



Efectes de les pertorbacions en la dinàmica dels bosc de pi roig a la península Ibèrica

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I. INTRODUCCIÓ GENERAL

Els arbres són un conjunt extremadament polifilètic, però comparteixen caràcters clau tals com una gran mida, altura i longevitat, així com una prodigiosa fecunditat que expliquen el seu èxit ecològic (Petit & Hampe, 2006). En efecte, la riquesa d'espècies arbòries a nivell global està xifrada al voltant de 100,000 taxons (Oldfield *et al.*, 1998) i actualment s'estima que els seus boscos cobreixen gairebé 4,000 milions d'hectàrees, el que representa prop del 31% de la superfície emergida del planeta (FAO, 2010). En aquest sentit, no és gens d'estranyar que els ecosistemes forestals siguin particularment rics en biodiversitat, albergant dos terços del total d'espècies terrestres (Millennium Ecosystem Assessment, 2005), que representin aproximadament el 45% i el 50% de les reserves de C i de la producció primària neta terrestres, respectivament, i que tinguin una incidència molt significativa en la regulació del cicle d'energia, el cicle hidrològic i la composició atmosfèrica a escala planetària (Bonan *et al.*, 2008). En aquest context, es fa palesa la funció crucial que tenen a escala global, així com els serveis ecològics, econòmics, socials i estètics que proporcionen als sistemes naturals i humans (Millennium Ecosystem Assessment, 2005). **En aquesta tesi ens centrem en aspectes ecològics dels boscos d'una important espècie arbòria àmpliament distribuïda al planeta.**

LA DEMOGRAFIA DELS BOSCOS

Fa 45 anys un destacat biòleg escrivia (Harper, 1967): *En contrast amb els vegetacionistes i la seva preocupació per descriure i interpretar àrees del territori, les observacions ecològiques de Darwin i les qüestions que es plantejava estaven basades en la consideració dels individus i de les poblacions, en una preocupació pels nombres.* D'aquesta manera, J.L. Harper va revolucionar el punt de vista descriptiu i fitosociològic que tradicionalment imperava l'ecologia de la vegetació. Des d'una visió evolutiva i darwinista, Harper va emfatitzar la necessitat d'estudiar les plantes des de la seva pròpia perspectiva, com a individus que constitueixen poblacions i la seva idoneïtat per als estudis demogràfics. Aquesta idea la va consolidar 10 anys més tard amb la publicació de la seva obra "Population biology of plants" que va significar el desenvolupament d'una demografia vegetal. **En aquesta tesi intentem profunditzar en la demografia poblacional dels boscos d'una espècie arbòria força important també a casa nostra.**

Tot i que els arbres són organismes sèssils, i malgrat que això sigui imperceptible per l'ull humà, els boscos són sistemes dinàmics resultat de la variació de les taxes d'establiment, creixement, reproducció i mortalitat dels seves poblacions. L'estructura i composició dels boscos, així com els seus patrons demogràfics reflecteixen la interacció de nombrosos factors biòtics i abiòtics, i una infinitat d'esdeveniments en la seva història. Les relacions de competència entre els arbres, les condicions climàtiques, els gradients en la disponibilitat de recursos, l'estrès ambiental i els règims de pertorbacions juguen un paper fonamental en l'estructura i la dinàmica dels boscos. Donada aquesta complexitat dels ecosistemes forestals, i de la creixent consciència social dels seus béns, serveis i funcionalitats (Terradas, 2005), la comprensió dels processos subjacents que en governen la demografia, com a aproximació a l'estudi de les poblacions i de la seva dinàmica, ha estat i és encara avui un objectiu central per a la recerca forestal.

LA COMPETÈNCIA PELS RECURSOS

En absència de pertorbacions, l'estructura de les poblacions forestals depèn directament de l'estadi de desenvolupament dels seus individus (i.e., l'estructura de mides) i com aquests s'organitzen en l'espai i en el temps. Al mateix temps, la capacitat dels individus per adquirir i utilitzar els recursos per a funcions vegetatives i reproductives, així com el balanç entre les taxes poblacionals d'establiment i mortalitat determinen la dinàmica del bosc. Aquests processos, però, estan condicionats en última instància per les interaccions biòtiques entre els individus de la població, on la capacitat per explotar els recursos disponibles i sobreviure sovint va lligada a adquirir una gran mida i esdevenir dominants dins la població. A mesura que els arbres creixen van ocupant més espai i utilitzen cada vegada més recursos, del que se'n deriva un augment de la competència i una reducció del creixement individual fins al punt que alguns individus queden estancats i suprimits, no podent obtenir els recursos que necessiten per sobreviure i, en conseqüència, moren. Aquest procés, conegut com autotala (Yoda *et al.*, 1963), depèn de la mida del individu, així com dels atributs estructurals de la població i en modula els processos demogràfics durant el seu desenvolupament (Peet & Christensen, 1987; Oliver & Larson, 1990). **En aquesta tesi fem especial èmfasi als factors biòtics i intrínsecs del bosc, com són l'estructura de les seves poblacions i la**

competència pels recursos entre els individus, i com aquests expliquen els patrons demogràfics de l'espècie arbòria estudiada.

ELS GRADIENTS AMBIENTALS I DE RECURSOS EN UN CONTEXT DE PERTORBACIÓ O D'ESTRÈS

A gran escala, el clima controla la disponibilitat d'aigua en el sòl i, per tant, la vegetació i els seus processos demogràfics. Tot i això, aquesta disponibilitat d'aigua pot ser modificada a escala local per factors edàfics i topogràfics els quals tenen un paper important en l'estructuració i dinàmica de la vegetació (Stephenson, 1990). Així doncs, les condicions climàtiques i l'heterogeneïtat espacial en la disponibilitat de recursos, afegits a l'estructura de la vegetació actuen de manera sinèrgica i tenen una gran influència en la demografia de les espècies (Hutchings *et al.*, 2000). En un context de pertorbació o d'estrès ambiental, en funció d'aquesta heterogeneïtat que determina la disponibilitat de recursos, de les relacions de competència entre els individus i dels atributs estructurals de la població en conjunt, un mateix tipus de comunitat forestal pot respondre diferencialment i mostrar diferents llimars de canvi en els patrons demogràfics (Tessier, 1988). La variació en la qualitat del lloc, d'aquesta manera, pot resultar en un mosaic de severitat conferint un mecanisme d'atenuació dels efectes davant d'una pertorbació o d'un estrès ambiental, on els individus supervivents poden assegurar la persistència de la població (Lloret *et al.*, 2012). Així, l'estructura forestal i la disponibilitat de recursos, operen de manera concomitant i interactiva, destacant que les direccions dels processos demogràfics i els canvis que experimenten induïts per les pertorbacions o per l'estrès poden divergir al llarg de diferents gradients ambientals. **En aquesta tesi explorem els patrons demogràfics de mortalitat, creixement, establiment i reproducció a escales regional, poblacional i individual de l'espècie estudiada. També, com aquests patrons canvien al llarg de diferents gradients ambientals (climàtics, de recursos i d'estructura del bosc) i d'estrès en resposta a les pertorbacions, i tractem d'esbrinar o explicar quins són els processos subjacents d'aquests patrons demogràfics que observem.**

DE LA MORT A L'ESTABLIMENT. LA DINÀMICA DE LES COMUNITATS FORESTALS

Petites o moderades pertorbacions naturals relacionades amb la mort d'un a uns pocs arbres adults i la creació d'obertures a la coberta forestal són processos clau en l'ecologia de les poblacions i de les comunitats de molts boscos (Franklin *et al.*, 1987). Sota capçades tancades, la mort d'individus adults provoca una variació de les condicions microambientals on pot iniciar-se una fase de substitució, per part de nous individus, de l'espai creat (Runkle, 1981). Els processos d'establiment, però, són molt sensibles i poden variar enormement al llarg dels gradients ambientals. Així, la disponibilitat de llum, les condicions climàtiques i edàfiques, així com les necessitats i trets específics de les espècies determinaran la trajectòria de la comunitat (Valladares, 2003; Ibáñez *et al.*, 2007). Si els nous individus establerts són de l'espècie dels individus adults morts, la substitució aportarà un mecanisme de compensació per a la població assegurant la seva futura permanència. D'altra banda, si les noves condicions afavoreixen l'establiment o desenvolupament d'altres espècies, el procés de substitució pot conduir a canvis permanents en la composició de la comunitat (Lertzman, 1992).

I què passa si la pertorbació és d'una gran mida? En aquest cas, la variació espacial en la intensitat de la pertorbació resultarà en un mosaic heterogeni d'individus supervivents. Així, els processos de regeneració dependran de la densitat dels supervivents, de la disponibilitat de llavors en els bancs permanents en el sòl i de les llavors dispersades pels supervivents o des dels límits del bosc on la pertorbació s'ha aturat (Turner *et al.*, 1998). En aquesta situació, la trajectòria de la població de l'espècie i de la comunitat dependrà de l'èxit o del fracàs dels mecanismes d'auto-substitució de l'espècie dominant i del potencial d'establiment i desenvolupament d'altres espècies.

En aquesta tesi dirigim l'atenció a com la mort dels arbres adults després d'una pertorbació (petita o gran) s'associa amb la regeneració de la pròpia espècie o, pel contrari, si altres espècies s'estan desenvolupant sota aquestes condicions i com aquests processos poden influir en la futura dinàmica de la població o de la comunitat.

L'ASSIGNACIÓ DELS RECURSOS I EL COST REPRODUCTIU

Sense desmerèixer els especuladors, tots els organismes responen a un principi bàsic de l'economia: l'administració dels recursos escassos per satisfer les seves necessitats. És un fet que els recursos són limitats i totes les activitats d'un organisme en requereixen. L'assignació d'un recurs a una determinada funció comporta pèrdues en la inversió potencial del recurs que es podria destinar a una altra funció (Levins, 1968). D'aquest procés emergeix el que s'anomena en anglès un *trade-off*, el qual reflecteix l'esforç en la inversió del recurs a una determinada activitat i el cost que suposa per a una altra activitat que competeix pel recurs.

Els *trade-offs* entre trets demogràfics sorgeixen de limitacions genètiques, morfològiques o funcionals dins dels individus, reflectint l'assignació dels recursos entre les diferents funcions vitals (Stearns, 1992). En biologia evolutiva és un axioma que la inversió en la reproducció és costosa i, per tant, els organismes s'enfronten a *trade-offs* entre la reproducció i altres funcions vitals (Reznick, 1985). En el cas dels arbres, degut al seu llarg període de vida i del continuat augment de la fecunditat amb la mida, la inversió dels recursos per a la reproducció pot suposar importants costos per a altres funcions com el creixement o el manteniment (Petit & Hampe, 2006). El cost reproductiu és força comú en les plantes però, atesa la dificultat en la seva medició i els múltiples factors que hi intervenen, s'han obtingut fins al moment una gran varietat de resultats moltes vegades ambigus i contradictoris (veure revisió a Obeso, 2002). **En aquesta tesi, ens hem centrat en l'emergència de *trade-offs* entre les funcions reproductiva i vegetativa i en el cost que pot tenir la producció de fruits sobre el creixement de l'espècie estudiada.**

L'assignació de recursos per a la funció reproductiva és, en essència, un procés al·lomètric, i.e., canvia amb la mida a mesura que creix l'individu (Niklas & Enquist, 2003). Per espècies arbòries, però, existeix poca informació sobre aquesta relació, encara que es preveu que l'esforç reproductiu disminueixi amb la mida degut a la gran quantitat de teixit estructural i dels òrgans d'emmagatzematge (Weiner *et al.*, 2009). D'altra banda, els *trade-offs* entre els trets demogràfics de les espècies poden variar al llarg dels gradients de recursos o ambientals (Russo *et al.*, 2008). No obstant això, i degut a la naturalesa al·lomètrica entre la mida i l'output reproductiu, només la variació

d'aquesta al·lometria al llarg d'un gradient ambiental podrà ser interpretada com una resposta diferencial entre els individus d'una espècie pel que fa a l'assignació dels recursos (Weiner, 2004). **En aquesta tesi abordem, per a l'espècie d'estudi i des d'un punt de vista al·lomètric, les qüestions de l'assignació de recursos entre les funcions reproductiva i vegetativa, de l'esforç reproductiu i els seus costos per al creixement, entre individus i dins d'individus, i en un gradient d'estrès ambiental tant individual com poblacional.**

DE L'ÈXIT AL DECLIVI DELS ARBRES. ELS PROCESSOS DEMOGRÀFICS DELS BOSCOS EN UN CONTEXT DE CANVI AMBIENTAL GLOBAL

El ràpid creixement de la població humana i el desmesurat ritme de consum dels recursos naturals han induït un canvi ambiental global (Vitousek, 1994) que té la potencialitat de causar grans canvis en la diversitat biològica amb importants conseqüències ecològiques (Hansen *et al.*, 2001). A nivell dels ecosistemes forestals, la desforestació és la principal causa de la pèrdua de boscos en països tropicals (Laurance, 1999; Malhi *et al.*, 2008), mentre que el retrocés de l'agricultura i de l'abandonament dels usos tradicionals del bosc durant l'últim segle han resultat en l'expansió i densificació dels boscos a l'hemisferi nord, especialment al continent europeu (MacDonald *et al.*, 2000; Pan *et al.*, 2011). D'altra banda, les tendències climàtiques actuals destaquen un augment de les temperatures i una major variabilitat climàtica (Easterling *et al.*, 2000), amb una elevada incidència d'esdeveniments extrems com les onades de calor i les sequeres (IPCC, 2007). Aquests fenòmens climàtics s'han associat, durant les últimes dècades i a escala global, als efectes devastadors de grans incendis forestals, així com a un estrès fisiològic dels arbres que s'ha traduït en episodis de declivi d'alguns boscos caracteritzats per una defoliació de les capçades dels seus arbres, reduccions del creixement i per elevades taxes de mortalitat (Dale *et al.*, 2001; Allen *et al.*, 2010). **En aquesta tesi, estudiem l'efecte d'aquestes pertorbacions derivades directa o indirectament de les activitats humanes en els processos demogràfics de l'espècie objecte d'estudi.** Més enllà d'actuar de manera diferenciada, el règim de pertorbacions associat al clima i als usos del territori tenen un efecte interactiu sobre l'estructura de la vegetació i el funcionament dels ecosistemes forestals (Lavorel *et al.*, 1998; Pausas & Fernández-Muñoz, 2012). Així, aquests processos

observats en la demografia dels boscos i de declivi d'algunes de les seves poblacions tant a escala local com regional són, presumiblement, el resultat de l'efecte combinat dels ràpids canvis, des d'un punt de vista estructural, que han experimentat els boscos durant els últims anys i del gradual canvi en el clima, així com de les pertorbacions que se'n deriven.

Si la demografia de les espècies arbòries pot veure's afectada a curt termini, la dinàmica de les seves poblacions i comunitats podria alterar-se a llarg termini desencadenant canvis en la vegetació. Aquesta idea ve suportada per treballs que descriuen canvis en la distribució de les espècies sota condicions climàtiques canviants (Allen & Breshears, 1998; Jump *et al.*, 2009), després de grans incendis forestals (Rodrigo *et al.*, 2004; Moser *et al.*, 2010) o com a resultat de les pràctiques històriques i actuals en els usos del territori (Chauchard *et al.*, 2007). No obstant això, els ecosistemes presenten processos a diferents nivells d'organització biològica que poden conferir resiliència al sistema en el seu conjunt. Així doncs, els canvis en la vegetació dependran també dels llindars ecològics i adaptatius de les espècies i dels processos demogràfics estabilitzadors que presentin les seves poblacions i comunitats davant de les pertorbacions (Lloret *et al.*, 2012). **En aquesta tesi ens interessem pels possibles canvis en la vegetació que podrien sorgir com a resultat d'aquestes pertorbacions. Ens centrem en els patrons d'establiment i regeneració de l'espècie estudiada i d'altres espècies que potencialment podrien substituir-la, amb els conseqüents canvis en la composició de les comunitats.**

EL CAS DE LA CONCA MEDITERRÀNIA

La conca mediterrània és un territori especialment idoni per estudiar els impactes que tenen les pertorbacions relacionades amb els usos del territori i el canvi climàtic sobre la demografia dels seus boscos. **Al nostre entendre, aquesta idoneïtat pot ser deguda a les següents raons:** (1) La disponibilitat d'aigua és un factor clau que limita els ecosistemes forestals de la conca mediterrània (Peñuelas *et al.*, 2001; Sarris *et al.*, 2007), on les sequeres hi són comunes i es preveu que hi esdevindran més freqüents i severes durant el pròxim segle (IPCC, 2007). (2) Aquesta regió representa el límit meridional de la distribució d'importants espècies arbòries de l'Hemisferi Nord, i

aquestes poblacions són, probablement, particularment vulnerables a l'augment de l'aridesa (Hampe & Petit, 2005). (3) Durant les darreres dècades, un augment generalitzat en la defoliació dels boscos i episodis localitzats de mortalitats molt elevades s'han associat a períodes de sequera (Lloret *et al.*, 2004; Bréda *et al.*, 2006; Carnicer *et al.*, 2011). (4) Els boscos d'aquesta regió han estat explotats i gestionats durant milers d'anys i les seves comunitats actuals difereixen àmpliament de les que existirien en absència dels humans (Blondel & Aronson, 1995). (5) Contràriament, l'expansió i densificació dels seus boscos després de l'abandonament agrícola i de la gestió forestal tradicional han estat particularment intenses durant l'últim segle (Margaris *et al.*, 1996; Grove & Rackham, 2001). Aquests canvis poden resultar en un augment de la competència entre els individus pels recursos, amb una tendència pels processos d'autotala (cf. Peet & Christensen, 1987) exacerbant la vulnerabilitat dels boscos als episodis de sequera (Linares *et al.*, 2009). (6) A la conca mediterrània el foc és un dels majors factors ecològics que determina la dinàmica i els patrons estructurals i paisatgístics de la vegetació (Naveh, 1975). L'escalfament i la sequera afecten la inflamabilitat del combustible i determinen, conjuntament amb els usos del territori i la composició atmosfèrica (Lavorel *et al.*, 1998), la vulnerabilitat dels boscos al foc, especialment durant l'estiu (Piñol *et al.*, 1998; Pausas, 2004). Per tant, l'augment previst de l'aridesa podria tenir un gran impacte en el règim de focs, sent els límits secs dels boscos particularment vulnerables (Czúcz *et al.*, 2011).

EL PI ROIG

En aquesta tesi, utilitzem el pi roig com a espècie model per estudiar les respostes demogràfiques dels boscos a les pertorbacions derivades del clima i dels canvis en els usos del territori i en la gestió forestal, en funció dels components estructurals de les poblacions i de gradients climàtics i de recursos. Creiem oportú dedicar un petit apartat sobre aquesta espècie.

El pi roig (*Pinus sylvestris* L.) és una espècie dominant en grans àrees boscoses de l'Hemisferi Nord, amb les poblacions més extenses localitzades en regions boreals (Figura 1.1a). Tot i això, el pi roig també ocupa extenses àrees a la conca mediterrània on el seu límit de distribució sud-oest correspon a la Península Ibèrica (Figura 1.1b). En

aquesta regió ocupa zones boscoses de muntanya amb una notable amplitud fitogeogràfica que inclou corologies submediterrànies, euro-siberianes i boreoalpines (Rivas-Martínez, 1983). La distribució de l'espècie s'estén del nord de la Península als sistemes Ibèric i Central, amb les poblacions més importants situades als Pirineus i amb algunes poblacions disperses en localitats més meridionals i seques (Castroviejo *et al.*, 1986). A Espanya, els boscos de pi roig ocupen unes 700,000 ha (Alía *et al.*, 2001). A Catalunya, el pi roig és la segona espècie forestal més abundant i ocupa 219,754 ha (18.4% de la superfície forestal total de Catalunya, Burriel *et al.*, 2004), amb grans extensions als Pirineus i algunes poblacions residuals al centre (muntanyes de Prades) i al sud (Ports de Beseit) de la regió (Figura 1.1c). Aquesta extensa distribució va lligada al fet que el pi roig és capaç d'ocupar un amplíssim gradient climàtic degut a l'alta variació de la seva arquitectura hidràulica (Martínez-Vilalta *et al.*, 2009) i a l'estrict control estomàtic que presenta sota condicions d'estrès hídric (Irvine *et al.*, 1998).

