*, *P. nigra*, *P. sylvestris*, *Q. ilex*, *Q. pyrenaica*, *S. aria*, and *T. baccata*. For each sapling individual, the following items were recorded:

1. Age (years). Age was estimated counting whorls for *Pinus* spp or growth scars on the main stem for the rest of the species (see Taylor & Aarssen 1989;

Boerner & Brinkman 1996; Zamora et al. 2001; and Gómez-Aparicio et al. 2005 for a similar method). Saplings were grouped into four age categories following a geometrical progression: category I (1-2 years), category II (3-4 years), category III (5-8 years), and category IV (more than 8 years).

2. Total height (cm). Size structures were established grouping individuals in four categories of 20-cm intervals from 0 to above 60 cm: category I (1-19 cm), category II (20-39 cm), category III (40-59 cm), and category IV (more than 60 cm).

3. Risk of herbivory. For each individual, we noted whether there was at least one browsed shoot (in the current or previous years).

Data analysis

- **Density of adults and saplings**

Densities of pooled adult trees were compared between landscape units using a one-way ANOVA and a later Fisher LSD post-hoc test. The same tests were used for pooled densities of saplings.

- **Age and height categories**

Chi-squared analyses were used to compare whether the landscape units differed in the frequency of each age or height category, only for the three species more abundant in the sapling bank: *A. granatense*, *P. sylvestris*, and *Q. ilex*. In the case of *Q. ilex*, chi-squared analyses were made only for reforestation stands in order to obtain a high enough number of sampled individuals.

- **Herbivore impact**

First, we pooled all species and compared the herbivory risk between landscape units using a chi-squared analysis. Then, herbivore impact was analysed for the four species with a high enough number of sampled saplings (*A. granatense*, *P. sylvestris*, *Q. ilex*, and *S. aria*) following two approaches. First, the variation with age in the risk of herbivory was calculated for non-fenced individuals using a logit

Table 1. Density of adults and saplings (individuals ha^{-1}), showing the relative percentage of each species in the total density of adults and saplings. Species absent from a landscape are denoted by *none*. Therefore, those values were not used to calculate the relative percentage, symbolized by – in the table. Values are mean ± standard error.

Landscape unit	Species	Adult density (individuals ha^{-1})	Sapling density (individuals ha^{-1})	Relative proportion of adults (%)	Relative proportion of saplings (%)
native forest	*P. sylvestris*	83.25 ± 5.21	33.33 ± 6.67	78.23 ± 15.66	7.83 ± 5.20
	P. nigra	none	none	–	–
	Q. ilex	3.48 ± 2.77	280.00 ± 120.55	3.42 ± 2.95	54.77 ± 24.94
	A. granatense	10.90 ± 10.18	593.33 ± 573.33	7.25 ± 6.49	29.44 ± 23.16
	T. baccata	16.85 ± 16.13	26.67 ± 26.67	11.10 ± 10.33	1.16 ± 1.16
	S. aria	none	86.67 ± 76.88	–	6.51 ± 3.28
	Q. pyrenaica	none	6.67 ± 6.67	–	0.29 ± 0.29
	All species pooled	114.48 ± 20.17	1026.67 ± 644.19		
dense ref. stands	*P. sylvestris*	929.65 ± 41.83	6.67 ± 6.67	90.09 ± 5.33	0.44 ± 0.44
	P. nigra	109.97 ± 60.26	none	9.69 ± 5.30	–
	Q. ilex	1.63 ± 1.63	833.33 ± 389.24	0.14 ± 0.14	82.77 ± 8.08
	A. granatense	none	26.67 ± 6.67	–	7.15 ± 4.80
	T. baccata	none	none	–	–
	S. aria	0.81 ± 0.81	33.33 ± 17.64	0.07 ± 0.07	2.61 ± 1.49
	Q. pyrenaica	none	26.67 ± 6.67	–	7.02 ± 4.83
	All species pooled	1042.06 ± 92.27	926.67 ± 415.10		
cleared ref. stands	*P. sylvestris*	455.61 ± 53.05	966.67 ± 966.67	88.12 ± 2.66	23.02 ± 23.02
	P. nigra	65.03 ± 24.66	none	11.69 ± 2.60	–
	Q. ilex	none	926.67 ± 159.30	–	61.73 ± 16.45
	A. granatense	none	20.00 ± 0.00	–	1.51 ± 0.51
	T. baccata	none	none	–	–
	S. aria	none	113.33 ± 54.57	–	10.37 ± 6.18
	Q. pyrenaica	1.08 ± 0.62	33.33 ± 17.64	0.18 ± 0.10	3.37 ± 1.79
	All species pooled	521.72 ± 78.17	2060.00 ± 1070.02		
fenced ref. stands	*P. sylvestris*	444.60 ± 145.93	440.00 ± 390.04	39.15 ± 5.25	6.67 ± 5.88
	P. nigra	490.08 ± 212.55	13.33 ± 6.67	40.21 ± 13.84	0.19 ± 0.09
	Q. ilex	137.67 ± 117.22	5833.33 ± 833.97	20.65 ± 19.00	90.26 ± 5.56
	A. granatense	none	73.33 ± 24.04	–	1.08 ± 0.23
	T. baccata	none	6.67 ± 6.67	–	0.10 ± 0.10
	S. aria	none	93.33 ± 17.64	–	1.53 ± 0.45
	Q. pyrenaica	none	13.33 ± 13.33	–	0.17 ± 0.17
	All species pooled	1072.36 ± 249.04	6473.33 ± 823.12		
post-fire stands	*P. sylvestris*	17.23 ± 2.76	120.00 ± 20.00	82.36 ± 14.63	41.06 ± 3.04
	P. nigra	3.94 ± 3.26	100.00 ± 40.00	17.64 ± 14.63	29.95 ± 9.75
	Q. ilex	none	40.00 ± 11.55	–	16.53 ± 8.47
	A. granatense	none	26.67 ± 6.67	–	9.12 ± 1.47
	T. baccata	none	none	–	–
	S. aria	none	none	–	–
	Q. pyrenaica	none	13.33 ± 13.33	–	3.33 ± 3.33
	All species pooled	21.16 ± 1.24	300.00 ± 64.29		

model. The response variable was the presence/absence of at least one shoot browsed, following a binomial distribution. The species and the age category nested within species (fixed factors) were the categorical predictors. We pooled all landscape units to obtain a large enough sample size and we used pairwise χ^2 tests with Bonferroni technique (Rice 1989) for multiple comparisons.

Second, differences in growth rates within species were compared for fenced vs. non-fenced individuals only in reforestation stands, so that factors other than fencing would not influence sapling growth. Height increase is considered to follow an exponential function of age, i.e. $\text{height} = ae^{b*age}$ (Zamora et al. 2001; Gómez-Aparicio et al. 2005 and references therein). This equation takes the form of a straight line when plotted semi-logarithmically, with the growth rate being the slope of the resulting regression line (Leopold & Kriedeman 1975). To compare growth rates between fenced and non-fenced individuals within a species, we used ANCOVAs with interaction terms to contrast the slopes of the semi-logarithmic lines (Dowdy & Wearden 1991). For the ANCOVAs, fencing was the independent variable, age the covariate, and natural logarithm of height the dependent one. We assumed that saplings were growing at different rates if the interaction term was significant.

Mean values are given ± standard error throughout this paper. For all these analyses explained above, we used R 2.4.1 software (R Development Core Team 2006) or STATISTICA 7.1 (StatSoft Inc. 2005).

RESULTS

Adult composition

The adult density of pooled tree species was significantly different between landscape units (R^2 adjusted = 0.98, F = 190.374, d.f. = 4, $P < 0.0001$; Table 1). Native forest presented intermediate values of adult densities (115 adults ha^{-1}; Table 1), whereas dense and fenced reforestation stands had the densest canopies (≈ 1000 adults ha^{-1}). Clearing reduced the density of adults to almost a half compared with the other two types of reforestation stands (521 adults ha^{-1}) and

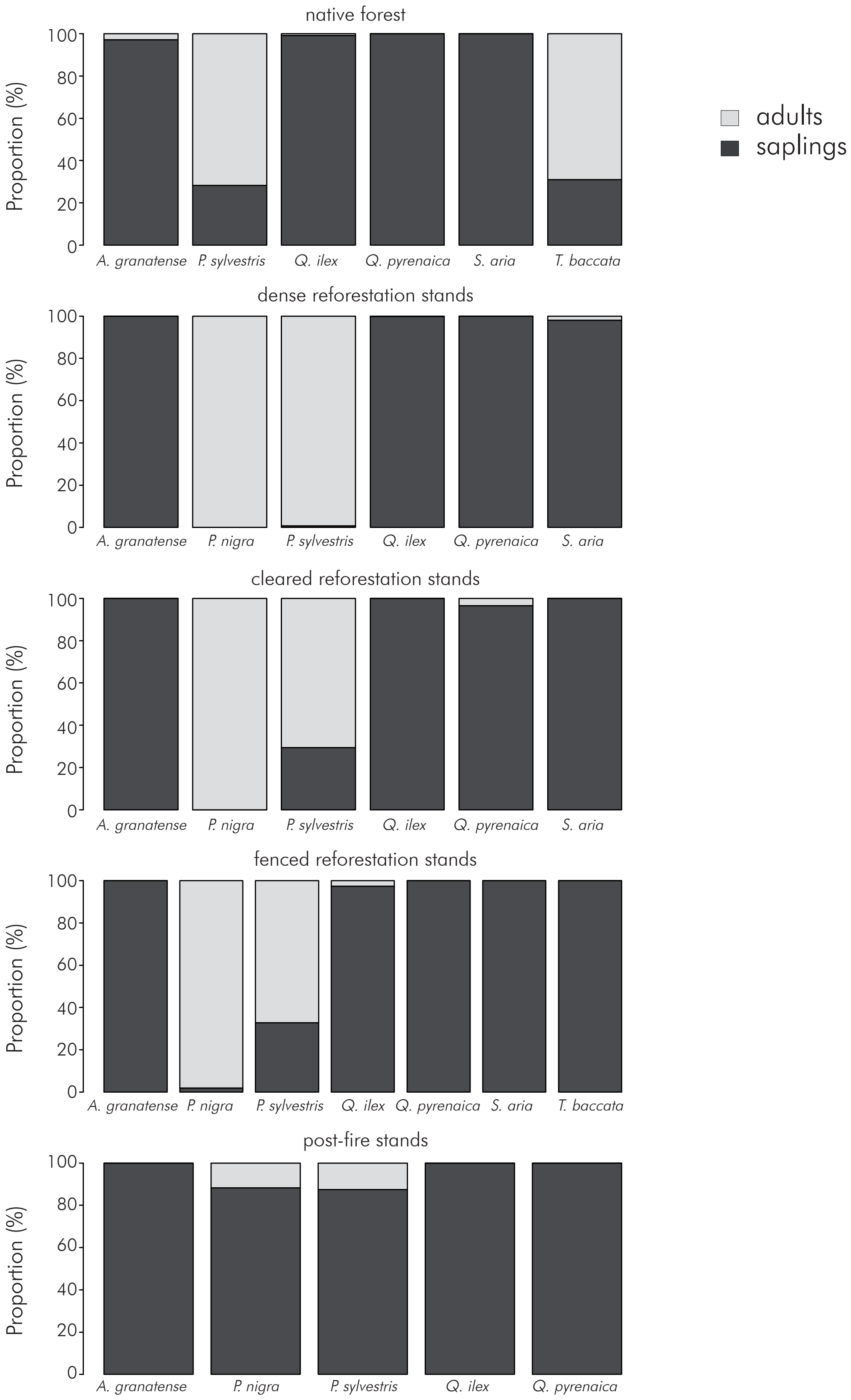

Figure 1. For each species, the percentage of the total number of individuals that were adults (grey bars) and saplings (black bars) is represented in each landscape unit

lastly, post-fire stands showed the least dense canopy of all landscape units (21 adults ha^{-1}).

The five studied landscape units greatly differed with respect to each other in terms of adult composition. The adult canopy in the native forest was the most heterogeneous; although *P. sylvestris* dominated a 78% of the canopy, *T. baccata* (11 %), *A. granatense* (7%) and, to a lesser extent, *Q. ilex* (3.5%) appeared with relatively medium densities (Table 1). A very different pattern appeared in the adult composition of dense and cleared reforestation stands; the canopy was almost completely composed of *P. sylvestris* (~90 %) and, to a lesser extent, by *P. nigra* (~10%). Other tree species such as *Q. ilex*, *S. aria*, and *Q. pyrenaica* appeared only as remnant trees, being non-relevant for the adult canopy. Fenced reforestation stands were dominated by *P. sylvestris* (40%) and *P. nigra* (40%), solely accompanied by *Q. ilex* (20%). Lastly, post-fire stands contained scattered trees of *P. sylvestris* and *P. nigra*.

Sapling composition

The density of pooled species of saplings significantly differed between landscape units (R^2 adjusted = 0.77, F = 12.88, d.f. = 4, $P < 0.001$; Table 1). Fenced reforestation stands significantly differed from the rest of landscape units because the sapling bank there was the densest.