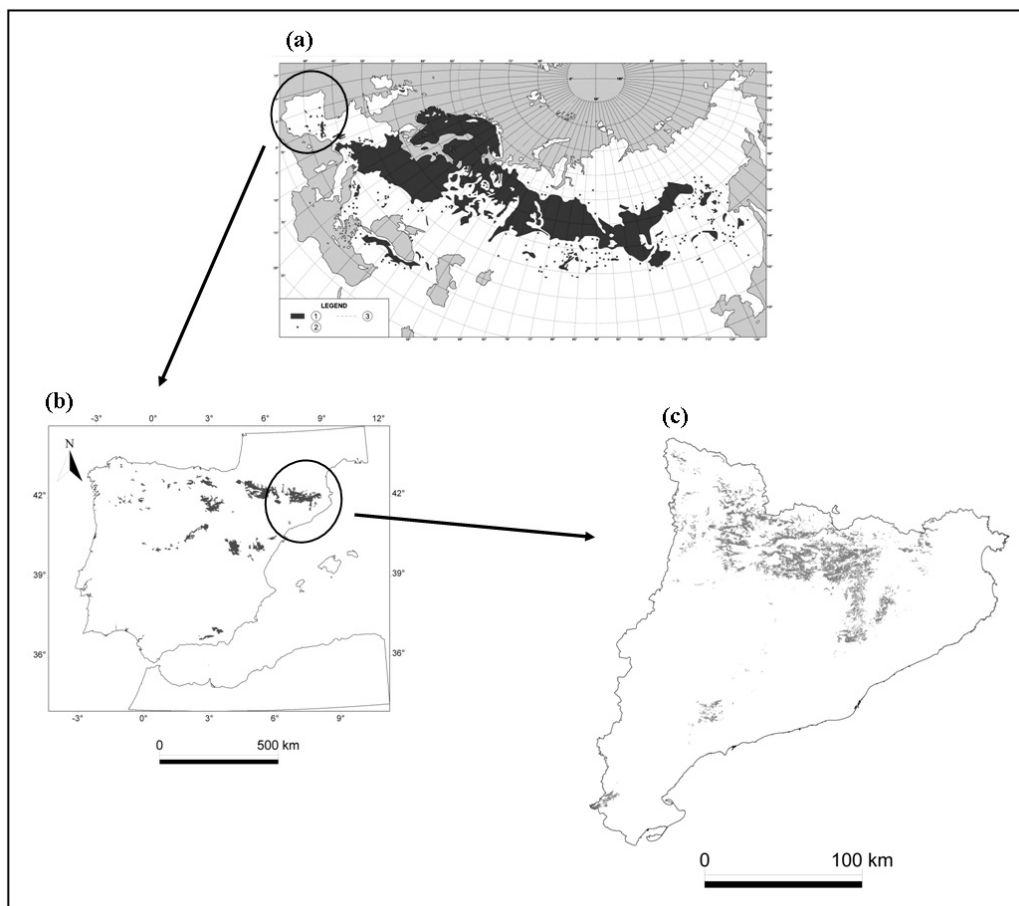


Figura 1. Mapes de distribució del pi roig (*Pinus sylvestris* L.): (a) Distribució global. Modificat a partir de B. Navez sota *Creative Commons license*; (b) Distribució a la Península Ibèrica; (c) Distribució a Catalunya. En els 3 mapes la superfície més fosca correspon a la distribució dels boscos de l'espècie.

El pi roig és una espècie monoica, anemòfila, de tronc dret i de capçada estreta i cònica. Sota condicions òptimes, l'alçada de l'arbre pot arribar als 40 m, tot i que normalment varia entre 10 i 20 m. Les fulles, de color verd blavís, són curtes (3-6 cm) i es mantenen 3 o 4 anys a l'arbre (per una descripció més detallada consulteu Gracia & Ordóñez, 2011). Cal destacar-ne també la incapacitat de germinar després d'un foc (Retana *et al.*, 2002) i l'absència de pinyes seròtines (Tapias *et al.*, 2004). El període de floració i la pol·linització es produeixen a la primavera (Abril-Juny) i la formació del con femení dura fins la primavera de l'any següent, quan es produeix la fecundació. En aquest moment pren la forma i coloració verda de la pinya nova. La inversió de recursos en la formació de la pinya es produeix majoritàriament durant aquest segon any (Abril-Novembre), i la maduració de la pinya i la dispersió de les llavors comença a finals de la tardor i dura fins a la primavera de l'any següent (Causens, 1988; Gracia & Ordóñez, 2011).

Durant l'últim segle hi ha hagut importants canvis en els usos del territori que han afectat la distribució del pi roig i l'estructura dels seus boscos a la península Ibèrica. L'abandonament de les activitats agràries i de l'explotació forestal en zones de muntanya (García-Ruíz *et al.*, 1996) i les reforestacions massives durant els 1960s i dècades posteriors (Martínez-García, 1999) han portat a una densificació dels boscos de pi roig i la seva àrea de distribució s'ha expandit notablement (Martínez-García, 1999; Poyatos *et al.*, 2003). Els canvis relacionats amb el clima també han tingut un cert impacte en els boscos de pi roig. Esdeveniments de sequera i condicions d'estrès hídric s'han associat a reduccions en el creixement, a episodis de mortalitat i defoliació d'individus adults, a una limitada taxa d'establiment i al fracàs reproductiu en algunes poblacions de pi roig d'Europa (Bigler *et al.*, 2006; Thabeet *et al.*, 2009), i en algunes poblacions de la Península Ibèrica (Martínez-Vilalta & Piñol, 2002; Hódar *et al.*, 2003; Castro *et al.*, 2004; Galiano *et al.*, 2010; Hereş *et al.*, 2012; Martínez-Vilalta *et al.*, 2012). D'altra banda, tot i que els boscos de pi roig en diferents parts d'Europa s'han mantingut en gran mesura fora de l'afectació dels focs de capçada durant segles, els focs de sotabosc hi són freqüents en algunes regions (Niklasson & Granström, 2000; Niklasson *et al.*, 2010) i durant les últimes dècades els focs de capçada han afectat algunes poblacions de l'espècie a la península Ibèrica (Pausas *et al.*, 2004). Tots aquests canvis i pertorbacions estan alterant els processos demogràfics dels boscos de pi roig,

amb importants conseqüències en algunes de les seves poblacions i amb la potencialitat de produir canvis en la seva distribució (Matías & Jump, 2012).

OBJECTIUS

Amb aquesta tesi pretenem aprofundir en l'estudi dels patrons demogràfics de creixement, mortalitat, establiment i reproducció dels boscos de pi roig (*Pinus sylvestris* L.) en resposta a les pertorbacions, com aquests varien amb els gradients ambientals al llarg de diferents escales espacials i si aquests processos poden originar canvis en la vegetació (Fig. 1.2).

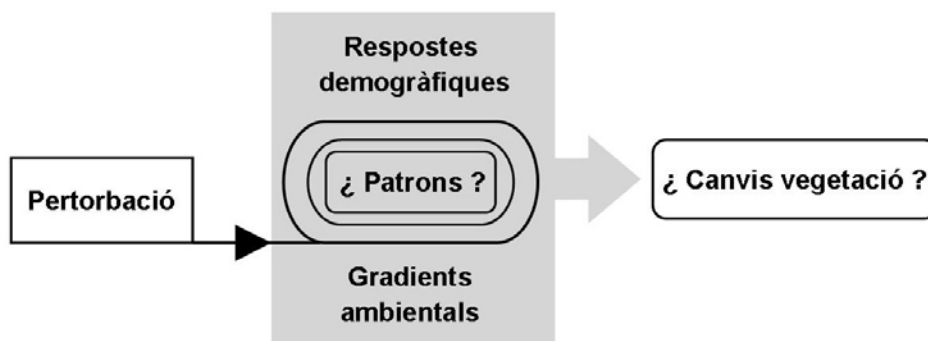


Figura 2. Il·lustració conceptual dels patrons que poden emergir en la demografia al llarg dels gradients ambientals en resposta a una pertorbació i els possibles canvis en la vegetació.

Podem imaginar un gran microscopi a través del qual hem anat augmentant el poder de resolució per observar aquests patrons demogràfics d'una escala gran a una escala més detallada. Per anar al gra plantejarem un seguit de preguntes que ens ajudaran a exposar els principals objectius d'aquesta tesi:

1. El pi roig i els seus boscos són vulnerables al foc? El foc pot induir canvis en la vegetació en zones actualment dominades pel pi roig?
2. Com són els patrons demogràfics dels boscos de pi roig de la península Ibèrica al llarg dels gradients climàtics i estructurals del bosc? Hi tenen alguna cosa a dir les sequeres? Està en declivi el pi roig?
3. Com són els patrons de declivi entre poblacions de pi roig? I què passa dins de les poblacions? Quins factors n'expliquen la variabilitat? Quins patrons de

regeneració es relacionen amb el declivi? Hi ha indicis de canvis en la vegetació?

4. Si el declivi de les poblacions va associat a un estrès per sequera, com respon l'esforç reproductiu dels individus sota aquestes condicions?

Aquestes preguntes les intentem abordar i respondre en els següents capítols on exposem els objectius concrets de la tesi:

Capítol I. INTRODUCCIÓ GENERAL. En aquest primer capítol fem una introducció general de la temàtica de l'estudi de la tesi.

Capítol II. LA MANCA DE REGENERACIÓ I LA VULNERABILITAT CLIMÀTICA AL FOC DEL PI ROIG PODEN INDUIR CANVIS EN LA VEGETACIÓ AL SEU LÍMIT SUD DE DISTRIBUCIÓ (*Lack of regeneration and climatic vulnerability to fire of Scots pine may induce vegetation shifts at the southern edge of its distribution*).

En aquest capítol estudiem la distribució espacial i climàtica dels incendis de capçada que han afectat els boscos de pi roig durant les últimes 3 dècades a Catalunya. A partir d'aquí, hem construït un índex de vulnerabilitat climàtica al foc dels boscos de pi roig a la península Ibèrica i hem vist què passaria amb aquesta vulnerabilitat en un context de canvi climàtic. D'altra banda, hem visitat 9 boscos cremats per incendis de capçada i hi hem inventariat la vegetació actual. Amb aquesta informació hem pogut veure la capacitat regenerativa del pi roig després del foc, si s'han produït canvis en la vegetació i hem fet prediccions de la dinàmica futura de la vegetació després d'un incendi.

Capítol III. DETERMINANTS ESTRUCTURALS I CLIMÀTICS DE LES TAXES DEMOGRÀFIQUES DELS BOSCOS DE PI ROIG A TRAVÉS DE LA PENÍNSULA IBÈRICA (*Structural and climatic determinants of demographic rates of Scots pine forests across the Iberian Peninsula*).

L'objectiu és determinar les respostes de les taxes de mortalitat i creixement dels boscos de pi roig en tota la seva distribució a la península Ibèrica a la variació espacial del clima, les anomalies climàtiques, l'estructura del bosc i la gestió forestal durant les últimes dècades del segle XX. Finalment, per avaluar les implicacions potencials pels

patrons de mortalitat observats, també hem analitzat la seva relació amb la regeneració potencial de l'espècie.

Capítol IV. PATRONS DE DECLIVI I DE REGENERACIÓ A TRAVÉS DE POBLACIONS DE PI ROIG (*Patterns of forest decline and regeneration across Scots pine populations*).

En aquest capítol hem tractat d'esbrinar quines relacions hi ha entre els diferents factors biòtics (estructura del bosc i competència pels recursos), abiòtics relacionats amb la disponibilitat d'aigua (clima, sòl i topografia) i la gestió forestal del passat que podrien explicar els patrons de declivi a nivell de parcel·la entre i dins de quatre poblacions de pi roig a Catalunya. Sota aquest declivi, hem estudiat els patrons d'establiment o regeneració tant del pi roig com de les principals espècies que potencialment el podrien substituir sota les condicions de declivi.

Capítol V. ASSIGNACIÓ REPRODUCTIVA VS. VEGETATIVA EN POBLACIONS EN DECLIVI DE PI ROIG (*Reproductive vs. vegetative allocation in declining Scots pine populations*).

En aquest últim capítol hem analitzat els patrons reproductius a nivell individual al llarg de gradients d'estrès (declivi poblacional i defoliació individual) des d'un punt de vista al·lomètric. Concretament, hem intentat detectar diferències entre els individus en l'assignació dels recursos entre les funcions reproductiva i vegetativa al llarg dels gradients d'estrès. Finalment hem estudiat si a nivell intra-individual existeix un cost reproductiu per al creixement (*trade-off*) i si aquest cost varia segons el nivell d'estrès que experimenta l'individu.

Capítol VI. DISCUSSIÓ GENERAL. En aquesta part de la tesi fem una síntesi de les principals conclusions i patrons obtinguts durant el desenvolupament del treball.

REFERÈNCIES BIBLIOGRÀFIQUES

- Alía, R., Moro-Serrano, J. & Notivo, E. (2001)** Genetic Variability of Scots Pine (*Pinus sylvestris*) Provenances in Spain: Growth Traits and Survival. *Silva Fennica*, 35: 27-38.
- Allen C.D. & Breshears, D.D. (1998)** Drought-induced shift of a forestwoodland ecotone: rapid landscape response to climate variation. *Proceedings of the National Academy of Sciences, USA*, 95: 14839-14892.
- Allen, C.D., Makalady, A.K., Chenchouni H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J-H., Allard, G., Running, S.W., Semerci, A. & Cobb, N. (2010)** A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, 259: 660-84.
- Bigler, C., Bräker, O.U., Bugmann, H., Dobbertin, M. & Rigling, A. (2006).** Drought as an Inciting Mortality Factor in Scots Pine Stands of the Valais, Switzerland. *Ecosystems*, 9: 330-343.
- Blondel, J. & Aronson, J. (1995)** Biodiversity and ecosystem function in the Mediterranean basin: Human and nonhuman determinants (ed by G. W. Davis and D. M. Richardson). *Mediterranean-Type ecosystems: The function of biodiversity*, pp. 43-105, Springer-Verlag, Berlin.
- Bonan, G.B. (2008)** Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science*, 320: 1444-1449.
- Bréda, N., Huc, R., Granier, A. & Dreyer, E. (2006)** Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. *Annals of Forest Science*, 63: 625-644.
- Burriel, J.A., Gracia, C., Ibáñez, J.J., Mata, T. & Vayreda, J. (2000-2004)** Inventari ecològic i forestal de Catalunya. Catalunya, 10 Volumes. CREA, Bellaterra (Catalunya).
- Carnicer, J., Coll, M., Ninyerola, M., Pons, X., Sánchez, G. & Peñuelas, J. (2011)** Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought. *Proceedings of the National Academy of Sciences, USA*, 108: 1474-1478.
- Castro, J., Zamora, R., Hódar, J.A. & Gómez, J.M. (2004)** Seedling establishment of a boreal tree species (*Pinus sylvestris*) at the southernmost distribution limit: consequences of being in a marginal Mediterranean habitat. *Journal of Ecology*, 92: 266-277.
- Castroviejo, S., Lainz, M., López González, G., Montserrat, P., Muñoz Garmendia, F., Paiva, J. & Villar, L. (1986)** Flora ibérica: plantas vasculares de la Península Ibérica e Islas Baleares, Vol. 1. Madrid: CSIC.
- Chauchard, S., Carcaillet, C. & Guibal, F. (2007)** Patterns of land-use abandonment control tree-recruitment and forest dynamics in Mediterranean mountains. *Ecosystems*, 10: 936-948.
- Cousens, J.E. (1988)** Report of a 12-year study of litterfall and productivity in a stand of mature Scots pine. *Forestry*, 61:255-266.
- Czúcz, B., Gálhidy, L. & Mátyás, C. (2011)** Present and forecasted xeric climatic limits of beech and sessile oak distribution at low altitudes in central Europe. *Annals of Forest Science*, 68: 99-108.

- Dale, V.H., Joyce, L.A., McNulty, S., Neilson, R.P., Ayres, M.P., Flannigan, M.D., Hanson, P.J., Irland, L.C., Lugo, A.E., Peterson, C.J., Simberloff, D., Swanson, F.J., Stocks, B.J. & Wotton, B.M. (2001) Climate change and forest disturbances. *BioScience*, 51: 723-34.
- Easterling, D.R., Meehl, G.A., Parmesan, C., Changnon, S.A., Karl, T.R. & Mearns, L.O. (2000) Climate extremes: observations, modeling, and impacts. *Science*, 289: 2068-2074.
- FAO (2010) Food and agricultural organization of the United Nations and Forest Stewardship Council. <http://www.fao.org>.
- Franklin, J.D., Shugart, H.H. & Harmon, M.E. (1987) Tree death as an ecological process. *Bioscience*, 37: 550-556.
- Galiano, L., Martínez-Vilalta, J. & Lloret F. (2010) Drought induced multi-factor decline of Scots pine in the Pyrenees and potential vegetation change by the expansion of co-occurring oak species. *Ecosystems*, 7: 978-991.
- García-Ruiz, J.M., Lasanta, T., Ruiz-Flaño, P., Ortigosa, L., White, S., González, C. & Martí, C. (1996) Land-use changes and sustainable development in mountain areas: A case study in the Spanish Pyrenees. *Landscape Ecology*, 11: 267-277.
- Gràcia, M. & Ordóñez, J.L. (2011) Les pinesdes de pi roig. Manuals de gestió d'hàbitats. Diputació de Barcelona.
- Grove, A.T. & Rackham, O. (2001) The nature of Mediterranean Europe: an ecological history. Yale University Press, New Haven.
- Hampe, A. & Petit, R.J. (2005) Conserving biodiversity under climate change: the rear edge matters. *Ecology Letters*, 8: 461-467.
- Hansen, A.J., Neilson, R.P., Dale, V.H., Flather, C.H., Iverson, L.R., Currie, D.J., Shafer, S., Cook, R. & Bartlein, P.J. (2001) Global change in forests: responses of species, communities, and biomes. *Bioscience*, 51: 765-779.
- Harper, J.L. (1967) A darwinian approach to plant ecology. *Journal of Animal Ecology*, 36: 495-518.
- Harper, J.L. (1977) Population biology of plañis. Academic Press, Londres.
- Hereş, A.M., Martínez-Vilalta, J. & López, J.C. (2012) Growth patterns in relation to drought induced mortality at two Scots pine (*Pinus sylvestris* L.) sites in NE Iberian Peninsula. *Trees*, 26: 621-630.
- Hódar, J.A., Castro, J. & Zamora, R. (2003) Pine processionary caterpillar *Thaumetopoea pityocampa* as a new threat for relict Mediterranean Scots pine forests under climatic warming. *Biological Conservation*, 110: 123-129.
- Hutchings, M.J., John, E.A. & Stewart, A.J.A., eds. (2000) The Ecological Consequences of Environmental Heterogeneity. Blackwell Science, Oxford, UK.
- Ibáñez, I., Clark, J.S., LaDeau, S. & Hille Ris Lambers, J. (2007) Exploiting temporal variability to understand tree recruitment response to climate change. *Ecological Monographs*, 77: 163-177.
- IPCC (2007) Climate change 2007: the physical science basis. Contribution of Working Group I to the Forth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge
- Irvine, J., Perks, M.P., Magnani, F. & Grace, J. (1998) The response of *Pinus sylvestris* to drought: stomatal control of transpiration and hydraulic conductance. *Tree Physiology*, 18: 393-402.

- Jump, A.S., Matyas, C. & Peñuelas, J. (2009)** The altitude-for-latitude disparity in the range retractions of woody species. *Trends in Ecology and Evolution*, 24: 694-701.
- Laurance, W.F. (1999)** Reflections on the tropical deforestation crisis. *Biological Conservation*, 91: 109-117.
- Lavorel, S., Canadell, J., Rambal, S. & Terradas, J. (1998)** Mediterranean terrestrial ecosystems: research priorities on global change effects. *Global Ecology and Biogeography*, 7: 157-166.
- Lertzman, K.P. (1992)** Patterns of gap-phase replacement in a subalpine, old-growth forest. *Ecology*, 73: 657-669.
- Levins, R. (1968)** Evolution in changing environments. Some theoretical explorations. Princeton University Press, New York.
- Linares, J.C., Camarero, J.J. & Carreira, J.A. (2009)**. Interacting effects of changes in climate and forest cover on mortality and growth of the southernmost European fir forests. *Global Ecology and Biogeography*, 18: 485-497.
- Lloret, F., Siscart, D. & Dalmases, C. (2004)** Canopy recovery after drought dieback in holm-oak Mediterranean forests of Catalonia (NE Spain). *Global Change Biology*, 10: 2092-2099.
- Lloret, F., Escudero, A., Iriondo, J.M., Martínez-Vilalta, J. & Valladares, F. (2012)** Extreme climatic events and vegetation: the role of stabilizing processes. *Global Change Biology*, 18: 797-805.
- MacDonald, D., Crabtree, J.R., Wiesinger, G., Dax, T., Stamou, N., Fleury, P., Gutierrez Lazpita, J. & Gibon, A. (2000)** Agricultural abandonment in mountain areas of Europe: Environmental consequences and policy response. *Journal of Environmental Management*, 59: 47-69.
- Malhi, Y., Roberts, J.T., Betts, R.A., Killeen, T.J., Li, W. & Nobre, C.A.. (2008)** Climate change, deforestation, and the fate of the Amazon. *Science*, 319: 169-172.
- Margaris, N. S., Koutsidou, E., & Giourga, Ch. (1996)**. Changes in traditional Mediterranean land-use systems (ed. by C. J. Brandt and J. B. Thornes), *Mediterranean Desertification and Land Use*, pp. 29-42, Chichester: Wiley.
- Martínez-García, F. (1999)** Los bosques de *Pinus sylvestris* L. del Sistema Central español. Distribución, historia, composición florística y tipología. PhD Thesis, Universidad Complutense de Madrid, Madrid, Spain.
- Martínez-Vilalta, J. & Piñol, J. (2002)**. Drought-induced mortality and hydraulic architecture in pine populations of the NE Iberian Peninsula. *Forest Ecology and Management*, 161: 247-256.
- Martínez-Vilalta, J., Cochard, H., Mencuccini, M., Sterck, F., Herrero, A., Korhonen, J.F.J., Llorens, P., Nikinmaa, E., Nolé, A., Poyatos, R., Ripullone, F., Sass-Klaassen, U. & Zweifel, R. (2009)** Hydraulic adjustment of Scots pine across Europe. *New Phytologist*, 184: 353-364.
- Martínez-Vilalta, J., López, B.C., Loepfe, L. & Lloret, F. (2012)** Stand- and tree-level determinants of the drought response of Scots pine radial growth. *Oecologia*, 168: 877-888.
- Matías, L. & Jump, A.S. (2012)** Interactions between growth, demography and biotic interactions in determining species range limits in a warming world: The case of *Pinus sylvestris*. *Forest Ecology and Management*, 282: 10-22.
- Millennium Ecosystem Assessment (2005)** Ecosystems and Human Well-being: Biodiversity Synthesis. World Resources Institute, Washington, DC.

- Moser, B., Temperli, C., Schneider, G. & Wohlgemuth, T. (2010)** Potential shift in tree species composition after interaction of fire and drought in the Central Alps. *European Journal of Forest Research*, 129: 625-633.
- Naveh, Z. (1975)** The evolutionary significance of fire in the Mediterranean region. *Vegetatio*, 29: 199-208.
- Niklas, K.J. & Enquist, B.J. (2003)** An allometric model for seed plant reproduction. *Evolutionary Ecology Research*, 5: 79-88.
- Niklasson, M. & Granström, A. (2000)** Numbers and sizes of fires: long-term spatially explicit fire history in a Swedish boreal landscape. *Ecology*, 81: 1484-1499.
- Niklasson, M., Zin, E., Zielonka, T., Feijen, M., Korczyk, A.F., Churski, M., Samojilik, T., Jędrzejewska, B., Gutowski, J.M. & Brzeziecki, B. (2010)** A 350-year tree-ring fire record from Białowieża Primeval Forest, Poland: implications for Central European lowland fire history. *Journal of Ecology*, 98: 1319-1329.
- Obeso, J.R. (2002)** The costs of reproduction in plants. *New Phytologist*, 155: 321-348.
- Oldfield, S., Lusty, C. & MacKinven, A. (1998)** The world list of threatened trees. Cambridge, UK: World Conservation Press.
- Oliver, C.D. & Larson, B.C. (1990)** Forest stand dynamics. McGraw-Hill, New York, NY.
- Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A., Phillips, O.L., Shvidenko, A., Lewis, S.L., Canadell, J.G., Ciais, P., Jackson, R.B., Pacala, S.W., McGuire, A.D., Piao, S., Rautiainen, A., Sitch, S. & Hayes, D. (2011)** A large and persistent carbon sink in the World's forests. *Science*, 333: 988-993.
- Pausas, J.G. (2004)** Changes in fire and climate in the eastern Iberian Peninsula (Mediterranean basin). *Climatic Change*, 63: 337-350.
- Pausas, J.G. & Fernández-Muñoz, S. (2012)** Fire regime changes in the Western Mediterranean basin: from fuel-limited to drought-driven fire regime. *Climatic Change*, 110: 215-226.
- Peet, R.K. & Christensen, N.L. (1987)** Competition and tree death. *Bioscience*, 37: 586-595.
- Peñuelas, J., Lloret, F. & Montoya, R. (2001)** Severe drought effects on Mediterranean woody flora in Spain. *Forest Science*, 47: 214-218.
- Petit, R.J. & Hampe, A. (2006)** Some evolutionary consequences of being a tree. *The Annual Review of Ecology, Evolution, and Systematics*, 37: 187-214.
- Piñol, J., Terradas, J. & Lloret, F. (1998)** Climate warming, wildfire hazard, and wildfire occurrence in coastal eastern Spain. *Climatic Change*, 38: 345-357.
- Poyatos, R., Latron, J. & Llorens, P. (2003)**. Land Use and Land Cover Change After Agricultural Abandonment. The Case of a Mediterranean Mountain Area (Catalan Pre-Pyrenees). *Mountain Research and Development*, 23: 362-368.
- Retana, J., Espelta, J.M., Habrouk, A., Ordóñez, J.L. & Solà-Morales, F. (2002)** Regeneration patterns of three Mediterranean pines and forest changes after a large wildfire in northeastern Spain. *Écoscience*, 9: 89-97.
- Reznick, D. (1985)** Costs of reproduction: An evaluation of the empirical evidence. *Oikos*, 44: 257-267.

- Rodrigo, A., Retana, J. & Picó, F.X. (2004)** Direct regeneration is not the only response of Mediterranean forests to large fires. *Ecology*, 85: 716-729.
- Runkle, J.R. (1981)** Gap regeneration in some old-growth forests of the eastern United States. *Ecology*, 62: 1041-1051.
- Russo, S.E., Brown, P., Tan, S. & Davies, S.J. (2008)** Interspecific demographic trade-offs and soil-related habitat associations of tree species along resource gradients. *Journal of Ecology*, 96: 192-203.
- Sarris, D., Christodoulakis, D. & Körner, Ch. (2007)** Recent decline in precipitation and tree growth in the eastern Mediterranean. *Global Change Biology*, 13: 1187-1200.
- Stearns, S.C. (1992)** The Evolution of Life Histories. Oxford University Press, Oxford.
- Stephenson, N.L. (1990)** Climatic control of vegetation distribution: the role of water balance. *American Naturalist*, 135: 649-670.
- Tapias, R., Climent, J., Pardos, J. & Gil, L. (2004)** Life histories of Mediterranean pines. *Plant Ecology*, 171: 53-68.
- Terradas, J. (2005)** Forest dynamics: a broad view of the evolution of the topic, including some recent regional contributions. *Investigación agraria. Sistemas y recursos forestales*, 14: 525-537.
- Tessier, L. (1989)** Spatio-temporal analysis of climate-tree ring relationships. *New Phytologist*, 111: 517-529.
- Thabeet, A., Vennetier, M., Gadbin-Henry, C., Denelle, N., Roux, M., Caraglio, Y. & Vila, B. (2009)** Response of *Pinus sylvestris* L. to recent climatic events in the French Mediterranean region. *Trees*, 23: 843-853.
- Turner, M.G., Baker, W.L., Peterson, C.J. & Peet, R.K. (1998)** Factors influencing succession: lessons from large, infrequent natural disturbances. *Écosystems*, 1: 511-523.
- Valladares, F. (2003)** Light heterogeneity and plants: from ecophysiology to species coexistence and biodiversity. Progress in Botany (eds K. Esser, U. Lüttge, W. Beyschlag & F. Hellwig), pp. 439-471. Springer Verlag, Heidelberg, Germany.
- Vitousek, P.M. (1994)** Beyond global warming: ecology and global change. *Ecology*, 75: 1861-1876.
- Weiner, J. (2004)** Allocation, plasticity and allometry in plants. *Perspectives in Plant Ecology Evolution and Systematics*, 6: 207-215.
- Weiner, J., Campbell, L.G., Pino, J. & Echarte, L. (2009)** The allometry of reproduction within plant populations. *Journal of Ecology*, 97: 1220-1233.
- Yoda, K., Kira, T., Ogawa, H. & Hozumi, K. (1963)** Intraspecific competition among higher plants. XI. Self-thinning in overcrowded pure stands under cultivated and natural conditions. *Journal of the Institute of Polytechnics, Osaka City University, Series D.*, 14:107-129.

II. LACK OF REGENERATION AND CLIMATIC VULNERABILITY TO FIRE OF SCOTS PINE MAY INDUCE VEGETATION SHIFTS AT THE SOUTHERN EDGE OF ITS DISTRIBUTION

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ABSTARCT

Aim Forest ecosystems dominated by fire-sensitive species could suffer shifts in composition under altered crown fire regimes mediated by climate change. The aims of this study were to: (1) study the spatio-temporal patterns and the climatic distribution of fires in Scots pine (*Pinus sylvestris* L.) forests during the last 31 years in Catalonia (NE Spain), (2) evaluate the climatic vulnerability to fire of these forests in Spain, (3) analyse the regeneration of Scots pine after fire, and (4) predict the mid-term maintenance or replacement of Scots pine in burned areas.

Location Catalonia (NE Spain): the southern distribution limit of Scots pine.

Methods We characterized the spatio-temporal and the climatic distribution of fires that occurred in Catalonia between 1979 and 2009. We used a generalized linear model to characterize the climatic vulnerability to fire of Scots pine in the whole of Spain. We assessed the regeneration of the species after crown fires in nine burned areas in Catalonia. The resulting data were integrated into a stochastic matrix model to predict the mid-term maintenance or replacement of Scots pine in burned areas.

Results During the last three decades, Scots pine forests distributed in dry sites were most affected by fire. Our assessment of the vulnerability to fire of Scots pine forests in Spain as a whole, based on climatic and topographical variables, showed that 32% of these forests are vulnerable to fire, and that this proportion could increase to 66% under a conservative climate change scenario. Field data showed almost no regeneration of Scots pine after crown fires, and a limited capacity to recolonize from unburned edges, even in relatively old fires, with 90% of recruits located in the first 25 m from the edge. This process could be delayed by the elapsed time for new recruits to achieve reproductive maturity, which we estimated to be approximately 15 years. Finally, our matrix model predicted the replacement of burned Scots pine forests by oak (*Quercus* sp.) forests, shrublands or mixed resprouters forests.

Main conclusions Increased vulnerability to fire of Scots pine forests under future, warmer conditions may result in vegetation shifts at the southern edge of the distribution of the species.

Keywords: Climatic vulnerability, fire regime, *Pinus sylvestris*, recolonization, regeneration, southern distribution limit, Spain, species range, vegetation shifts.

INTRODUCTION

Fire is one of the most important ecological factors determining vegetation dynamics and landscape patterns over large areas of the Earth (Bond *et al.*, 2005; Pausas & Keeley, 2009). In the Mediterranean Basin, warming and drought affect fuel flammability and determine, together with changes in land uses and atmospheric composition (Lavorel *et al.*, 1998), the vulnerability of forests to fire, especially during the summer (Piñol *et al.*, 1998; Pausas, 2004). Indeed, during the second half of the 20th century the frequency of fires and the area burned have increased concomitantly with fire weather risk (Piñol *et al.*, 1998). Thus, the aridity increase predicted by most climate models (Bates *et al.*, 2008) could have a large impact on fire regimes, the dry edge of forests being particularly vulnerable (Czúcz *et al.*, 2011). The effect of these changes could be more pronounced in sub-Mediterranean montane areas (Loepfe *et al.*, 2011), where crown fires are relatively uncommon at present and forests are dominated by species without specific post-fire regeneration mechanisms.

Many species are able to survive or reestablish after disturbances and, in Mediterranean ecosystems, propagule-persistence and resprouting capacity are the two main fire response traits of plants (Pausas *et al.*, 2004). These traits provide Mediterranean plant communities with the ability to recover and persist after fire. Thus, some Mediterranean plant communities can return to the pre-fire composition and structure several decades after fire (Hanes, 1971). Although this process has been observed in many representative Mediterranean species (Trabaud & Lepart, 1980; Lloret, 1998; Arnan *et al.*, 2007), a decline in plant resilience and shifts in community composition may also occur in Mediterranean communities, depending on fire regimes, environmental conditions and the presence of species-specific post-fire regeneration mechanisms (Díaz-Delgado *et al.*, 2002; Lloret *et al.*, 2005; Arnan *et al.*, 2007).

Pine species cover large areas of the Northern Hemisphere and about 25% of the forested area in the Mediterranean Basin (Barbero *et al.*, 1998). Pine forests have an ancient history of human intervention that has shaped their current structure,

composition and distribution (Richardson *et al.*, 2007). The marked decline of agriculture, changes in forest exploitation, afforestation policies and long-term fire suppression during the 20th century have changed fire regimes in the Mediterranean Basin, with pine forests becoming the most fire-sensitive ecosystems (Pausas *et al.*, 2008). Some pine species such as *Pinus halepensis* and *Pinus pinaster* show good regeneration capacity after fire (Herranz *et al.*, 1997; Nathan & Ne'eman, 2004; Rodrigo *et al.*, 2004; Calvo *et al.*, 2008), based on the canopy seed bank stored in serotinous cones (Tapias *et al.*, 2001). Even in forests dominated by these species, however, time intervals between successive fires shorter than the period required for population replacement can lead to changes in community composition (Eugenio *et al.*, 2006). In other pine species, such as *Pinus nigra* or *Pinus pinea*, the lack of serotinous cones limits regeneration capacity after crown fires (Retana *et al.*, 2002; Rodrigo *et al.*, 2004, 2007), stressing the importance of unburned islands and edges as seed sources (Ordóñez *et al.*, 2005).

Scots pine (*Pinus sylvestris* L.) forests in different parts of Europe have remained largely unaffected by crown wildfires in centuries, although understorey fires have been frequent in some regions (Niklasson & Granström, 2000; Niklasson *et al.*, 2010). However, during the last decades of the 20th century, crown wildfires have affected the south-western distribution limit of this species (Pausas *et al.*, 2008). Given the apparent inability of Scots pine to germinate after fire (Retana *et al.*, 2002) and that serotiny is absent in this species (Tapias *et al.*, 2004), vegetation shifts may occur in areas where Scots pine is currently the dominant tree species (cf. Rodrigo *et al.*, 2004). Here, we study for the first time the spatio-temporal patterns and the climatic distribution of fires in Scots pine forests on a large regional scale at the southern (and dry) limit of the species distribution. Our specific aims were to: (1) evaluate the climatic vulnerability to crown fire of Scots pine forests across the whole distribution of the species in Spain, (2) analyse the success of regeneration of Scots pine as a function of fire size and time since burning, and (3) integrate the previous information into a matrix model to predict the mid-term maintenance or replacement of this species in burned areas.

MATERIALS AND METHODS

Regional analysis and climatic vulnerability to fire of Scots pine forests

This part of the study was carried out in Catalonia (NE Spain; Fig. 1a), where Scots pine is the second most abundant tree species, covering 219,754 ha (18.4% of total forested area; Burriel *et al.*, 2004). Scots pine forests occupy an important climatic gradient, ranging from relatively cold and humid locations in the Pyrenees to warmer and drier locations in the pre-Pyrenees and scattered populations in the south (Fig. 1b). The species is present from 200 to 2100 m a.s.l., but it is mainly distributed between 800 and 1600 m a.s.l. Annual precipitation in its distribution area ranges from 520 to 1330 mm and average annual temperature between 3.6 and 14.3 °C.

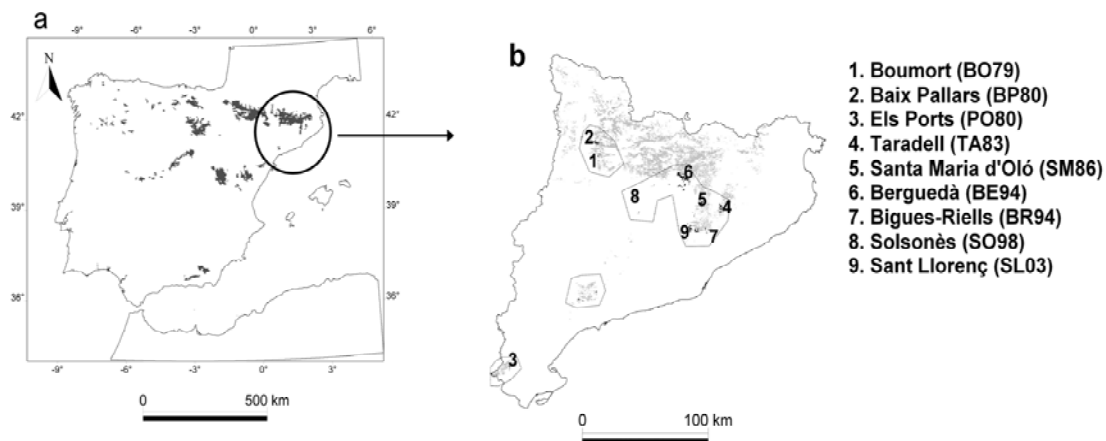


Figure 1. (a) Scots pine (*Pinus sylvestris* L.) distribution across Spain (grey surface). (b) Distribution of Scots pine in Catalonia (in grey) and location of the main wildfires affecting this species (in black) during the last 31 years (dotted circles). The numbers correspond to the nine fires sampled in this study (Table 1). Each sampled fire is defined by a code that includes the initials of the location and the year of the fire.

To characterize the regional fire patterns in Scots pine forests during the last three decades in Catalonia, the perimeters of wildfires that have occurred since 1979 were obtained from LANDSAT satellite images (Salvador *et al.*, 2000 and successive updates) and overlaid on land-cover maps. Two different maps were used: for fires that occurred between 1979 and 1988 we used the Land Cover Map of Spain from 1978 (MAPA, 1980) and for fires that occurred between 1989 and 2009 we used a more recent Forest Map of Catalonia (DARP, 1996). This methodology ensured that Scots

pine was the dominant species before the fire and allowed us to characterize the fire regime in this forest type over the last 31 years. The resulting map was overlaid on a water availability map to study the distribution of Scots pine wildfires as a function of climate. Water availability was defined as: $WAI = ((P - PET)/PET) \cdot 100$, where P is annual rainfall (mm year^{-1}) and PET is potential evapotranspiration (mm year^{-1}) calculated with the Hargreaves & Samani (1982) equation. Climate was classified in terms of WAI in four main categories: Dry ($WAI < -20$), Dry-Subhumid ($-20 \leq WAI < 0$), Subhumid ($0 \leq WAI < 20$) and Humid ($WAI \geq 20$). Climatic (P and PET) data were obtained from the Digital Climatic Atlas of Catalonia (Ninyerola *et al.*, 2000), with a spatial resolution of 180 m.

We then expanded the previous analysis to evaluate the climatic vulnerability to fires of Scots pine forests across the whole distribution of the species in Spain (Fig. 1a). The following methodology was used. First, we characterized the whole distribution of Scots pine in Catalonia in terms of annual rainfall (mm year^{-1}), mean annual temperature ($^{\circ}\text{C}$), annual thermal amplitude ($^{\circ}\text{C}$) and terrain slope (%). Climatic variables were obtained from the Digital Climatic Atlas of Catalonia (Ninyerola *et al.*, 2005), as before, and the slope was obtained from a digital elevation model with a resolution of 30 m. These variables were used as explanatory factors in a generalized linear model (GLM) of the probability of being affected by fire, modelled as a binomial function. Interaction terms were not considered in the final model as they did not improve model fit. As unburned area was much greater than burned area, data points consisted of 200 points selected randomly within the area of Scots pine burned during the last 31 years and 500 points randomly located across the whole unburned distribution of Scots pine in Catalonia. The distributions of the explanatory variables for the selected points were always very similar to those for the whole distribution of Scots pine in the study region, thus ensuring their representability. A preliminary GLM analysis accounting for differences across the main areas occupied by Scots pine forests in Catalonia (Ports de Beseit, Prades Mountains and Pyrenees, from south to north in Fig.1b) showed no spatial effects.

The previous GLM function was used to classify the 2397 plots from the National Forest Inventory of Spain (IFN, Villaescusa & Díaz, 1998) where Scots pine was the dominant species and that had previously been characterized using the same predictor

variables. In this case the climatic variables were obtained from the Digital Climatic Atlas of the Iberian Peninsula (Ninyerola *et al.*, 2005) and the slope from a digital elevation model with a resolution of 30 m. Plots with a probability of being affected by fire ≥ 0.5 according to the GLM were considered vulnerable, whereas plots with a probability < 0.5 were considered not vulnerable to fire. We computed the proportion of plots classified into each group within each climate type, defined as above. To visualize these results we produced a raster with a 10×10 km resolution in which the average value of the GLM probabilities for plots within each cell was computed. As an additional exploratory exercise to investigate the impact of climate change, we repeated the previous classification of the IFN plots assuming an increase of 4°C in mean annual temperature, consistent with the regionalized climate scenarios for Spain (period 2071-2100; Brunet *et al.*, 2009). All statistical analyses were carried out with the R software (R version 2.10.0; R Development Core Team, 2009).

Post-fire regeneration and recolonization from unburned edges

To study the success of post-fire regeneration of Scots pine within burned areas, we selected 9 of the 11 crown fires that occurred in Catalonia from 1979 to 2009 and had affected an area of at least 100 ha of Scots pine forest (Table 1; Fig. 1b). Ten circular plots of 10 m radius were established at random in spring 2010 within each of these burned areas. Plots were located at a distance of at least 70 m from the margin of the fire to prevent the arrival of pine seeds dispersed by the wind. This distance was chosen because the distance at which seeds of other pine species are dispersed is typically less than 30 m (Nathan *et al.*, 2000; Ordóñez *et al.*, 2006; Rodrigo *et al.*, 2007). Within each plot we counted the number of individuals (either seedlings or saplings) of Scots pine and also of all other tree species. In the case of resprouting species we also counted the number of individuals already present before the fire that had resprouted after fire.

Table 1. Characteristics of the burned areas included in the analysis of the success of post-fire regeneration of Scots pine (*Pinus sylvestris*) after fire in Catalonia. Each burned area is defined by a code that includes the initials of the location and the year of the fire. Post-fire densities (individuals ha⁻¹ ± SE) of Scots pine and the other tree species recorded in each burned area are shown. Oak densities refer to resprouts.