The sapling bank was discordant with adult canopy in all landscape units (Fig. 1; Table 1). In the native forest, discordance was referred to in terms of abundance instead of composition; the sapling bank was dominated by *Q. ilex* (55%) and *A. granatense* (30%), whereas the most abundant species of the adult canopy, *P. sylvestris*, had few saplings (7%). In the rest of degraded landscape units, adults and saplings were discordant both in abundance and composition. In general, *Pinus* spp were absent in sapling banks but, in contrast, there were more species than in the canopy, thanks to the presence of deciduous trees such as *A. granatense* and *S. aria*, which were absent as adults. In dense and fenced reforestation stands, the sapling bank was dominated by *Q. ilex* (> 90%) and the two dominant species of the canopy, *P. sylvestris* and *P. nigra,* were almost absent as saplings. *P. sylvestris* was important in the sapling bank only in cleared refores-

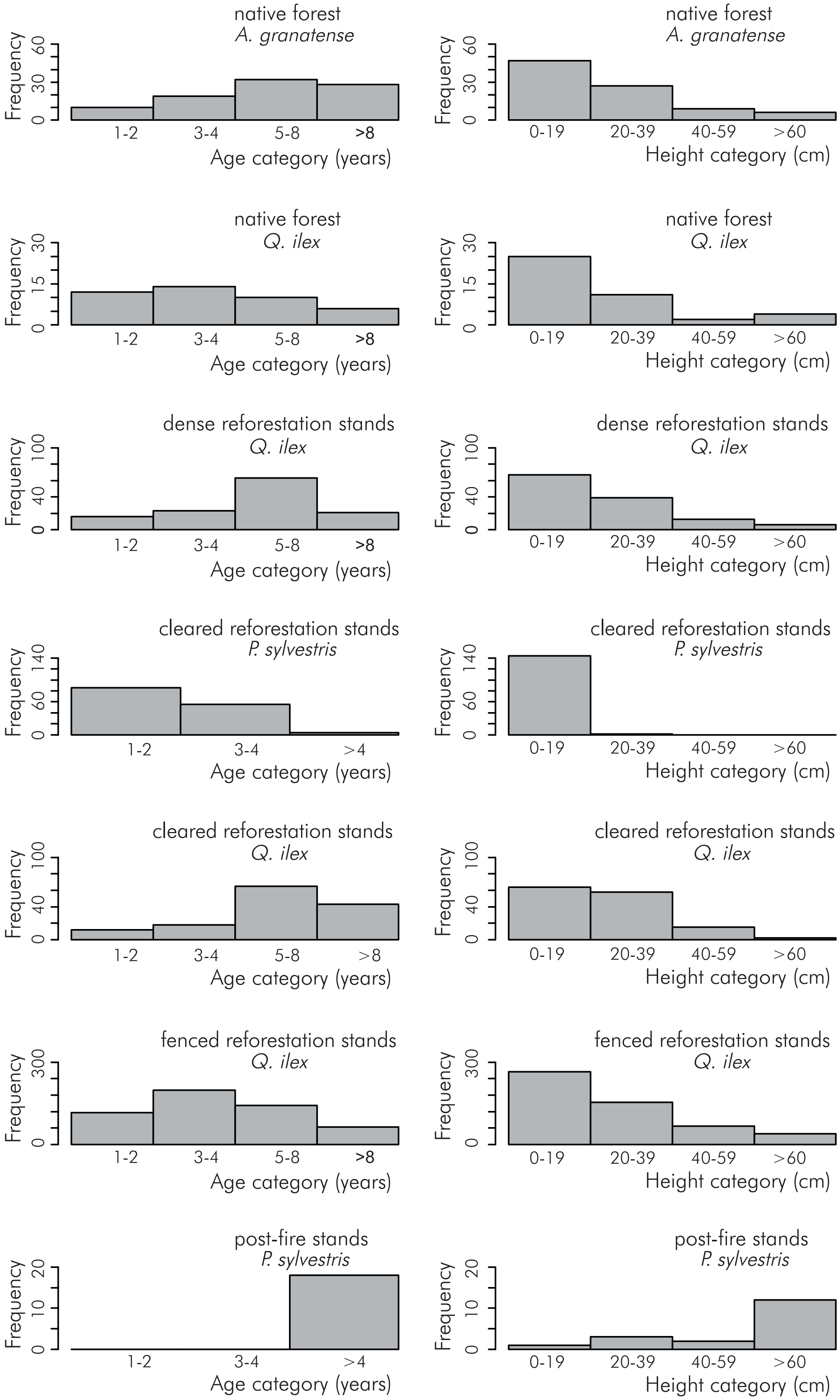

Figure 2. Age and height categories of the main components of the sapling bank in each landscape unit.

tation stands (23%). The few saplings appearing in post-fire stands were mostly *P. sylvestris* (41%), *P. nigra* (30%), and *Q. ilex* (17%).

Age and height categories of saplings

Age as well as height categories of a species differed across landscape units in the case of *Q. ilex* and *P. sylvestris*, but not for *A. granatense* (Table 2). Also, when we compared each landscape unit with the rest using the age and size structure of the dominant species appearing in each one, the age-size structure of the dominant species varied (Fig. 2). The most general pattern for the population of the dominant species in the sapling bank was to be composed of individuals that were relatively old (> 4 years) and short (< 20 cm). That was the case of *A. granatense* and *Q. ilex* in the native forest (Fig. 2), as well as of *Q. ilex* in dense, cleared, and fenced reforestation stands (although in this last case, individuals were slightly younger). However, the population of *P. sylvestris* in cleared reforestation stands was composed mainly of young (< 5 years) and short (< 20 cm) saplings, while individuals in post-fire stands were old (> 4 years) and tall (> 60 cm).

Table 2. Results of the chi-squared (χ^2) analysis comparing age or height categories of each species in the different landscape units. The null hypothesis is that the distribution of age/height categories is uniform in all landscape units. Significant *P* values are shown in bold.

	d.f.	χ^2	*P*
Age categories			
Acer granatense	8	14.438	0.07
Pinus sylvestris	8	230.946	**<0.0001**
Quercus ilex	6	103.315	**<0.0001**
Height categories			
Acer granatense	12	12.702	0.3911
Pinus sylvestris	12	266.721	**<0.0001**
Quercus ilex	6	14.680	**<0.0229**

Risk of herbivory by ungulates

For all tree species pooled, the landscape units significantly differed in their risk of herbivory ($\chi^2 = 52.09$, d.f. = 3, $P < 0.0001$), following a range of intensity: native (33.79 ± 12.35) > cleared (32.83 ± 11.05) = post-fire stands (24.83 ± 1.46) > dense (7.76 ± 7.76).

The herbivory risk varied among species and age categories within a species (Table 3). Among species, the percentage of saplings with a least one shoot browsed showed the following ranking: *S. aria* (52 %) > *A. granatense* (38 %) > *Q. ilex* (34 %) > *P. sylvestris* (1 %). Within species, the risk of herbivory increased significantly with age (Fig. 3), the highest risk of herbivory appearing for *S. aria* (even reaching values of 100%) and *A. granatense*, and the lowest for *Q. ilex*.