Locality	Code of fire	Year of fire	Area burned (ha)	Unburned edges	Climate	<i>Pinus sylvestris</i>	<i>Quercus ilex</i>	Deciduous oaks
1. Boumort	BO79	1979	250.0	—	Subhumid / Humid	25 ± 9	0	0
2. Baix Pallars	BP80	1980	779.5	3	Subhumid	0	210 ± 65	51 ± 32
3. Els Ports	PO80	1980	329.1	—	Subhumid / Humid	0	0	0
4. Taradell	TA83	1983	643.5	2	Dry-Subhumid	51 ± 22	70 ± 25	875 ± 137
5. Santa Maria d'Oló	SM86	1986	245.9	3	Dry / Dry-Subhumid	25 ± 10	6 ± 4	1435 ± 232
6. Berguedà	BE94	1994	2403	—	Dry-Subhumid	0	824 ± 158	716 ± 225
7. Bigues-Riells	BR94	1994	103.3	—	Dry-Subhumid	0	1085 ± 192	70 ± 25
8. Solsonès	SO98	1998	179.0	—	Dry	0	13 ± 8	2736 ± 285
9. Sant Llorenç	SL03	2003	985.2	—	Dry / Dry-Subhumid	0	1490 ± 210	528 ± 95

Recolonization patterns from the unburned edges were assessed during spring 2010 in three areas burned more than 20 years ago (Table 1): Baix Pallars (BP80), Taradell (TA83) and Santa Maria d'Oló (SM86). We located three unburned edges both in BP80 and in SM86, and two unburned edges in TA83. In all cases Scots pine was the main tree species in the canopy before the fire, and there was no effect of other edges or groups of surviving individuals in the sampled area. At each unburned edge we established a perpendicular transect from the margin into the burned area. Starting from the unburned edge, we established successive sampling plots of 10 x 10 m until we found null Scots pine establishment. In each sampling plot we counted the number of Scots pine recruits.

Trees need to attain a certain age before they can produce reproductive structures, and this species-specific time lag conditions the progressive recolonization rate by successive generations within the burned area. For this reason we estimated the age and the presence/absence of cones of each Scots pine recruit sampled within the burned area. With these data we estimated the probability of presence of cones, depending on the age of the tree, using a GLM. We modelled the presence/absence of cones as a binomial response, with age as fixed effect and transect within the burned area as a random effect to account for the spatial autocorrelation between recruits within transects and between transects within burned areas.

Predicting forest composition 30 years after fire

To predict the post-fire maintenance or replacement of Scots pine in the canopy we used a matrix model developed by Rodrigo *et al.* (2004) to simulate the success or failure of the post-fire regeneration of the main tree species in north-eastern Spain. To estimate the probability of forest type change 30 years after fire, the following data inputs were used.

- I. Vectors of the initial post-fire densities of seedlings or resprouting individuals of each species in the 90 plots sampled. Following Rodrigo *et al.* (2004), we assumed that mortality of resprouter individuals surviving fire was nil during the time interval considered (30 years). Thus, the density of resprouting individuals measured in each plot was assumed to be the initial post-fire density of resprouting species. To obtain the initial density of seedlings at each plot, we divided the

measured density values by the mean survival since the occurrence of fire [using survival rates estimated by Rodrigo *et al.* (2004) for *Pinus* species using survival functions]. We assumed nil seedling density of *Quercus* species immediately after fire (Rodrigo *et al.*, 2004).

- II. Vector of the number of stems per individual of resprouting species 30 years after fire obtained from Rodrigo *et al.* (2004) for *Q. ilex* (data from 95 individuals) and *Q. cerrioides* (data from 60 individuals).
- III. Vector of seedling survival rates 30 years after fire. For *P. halepensis*, we used data from survivorship functions obtained from 14 burned plots (Rodrigo *et al.*, 2004). Similarly, vectors of survival rates for *P. pinea* and *P. pinaster* seedlings were determined in four plots for each species (Rodrigo *et al.*, 2004). As post-fire regeneration of *Pinus sylvestris* and *P. nigra* was usually very low or nil, it was not possible to have detailed seedling survival rates for these species, and we used the vector of survival rates for *P. halepensis* as a maximum estimate of the survival rate for these two species.

The output of the model included 1000 simulated plots. For each simulation and species the model selected at random a density value from the vectors of initial seedling density or initial number of resprouting individuals after fire. For *Pinus* species (non-resprouters) this value was multiplied by a seedling survival rate chosen at random from vector II above, whereas for *Quercus* species it was multiplied by a number of stems per individual chosen at random from vector III. This procedure assumed density-independent germination, resprouting, and survival processes (Rodrigo *et al.*, 2004).

We assigned different post-fire forest types to each simulated plot according to the relative density values of species and crown cover. Crown cover data per plot were estimated from tree density values by using the regression equations between cover and density for each species obtained from the Ecological Forest Inventory of Catalonia (Burriel *et al.*, 2004; Rodrigo *et al.*, 2004). When two or more species occurred in a given plot, we used the weighted cover values according to the proportion of each species in the plot. The following forest types were considered: (1) shrublands, defined as those with < 10% of tree cover; (2) monospecific forests, defined as those with a density of the most abundant species or group of species > 66.6% of the total tree density; (3) mixed forests, defined as those not considered monospecific. The likelihood

of *Pinus sylvestris* forests remaining in the same forest type or shifting to another one 30 years after fire was computed as the proportion of these 1000 simulated plots that yielded the same or different forests types.

RESULTS

Regional patterns in Catalonia

During the past 31 years (1979-2009), 32 fires affected Scots pine forests in Catalonia, burning a total of 6700 ha. This area represents 3.6% of the whole distribution of Scots pine in Catalonia. Fires were concentrated in the pre-Pyrenees and in the scattered southern populations (Fig. 1b), which represent the southern distribution limit of the species in the region. Both the number of fires and the area burned were lower in the last 10 years than in the two previous decades: 2722 ha and 13 fires in the 1980s, 2908 ha and 11 fires in the 1990s, 1070 ha and 8 fires in the 2000s, reflecting in part the effect of a single large fire that occurred in 1994 (Table 1). It should be noted, however, that the percentage of total burned area affecting Scots pine forests has remained approximately stable: 2.4% in the 1970s, 2.2% in the 1990s and 2.6% in the 2000s. Regarding the distribution of fires across the climatic gradient, the area burned was concentrated in Dry-Subhumid regions (Fig. 2).

Vulnerability to fire of the Scots pine forests in Spain

The GLM used to model the vulnerability to fire of Scots pine forests in Catalonia explained 32.7% of variability in fire occurrence. Annual precipitation and slope had a negative effect on the probability of burning ($\beta = -0.0086$, $P < 0.001$; $\beta = -0.0145$, $P < 0.05$, respectively), whereas mean annual temperature had a positive effect ($\beta = 0.3875$, $P < 0.001$) and the effect of thermal amplitude was not significant ($P = 0.58$). Thus, annual precipitation and mean annual temperature were the main predictors, with low precipitations and high temperatures being characteristic of samples within burned areas.

According to the GLM function, 32% of the Scots pine plots in the Spanish Forest Inventory were classified as vulnerable to fire. These plots were mostly concentrated in Dry sites (Table 2; Fig. 3). Under the climate warming scenario (4°C increment in mean

annual temperature), the percentage of vulnerable plots increased to 66%. This increment was concentrated in Dry sites and, especially, in Dry-Subhumid locations (Table 2).

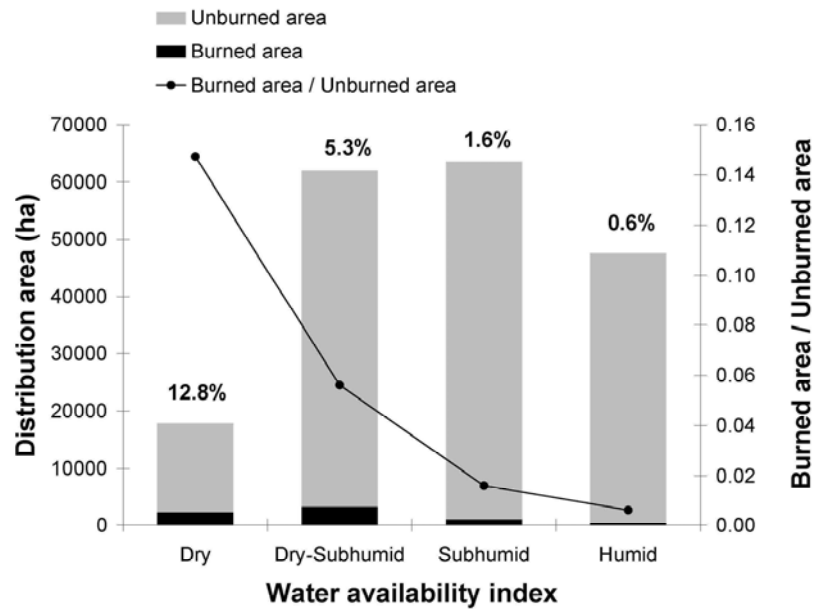


Figure 2. Area burned /unburned (in ha, vertical bars) and area burned /unburned ratio (solid line) of Scots pine (*Pinus sylvestris*) forests in each climate type in Catalonia. Climate categories are based on water availability (see text for further details). The numbers over the bars indicate the percentage of the area of Scots pine forests affected by fire in relation to the whole area occupied by the species in climate type.

Table 2. Vulnerability to fire of the Scots pine (*Pinus sylvestris*) plots in the Spanish Forest Inventory as a function of climate type based on a generalized linear model (GLM), which models fire occurrence as a function of climate predictors and terrain slope (see text for further details). Number of plots and the percentage they represent of the total number in each climate category are shown. The results under current climatic conditions are compared with predictions under a warming scenario consisting of a 4 °C rise in mean annual temperature. VU, plots vulnerable to fire; NV, plots not vulnerable to fire.

Scenario	Current climate		Climate warming (4°C)	
Vulnerability	VU (%)	NV (%)	VU (%)	NV (%)
Dry	735 (72.7)	276 (27.3)	1009 (99.8)	2 (0.2)
Dry-Subhumid	28 (3.3)	825 (96.3)	553 (64.8)	300 (35.2)
Subhumid	0 (0.0)	279 (100.0)	7 (2.5)	272 (97.5)
Humid	0 (0.0)	254 (100.0)	0 (0.0)	254 (100.0)
Total	763 (31.8)	1634 (68.2)	1569 (65.5)	828 (34.5)

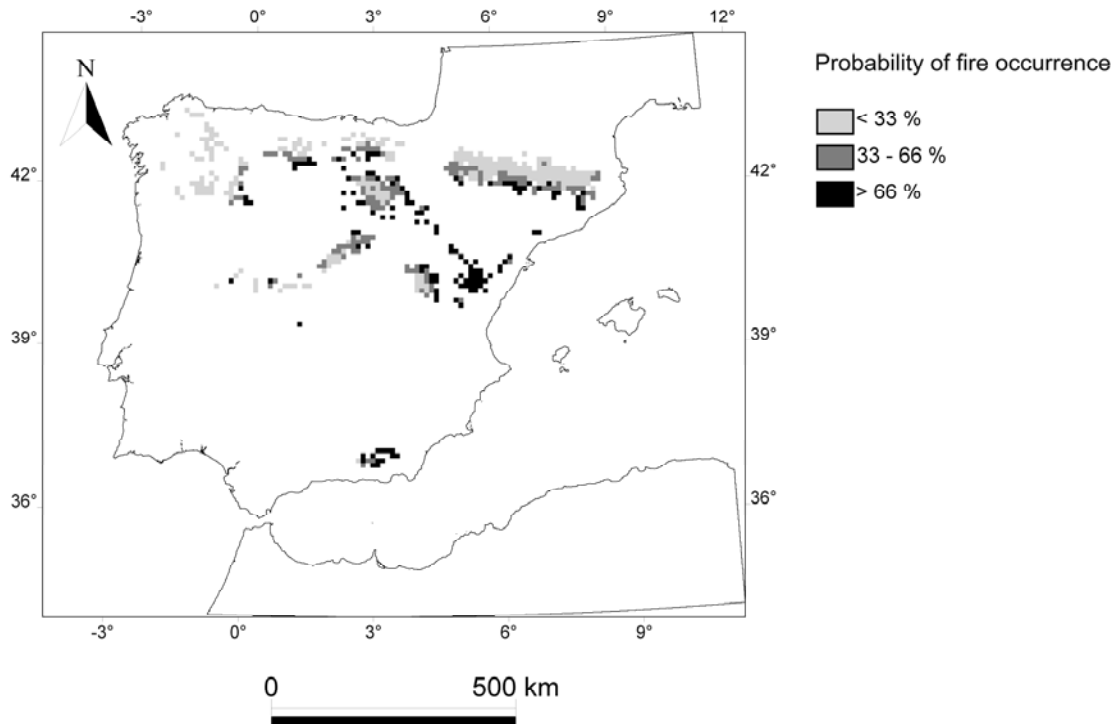


Figure 3. Map of the climatic vulnerability of the Scots pine (*Pinus sylvestris*) forests in Spain based on the fitted generalized linear model for Catalan Scots pine forests (see text for further details).

Post-fire regeneration and recolonization from the unburned edges

Post-fire regeneration of Scots pine was nil in six out of the nine study sites, while the remaining three showed very low regeneration values (Table 1). This low regeneration was not dependent on climate or time since fire, as the studied burned areas were located in all WAI categories and nil Scots pine regeneration was observed for fires that occurred up to 30 years ago (Table 1).

Concerning recruitment from the unburned edges, 55% of new recruits were located in the first 10 m from the limit of the forest, at densities ranging from 200 to 8400 recruits ha^{-1} , while 90% of recruits were distributed in the first 25 m from unburned edges (Fig. 4). The shape of the relationship between recruit density and distance to the edge was similar for the three studied fires. The maximum distance from the unburned edge at which we found Scots pine recruits was 68 m. Tree age was related significantly with the presence of cones ($\beta = 0.375$, $P < 0.001$), so that the likelihood of a given tree producing cones increased with tree age, this probability reaching 50% at about 15 years of age.

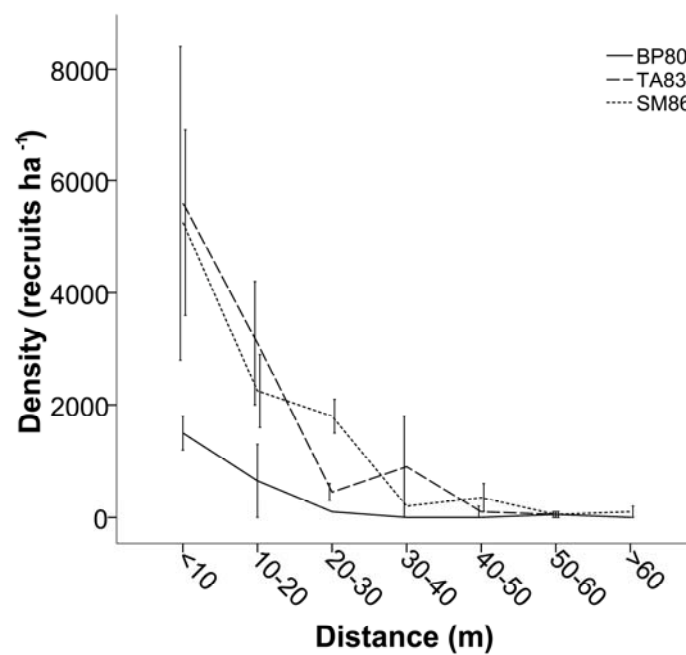


Figure 4. Density ($\pm$ SE) of Scots pine (*Pinus sylvestris*) recruits in Catalonia in each sampling plot along the transects established in three old burned areas to analyse the recruitment patterns of Scots pine from unburned edges. Abbreviations of fires: Baix Pallars (BP80), Taradell (TA83) and Santa Maria d'Oló (SM86).

Predicted vegetation shifts

The results obtained from the stochastic simulation model of forest composition 30 years after fire confirmed the regeneration failure of burned Scots pine forests and the consequent vegetation shifts (Fig. 5). The initial establishment of this species was not enough to recover the same forest type after fire and the model predicted changes in species composition in nearly all cases. Only 0.1% of formerly Scots pine plots were able to regenerate as mixed Scots pine forest. In all other cases, monospecific forests of *Quercus ilex*, deciduous oak forests, shrublands and mixed resprouters forests were expected to be the dominant vegetation types 30 years after the fire (Fig. 5).

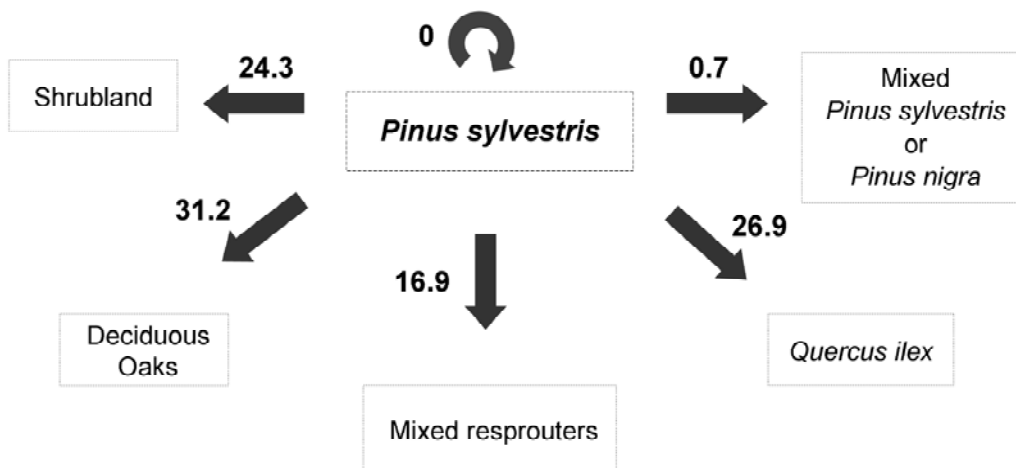


Figure 5. Model predictions of the percentage of burned Scots pine (*Pinus sylvestris*) forests in Catalonia recovering to the same forest type or changing to other forest types 30 years after fire.

DISCUSSION

During the last 31 years crown fire has affected a small proportion of the forests dominated by Scots pine in Catalonia. Although the surface burned has not been large, it cannot be regarded as negligible considering that this species occupies montane areas where crown fire is not as common as in lowland Mediterranean forests (Pausas *et al.*, 2008). The fact that during the study period fires have mostly affected forests located in dry and subhumid areas of this region implies that climate contributes to limit fire occurrence (Pausas & Fernández-Muñoz, 2011) and, therefore, that changes in climate will be likely to modify the fire regime, and, consequently, the vulnerability to fire of Scots pine forests in the study area.

The previous interpretation was supported by the GLM results, which allowed us to expand our assessment to Spanish Scots pine forests as a whole, and showed that 32% of these forests are climatically similar to the burned Scots pine forests in Catalonia. Additionally, our results showed that the proportion of vulnerable Scots pine forests could increase dramatically to 66% under a conservative climate change scenario assuming no reduction in rainfall. However, other components linked to human pressures on land resources and fire suppression policies also affect current fire regimes

through fuel accumulation and connectivity (Debussche *et al.*, 1999; Badia *et al.*, 2002; Pausas & Fernández-Muñoz, 2011) and should be considered in fire risk predictions (Flannigan *et al.*, 2006; Loepfe *et al.*, 2011).

Our field data showed an almost nil regeneration of Scots pine after crown fire, highlighting the sensitiveness to fire of this species. As Scots pine lacks serotinous cones (Tapias *et al.*, 2004), only seeds present in the current year's cones or in the soil could be potential sources for regeneration after crown fire. In water-limited regions, such as Spain, there is an uncoupling between the species' phenology and crown fires, because seed dispersal occurs from late winter to spring (Castro *et al.*, 1999), just before the summer wildfire season. Thus, during crown fires the canopy seed bank is empty. Additionally, seedlings and the seeds remaining in the soil are normally killed by the fire and cannot contribute to the regeneration of the species (Habrouk *et al.*, 1999).

In the current scenario of increased occurrence and size of crown wildfires in the Mediterranean Basin (Pausas & Fernandez-Muñoz, 2011), in which most of the trees within the burned area die (Rodrigo *et al.*, 2004; Ordóñez *et al.*, 2005), unburned edges are frequently the main (or only) source of propagules (Turner *et al.*, 1998). However, the establishment patterns from the unburned edges observed in this study show a very limited dispersal capacity of Scots pine. The majority of new recruits were located at distances < 25 m from the unburned edges, even for fires that occurred 25 years ago or more, which agrees with the studies carried out for other pine species (Nathan *et al.*, 2000; Rodrigo *et al.*, 2007). The elapsed time until a new recruit of Scots pine achieves reproductive maturity, estimated here at around 15 years, limits the dispersal capacity of the species after fire and the recolonization rate from the unburned edges. The previous estimate should be considered as an average across our study sites, as cone production is affected by local conditions (e.g. stand structure, site quality, biotic interactions) (Shmida *et al.*, 2000).