Herbivory significantly affected the sapling growth rate of *P. sylvestris* and *Q. ilex* (significant fencing x age interaction; Table 4). Fenced individuals grew faster than non-fenced ones for saplings of *P. sylvestris* ($\text{height} = 1.12e^{0.33\text{age}}$ for non-fenced vs. $\text{height} = 1.12e^{0.45\text{age}}$ for fenced) and *Q. ilex*. ($\text{height} = 2.3e^{0.11\text{age}}$ for non-fenced vs. $\text{height} = 2.16e^{0.19\text{age}}$ for fenced).

Table 3. Results of the logit model analysing the herbivory risk for the saplings of the four most abundant species. The effects tested in the first analysis were species and age category nested within species. Degrees of freedom, Wald statistic and *P* values are shown. All the predictor variables, and the Likelihood ratio χ^2 statistic of the model were significant (in bold).

Herbivory Risk	d.f.	Wald Statistic	*P*
Intercept	1	5.00	**0.0254**
Species	3	35.959	**<0.0001**
Age category [Species]	4	56.475	**<0.0001**
Model	7	168.845	**<0.0001**

Table 4. Summary of the ANCOVA model to compare the age-height regression slopes between saplings inside and outside an exclosure set up in 1982. Age ranged from 2 to 20 years. Analyses were performed separately for each specie with enough number of individuals appearing in reforestation stands (*A. granatense*, *P. sylvestris*, *Quercus ilex*, and *Sorbus aria*).

Species	d.f.	SS	F	*P*
Acer granatense[a]				
Fencing	1	0.29	1.36	**0.041**
Age	1	3.38	15.81	**0.002**
Fencing x Age	1	0.79	3.70	**0.08**
Error	12	2.56		
Pinus sylvestris[b]				
Fencing	1	4.16	55.56	**<0.0001**
Age	1	10.36	138.32	**<0.0001**
Fencing x Age	1	1.09	14.59	**0.0002**
Error	208	15.57		
Quercus ilex[c]				
Fencing	1	0.77	3.65	**0.06**
Age	1	133.23	628.29	**<0.0001**
Fencing x Age	1	11.27	53.20	**<0.0001**
Error	1014	215.01		
Sorbus aria[d]				
Fencing	1	0.02	0.11	0.7
Age	1	13.01	70.92	**<0.0001**
Fencing x Age	1	0.29	1.61	0.22
Error	29	0.18		

[a] *Acer granatense* whole model: $F_{3,12} = 17.08$, $P < 0.0001$, $R^2 = 0.81$

[b] *Pinus sylvestris* whole model: $F_{3,208} = 223.08$, $P < 0.0001$, $R^2 = 0.76$

[c] *Quercus ilex* whole model: $F_{3,1014} = 270.08$, $P < 0.0001$, $R^2 = 0.44$

[d] *Sorbus aria* whole model: $F_{3,29} = 31.63$, $P < 0.0001$, $R^2 = 0.77$

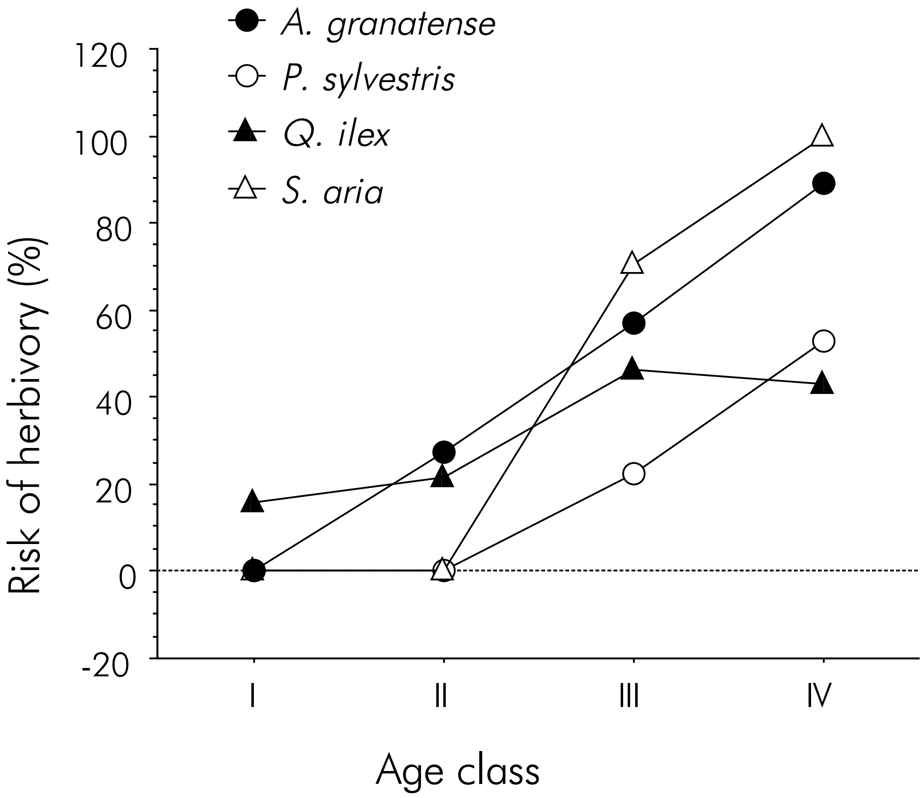

Figure 3. Variation with age in the risk of herbivory (%) undergone by four tree species. Different letters indicate significant differences between species for the same age category (after Bonferroni correction at $\alpha < 0.05$) according to pairwise χ^2 tests.

DISCUSSION

Degree of concordance between adults and saplings

Our results have shown that native forest as well as reforestation stands presented a diverse and abundant sapling bank, indicating a general pattern of active regeneration under current conditions. Native forest, reforestation stands, and post-fire stands shared the same local pool of species, presumably because all landscape units were very close to one another and formed a mosaic of similar altitude, exposure, and soil type among patches.

However, the canopy and sapling bank were discordant in all landscape units (Fig. 1). In the native forest, adults and saplings were discordant in terms of abundance rather than composition. The dominant adults in the canopy (*P. sylvestris* and *T. baccata*) were almost absent in the sapling bank; contrarily, *Q. ilex*, *A. granatense*, and *S. aria* dominated the sapling bank and were rare in the canopy. By contrast, the adults and saplings in degraded landscape units were discordant both in terms of composition and abundance; adult canopy was dominated by *P. sylvestris* and *P. nigra*, whereas the sapling bank was dominated by *Q. ilex*, and it was more diverse than the canopy due to the presence of *A. granatense*, *S. aria*, and *Q. pyrenaica*. Therefore, according to our working hypothesis, the canopy and the sapling bank were more discordant in degraded landscape units than in the native forest, because reforestation stands and post-fire stands were discordant both in terms of composition as well as sapling abundance. These results indicate that the most probable succession trend in the native forest is autosuccession (*sensu* Hanes 1971) because it implies a structural shift in the community without significant species turnover but rather a change in species abundance. Contrarily, our results suggest a secondary succession in degraded landscape units (based on the classical ideas of Clements 1916, 1936), implying species turnover in the community, which therefore goes through a mixed forest stage.