Here, we have expanded the spatial scale of previous studies (Retana *et al.*, 2002; Rodrigo *et al.*, 2004) to confirm the lack of post-fire regeneration of Scots pine after crown fire in a wide range of climates and water availability conditions. Taken together with our assessment of the current and future climatic vulnerability to fire of Scots pine forests in Spain, this result suggests that vegetation shifts are likely to occur. According

to our matrix model, oak forests and shrublands are the vegetation types most likely to replace burned Scots pine forests, a trend that has been already observed in some areas (Espelta *et al.*, 2002). These potential vegetation shifts are likely to be influenced by historical management and land use practices (Richardson *et al.*, 2007).

In conclusion, our study shows that the expected increase in the climatic vulnerability to crown fire of Scots pine forests can put the persistence of its southern populations at risk and lead to its potential replacement by other tree or shrub species. Such a change would have cascading effects on the recovery of the whole plant and animal communities after fire (Arnan *et al.*, 2006, 2007; Rodrigo & Retana, 2006; Rodrigo *et al.*, 2008). The previous considerations should be taken into account in forest planning in Mediterranean montane regions, in addition to other factors currently shaping the distribution of pine forests (Richardson *et al.*, 2007).

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LITERATURE CITED

- Arnan, X., Rodrigo, A. & Retana, J. (2006) Post-fire recovery of Mediterranean ground ant communities follows vegetation and dryness gradients. *Journal of Biogeography*, 33: 1246-1258.
- Arnan, X., Rodrigo, A. & Retana, J. (2007) Post-fire regeneration of Mediterranean plant communities at a regional scale is dependent on vegetation type and dryness. *Journal of Vegetation Science*, 18: 111-122.
- Badia, A., Saurí, D., Cerdan, R. & Llurdés, J.C. (2002) Causality and management of forest fires in Mediterranean environments: an example from Catalonia. *Global Environmental Change Part B: Environmental Hazards*, 4: 23-32.
- Barbero, M., Loisel, R., Quézel, P., Richardson, D.M. & Romane, P. (1998) Pines of the Mediterranean Basin. Ecology and biogeography of *Pinus* (ed. by D. M. Richardson), pp. 153-170. Cambridge University Press, Cambridge.

- Bates, B.C., Kundzewicz, Z.W., Wu, S., Palutikof, J.P. (2008) Climate change and water. Technical Paper VI of the Intergovernmental Panel on Climate Change. IPCC Secretariat, Geneva.
- Bond, W.J., Woodward, F.I. & Midgley, G.F. (2005) The global distribution of ecosystems in a world without fire. *New Phytologist*, 165: 525-538.
- Brunet, M., Casado, M.J., de Castro, M., Galán, P., López, J.A., Martín, J.M., Pastor, A., Petisco, E., Ramos, P., Ribalaygua, J., Rodríguez, E., Sanz, I. & Torres, L. (2009) Generación de escenarios regionalizados de cambio climático para España. Agencia Estatal de Meteorología, Madrid.
- Burriel, J.A., Gracia, C., Ibáñez, J.J., Mata, T. & Vayreda, J. (2000-2004) Inventari ecològic i forestal de Catalunya. Catalunya, 10 Volumes. CREAF, Bellaterra (Catalunya).
- Calvo, L., Santalla, S., Valbuena, L., Marcos, E., Tárrega, R. & Luis-Calabuig, E. (2008) Post-fire natural regeneration of a *Pinus pinaster* forest in NW Spain. *Plant Ecology*, 197: 81-90.
- Castro, J., Gómez, J.M., García, D., Zamora, R. & Hódar, J.A. (1999) Seed predation and dispersal in relict Scots pine forests in southern Spain. *Plant Ecology*, 145: 115-123.
- Czúcz, B., Gálhidy, L. & Mátyás, C. (2011) Present and forecasted xeric climatic limits of beech and sessile oak distribution at low altitudes in central Europe. *Annals of Forest Science*, 68: 99-108.
- DARP (1996) Mapa Forestal de Catalunya 1:100000. Departament d'Agricultura, Ramaderia i Pesca, Barcelona.
- Debussche, M., Lepart, J. & Dervieux, A. (1999) Mediterranean landscape changes: evidence from old postcards. *Global Ecology and Biogeography*, 8: 3-15.
- Díaz-Delgado, R., Lloret, F., Pons, X. & Terradas, J. (2002) Satellite evidence of decreasing resilience in Mediterranean plant communities after recurrent wildfires. *Ecology*, 83: 2293-2303.
- Espelta, J.M., Rodrigo, A., Habrouk, A., Mighelli, N., Ordóñez, J.L. & Retana, J. (2002) Land use changes, natural regeneration patterns, and restoration practices after a large wildfire in NE Spain: challenges for fire ecology and landscape restoration. Fire and biological processes (ed. by L. Traubaud and R. Prodon), pp. 315-324. Backhurs Publishers, Leiden.
- Eugenio, M., Verkaik, I., Lloret, F. & Espelta, J.M. (2006) Recruitment and growth decline in *Pinus halepensis* populations after recurrent wildfires in Catalonia (NE Iberian Peninsula). *Forest Ecology and Management*, 231: 47-54.
- Flannigan, M.D., Amiro, B.D., Logan, K.A., Stocks, B.J. & Wotton, B.M. (2006) Forest fires and climate change in the 21st century. *Mitigation and Adaptation Strategies for Global Change*, 11: 847-859.
- Habrouk, A., Retana, J. & Espelta, J.M. (1999) Role of heat tolerance and cone protection of seeds in the response of three pine species to wildfires. *Plant Ecology*, 145: 91-99.
- Hanes, T.L. (1971) Succession after fire in the chaparral of southern California. *Ecological Monographs*, 41: 27-52.
- Hargreaves, G.H. & Samani, Z.A. (1982) Estimating potential evapotranspiration. *Journal of Irrigation and Drainage Engineering*, 108: 225-230.
- Herranz, J.M., Martínez-Sánchez, J.J., Marín, A. & Ferrandis, P. (1997) Postfire regeneration of *Pinus halepensis* Miller in a semi-arid area in Albacete province (southeastern Spain). *Écoscience*, 4: 86-90.

- Lavorel, S., Canadell, J., Rambal, S. & Terradas, J. (1998)** Mediterranean terrestrial ecosystems: research priorities on global change effects. *Global Ecology and Biogeography*, 7: 157-166.
- Lloret, F. (1998)** Fire, canopy cover and seedling dynamics in Mediterranean shrubland of northeastern Spain. *Journal of Vegetation Science*, 9: 417-430.
- Lloret, F., Estevan, H., Vayreda, J. & Terradas, J. (2005)** Fire regenerative syndromes of forest woody species across fire and climatic gradients. *Oecologia*, 146: 461-468.
- Loepfe, L., Martínez-Vilalta, J., & Piñol J. (2011)** An integrative model of human influenced fire regimes and landscape dynamics. *Environmental Modelling & Software*, 26: 1028-1040.
- MAPA (1980)** Mapa de Cultivos y Aprovechamientos, 1:50000. Ministerio de Agricultura, Pesca y Alimentación (MAPA), Madrid.
- Nathan, R., Safriel, U.N., Noy-Meir, I. & Schiller, G. (2000)** Spatiotemporal variation in seed dispersal and recruitment near and far from *Pinus halepensis* trees. *Ecology*, 81: 2156-2169.
- Nathan, R. & Ne'eman, G. (2004)** Spatiotemporal dynamics of recruitment in Aleppo pine (*Pinus halepensis* Miller). *Plant Ecology*, 171: 123-137.
- Niklasson, M. & Granström, A. (2000)** Numbers and sizes of fires: long-term spatially explicit fire history in a Swedish boreal landscape. *Ecology*, 81: 1484-1499.
- Niklasson, M., Zin, E., Zielonka, T., Feijen, M., Korczyk, A.F., Churski, M., Samojilik, T., Jędrzejewska, B., Gutowski, J.M. & Brzeziecki, B. (2010)** A 350-year tree-ring fire record from Białowieża Primeval Forest, Poland: implications for Central European lowland fire history. *Journal of Ecology*, 98: 1319-1329.
- Ninyerola, M., Pons, X. & Roure, J.M. (2000)** A methodological approach of climatological modelling of air temperature and precipitation through GIS techniques. *International Journal of Climatology*, 20: 1823-1841.
- Ninyerola, M., Pons, X. & Roure, J.M. (2005)** Atlas Climático Digital de la Península Ibérica. Metodología y aplicaciones en bioclimatología y geobotánica. Universidad Autónoma de Barcelona, Bellaterra.
- Ordóñez, J.L., Retana, J. & Espelta, J.M. (2005)** Effects of tree size, crown damage, and tree location on post-fire survival and cone production of *Pinus nigra* trees. *Forest Ecology and Management*, 206: 109-117.
- Ordóñez, J.L., Molowny-Horas, R. & Retana, J. (2006)** A model of the recruitment of *Pinus nigra* from unburned edges after large wildfires. *Ecological Modelling*, 197: 405-417.
- Pausas, J.G. (2004)** Changes in fire and climate in the eastern Iberian Peninsula (Mediterranean basin). *Climatic Change*, 63: 337-350.
- Pausas, J.G., Bradstock, R.A., Keith, D.A. & Keeley, J.E. (2004)** Plant functional traits in relation to fire in crown-fire ecosystems. *Ecology*, 85: 1085-1100.
- Pausas, J.G., Llovet, J., Rodrigo, A. & Vallejo, R. (2008)** Are wildfires a disaster in the Mediterranean basin? – A review. *International Journal of Wildland Fire*, 17: 713-723.
- Pausas, J.G. & Keeley, J.E. (2009)** A burning story: the role of fire in the history of life. *BioScience*, 59: 593-601.

- Pausas, J.G. & Fernández-Muñoz, S. (2012)** Fire regime changes in the Western Mediterranean basin: from fuel-limited to drought-driven fire regime. *Climatic Change*, 110: 215-226.
- Piñol, J., Terradas, J. & Lloret, F. (1998)** Climate warming, wildfire hazard, and wildfire occurrence in coastal eastern Spain. *Climatic Change*, 38: 345-357.
- R Development Core Team (2009)** R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. URL www.r-project.org/.
- Retana, J., Espelta, J.M., Habrouk, A., Ordóñez, J.L. & Solà-Morales, F. (2002)** Regeneration patterns of three Mediterranean pines and forest changes after a large wildfire in northeastern Spain. *Écoscience*: 9, 89-97.
- Richardson, D. M., Rundel, P.W., Jackson, S.T., Teskey, R.O., Aronson, J., Bytnerowicz, A., Wingfield, M.J. & Procheş, Ş. (2007)** Human impacts in pine forests: past, present, and future. *Annual Review of Ecology, Evolution, and Systematics*, 38: 275-297.
- Rodrigo, A., Retana, J. & Picó, F.X. (2004)** Direct regeneration is not the only response of Mediterranean forests to large fires. *Ecology*, 85: 716-729.
- Rodrigo, A. & Retana, J. (2006)** Post-fire recovery of ant communities in Submediterranean *Pinus nigra* forests. *Ecography*, 29: 231-239.
- Rodrigo, A., Quintana, V. & Retana, J. (2007)** Fire reduces *Pinus pinea* distribution in the northeastern Iberian Peninsula. *Écoscience*, 14: 23-30.
- Rodrigo, A., Sardà-Palomera, F., Retana, J. & Bosch, J. (2008)** Changes of dominant ground beetles in black pine forests with fire severity and successional age. *Écoscience*, 15: 442-452.
- Salvador, R., Valeriano, J., Pons, X. & Díaz-Delgado, R. (2000)** A semi-automatic methodology to detect fire scars in shrubs and evergreen forests with Landsat MSS time series. *International Journal of Remote Sensing*, 21: 655-671.
- Shmida, A., Lev-Yadun, S., Goubitz, S. & Ne'eman, G. (2000)** Sexual allocation and gender segregation in *Pinus halepensis*, *P. brutia* and *P. pinea*. (ed. by G. Ne'eman and L. Trabaud), pp. 91-104. Ecology, biogeography and management of *Pinus halepensis* and *P. brutia* forest ecosystems in the Mediterranean Basin. Backhuys Publishers, Leiden.
- Tapias, R., Gil, L., Fuentes-Utrilla, P. & Pardos, J.A. (2001)** Canopy seed banks in Mediterranean pines of south-eastern Spain: a comparison between *Pinus halepensis* Mill., *P. pinaster* Ait., *P. nigra* Arn. and *P. pinea* L. *Journal of Ecology*, 89: 629-638.
- Tapias, R., Climent, J., Pardos, J. & Gil, L. (2004)** Life histories of Mediterranean pines. *Plant Ecology*, 171: 53-68.
- Trabaud, L. & Lepart, J. (1980)** Diversity and stability in garrigue ecosystems after fire. *Plant Ecology*, 43: 49-57.
- Turner, M.G., Baker, W.L., Peterson, C.J. & Peet, R.K. (1998)** Factors influencing succession: lessons from large, infrequent natural disturbances. *Écosystems*, 1: 511-523.
- Villaescusa, R. & Díaz, R. (1998)** Segundo Inventario Forestal Nacional (1986-1996). España. Ministerio de Medio Ambiente, Instituto para la Conservación de la Naturaleza (ICONA), Madrid.

III. STRUCTURAL AND CLIMATIC DETERMINANTS OF DEMOGRAPHIC RATES OF SCOTS PINE FORESTS ACROSS THE IBERIAN PENINSULA

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ABSTRACT

Aim The demographic rates of tree species typically show large spatial variation across their range. Understanding the environmental factors underlying this variation is a key topic in forest ecology, with far-reaching management implications. Scots pine (*Pinus sylvestris* L.) covers large areas of the Northern Hemisphere, being the Iberian Peninsula its south-western distribution limit. In recent decades, an increase of severe droughts and a densification of forests as a result of changes in forest uses have occurred in this region. Our aim was to use climate and stand structure data to explain mortality and growth patterns of Scots pine forests across the Iberian Peninsula.

Location Iberian Peninsula: the southern distribution limit of Scots pine.

Methods We used data from 2392 plots dominated by Scots pine, sampled for the National Forest Inventory of Spain. Plots were sampled from 1986 to 1996 (IFN2) and re-sampled from 1997 to 2007 (IFN3), allowing for the calculation of growth and mortality rates. We fitted linear models to assess the response of growth and mortality rates to the spatial variability of climate, climatic anomalies and forest structure.

Results Over the period of approximately 10 years between the IFN2 and IFN3, the amount of standing dead trees increased eleven-fold. Higher mortality rates were related to dryness and growth was lower with increasing dryness and temperature, but results also suggested that effects of climatic stressors were not restricted only to dry sites. Forest structure was strongly related to demographic rates, suggesting that stand development and competition are the main factors associated with demography. In the case of mortality, forest structure interacted with climate, suggesting that competition for water resources induces tree mortality in dry sites. A slight negative relationship was found between mortality and growth, indicating that both rates are likely to be affected by the same stress factors. Additionally, regeneration tended to be lower at plots with higher mortality.

Main conclusions Taken together, our results suggest a large-scale self-thinning related to the recent densification of Scots pine forests. This process appears to be enhanced by dry conditions and may lead to a mismatch in forest turnover. Forest management may

be an essential adaptive tool under the drier conditions predicted by most climate models.

Keywords

Dryness, forest structure, growth, land use changes, mortality, National Forest Inventory of Spain, *Pinus sylvestris*, regeneration.

INTRODUCTION

Understanding the underlying processes driving forest demography is a central goal for forest research. This is becoming increasingly important in the face of global change and the many disturbances to which forests are being subjected, and the need to forecast how forests will change in the future (Bonan, 2008; Purves & Pacala, 2008). Given the long lifespan of trees, one of the main complications of this type of research is the need of extensive monitoring of relatively large populations over long periods of time.

Without disturbances, forest demography (survival, growth, recruitment) is determined by climate and by biotic interactions (Harper, 1977; Ibáñez *et al.*, 2007). During forest development, structural attributes modulate forest demography via competition and natural thinning processes, which favour the most vigorous trees and allow the emergence of new recruits (Peet & Christensen, 1987). In the face of disturbance, and depending on the climate conditions and competitive relations, the same type of forest community may respond differently and display different thresholds of change in demography patterns (Tessier, 1989). These two components, climate and forest structure, operate simultaneously and interactively, highlighting the need of taking them both into account in studies of forest dynamics (Linares *et al.*, 2009; 2010).

The ecological thresholds (cf., Anderesen *et al.*, 2008) of forest communities deserve special attention, as abrupt environmental changes could lead forests to exceed their adaptation capacity (Linares *et al.*, 2010). Changing environmental conditions may lead to alterations in the structure and dynamics of forests, as well as induce changes in species distributions (Hansen *et al.*, 2001). This is reflected by the recent episodes of forest dieback observed across a broad range of forest types around the globe (Allen *et*

al., 2010), as well as by the recent changes in tree growth and forest productivity observed worldwide, suggesting long-term alterations of forest-atmosphere interactions (Bonan, 2008).

The forests in the western Mediterranean have been managed for millennia, and current communities differ widely from those that would exist in the absence of humans (Blondel & Aronson, 1995). Forest expansions after agricultural abandonment and modifications in forest management have been particularly intense during the last century (Margaris *et al.*, 1996; Grove & Rackham, 2001), resulting in denser stands with increased competition for resources and potentially exacerbating the vulnerability of forests to drought periods (Linares *et al.*, 2009). This is critical if we consider that many Mediterranean forests are currently water-limited (Peñuelas *et al.*, 2001; Sarris *et al.*, 2007) and that climate models predict that conditions will get drier in the future, with temperature increases of 3-4°C during the next century and large reductions of annual precipitation, reaching 50% during the summer (EEA, 2008). The impact of climatic stressors on these forests could thus be dramatic (Aber *et al.*, 2001; Bréda *et al.*, 2006; Hartmann, 2010), particularly if we consider that many Mediterranean woodlands are in the low-latitude edge of their distribution and are likely to be particularly vulnerable to increased aridity (Hampe & Petit, 2005). In this context, understanding the regional patterns of forest demography in relation to the structural attributes and climate could be a relevant management tool to inform adaptation and mitigation strategies.

Human activities have affected the distribution, composition, and structure of pine forests for millennia (Richardson *et al.*, 2007). Scots pine (*Pinus sylvestris* L.) is the dominant tree species in large areas of the Northern Hemisphere, with the largest populations located in boreal regions. However, Scots pine also occupies large areas in the Mediterranean basin, with the Iberian Peninsula being the southwestern limit to its distribution. Scots pine forest dieback has been related to extreme drought episodes in European forests (Bigler *et al.*, 2006), including several populations in the Iberian Peninsula (Martínez-Vilalta & Piñol, 2002; Hódar *et al.*, 2003). At the same time, competition-induced mortality has also been documented for Scots pine (Bravo-Oviedo *et al.*, 2006), probably as a result of changes in land use and forest management. Regarding growth, several studies have documented that the relationship between water

availability and demand during the summer is the main climatic factor limiting Scots pine (Martínez-Vilalta *et al.*, 2008). Negative relationships have also been found between competition and growth of Scots pine in Mediterranean mountain areas (García-Abril *et al.*, 2007).

In this study we explore the recent dynamics of mortality and growth throughout the distribution of Scots pine in the Iberian Peninsula, using the extensive data base of the National Forest Inventory of Spain. This is one of the first times the intraspecific variation of demographic rates has been studied at such a large scale, and the first time these rates are studied extensively at the dry edge of the distribution of an important forest species such as Scots pine. Specifically, our main objective was to evaluate the response of mortality and growth rates to spatial variability of climate, climatic anomalies and forest structure during the last decades of the twentieth century. We addressed three main hypotheses: (1) Mortality rates would be relatively high and concentrated in more arid sites suffering higher climatic anomalies; (2) Given the recent increase in severe droughts we expect that the spatial variability in mortality and growth rates would be more related to climatic differences across sites and climatic anomalies than to differences in forest structure; (3) Mortality and growth would be negatively related across sites, indicating that the qualitative response of these rates to the major stress factors is similar. To evaluate the potential implications of the observed mortality patterns on forest dynamics, we also analyzed the relationship between mortality and potential regeneration of Scots pine.

MATERIAL AND METHODS

Study system

The studied area encompasses the forested territories of Spain (493720 km²) located in the Iberian Peninsula (western Mediterranean basin, between 10° W and 3° E longitude, and between 43° N and 35° N latitude). This geographic location, together with the range of influences and the mountainous orography, produces a very heterogeneous climate. According to Capel Molina (2000), there are two major climatic domains: the temperate-oceanic, and the Mediterranean. The temperate-oceanic climate, with a dominant Atlantic influence, occurs in the north of the area, and has relatively wet and

cold weather, with mean annual temperatures ranging from 9 to 15°C, and annual precipitation ranging between 900 and 3000 mm. The rest of Spain falls within the Mediterranean domain, which is characterized by mild winters and hot and dry summers. Mean annual temperatures range from 15 to 19°C, and annual precipitation ranges from 200 to 900 mm. There is also a continental gradient from the coast inland with increasing thermal amplitudes. This climate variability and the geographic location of the Iberian Peninsula are the main factors explaining the existence of a rich and varied flora. Vegetation types across the climatic-topographic gradients include: Atlantic, sub-Atlantic and sub-Mediterranean deciduous forests; montane, sub-alpine, and Mediterranean coniferous forests; sclerophyllous and evergreen shrublands and forests (Blanco *et al.*, 1997).

Scots pine (*Pinus sylvestris* L.) occupies large areas in the Spanish mountain forested areas, with a large phytogeographic region including sub-Mediterranean, Eurosiberian, and Boreoalpine chorologies (Rivas-Martínez, 1983). The distribution extends from the north to the Iberian and Central mountain ranges, with the most extensive populations located in the Pyrenees. According to Martínez-García (1999) Scots pine forests in Spain are distributed in eight major regions (Fig. 1). There have been important land use changes in the Iberian Peninsula during the last century, including the abandonment of agropastoral activities in mountain areas, the abandonment of forest exploitation (García-Ruiz *et al.*, 1996), and a large-scale afforestation starting in the 1940s that intensified during the 1950s and has continued albeit at lower rates until recent decades (Martínez-García, 1999). As a result, stand density has increased in many forests and the range of Scots Pine has expanded noticeably (Martínez-García, 1999; Poyatos *et al.*, 2003).

The data set: the National Forest Inventory of Spain (IFN)

The IFN is an extensive database of periodical forest surveys distributed systematically across the forested area of Spain (Villaescusa & Díaz, 1998). The IFN is based on a network of fixed circular plots at a density of 1 plot km⁻², which allows forest characterization and includes exhaustive information on the composition of canopy and understory woody species, as well as on forest structure and production. Within the plots, all trees ≥ 7.5 cm in diameter at breast height (dbh) were labelled, measured for dbh and height, identified to species and censused for mortality. Sampling followed a

nested circular plot design. Thus, all trees with dbh > 7.5 cm were measured within 5 m of the centre of the plot, trees with dbh > 12.5 cm were also measured between 5 and 10 m around the centre of the plot, whereas trees with dbh > 22.5 cm and dbh > 42.5 cm were considered within 10-15 m and 15-25 m around the centre of the plots, respectively. Individuals with dbh between 2.5 and 7.5 cm were also counted (but not individually labelled) within the central 5 m plot. The first National Forest Inventory (IFN1) was conducted between 1965 and 1975, the second (IFN2) from 1986 to 1996, and the third (IFN3) from 1997 to 2007. The plots sampled during the IFN1 were different from those sampled during the IFN2 and IFN3, as the continuous character of the project started with the IFN2. We used data from the permanent plots surveyed in the IFN2 and revisited again in the IFN3.

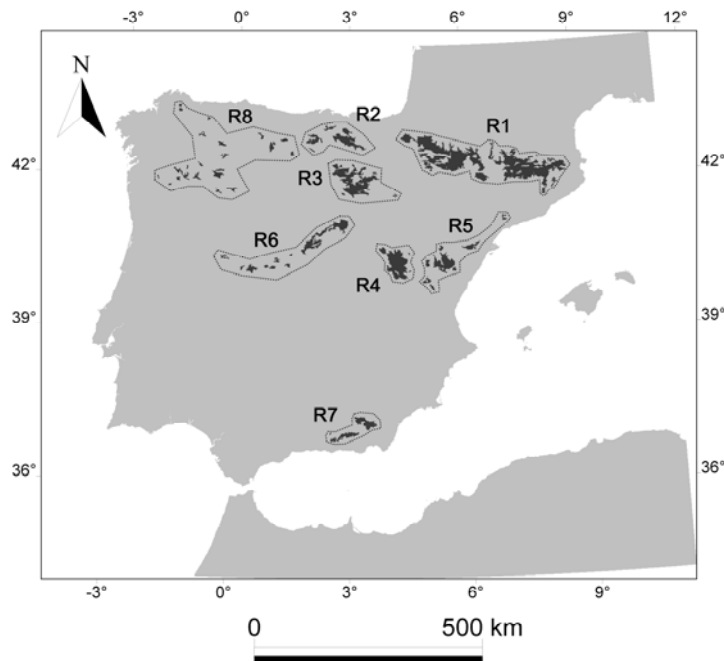


Figure 1. Map of the Iberian Peninsula showing the distribution of Scots pine, *Pinus sylvestris* (black), and regions of provenance: R1, Pyrenees; R2, eastern Cantabrian mountain range to western Basque mountains; R3, northern Iberian mountain range; R4, southern Iberian mountain range; R5, southeastern Iberian mountain range to Catalan coastal mountain range; R6, Central mountain range; R7, Betic mountain range; R8, Cantabrian mountain range.

For the present study we selected plots according to the following criteria:

- a) Scots pine basal area $\geq 50\%$ of the total plot basal area.
- b) At least 10 Scots pine individuals were tracked through the two repeated censuses (IFN2 and IFN3). This criterion was introduced to reduce variation in plot-level demographic rates.
- c) No evidence of forest management (cutting or thinning) nor recent disturbances (i.e., fires) was detected during the IFN3 survey. Forest management as detected in the IFN2 survey was used to study the influence of previous management in our results.

This filtering resulted in a total of 2392 plots with basal areas ranging from 5.6 to 80.8 $\text{m}^2 \text{ha}^{-1}$ and densities between 305 and 3400 trees ha^{-1} .

Demographic rates

Mortality (MR) at the plot level was calculated as $N_{\text{IFN2}} - N_{\text{IFN3}}$, where N_{IFN2} is the number of living Scots pines at the IFN2 and N_{IFN3} the number of those that survived to the IFN3 survey. MR was averaged taking into account the unequal sampling effort across tree sizes (i.e. weighting the contributions of each size class by plot size), and was standardized for a period of 10 years to take into account differences among plots in the time interval (9-12 years) between the two censuses. Although annual mortality data were not available, we calculated the average annual mortality rate during the period between the two inventories (10 years) following Sheil *et al.* (1995). We also computed standing mortality (i.e., the percentage of dead trees per plot) as detected at the IFN2 and IFN3 surveys. It should be noted that in this case the period during which this mortality occurred is unknown, unlike what happens for MR as described above.

Mean annual basal area increment of surviving trees per plot, relative to mean tree size (mean dbh per plot, again taking into account the unequal sampling effort across tree sizes), was used as a measure of growth rate (GR, in $\text{cm}^2 \text{cm}^{-1} \text{year}^{-1}$). GR was calculated using the following equation:

$$\text{GR} = ([\text{BA}_{\text{IFN3}} / N_{\text{IFN3}}] - [\text{BA}_{\text{IFN2}} / N_{\text{IFN3}}]) / (t * \text{dbh}_{\text{IFN2}})$$

where BA_{IFN2} and BA_{IFN3} are the plot basal areas at the second and third national inventories, respectively, N_{IFN3} is the number of living pines per plot at the third

national inventory, dbh_{IFN2} is the mean diameter at breast height at the IFN2 and t is the time interval between the two measurements (9-12 years). Basal area increment was normalized by the number of trees and by mean dbh to account for differences in forest development. This normalization was preferred over more conventional approaches using relative basal area increments because in our case dividing basal area increment by basal area over-corrected for size effects. Unequal sampling effort across tree sizes was also accounted for in the calculation of GR.

Finally, we used the number of Scots pine individuals with dbh between 2.5 and 7.5 cm detected at each plot during the IFN3 as an indicator of potential regeneration. It should be noted, however, that this count is not a measure of recruitment rate, as the age distribution of the counted saplings is unknown.

Climatic and forest structural data

Two climatic data sets were used, the first one to characterize the spatial variability of climate across the Iberian Peninsula, and the second to describe the climatic anomalies occurred during the time interval between the two surveys. Climatic variables associated with each individual plot were obtained from the Digital Climatic Atlas of the Iberian Peninsula (Ninyerola *et al.*, 2005), with a spatial resolution of 180 m. Two variables were used to characterize the climate at each plot (period 1950–1999): mean annual temperature (in °C) and summer P/PET, defined as the average ratio of precipitation to potential evapotranspiration (the latter calculated following the Hargreaves-Samani method; Hargreaves & Samani, 1982) from June to August. Low values of summer P/PET correspond to dry sites, and high values to wet sites. The studied plots covered a wide climatic gradient, with mean annual temperatures ranging from 5 to 13.7°C and mean summer P/PET from 0.04 to 1.12.

Climatic anomalies, defined as the difference between the value of a climate variable in a given period with respect to the mean value for a reference period, divided by the standard deviation, were obtained from the gridded 0.5x0.5° dataset produced by Willmott & Matsuura (<http://climate.geog.udel.edu>). Values of the positive (i.e., above average) and negative (below average) temperature and precipitation anomalies were computed for the period March-August of each year. We used cumulative anomalies of temperature and precipitation, calculated as the sum of the yearly anomalies with the

same sign (either < 0 or ≥ 0) for the time interval between surveys for each study plot, resulting in four variables: negative anomaly of precipitation (NAP), positive anomaly of precipitation (PAP), negative anomaly of temperature (NAT), and positive anomaly of temperature (PAT). As periods between surveys varied between 9 and 12 years, all values were standardized to a period of 10 years. The absolute value of the anomalies was used in all analyses to facilitate the interpretation of the results.

To characterize the forest structure of each plot, we used total stand density (Density, in trees ha^{-1}) and mean Scots pine dbh (in cm) as measures of stand structure and competition intensity, both extracted from the IFN2 dataset and corrected for the unequal distribution of sampling effort across size classes (cf. above).

Statistical analyses

Statistical models to analyze MR and GR were constructed separately using the same predictor variables in both cases. We modelled demographic rates as a function of the following fixed factors: Density, dbh, mean annual temperature, summer P/PET, PAT, NAP, PAP, NAT and prior management (Management, dichotomic variable). The following interactions were also considered: Density x summer P/PET, dbh x summer P/PET, Density x NAP and dbh x NAP, as high competition may intensify the effect of water scarcity; and summer P/PET x NAP and summer P/PET x PAT to evaluate if there was a differential effect of anomalies along the climatic gradient. Region was introduced in the models as a random factor to account for spatial autocorrelation. Starting from the saturated model, we created the fully crossed set of models and ranked them from lowest to highest BIC (Bayesian Information Criterion). Models within 4 BIC units of the best model were considered equivalent in terms of fit and are all reported. Logarithmic transformations of GR, Density, and dbh were used to satisfy the normality assumption. The correlation among explanatory variables was always ≤ 0.4 , suggesting that collinearity was not a problem in our models. Significance was accepted at $\alpha = 0.01$ given the large sample size. Statistical analyses were carried out with the R software (packages nlme and lme4, R 2.10.0, The R Foundation for Statistical Computing). Throughout the manuscript all values are given as mean $\pm$ standard error.

We used generalized linear mixed models (GLMM) to analyze the dependence of Scots pine mortality on climate and forest structure. Counts of demographic events (death)

were modelled as a Poisson distribution with a log link function by using the Laplace approximation to estimate parameters. Since the variance of the counts was significantly greater than the mean, indicating overdispersion, we refitted the data with a quasi-Poisson model with Laplace approximation. An offset of $\ln[\text{Scots pine population size}]$ in the first census (IFN2) was included in the model to account for the different population size across plots. A mixed linear model was used to study the relationship between $\ln(\text{GR})$ and the explanatory variables. Parameters were estimated by maximum likelihood.

To evaluate the relationship between growth or regeneration and mortality (the latter expressed as the percentage of individuals dying between the two censuses: MR%), as well as to check the effect of region and management on the previous relationships, we fitted linear models with GR (general linear model) or regeneration (negative binomial GLM) as dependent variables, Region and Management as factors, and MR% and the interactions Region x MR% and Management x MR% as covariates.

RESULTS

Mortality

The weighted percentage of dead Scots pines (standing mortality) increased from 0.39% in the IFN2 to 4.39% in the IFN3, and the number of plots with mortality also increased, from 89 (3.7% of the IFN2 plots) to 858 (35.8% of the IFN3 plots). The same pattern was observed at the plot level: mean mortality percentage per plot was $0.35 \pm 0.05\%$ in the IFN2, increasing to $3.99 \pm 0.17\%$ in the IFN3, implying that the amount of dead trees increased eleven-fold between the two surveys (Fig. 2). Prior management (before the IFN2) affected 27.3% of our plots but apparently did not bias our results, as the percentage of dead Scots pines increased dramatically between the two inventories both in unmanaged (from 0.45% to 4.57%) and in managed plots (0.18% to 3.86%).

Considering only the mortality occurred between the two censuses, mean annual mortality rate was $0.45 \pm 0.02\%$ per year for all plots, $0.48 \pm 0.02\%$ per year in unmanaged plots and $0.38 \pm 0.03\%$ per year in managed plots. Mortality rates showed a right-skewed distribution (Fig. 3), with most plots showing no mortality and a 14.5% of

plots with mortality rates $> 1\%$ per year. Mortality rate was highest in small trees (7.5-12.5 cm size class), but values remained relatively high also in larger size classes (Appendix 1).

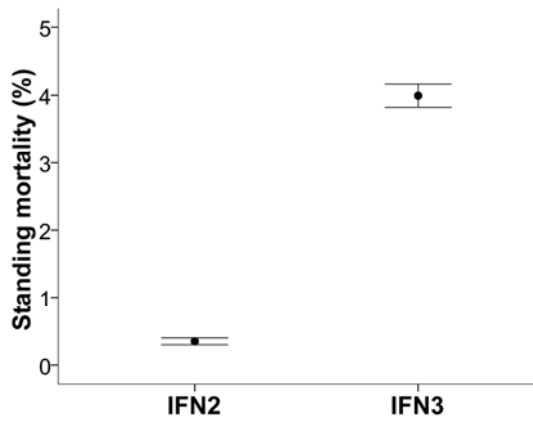


Figure 2. Standing mortality calculated as the percentage of dead trees per plot (mean $\pm$ SE) of Scots pine detected during the surveys. IFN2 represents plots sampled from 1986 to 1996; IFN3 represents plots resampled from 1997 to 2007.

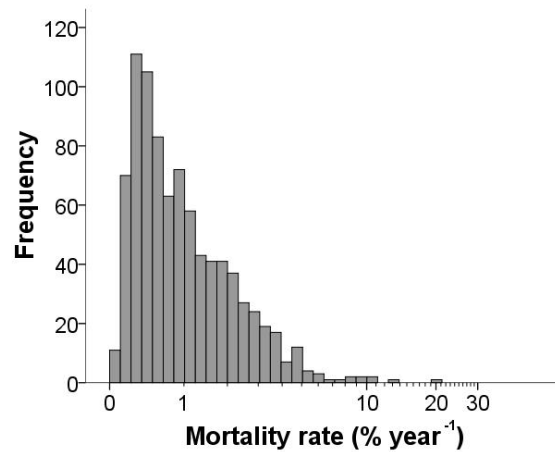


Figure 3. Distribution of annual mortality rate of Scots pine on a logarithmic scale. Only plots with mortality > 0 are shown ($N = 858$ plots out of a total of 2392 plots).

Regarding the distribution of mortality occurred in the period between surveys (MR), there were 10 models within 4 BIC units that always incorporated the effect of Density, dbh, summer P/PET, NAP and the interactions dbh $\times$ summer P/PET and dbh $\times$ NAP (Appendix 2; Table 1 for the model with lowest BIC). Denser stands showed higher levels of mortality (Appendix 2; Table 1). The interaction between dbh and summer P/PET revealed that the effect of increasing dbh on MR was stronger at dry sites (Fig. 4a). Similarly, the effect of NAP (periods of low precipitation) on MR was more intense in stands with high dbh values (Fig. 4b). Regarding this last interaction, it should be noted that MR tended to increase at low NAP when dbh was large. All the other explanatory factors were either not retained in the best model set or had inconsistent effects across models. .

Table 1 Summary of the mortality (MR) model for Scots pine (*Pinus sylvestris*) with lowest BIC (Bayesian information criterion). Key to abbreviations: dbh, mean Scots pine diameter at breast height; NAP, negative anomaly of precipitation; PAT, positive anomaly of temperature; summer P/PET, average ratio of precipitation to potential evapotranspiration from June to August.

Effects	Estimate	SE	T-value
Intercept	– 22.6918	2.1464	– 10.572
dbh	4.3017	0.7116	4.301
Density	0.8739	0.0605	14.452
Summer P/PET	6.8993	1.7747	3.887
NAP	0.5952	0.1956	3.042
PAT	0.0551	0.0179	3.078
dbh x Summer P/PET	– 2.2172	0.6196	– 3.579
dbh x NAP	– 0.2066	0.0679	– 3.040

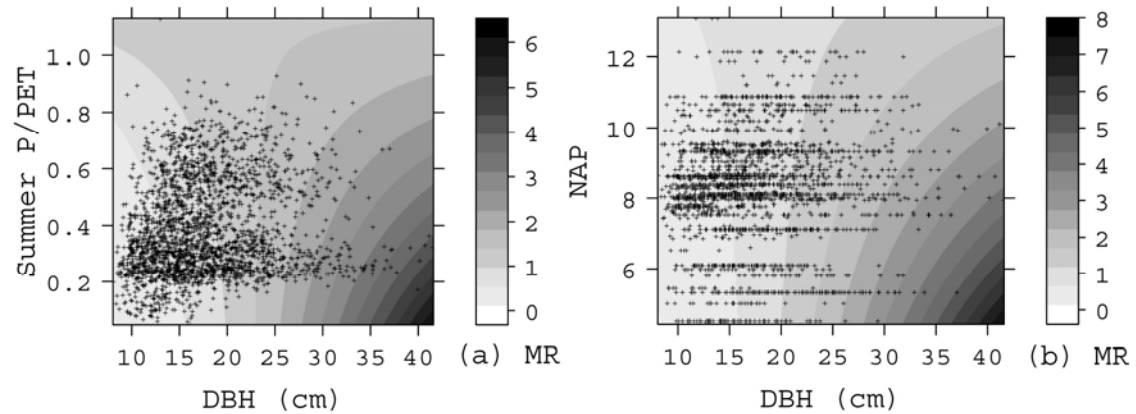


Figure 4. Surface plot showing the predicted effects on Scots pine mortality (MR) of the interactions (a) dbh x summer P/PET (the average ratio of precipitation to potential evapotranspiration from June to August) and (b) dbh x NAP (the negative anomaly of precipitation). Crosses represent each observation. Summer P/PET and NAP are dimensionless variables.

Growth

Annual growth rate covered a range between 0.08 and 2.52 $\text{cm}^2 \cdot \text{cm}^{-1} \cdot \text{year}^{-1}$, with an average of $0.57 \pm 0.01 \text{ cm}^2 \cdot \text{cm}^{-1} \cdot \text{year}^{-1}$ (Fig. 5). If the plots are split depending on whether they were recorded as managed during the IFN2, mean annual growth rate in unmanaged plots was $0.59 \pm 0.01 \text{ cm}^2 \cdot \text{cm}^{-1} \cdot \text{year}^{-1}$, while in managed plots it was $0.50 \pm 0.01 \text{ cm}^2 \cdot \text{cm}^{-1} \cdot \text{year}^{-1}$. Growth of individual trees in terms of basal area increment tended to increase with tree size (Appendix 3).

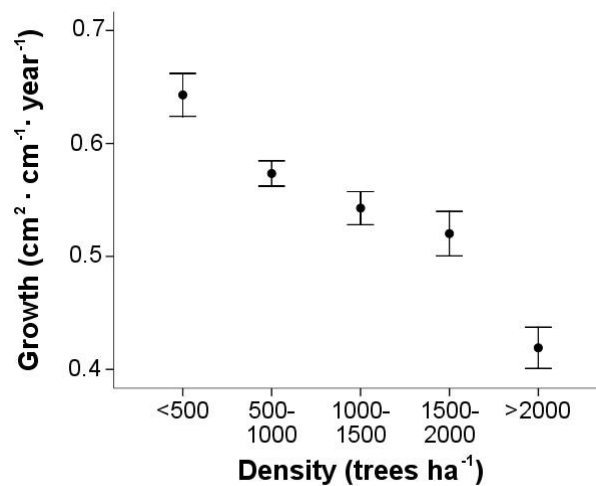


Figure 5 Annual growth rate (GR) of Scots pine (mean $\pm$ SE) per range of tree densities.

Overall, the best model for GR included the effect of Density, dbh, annual temperature, summer P/PET, NAP and the interaction summer P/PET $\times$ NAP (Table 2). There were no other models within 4 BIC units. Forest structure had a strong effect on Scots pine growth. GR was significantly lower with increasing density and dbh (Table 2). Regarding the climatic variables, annual temperature had a significant negative effect on GR, indicating that GR was lower with increasing temperature (Table 2). Finally, the interaction between summer P/PET and NAP indicated that pines at dry sites tended to grow less and that the negative effect of NAP on GR was more intense at wet sites (Fig. 6).

Table 2. Summary of the Scots pine growth rate (GR) model with lowest BIC. Growth was log-transformed. Key to abbreviations: dbh, mean Scots pine diameter at breast height; NAP, negative anomaly of precipitation; summer P/PET, average ratio of precipitation to potential evapotranspiration from June to August.