The discordant dominance of the canopy vs. sapling bank surely reflects a land-use change that favours *Q. ilex*, *A. granatense*, and *S. aria* instead of *P. sylvestris* (Chauchard et al. 2007). In our study area, as well as in the Mediterranean Basin, traditional land uses have became progressively non-profitable, so there has been a trend towards agriculture abandonment, logging reduction because of the switch to other energy sources instead of charcoal, and browsing cessation (Barbero et al. 1990; Debussche et al. 1999). Indeed, the area was declared as National Park in 1999, a conservation measure that has reduced the human impact and that restricts domestic livestock.

Forest regeneration under different types of habitat degradation

The type of degradation of each landscape unit differently affected the regeneration dynamics of the most dominant species present therein. In the native forest, the main threat for sapling regeneration was herbivore damage, as the population structures of the dominant species (*Q. ilex* and *A. granatense*) were composed mainly of old, short, and hence browsed individuals (García et al. 1999; Gómez-Aparicio et al. 2005). Presumably, the presence of a more diverse community in the native forest increased the herbivore pressure, because herbivores are influenced by context and they prefer vegetation with species more apt for consumption (Grubb 1992; Gómez et al. 2001; Björkman & Hambäck 2003; Baraza et al. 2006).

When no management was applied, as in dense reforestation stands, the sapling bank of the most abundant species (*Q. ilex*) was also predominantly composed of old and short individuals. Herbivore pressure proved comparatively low in this landscape unit compared with the rest, probably because the dense canopy diminished the food accessible for ungulates in the understory. Therefore, if saplings older than 15 years were lacking despite that the reforestation stands were 55 years old, the reason was not herbivore pressure. Other studies in the north-eastern Iberian Peninsula (Espelta et al. 1995) have reported that *Q. ilex* is limited in growth and survival by light scarcity, a phenomenon apparently occurring in our study area; i.e. the dense canopy of the reforestation stands constrained the survival of old saplings of *Q. ilex*. The result is an arrested sapling bank unable to reach the adult stage. This fact indicates that reforestation stands, although providing favourable microsites for seed germination and seedling establishment (Gómez 2003, Puerta-Piñero et al. 2007), are not the most suitable landscape units for long-term regeneration of oaks, at least if the canopy is not thinned. Contrarily, when clearing was applied, an active regeneration appeared mainly for the light-demanding *P. sylvestris* (Castro et al. 2004; Weber et al. 2007). *P. sylvestris* responded quickly, because clearing was performed 6 years before this study and saplings that were 2-4 years old abounded (i.e. they recruited just after clearing).

Fencing greatly increased the density of the sapling bank, signalling that ungulates diminish sapling performance in our study area, as reflected in other studies (Zamora et al. 2001; Baraza 2005; Gómez-Aparicio et al. 2005, 2007b; Quero et al. 2007). Sapling abundance was especially remarkable for *Q. ilex* for two probable reasons: on the one hand, fenced plots showed more adults of *Q. ilex* in the canopy than in the other landscape units (Table 1), and consequently many acorns were dispersed; on the other hand, fencing excluded wild boar, a major acorn predator (Matías et al. *submitted*; Chapter 2). However, the numerous saplings appearing in fenced reforestation stands were rarely older than 15 years, as in the rest of reforestation stands, supporting the contention that the factor limiting recruitment under dense plantations is light scarcity, not herbivory pressure.

Another negative impact of browsing pressure is that herbivores were also responsible of sapling-growth limitation, because fenced individuals grew faster than non-fenced ones (see Zamora et al. 2001, Gómez-Aparicio 2004, Gómez-Aparicio et al. 2007b for similar results). A direct consequence of this is that the time necessary to reach the threshold of 150 cm, necessary to escape from mammalian herbivores (Zamora et al. 2001), was faster for fenced individuals of *A. granatense* (19 vs. 12 years) and *Q. ilex* (26 vs. 18 years). Also, as other studies have already shown (Crawley 1997; Zamora et al. 2001; Nomiya et al. 2003; Chauchard et al. 2006; Gómez-Aparicio et al. 2007b), herbivores preferred old, larger individuals, presumably because young saplings were not apparent to herbivores (Baraza 2005). Consequently, mammalian herbivores are more intensively affecting the saplings with more potential for growth because their larger size, significantly retarding their ability to reach the threshold of height necessary to escape from herbivores.

Lastly, the sapling bank in post-fire stands was the least dense one. Surely, the lack of adults exerted a severe limitation on tree recruitment, diminishing seed rain (Mendoza et al. *submitted*; Chapter 1). In addition, population of *P. sylvestris* in post-fire stands was composed only of old and tall individuals, suggesting that a favourable event for recruitment happened around 10 years before this study. *P. sylvestris* is able to recruit only in the southernmost area of its distribution range after a rare event of rainy summer, because seedlings of this species need an extra amount of rainfall to survive the critical first-summer drought in harsh environments (Castro el al. 2005; Chapters 3 & 4). This is consistent with the fact that the year 1996 was an extremely rainy year, reaching the maximum value of rainfall in a 15-year series (1793 mm; data series from 1990 to 2006 taken in a meteorological station placed in the study area). However, the lack of individuals younger than 8 years indicates that another recruitment event for *P. sylvestris* did not happen in post-fire stands in the last 8 years, probably because all summers have been dry since 1997.

Consequences for forest dynamics

Our results pointed out two main factors that hamper sapling transitions into adults. First, strong differences in tree densities result in different light environments. We have shown that dense reforestation stands presented the same pool of species as the rest of landscape units; however, sapling abundance was much lower because the high density of planted trees strongly limits the access of light to the understory and hence restricts sapling establishment. A positive effect of the low sapling density in the understory was that this landscape unit proved less attractive for herbivores because of the lack of food. On the contrary, clearing increased the presence of light-demanding species in the understory, mainly *P. sylvestris*, and cleared reforestation stands became more attractive for herbivores because more saplings and shrubs (and herbs) were appearing in the understory.

Secondly, herbivore pressure constrained sapling recruitment of species in the following way: *S. aria* > *A. granatense* > *Q. ilex* > *P. sylvestris*. Previous studies in the same area (Baraza 2005; Baraza et al. 2006; Gómez-Aparicio et al. 2007b) showed the same gradient of herbivore preferences for the species in common (all except *S. aria*). As a consequence of this selection of species, herbivores are in part presumably responsible for the discordance between adults and saplings. The most severe intensity of consumption of saplings of *A. granatense*, *S. aria*, and *Q. ilex* precluded their recruitment into adult trees. Contrarily, since *P. sylvestris* was less preferred by ungulates, the few saplings of former species had a higher probability of becoming adults. Probably, the reduction of browsing pressure in our study area as consequence of a land-use change has increased the recruitment probabilities of *A. granatense*, *S. aria*, and *Q. ilex* (more palatable species) against *P. sylvestris* (non-palatable species; see Weber et al. 2008 for a similar results with *Quercus pubescens* and *P. sylvestris* in alpine forests).

In conclusion, even in the remnant fragments of native forest the most abundant species in the canopy are scarce in the sapling bank and vice versa, while in all degraded landscape units (dense, cleared, and fenced reforestation stands, and post-fire stands) adults and saplings differed in composition as well as in abundance. These discordances suggest that the future forest of the mosaic landscape will be different depending on the type of degradation of each landscape unit. In the case of the native forest, the sapling bank shows a trend from a pine-dominated forest towards a mixed forest of *P. sylvestris* with more importance of *Q. ilex*, *A. granatense*, and *S. aria*. In reforestation stands, there is a probable shift from a canopy completely dominated by *Pinus* spp towards a mixed forest. In post-fire stands, heliophilous trees such as *Pinus* spp would be more important in abundance. Therefore, each patch in the mosaic landscape would have a different successional trend, the resulting landscape being strongly dependent on patch dynamics (Pickett & Thompson 1978), which seems to be an usual successional driver in other stressful Mediterranean habitats such as calcareous communities (Escudero 1996), salt marsh communities (Castellanos et al. 1994), and semiarid shrublands (Pugnaire et. al 1996).

In short, the final composition of future forests in all landscape units will depend upon whether the management practices are able to diminish the regeneration constraints imposed by light scarcity in dense reforestation stands, recruitment limitations in post-fire stands, and a high herbivore pressure in nearly all stands.

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DISCUSIÓN GENERAL

El objetivo de esta tesis doctoral es conocer las limitaciones para la regeneración que se producen como consecuencia de la degradación del hábitat en un paisaje en mosaico mediterráneo. Para ello, se han estudiado todas las fases tempranas del ciclo de vida de las plantas, así como los principales factores abióticos (agua y tipo de hábitat) y bióticos (interacciones planta-animal e interacciones planta-planta) que pueden limitar el éxito de transición a la fase siguiente. Gracias a este conocimiento se pretenden proponer medidas de gestión que potencien la recuperación del bosque autóctono de montaña a partir de los hábitats degradados que le rodean, teniendo en cuenta además el contexto de cambio global en el que nos vemos inmersos.

Limitación en el reclutamiento producida por la dispersión de semillas

En los sistemas mediterráneos, al contrario que en los templados o tropicales, normalmente se ha minusvalorado la importancia de la limitación en el reclutamiento producida por la dispersión de semillas, otorgándosele un mayor peso a la limitación en el establecimiento de plántulas. Este paradigma se ha extraído de un gran número de estudios realizados en diferentes hábitats mediterráneos tales como bosques (Herrera et al. 1994; Traveset et al. 2003; Castro et al. 2005; Pulido & Díaz 2005), matorrales (García et al. 1999; Rey & Alcántara

2000) o sistemas semiáridos (Escudero et al. 2000; Lloret et al. 2005; García-Fayos & Gasque 2006). De ellos se desprende que el establecimiento se encuentra normalmente muy limitado por la escasa supervivencia de las plántulas en el transcurso del primer verano. Sin embargo, los resultados de esta tesis doctoral muestran que la limitación por la llegada de semillas puede ser más importante de lo que se ha tenido en cuenta en los últimos años (Capítulo 1). Esto no quiere decir que el reclutamiento no esté limitado por el establecimiento, sino que también puede estarlo por la escasez de semillas. Estos resultados concuerdan con el estudio pionero de Herrera en 1985 que destacaba a los animales dispersores de semillas como los primeros “arquitectos” del hábitat. Asimismo, algunos otros trabajos en ambientes mediterráneos han señalado la importancia de la limitación en la dispersión de semillas, aunque se han centrado en una sola especie (por ejemplo, Gómez-Aparicio et al. 2007 para A. granatense o Sánchez & Peco 2007 para Lavandula stoechas subsp. pedunculata).

La limitación por la dispersión de semillas ocurre principalmente en aquellas unidades de paisaje en las que la degradación del hábitat ha provocado una baja densidad de adultos, como es el caso de las especies de matorral en las repoblaciones, o las especies arbóreas en el matorral (Capítulo 1). Esta falta de adultos reproductores origina que la densidad de semillas dispersada sea muy baja o prácticamente nula (Clark et al. 1998). Por el contrario, cuando el tipo de manejo humano ha incrementado la densidad de los árboles y arbustos adultos (por ejemplo, Pinus spp. en las repoblaciones o las especies de matorral en los matorrales), el reclutamiento estuvo mucho más limitado en el establecimiento que en la dispersión de semillas.

A pesar de que haya un patrón general que relacione la baja dispersión de semillas con el tipo de manejo humano, existen diferencias según el vector de dispersión de cada especie. Cuando se trata de vectores aleatorios (es decir, el viento o la gravedad), las semillas no suelen llegar a áreas que estén alejadas más de unas decenas de metros de los individuos adultos (Sánchez & Peco 2002; Gómez-Aparicio et al. 2007), con lo que la expansión poblacional está seriamente constreñida. Así, por ejemplo, estudios en la misma zona han determinado que la distancia media de dispersión de semillas de Pinus sylvestris y Acer opalus subsp. granatense (a partir de ahora llamado A. granatense) raramente es mayor de 20 m (Castro et al. 1999; Gómez-Aparicio et al. 2007). No obstante, la lluvia de semillas recogida durante dos años muestra que también se producen algunos eventos de dispersión a larga distancia para las especies anemócoras, los cuales son de enorme importancia para la expansión forestal (Nathan 2006).

Por el contrario, si el vector es un ave frugívora, se produce un patrón de dispersión no aleatorio, no sólo en cuanto a la distancia, sino también en cuanto a la dirección (García et al. 2007). En consecuencia, las distancias de dispersión de las aves suelen ser mayores que cuando la dispersión es por el viento (García et al. 2005; Jordano et al. 2007), y se ha demostrado por medio de marcadores moleculares que los eventos de dispersión a larga distancia no son tan infrecuentes (García et al. 2007). Debido a que las aves frugívoras prefieren los hábitats en los que encuentran refugio y alimento (García et al. 2000), el patrón la lluvia de semillas depende de las características del hábitat y el comportamiento de cada especie animal y no está tan directamente relacionado con la densidad de adultos (Schupp & Fuentes 1995; Jordano & Schupp 2000; Russo & Augspurger 2004). Los hábitats preferidos por las aves frugívoras en nuestra zona de estudio son el bosque autóctono (de estructura abierta y con un abundante sotobosque) y el matorral (Hódar et al. observación personal). Por el contrario, las repoblaciones resultan menos atractivas, seguramente porque la alta densidad de pinos provoca una menor fructificación en el sotobosque. De esta manera, a pesar de que el bosque autóctono presente una abundancia media de especies de matorral (Capítulo 1), la lluvia de semillas de especies con dispersión zoócora es mayor que en las parcelas de matorral, presumiblemente por el patrón de abundancia y selección de hábitats de los frugívoros.