Effects	Estimate	SE	P-value
Intercept	4.2554	0.2801	< 0.001
dbh	− 1.0210	0.0331	< 0.001
Density	− 0.4052	0.0176	< 0.001
Summer P/PET	2.2606	0.3862	< 0.001
Temperature	− 0.0263	0.0074	< 0.001
NAP	0.0777	0.0221	< 0.001
Summer P/PET x NAP	− 0.1845	0.0473	< 0.001

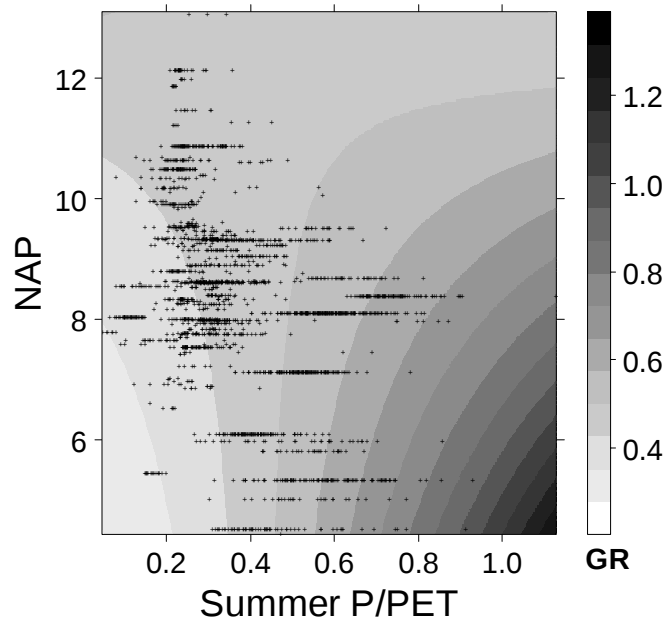


Figure 6. Surface plot showing the predicted effects on growth of the interaction Summer P/PET x NAP. Crosses represent each observation. GR, growth rate; NAP, negative anomaly of precipitation; Summer P/PET, average ratio of precipitation to potential evapotranspiration from June to August. Summer P/PET and NAP are variables dimensionless.

Relationships between demographic rates

MR% and GR were negatively associated ($\beta = -0.022$, $P < 0.001$) indicating a lower growth of Scots pine in plots with high mortality levels. GR varied among regions ($P < 0.001$), but the interaction MR% x Region was only marginally significant ($P = 0.011$), indicating that the slope of the relationship between MR% and GR did not vary substantially across regions. GR did not vary as a function of prior management ($P = 0.738$), and the interaction term was marginally significant with a positive effect ($\beta = 0.012$, $P = 0.028$), suggesting a less marked relationship between GR and MR% in managed plots.

Only 46.3% of the IFN3 plots showed any Scots pine regeneration. Moreover, mortality was negatively related to regeneration, indicating low regeneration where mortalities were high ($\beta = -0.046$, $P < 0.001$). Additionally, regeneration also varied among regions ($P < 0.001$), but the interaction term was not significant ($P = 0.329$), i.e. that the slope of the regeneration–MR% relationship did not differ across regions. Regeneration did not vary as a function of management ($P = 0.268$) and the interaction term was not significant ($P = 0.138$).

DISCUSSION

Tree mortality between the two forest inventories considered in this study was $0.45 \pm 0.02\%$ per year on average. Unfortunately, annual mortality data were not available in our study and the previous figure masks year to year differences, which can be large. As a comparison, annual tree mortality in French coniferous forests has been around 0.2% since 1989, with some pulses of 0.4-0.5% (years 1991, 2005 and 2006), and only one pulse with higher mortality (around 1.2%) in 2004 (Bréda & Badeau, 2008). In a recent study, van Mantgem *et al.* (2009) have reported a rapid increase in pine mortality across Western USA, from a low value of around 0.25% per year in the mid 1950s to extremely high current values of around 2% per year. Although the overall mortality rates reported here are not as high, it should be noted that our mortality values correspond to an average over 10 years and across a very large area, and that there was a large number of plots with mortality rates far above the average (Fig. 3). This is

consistent with some local observations of high mortality associated with drought episodes (Martínez-Vilalta & Piñol, 2002; Hódar *et al.*, 2003).

The amount of standing dead Scots pine trees increased dramatically (11-fold) over the 10 year period between IFN2 and IFN3. Although the difference between the two censuses is impressive, the interpretation of this result is limited by at least two facts. Firstly, as we only have data from two points in time it is impossible to draw strong conclusions about time trends. Secondly, the causes of this increase are likely to be multiple and complex. A large part of the difference between the two censuses could be due to changes in forest management and, in particular, in the way dead stems are dealt with, as they may have been more readily removed in the past, when forests were more intensively used. However, given the relatively low percentage of plots with management prior to the IFN2 (27%) and that the increase in standing mortality affected both managed and unmanaged stands in a similar manner, our results suggest that other factors besides management may have contributed to this recent increase in standing dead trees at such regional scale. Directional changes in climate and forest structure during the second half of the 20th century could have also contributed to the observed increase in standing dead trees. Regardless of the ultimate cause of the observed pattern, the observed increase in standing dead trees is large enough to have perceptible implications for the studied forests in terms of functioning and biotic interactions.

Mortality and growth in relation to forest structure and climate

In agreement with our first hypothesis, higher levels of Scots pine mortality were associated with climate dryness and climate anomalies characterized by low precipitation and high temperatures. The effect of recurrent and severe droughts on forest survival has been shown in other studies (Breshears *et al.*, 2005; van Mantgem *et al.*, 2009), including several studies on Scots pine forests (Martínez-Vilalta & Piñol, 2002; Bigler *et al.*, 2006). As expected, higher growth rates were associated with high water availability, both in space and time. Similar relationships have been observed for other species in Mediterranean regions (Sarris *et al.*, 2007) and for Scots pine populations at higher latitudes (Linderholm, 2001). Our results add to the evidence suggesting that the balance between water availability and demand during the summer (summer P/PET) is a key climatic factor controlling tree growth (as also observed by Bréda *et al.*, 2006; Martínez-Vilalta *et al.*, 2008). Finally, our MR and GR models

provided some evidence that the detrimental effects of climatic anomalies are not restricted to dry sites, suggesting that populations under relatively wet climates may be equally vulnerable to periods of drought stress.

However, forest structure explained a much larger % of the spatial variation in MR and GR than climate, contradicting our second hypothesis. These results were unexpected considering that we studied mostly populations at the dry limit of the distribution of a drought-sensitive species such as Scots pine. On the other hand, our findings are not surprising in the context of forest development theory, as many of the studied stands are relatively young and dense (see Appendix 4) and could be at the “stem-exclusion stage” (Oliver & Larson, 1990). Thus, endogenous processes, such as self-thinning, could be the main driving force behind demographic rates (Lutz & Halpern, 2006), particularly considering the shade-intolerant nature of Scots pine (Ceballos & Ruiz de la Torre, 1971). The current structure of many Scots pine forests in Spain, associated with relatively homogenous and dense stands, is to a large extent the result of plantation policies and the abandonment of traditional agricultural and forest uses during the 20th century (Martínez-García, 1999; OSE, 2007).

Our study indicates that climatic effects interact with forest structure, particularly in older forests, and thus complements previous work showing that competition for resources might have a negative effect on tree survival (Bravo-Oviedo *et al.*, 2006) or could exacerbate the effects of strong and punctual periods of water deficit on forest dynamics (Klos *et al.*, 2009; Linares *et al.*, 2009). Overall, these studies suggest that forest structure may act as an intrinsic continuous stressor on trees through increased competition for resources, and that this condition could intensify under more extreme climatic conditions. Clearly, forest structure should be given a prominent role in the study of forest dynamics under environmental change, as structural attributes modulate the adaptation and vulnerability of forests to climate-induced stress (Linares *et al.*, 2010).

Finally, our results also show that mortality and growth rates were affected by similar environmental factors, so that conditions that were associated with high mortality (dense forests with high basal area, dry climates, periods of low precipitation) were also associated with low growth rates. In agreement with this, growth and mortality rates

were negatively related at the plot level, in accordance with similar results obtained by previous studies relating low growth rates with increased mortality (Kobe, 1996; Bigler *et al.*, 2004; Das *et al.*, 2007).

Forest dynamics and management implications

Fewer than 50% of our study plots showed Scots pine regeneration. This result should be interpreted in the context of current stand development of the studied Scots pine forests (see previous section; Oliver & Larson, 1990). However, the fact that low regeneration was associated with high levels of tree mortality suggests that the interacting effects of structural and climatic stressors on Scots pine survival could be also acting negatively on its regeneration, indicating a potential mismatch in forest turnover, as already reported for other pine species (Gworek *et al.*, 2007).

Mitigation strategies such as thinning treatments and sustainable harvest activities to enhance structural diversity may release competition within denser stands (Bravo-Oviedo *et al.*, 2006), and could likely reduce vulnerability of forests to drought (Dale *et al.*, 2001). A release of competition for resources on the surviving trees can occur after mortality episodes (Martínez-Vilalta & Piñol, 2002), which could allow higher growth rates of surviving trees (Olano & Palmer, 2003). The key role of forest structure and structure-climate interactions observed in our study clearly shows the potential of forest management to modulate the demographic response of southern Scots pine forests to increased aridity.

Mediterranean forests have been in constant change for millennia, and especially during the last century, as a result of human impacts (Grove & Rackham, 2001). These changes are now accelerating in the context of global environmental change (Bonan, 2008). Our study indicates that forest management based on a sound understanding of how forests are responding to the different components of global change could be used to help forests accommodate to the expected new conditions (Millar *et al.*, 2007).

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LITERATURE CITED

- Aber, J., Neilson, R.P., McNulty, S., Lenham, J.M., Bachelet, D. & Drapek, R.J. (2001) Forest processes and global environmental change: the effects of individual and multiple stressors on forests. *BioScience*, 51: 735-751.
- Allen, C.D., Makalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.H., Allard, G., Running, S.W., Semerci, A. & Cobb, N. (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest ecology and Management*, 259: 660-684.
- Andersen, T., Carstensen, J., Hernández-García, E. & Duarte, C.M. (2008) Ecological thresholds and regime shifts: approaches to identification. *Trends in Ecology and Evolution*, 24: 49-57.
- Bigler, C., Gricar, J., Bugmann, H. & Cufar, K. (2004) Growth patterns as indicators of impending tree death in silver fir. *Forest Ecology and Management*, 199: 183-190.
- Bigler, C., Bräker, O.U., Bugmann, H., Dobbertin, M. & Rigling, A. (2006) Drought as an Inciting Mortality Factor in Scots Pine Stands of the Valais, Switzerland. *Ecosystems*, 9: 330-343.
- Blanco, E., Casado, M.A., Costa, M., Escribano, R., García, M., Génova, M., Gómez, F., Moreno, J.C., Morla, C., Regato, P. & Sáinz, H. (1997) Los bosques ibéricos: Una interpretación geobotánica. Planeta, Barcelona.
- Blondel, J. & Aronson, J. (1995) Biodiversity and ecosystem function in the Mediterranean basin: Human and nonhuman determinants (ed by G. W. Davis and D. M. Richardson). *Mediterranean-Type ecosystems: The function of biodiversity*, pp. 43-105, Springer-Verlag, Berlin.
- Bonan, G.B. (2008) Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science*, 320: 1444-1449.
- Bravo-Oviedo, A., Sterba, H., del Río, M. & Bravo, F. (2006) Competition-induced mortality for Mediterranean *Pinus pinaster* Ait. and *Pinus sylvestris* L. *Forest Ecology and Management*, 222: 88-98.

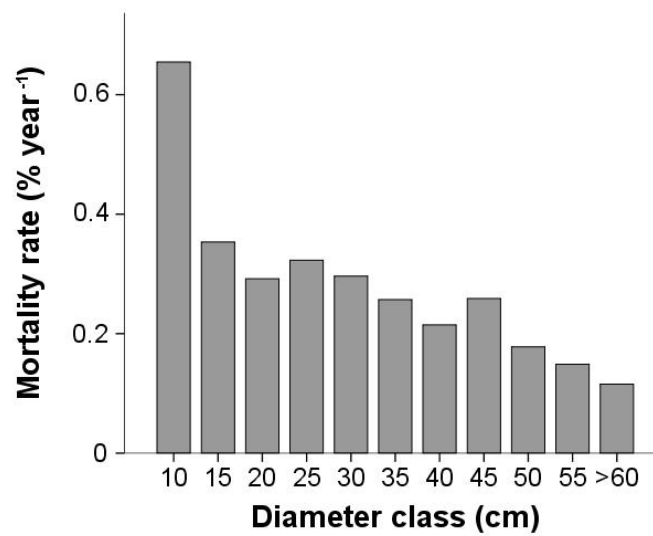
- Bréda, N., Huc, R., Granier, A. & Dreyer, E. (2006)** Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. *Annals of Forest Science*, 63: 625-644.
- Bréda, N. & Badeau, V. (2008)** Forest tree responses to extreme drought and some biotic events: towards a selection according to hazard tolerance? *C.R. Geoscience*, 340: 651-662.
- Bresheras, D.D., Cobb, N.S., Rich, P.M., Price, K.P., Allen, C.D., Balice, R.G., Romme, W.H., Kastens, J.H., Floyd, M.L., Belnap, J., Anderson, J.J., Myers, O.B. & Meyer, C.W. (2005)** Regional vegetation die-off in response to global-change-type drought. *Proceedings of the National Academy of Sciences of the United States of America, USA*, 102: 15144-15148.
- Capel Molina, J.J. (2000)** *El Clima de la Península Ibérica*. Ariel, Barcelona.
- Ceballos, L. & Ruiz de la Torre, J. (1971)** Árboles y arbustos de la España peninsular. Madrid: Instituto Forestal de Investigaciones y Experiencias.
- Dale, V.H., Joyce, L.A., McNulty, S., Neilson, R.P., Ayres, M.P., Flannigan, M.D., Hanson, P.J., Irland, L.C., Lugo, A.E., Peterson, C.J., & others (2001)** Climate change and forest disturbances. *BioScience*, 51: 723-34.
- Das, A., Battles, J.J., Stephenson, N.L. & van Mantgem, P.J. (2007)** The relationship between tree growth patterns and likelihood of mortality: a study of two tree species in the Sierra Nevada. *Canadian Journal of Forest Research*, 37: 580-597.
- EEA (2008)** Impacts of Europe's changing climate-2008 indicator-based assessment. European Environment Agency summary. Report No. 4 / 2008. European Environment, Agency, Copenhagen, Denmark.
- García-Abril, A., Martín-Fernández, S., Grande, M.A. & Manzanera, J.A. (2007)** Stand structure, competition and growth of Scots pine (*Pinus sylvestris* L.) in a Mediterranean mountainous environment. *Annals of Forest Science*, 64: 825-830.
- García-Ruiz, J.M., Lasanta, T., Ruiz-Flaño, P., Ortigosa, L., White, S., González, C & Martí C. (1996)** Land-use changes and sustainable development in mountain areas: A case study in the Spanish Pyrenees. *Landscape Ecology*, 11: 267-277.
- Grove, A.T. & Rackham, O. (2001)** The nature of Mediterranean Europe: an ecological history. Yale University Press, New Haven.
- Gworek, J.R., Vander Wall, S.B. & Brussard, P.F. (2007)** Changes in biotic interactions and climate determine recruitment of Jeffrey pine along an elevation gradient. *Forest Ecology and Management*, 239: 57-68.
- Hampe, A. & Petit, R.J. (2005)** Conserving biodiversity under climate change: the rear edge matters. *Ecology Letters*, 8: 461-467.
- Hansen, A.J., Neilson, R.P., Dale, V.H., Flather, C.H., Iverson, L.R., Currie, D.J., Shafer, S., Cook, R. & Bartlein, P.J. (2001)** Global change in forests: responses of species, communities, and biomes. *Bioscience*, 51: 765-779.
- Hargreaves, G.H. & Samani, Z.A. (1982)** Estimating potential evapotranspiration. *Journal of Irrigation and Drainage Engineering*, 108: 225-230.
- Harper, J.L. (1977)** Population Biology of Plants. Academic Press, London.

- Hartmann, H. (2011)** Will a 385 million year-struggle for light become a struggle for water and for carbon? - How trees may cope with more frequent climate change-type drought events. *Global Change Biology*, 17: 642-655.
- Hódar, J.A., Castro, J. & Zamora, R. (2003)** Pine processionary caterpillar *Thaumetopoea pityocampa* as a new threat for relict Mediterranean Scots pine forests under climatic warming. *Biological Conservation*, 110: 123-129.
- Ibáñez, I., Clark, J.S., LaDeau, S., & Hill Ris Lambers, J. (2007)** Exploiting temporal variability to understand tree recruitment response to climate change. *Ecological Monographs*, 77: 163-177.
- Klos, R.J., Wang, G.G., Bauerle, W.L. & Rieck, J.R. (2009)** Drought impact on forest growth and mortality in the southeast USA: an analysis using Forest Health and Monitoring data. *Ecological Applications*, 19: 699-708.
- Kobe, R.K. (1996)** Intraspecific variation in sapling mortality and growth predicts geographic variation in forest composition. *Ecological Monographs*, 66: 181-201.
- Linares, J.C., Camarero, J.J. & Carreira, J.A. (2009)** Interacting effects of changes in climate and forest cover on mortality and growth of the southernmost European fir forests. *Global Ecology and Biogeography*, 18: 485-497.
- Linares, J.C., Camarero, J.J. & Carreira, J.A. (2010)** Competition modulates the adaptation capacity of forests to climatic stress: insights from recent growth decline and death in relict stands of the Mediterranean fir *Abies pinsapo*. *Journal of Ecology*, 98: 592-603.
- Linderholm, H.W. (2001)** Climatic influence on Scots pine growth on dry and wet soils in the central Scandinavian mountains, interpreted from tree-ring widths. *Silva Fennica*, 35: 415-424.
- Lutz, J.A. & Halpern, C.B. (2006)** Tree mortality during early forest development: A long-term study of rates, causes, and consequences. *Ecological Monographs*, 76: 257-275.
- Margaris, N. S., Koutsidou, E., & Giourga, Ch. (1996)** Changes in traditional Mediterranean land-use systems (ed. by C. J. Brandt and J. B. Thornes), *Mediterranean Desertification and Land Use*, pp. 29-42, Chichester: Wiley.
- Martínez-García, F. (1999)** Los bosques de *Pinus sylvestris* L. del Sistema Central español. Distribución, historia, composición florística y tipología. PhD Thesis, Universidad Complutense de Madrid, Madrid, Spain.
- Martínez-Vilalta, J. & Piñol, J. (2002)** Drought-induced mortality and hydraulic architecture in pine populations of the NE Iberian Peninsula. *Forest Ecology and Management*, 161: 247-256.
- Martínez-Vilalta, J., López, B.C., Adell, N., Badiella, L. & Ninyerola, M. (2008)** Twentieth century increase of Scots pine radial growth in NE Spain shows strong climate interactions. *Global Change Biology*, 14: 2868-2881.
- Millar, C.I., Stephenson, M.L. & Stephens, S.L. (2007)** Climate change and forests of the future management in the face of uncertainty. *Ecological Applications*, 17: 2145-2151.
- Ninyerola, M., Pons, X. & Roure, J.M. (2005)** *Atlas Climático Digital de la Península Ibérica. Metodología y aplicaciones en bioclimatología y geobotánica*. ISBN 932860-8-7. Universitat Autònoma de Barcelona, Bellaterra, Spain.

- Olano, J.M. & Palmer, M.W. (2003)** Stand dynamics of an Appalachian old-growth forest during a severe drought episode. *Forest Ecology and Management*, 174: 139-148.
- Oliver, C.D. & Larson, B.C. (1990)** Forest Stand Dynamics. McGraw-Hill, New York, NY.
- OSE (Observatorio de la Sostenibilidad en España) (2007)** *Sostenibilidad en España 2007*. Universidad de Alcalá, Alcalá de Henares (Madrid), Spain.
- Peñuelas, J., Lloret, F. & Montoya, R. (2001)** Severe drought effects on Mediterranean woody flora in Spain. *Forest Science*, 47: 214-218.
- Peet, R.K. & Christensen, N.L. (1987)** Competition and tree death. *Bioscience*, 37: 586-595.
- Poyatos, R., Latron, J. & Llorens, P. (2003)** Land Use and Land Cover Change After Agricultural Abandonment. The Case of a Mediterranean Mountain Area (Catalan Pre-Pyrenees). *Mountain Research and Development*, 23: 362-368.
- Purves, D. & Pacala, S. (2008)** Predictive Models of Forest Dynamics. *Science*, 320: 1452-1453.
- Richardson, D.M., Rundel, P.W., Jackson, S.T., Teskey, R.O., Aronson, J., Bytnerowicz, A., Wingfield, M.J. & Proches, S. (2007)** Human impacts in pine forests: Past, present, and future. *Annual review of ecology evolution and systematics*, 38: 275-297.
- Rivas-Martínez, S. (1983)**. Pisos bioclimáticos de España. *Lazaroa*, 5: 33-43.
- Sarris, D., Christodoulakis, D. & Körner, Ch. (2007)** Recent decline in precipitation and tree growth in the eastern Mediterranean. *Global Change Biology*, 13: 1187-1200.
- Sheil, D., Burslem, D.F.R.P. & Alder, D. (1995)** The interpretation and misinterpretation of mortality rate measures. *Journal of Ecology*, 83: 331-333.
- Tessier, L. (1989)** Spatio-temporal analysis of climate-tree ring relationships. *New Phytologist*, 111: 517-529.
- van Mantgem, P.J., Stephenson, N.L., Byrne, J.C., Daniels, L.D., Franklin, J.F., Fulé, P.Z., Harmon, M.E., Larson, A.J., Smith, J.M., Taylor, A.H. & Veblen, T.T. (2009)** Widespread increase of tree mortality rates in the western United States. *Science*, 323: 521-524.
- Villaescusa, R. & Díaz, R. (eds.) (1998)** *Segundo Inventario Forestal Nacional (1986-1996)*. España. Ed. Ministerio de Medio Ambiente, ICONA, Madrid.