Limitación en el reclutamiento producida por la depredación post-dispersiva de semillas

Los resultados del experimento de depredación post-dispersiva de semillas mostraron que la limitación ejercida por los depredadores es relativamente importante (un 44% de las semillas fueron depredadas, tomando valores medios entre especies, unidades de paisaje y años). No obstante, la depredación post-dispersiva de semillas no fue la misma en todas las unidades de paisaje, existiendo una selección que dependía del tipo de degradación y que en parte se pudo explicar por la cobertura del matorral (Capítulo 2). De esta manera, aquellas unidades de paisaje en las que el tipo de manejo aumentó la cobertura de matorral (es decir, matorral, bosque autóctono y repoblaciones cercadas) presentaron mayor tasa de depredación de semillas que las repoblaciones aclaradas y densa, donde la cobertura de matorral es menor. Presumiblemente, al ofrecer los matorrales refugio y alimento a los roedores, incrementan su abundancia y actividad y, por lo tanto, hay mayor depredación de semillas (Simonetti 1989; Fedriani & Manzaneda 2005; Mortelliti & Biotani 2006).

A pesar de que la tasa de depredación pudiera explicarse en parte por el tipo de unidad de paisaje, el factor que tuvo más importancia en el modelo de depredación era la especie a la que pertenecía cada semilla (Capítulo 2). De esta manera, las características estructurales y bioquímicas de las semillas conllevaron que los roedores seleccionasen las especies siguiendo un mismo patrón que permaneció muy consistente entre unidades de paisajes y años (Quercus ilex > Pinus sylvestris > Sorbus aria > Berberis vulgaris > Acer granatense > Crataegus monogyna). El bajo consumo de A. granatense y de C. monogyna se puede explicar por la gruesa cubierta que protege al endospermo en estas dos especies, con lo que las semillas resultan menos apetecibles para los depredadores porque supone más costo la extracción del endospermo. B. vulgaris presenta asimismo diversas toxinas (Kollmann et al. 1998) que pueden provocar rechazo por parte de los roedores. Por el contrario, S. aria, P. sylvestris y, especialmente, Q. ilex no presentan defensas físico-químicas que eviten su consumo y resultan recursos apetecibles para los roedores por su valor nutritivo. El gran tamaño de las bellotas de Q. ilex promueve que esta especie sea muy consumida por los depredadores (proporciona más energía que otras semillas más pequeñas), y además amplia el espectro de depredadores hasta el jabalí.

Limitación en el establecimiento de las plántulas

En concordancia con otros trabajos en ambientes mediterráneos (Herrera et al. 1994; García et al. 1999; Rey & Alcántara 2000; Traveset et al. 2003; Castro et al. 2005; Lloret et al. 2005; Pulido & Díaz 2005; García-Fayos & Gasque 2006), los resultados observacionales y experimentales coincidieron en señalar las negativas consecuencias de la sequía estival para la supervivencia de las plántulas. Tanto los resultados obtenidos de los censos de plántulas emergidas en condiciones naturales (Capítulo 1) como del experimento de siembra de semillas en distintos tipos de hábitats y niveles de riego (Capítulos 3 y 4) mostraron que la limitación en el establecimiento de las plántulas es muy alta, aunque existen diferencias según la especie y tipo de hábitat.

Las especies boreo-alpinas (P. sylvestris y T. baccata) están más limitadas en el establecimiento que el resto de las especies que componen la comunidad de leñosas. El caso más dramático fue el de T. baccata, porque en dos años consecutivos de observaciones (en los que no se produjo ningún verano lluvioso), no se observó ninguna plántula de T. baccata emergida en condiciones naturales (Capítulo 1). Además, el experimento de siembra de semillas nos permitió determinar que la falta de emergencia de T. baccata en condiciones naturales no sólo se debe a que la lluvia de semillas es muy baja (Capítulo 1), sino también a que esta especie requiere un verano lluvioso para la emergencia (Capítulo 3). Tanto los resultados observacionales como experimentales con P. sylvestris coinciden en señalar que las plántulas emergidas de esta especie mueren masivamente después del primer verano. Estos resultados coinciden con trabajos previos que han destacado las limitaciones por la sequía de P. sylvestris (Castro 1999; Castro et al. 2004; Castro et al. 2005).

A pesar de que el establecimiento de las plántulas de las especies mediterráneas y submediterráneas (Quercus spp., A. granatense, S. aria y todas las especies de matorral) se vio seriamente limitado por la sequía, incluso en veranos secos estas especies fueron capaces de reclutar. Además, gracias a los censos de plántulas de especies de matorral (no incluidas en el experimento de siembra) se pudo observar que las plántulas de matorral eran capaces de sobrevivir en todos los tipos de unidades de paisaje, y es más, se establecieron plántulas de matorrales con fruto carnoso en el año extremadamente seco (2005). Estos resultados apuntan que las especies mediterráneas y/o submediterráneas son las que permiten la expansión forestal hacia hábitats más pioneros (matorrales y zonas abiertas), especialmente cuando el verano es lluvioso. Asimismo, la capacidad de las especies de fruto carnoso para establecer plántulas incluso cuando las condiciones meteorológicas son extremas apuntan al hecho de que, bajo un escenario de cambio global que predice una mayor aridez y frecuencia de eventos extremos (Moreno et al. 2005; IPCC 2007), existe una tendencia a la matorralización.

Limitación por herbivoría de ungulados

Los resultados obtenidos en esta memoria de tesis doctoral muestran que en la mayor parte de las unidades de paisaje que componen el paisaje en mosaico existe un banco de juveniles más diverso que la composición de adultos, e incluso en algunas unidades de paisaje, como la repoblación cercada o aclarada, la densidad de juveniles es muy alta (Capítulo 5). No obstante, esta reserva de reclutas no significa necesariamente un potencial real de regeneración para todas las especies, puesto que la herbivoría por ungulados limita severamente la capacidad de desarrollo y crecimiento de los juveniles hasta el estadio reproductivo. Normalmente, en estudios demográficos que analizan las estructuras de edades y tamaños como indicadores de la dinámica de regeneración de especies leñosas, la existencia de un banco de juveniles diverso y abundante se interpreta como una señal de regeneración activa (refs.). Por el contrario, las estructuras envejecidas de las poblaciones (es decir, con mayor representación de adultos que de juveniles) son interpretadas como el resultado de una baja y lenta tasa de incorporación de nuevos individuos a la población (Ogden 1985; Hutchings 1997). En esta situación, las poblaciones locales sobrevivirían durante largos periodos de tiempo bajo condiciones ecológicas desfavorables para el reclutamiento gracias a la longevidad de los adultos (estrategia de persistencia; García & Zamora 2003), mostrando dinámicas remanentes de regeneración (Eriksson 1996).

En el caso del paisaje en mosaico estudiado, a pesar de que el banco de juveniles es más abundante que los adultos, la mayor parte de las poblaciones de juveniles presentaban una estructura demográfica compuesta por individuos relativamente viejos (> 4 años) pero cortos (< 20 cm). Es decir, a pesar de que las estructuras poblacionales estuviesen caracterizadas por la existencia de una baja proporción de adultos en relación al potencial de juveniles, también eran indicadoras de dinámicas remanentes. La herbivoría resulta un cuello de botella que impide, a pesar de la existencia de reclutas, la incorporación de nuevos individuos adultos a la población y por tanto el cierre del ciclo de vida de las plantas y a efectos de dinámica poblacional equivaldría prácticamente a la ausencia de reclutamiento.

No obstante, los herbívoros no ejercen la misma presión para todas las especies, ya que existe una selección basada en las características nutricionales de las especies y el contexto que las rodea (Baraza 2005; Baraza et al. 2006, Gómez-Aparicio et el. 2007). Las especies más palatables (S. aria y A. granatense) son sistemáticamente las más comidas, aunque en todas las unidades de paisaje la presión de los herbívoros no era la misma. Así, el bosque autóctono, las repoblaciones aclaradas y el matorral tuvieron mayor porcentaje de juveniles con herbivoría que las repoblaciones densas (Capítulo 5). Esto se debe seguramente a que los herbívoros prefieren la vegetación que tiene más especies aptas para el consumo (Grubb 1992; Gómez et al. 2001; Björkman & Hambäck 2003; Baraza et al. 2006). La cerrada copa de los árboles en las repoblaciones densas provoca que el sotobosque sea menos escaso y por lo tanto, menos atractivo para los herbívoros.

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CONCLUSIONES

1. La degradación del hábitat limita la lluvia de semillas al reducir la abundancia de adultos reproductores. Por otra parte, la acción humana provoca también que los hábitats resulten poco atractivos para las aves frugívoras y por lo tanto, también se reduzca la dispersión de semillas. A pesar de que tradicionalmente se le ha dado más peso a la limitación por el establecimiento de las plántulas en los sistemas mediterráneos, nuestros resultados enfatizan el peso de la limitación en el reclutamiento por la falta de dispersión de semillas, especialmente en el caso de las especies arbóreas de dispersión anemócora, así como que esta amenaza se incrementa a medida que la degradación del hábitat esté más extendida.

2. El patrón de depredación post-dispersiva de semillas se mantuvo consistente entre unidades de paisaje, especies, y años. La degradación del hábitat influye en la medida que controla la abundancia de matorrales, y éstos a su vez favorecen a los roedores. Asimismo, las especies con cubierta más dura o sustancias tóxicas fueron menos depredadas que las especies sin ninguna defensa físico-química y mayor contenido nutritivo. Este patrón de selección por parte de los depredadores puede tener consecuencias para la diversidad de las comunidades vegetales, ya que implica que las semillas de especies arbóreas son sistemáticamente más depredadas que las especies de matorral (independientemente del año o unidad de paisaje).

3. La mayor parte de las plántulas de especies leñosas mueren en su primer año de vida, aunque existen diferencias según la especie considerada, el tipo de hábitat y las condiciones meteorológicas del año. Las especies boreo-alpinas fueron las menos tolerantes a la sequía, y las plántulas sólo se establecieron en el caso de un verano lluvioso, y principalmente en hábitats con cobertura vegetal. Por el contrario, las especies mediterráneas o sub-mediterráneas aumentaron su reclutamiento cuando el verano era lluvioso, aunque las plántulas fueron capaces de establecerse durante los típicos veranos secos, principalmente bajo bosque o matorral. Las plántulas de las especies de matorral con fruto carnoso fueron las únicas que sobrevivieron a un año excepcionalmente seco en condiciones naturales. A pesar de que las especies boreo-alpinas presenten una estrategia de permanencia gracias a la longevidad de sus individuos, la menor supervivencia de las plántulas en los años típicamente secos de los sistemas mediterráneos augura una progresiva disminución de la abundancia de estas especies, especialmente bajo un escenario de cambio global.

4. Nuestros resultados sugieren que los bosques montanos mediterráneos tienen una tendencia a que las especies de matorral con fruto carnoso predominen, debido a que: 1) poseen vectores de dispersión no aleatorios que llevan semillas a hábitats generalmente favorables para el reclutamiento, 2) las semillas son menos depredadas; y 3) las plántulas son las únicas capaces de establecerse en años especialmente secos.

5. La comparación del banco de juveniles con los adultos a lo largo de cinco tipos distintos de unidades de paisaje revela que las especies arbóreas poseen una dinámica de reclutamiento activa, siendo la abundancia de juveniles mayor que la de adultos. Las unidades de paisaje degradadas presentan un banco de juveniles que discuerda en composición con los adultos, apuntando un potencial cambio en el bosque en el que las especies de *Pinus* tienden a desaparecer, mientras que se predice una mayor abundancia de *Q. ilex*, *A. granatense* y *S. aria*. No obstante, la herbivoría por ungulados aparece como un importante cuello de botella de la regeneración, limitando el crecimiento de los juveniles y por tanto, a largo plazo, la incorporación de nuevos individuos adultos a las poblaciones. Por otra parte, las repoblaciones especialmente densas limitan la llegada de luz al sotobosque, y los juveniles se quedan estancados en el creci-

miento, sin poder llegar a adultos. Por lo tanto, la composición del bosque futuro dependerá del tipo de control que se haga sobre los herbívoros y el manejo forestal que se aplique a las repoblaciones densas.

6. La regeneración del bosque mixto autóctono de Sierra Nevada requiere por tanto la confluencia simultánea de un conjunto de circunstancias tales como abundante producción de semillas, baja depredación, y veranos relativamente lluviosos durante 2-3 años seguidos, confluencia que no es frecuente bajo las actuales condiciones climáticas mediterráneas y será todavía más rara bajo un escenario de cambio global.

7. La conservación de los últimos bosques autóctonos de pino silvestre del sur peninsular requiere una gestión adaptativa que conduzca a paliar en lo posible las causas que limitan la regeneración. Estas actuaciones deben favorecer la dispersión de las especies de fruto carnoso mediante la adecuación de la estructura del hábitat, la siembra de semillas, posibles plantaciones aprovechando eventos lluviosos, la conservación de los matorrales como elementos indispensables para el reclutamiento de las plántulas, así como planes de gestión y control de la carga ganadera. Asimismo, la tendencia anteriormente señalados que sugiere una mayor abundancia de especies con fruto carnoso debería tenerse en cuenta en los planes de conservación del bosque autóctono de Sierra Nevada, porque incrementa los riesgos para las especies arbóreas, de las cuales, cuatro están ya en peligro de conservación.