APPENDIXES

Appendix 1. Annual mortality rate of Scots pine per diameter class; x-axis numbers are the central value of the class, and classes are each 5 cm wide.

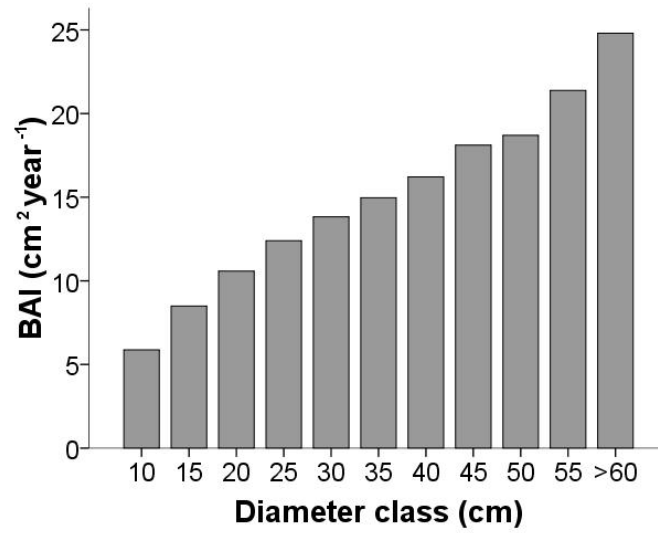


Appendix 2. Summary of the mortality (MR) models.

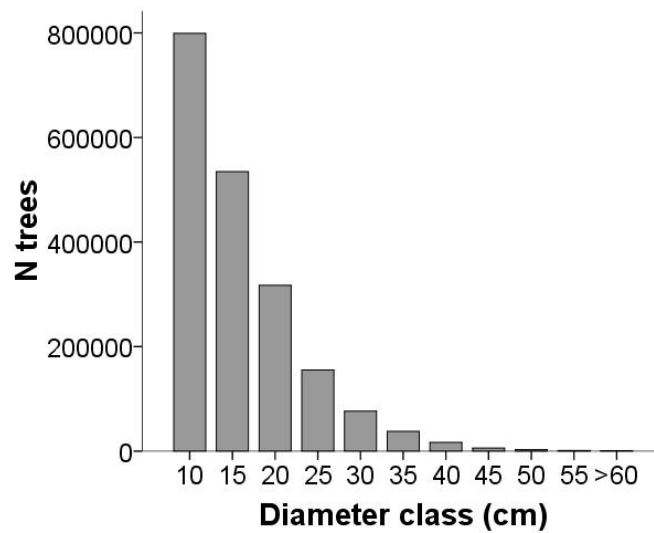
Models	Model 1	Model 2	Model 2	Model 4	Model 5	Model 6	Model 7	Model 8	Model 9	Model 10
BIC	5560	5561	5562	5562	5562	5563	5564	5564	5564	5564
Intercept	–	–	–	–	–	–	–	–	–	–
dbh	+	+	+	+	+	+	+	+	+	+
Density	+	+	+	+	+	+	+	+	+	+
Summer P/PET	+	+	+	+	+	+	+	+	+	+
NAP	+	+	+	+	+	+	+	+	+	+
PAT	+	n.i.	–	+	n.i.	+	–	n.i.	+	n.i.
NAT	n.i.	–	n.i.	n.i.	–	n.i.	n.i.	–	–	–
dbh x Summer P/PET	–	–	–	–	–	–	–	–	–	–
dbh x NAP	–	–	–	–	–	–	–	–	–	–
PAT x Summer PPET	n.i.	n.i.	+	n.i.	n.i.	n.i.	+	n.i.	n.i.	n.i.
NAP x Summer PPET	n.i.	n.i.	n.i.	n.i.	+	+	n.i.	n.i.	n.i.	+
Management	n.i.	n.i.	n.i.	–	n.i.	n.i.	–	–	n.i.	–

+, positive effect of the predictor on MR; –, negative effect of the predictor on MR; n.i., not included in the model. DBH, mean Scots pine diameter at breast height; NAP, negative anomaly of precipitation; PAT, positive anomaly of temperature; NAT, negative anomaly of temperature; Summer P/PET, average ratio of precipitation to potential evapotranspiration from June to August.

Appendix 3. Annual basal area increment of Scots pine per diameter class; x-axis numbers are the central value of the class, and classes are each 5 cm wide.



Appendix 4. Whole distribution of diameter classes in the IFN2. X-axis numbers are the central value of the class; classes are each 5 cm wide.



IV. PATTERNS OF FOREST DECLINE AND REGENERATION ACROSS SCOTS PINE POPULATIONS

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ABSTRACT

Aim To predict future changes in forest ecosystems it is crucial to understand the complex processes involved in decline of tree species populations and evaluate the implications for potential vegetation shifts. Here, we study patterns of decline (canopy defoliation and mortality of adults) of four Scots pine populations at the southern edge of its distribution and characterized by different combinations of climate dryness and intensity of past management.

Location Catalonia: the southern edge of Scots pine distribution.

Methods General linear and structural equation modeling were used to assess how biotic, abiotic and management components interacted to explain the spatial variability of Scots pine decline across and within populations. Regeneration patterns of Scots pine and co-occurring oak species were analyzed to assess potential vegetation shifts.

Results Decline trends were related to climatic dryness at the regional scale, but, ultimately, within-population forest structure, local site conditions and past human legacies could be the main underlying drivers of Scots pine decline. Overall, Scots pine regeneration was negatively related to decline both within and between populations, while oak species responded to decline idiosyncratically across populations.

Main conclusions Taken together, our results suggest that (1) patterns of decline are the result of processes acting at the plot level that modulate forest responses to local environmental stress and (2) decline of adult Scots pine trees seems not to be compensated by self-recruitment so that the future dynamics of these forest ecosystems are uncertain.

Keywords: climatic dryness; decline; defoliation; forest structure; management; mortality; *Pinus sylvestris*; site conditions; vegetation shifts.

Introduction

Forests around the world are changing at accelerated rates (cf. Sugden *et al.*, 2008). Two of the components of global change, climate change and land use changes, are believed to be the main drivers modifying forested ecosystems (Houghton, 1994; Dale *et al.*, 2001). Climate-related forest decline, characterized by crown defoliation and pulses of elevated tree mortality (Bréda *et al.*, 2006), has been observed in many parts of the world during the last decades (Allen *et al.*, 2010). Direct human activities also have large impacts on forests. In tropical countries deforestation is the main cause of forest loss (Laurance, 1999; Malhi *et al.*, 2008), while in Northern latitudes, and particularly in European countries, forests have increased in area and tree density as a result of widespread agricultural decline and abandonment of traditional forest uses (MacDonald *et al.*, 2000; Pan *et al.*, 2011).

One of the major potential implications of climate change on forests are changes in species distributions and the corresponding vegetation shifts (González *et al.*, 2010). Due to the long lifespan of trees, adult mortality plays a critical role in forest ecosystem processes and population dynamics (Franklin *et al.*, 1987). Under closed canopies, the death of an adult tree creates a new microenvironment where a gap-phase replacement may be initiated as the space created is occupied by new recruits (Lertzman, 1992). However, recruitment is highly dependent on climate (Ibáñez *et al.*, 2007) and historical or current management and land use practices (Chauchard *et al.*, 2007; Plieninger *et al.*, 2010). Thus, severe events of decline of a particular species sometimes can not be compensated because the new conditions may constrain its regeneration and favor other species, leading to changes in species composition.

Water availability is a key factor limiting forests in the Mediterranean basin, where droughts are a common disturbance and are predicted to become more frequent and severe during the next century (IPCC, 2007). This region represents the southern distribution limit of many important tree species in the northern hemisphere, and these southern populations are likely to be particularly vulnerable to increased aridity (Hampe & Petit 2005). In recent decades, a generalized increase in defoliation of forests has been associated to dry periods (Carnicer *et al.*, 2011) and episodes of drought-induced tree mortality and reduced recruitment have been documented (Castro *et al.*, 2004;

Lloret *et al.*, 2004; Bréda *et al.*, 2006). Environmental gradients related to microsite components such as soil and topography are expected to act as local modifiers of water availability, in some cases increasing stress for trees (e.g., Galiano *et al.*, 2010). Moreover, land-use changes during the last century, in particular crop abandonment and reduction of forest management, have shaped the current structure of Mediterranean forests (Grove & Rackham 2001), which have become denser and prone to self-thinning processes (cf. Peet & Christensen 1987). This change in the structural attributes of forests is likely to exacerbate the role of competition in modulating the effects of climatic stress on forests (Linares *et al.*, 2010; Vilà-Cabrera *et al.*, 2011).

If we are to predict future changes in forest ecosystems or try to mitigate them through management, it is critical (1) to characterize the role of climate, microsite conditions, management and their interaction on current episodes of forest decline, and (2) to assess how the effects of these factors at the local level change across large-scale gradients of climate and forest management. Here we aim at doing so by using Scots pine (*Pinus sylvestris* L.), a widely distributed temperate tree, as a model species. In recent years, drought-induced Scots pine decline has been recorded in several Mediterranean areas (Martínez-Vilalta & Piñol 2002; Hódar *et al.*, 2003), in some cases associated with enhanced recruitment of co-occurring oak species (Galiano *et al.*, 2010). At the same time, the variability of growth and mortality rates at the regional scale has been shown to be mostly dependent on plot-level structural attributes and, to a lesser extent, on their interaction with climate (Vilà-Cabrera *et al.*, 2011).

In order to understand the complex processes involved in Scots pine decline and evaluate the implications for potential vegetation shifts, four different Scots pine populations were selected throughout the southern range of its distribution. Each population was characterized by a combination of climate dryness and intensity of past management. We addressed the following questions: (1) How do biotic (tree competition), abiotic (climate, topography, soil) and management components interact to explain the spatial variability of Scots pine decline across and within populations? (2) Is the decline of adult Scots pine trees compensated by self-recruitment or current regeneration is dominated by other woody species that could potentially replace Scots pine?

MATERIAL AND METHODS

Study area

The study was carried out in Catalonia (NE Spain, Appendix 1), where Scots pine occupies large areas in the Pyrenees and some marginal locations in the center and south of the region (Appendix 1). Scots pine is the second most abundant tree species in Catalonia, covering 219,754 ha (18.4% of the total forested area, Burriel *et al.*, 2004) and encompassing a wide climatic gradient. The species is present from 200 to 2100 m a.s.l., but it is mainly distributed between 800 and 1600 m a.s.l. Annual precipitation in its distribution area ranges from 520 to 1330 mm and average annual temperature between 3.6 and 14.3 °C. As a result of abandonment of agropastoral activities and forest exploitation in mountain areas during the last century, stand density has increased in many forests and the range of Scots pine has expanded noticeably (Martínez-García, 1999; Poyatos *et al.*, 2003).

We selected four different Scots pine populations throughout the species distribution in Catalonia, which allowed us to compare sites under contrasted climates and with different management histories (Tables 1 and 2). Ports and Prades were located in the south and center of Catalonia, respectively, and Arcalís and Falgars were located in the Pyrenees (Appendix 1). Drought-induced forest decline has been related to severe summer droughts in Prades during 1994 and 1998 (Martínez-Vilalta & Piñol 2002) and in Arcalís during 2005 (Galiano *et al.*, 2010), while in the other two populations, Falgars and Ports, forest decline had not been documented. Forest management differed across sites. While Arcalís and Prades populations have remained largely unmanaged at least since the 1980s, Falgars and Ports have experienced recent (albeit moderate) logging practices (Tables 1 and 2).

Table 1. Combination of climate and intensity of management for the four studied populations.

Climate	Intensity of management	
	Low	High
Dry	Prades	Ports
Wet	Arcalís	Falgars

Table 2. Main characteristics of the studied Scots pine stands. Mean $\pm$ SE values are shown, N=30 in each site.

Stand characteristics	Prades	Ports	Arcalís	Falgars
Altitude (m)	846 – 1050	1047 – 1311	645 – 1383	1048 – 1347
Annual precipitation (mm)	698 $\pm$ 3	927 $\pm$ 4	932 $\pm$ 14	1008 $\pm$ 5
Annual temperature (°C)	11.6 $\pm$ 0.05	10.8 $\pm$ 0.05	9.5 $\pm$ 0.23	9.1 $\pm$ 0.09
Summer P/PET	0.32 $\pm$ 0.01	0.51 $\pm$ 0.01	0.61 $\pm$ 0.02	0.76 $\pm$ 0.01
Soil depth (cm)	55.6 $\pm$ 1.7	41.0 $\pm$ 1.2	42.4 $\pm$ 2.2	37.3 $\pm$ 1.2
Top Index	8.9 $\pm$ 0.2	8.4 $\pm$ 0.2	9.1 $\pm$ 0.2	7.9 $\pm$ 0.1
Stumps (%)	6.1 $\pm$ 1.3	11.9 $\pm$ 1.2	1.1 $\pm$ 0.5	18.2 $\pm$ 2.1
Tree density (trees ha⁻¹)	381 $\pm$ 27	600 $\pm$ 40	879 $\pm$ 71	758 $\pm$ 39
Mortality (%)	12.4 $\pm$ 1.6	3.6 $\pm$ 0.9	12.3 $\pm$ 2.6	9.8 $\pm$ 1.9
Defoliation (%)	44.9 $\pm$ 1.6	37.3 $\pm$ 1.0	49.1 $\pm$ 2.7	47.5 $\pm$ 1.0

Field sampling

During 2007 and 2008, 120 circular plots (30 in each Scots pine population) were established along an altitudinal gradient in each site. Within each population, we stratified the study area in three categories of altitude: low, intermediate and high. The area of the 3 altitude categories was approximately similar. Within each block we selected 10 plots at random. Plot size in Arcalís was 314 m² (10 m radius), while in Falgars, Ports and Prades was 491 m² (12.5 m radius). At each site, plots were located on north facing slopes within the same valley and were separated by more than 50 m from each other to reduce spatial autocorrelation. The sampling design aimed at capturing the overall range of environmental conditions in each studied valley. The altitudinal gradient varied among populations, being larger in Arcalís (Table 2).

Forest data: decline, recruitment, forest structure and management

Within each plot, all adult trees (diameter at breast height [dbh] $\geq$ 5 cm) were surveyed, identified to species and measured for dbh. In the case of Scots pine, all adult pine trees were censused for mortality and, for each pine, we visually estimated the percentage of green needles relative to a healthy canopy of a similar sized tree in the same population. Mortality and defoliation were used to assess Scots pine decline at the plot level in our

populations. Scots pine mortality was measured as the percentage of dead trees per plot ($[(N \text{ dead trees} / N \text{ total trees}] \times 100$) and defoliation as the mean percentage of crown defoliation per plot of all living individuals (Table 2). We calculated Scots pine density and basal area per plot. Because the two variables were correlated we used Scots pine density (trees ha^{-1}) as a measure of forest structure and intra-specific competition (Table 2). The number of Scots pine stumps was recorded for each plot as a measure of management intensity.

The abundance of seedlings and saplings in each plot was used as a measure of potential regeneration. Saplings ($\text{dbh} < 5 \text{ cm}$ and $\text{height} \geq 0.5 \text{ m}$) were identified to species and counted all over the plot, whereas seedlings (individuals $< 0.5 \text{ m}$ in height) were recorded in 1-m wide bands along the four axes of each circular plot. The abundance of seedlings and saplings of the two most abundant *Quercus* species, *Q. ilex* and *Q. pubescens*, considered together as *Quercus* spp., was used to evaluate potential vegetation changes (or shifts) in the studied Scots pine populations.

Environmental data

To characterize each plot climatically we obtained data from the Digital Climatic Atlas of Catalonia (Ninyerola *et al.*, 2000), with a spatial resolution of 180 m. As a measure of climatic summer drought we computed the average ratio of precipitation to potential evapotranspiration (calculated following the Hargreaves-Samani [1982] method) from June to August (Summer P/PET; Martínez-Vilalta *et al.*, 2008). Low values of Summer P/PET correspond to dry sites while high values correspond to wet sites (Table 2).

We used soil depth and a topographic wetness index as measures of water holding capacity of soils and local topography. With a metal bar (90 cm height and 2 cm wide) we carried out ten measures of soil depth per plot and from them we computed the average soil depth (Table 2). We used the topographic index (Top index) developed by Beven & Kirkby (1976) to characterize the spatial distribution of soil moisture conditions at the catchment scale (Table 2) which is defined at point 'i' as:

$$w_i = \ln \left(\frac{a}{\tan \beta} \right)$$

where a is the contributing area, and $\tan \beta$ is the local slope of the terrain.

We used a digital elevation model generated by the Cartographic Institute of Catalonia (ICC) with a resolution of 30 m to compute the topographic index.

Statistical analyses

To test decline average differences among populations we performed a generalized linear model (GLZ) of the number of dead Scots pines (negative binomial distribution with log-link function) including an offset of $\ln[\text{Scots pine population size}]$ to account for different tree densities, and a general linear model (GLM) for mean crown defoliation. Population was introduced in the models as factor. To evaluate the relationship between mortality and defoliation we fitted a negative binomial GLZ with log-link function with the number of dead Scots pines as dependent variable, population as factor and defoliation and the interaction population x defoliation as covariates. An offset of $\ln[\text{Scots pine population size}]$ was also introduced.

Scots pine Decline was defined as the average defoliation of Scots pines in each plot, where dead pines were considered to have 100% defoliation. Three groups of variables were selected on the basis that they could explain decline patterns across and within populations: *Abiotic factors* (Summer P/PET, Soil depth, Top index), *Management* (% Stumps) and *Biotic factors* (Tree density).

We used a general linear mixed model (GLMM) to test the effects of biotic and abiotic factors, and management on Scots pine decline across populations. We introduced in the model all the second order interactions between predictors. Population was introduced in the model as a random factor to account for the spatial autocorrelation (or homogeneity) among plots. Starting from the saturated model, we created the fully crossed set of models and ranked them from lowest to highest AICc (second-order Akaike information criterion). All best models (lowest AICc) within 2 AICc units were considered to be equivalents in terms of fit.

Structural equation modeling (SEM) is used to test complex hypotheses involving multiple causal pathways (relationships between inter-correlated variables), and evaluate whether data are consistent with the model (Grace, et al. 2006). We used SEM

to analyze the complex relationships between the four groups of variables considered: *Abiotic factors* (Summer P/PET, Soil depth, Top index), *Management* (% Stumps), *Biotic factors* (Tree density) and *Scots pine Decline*. We created a common conceptual model to explain decline patterns within each system (Figure 1). The general model assumed that the different *Abiotic factors* covaried with each other and that they could have direct effects on *Scots pine Decline* as well as indirect effects mediated through influences on *Biotic factors* (Figure 1). Finally, the model also considered that the effects of *Management* and *Abiotic factors* covaried and that *Management* could have indirect effects on *Scots pine Decline* mediated by *Biotic factors* (Figure 1).

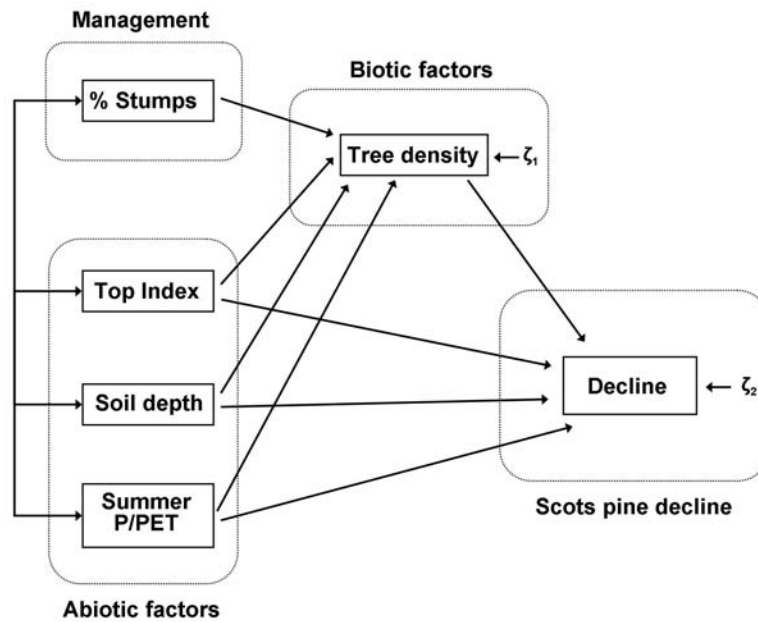


Figure 1. Conceptual structural equation model relating *Scots pine Decline* with three groups of variables representing *Biotic factors*, *Abiotic factors* and *Management* (dotted lines). Rectangles correspond to measured variables representing each group. Symbols: ζ_1 , error associated to Tree density; ζ_2 , error associated to Decline.

The theoretical relationships between variables in our conceptual model for each population were tested by goodness-of-fit tests between the observed covariance matrix and that expected if the model was correct. We evaluated the overall fit of the models by the χ^2 and the corresponding p-value, by the GFI (goodness-of-fit index), by the CFI (Bentler's comparative fit index) and by the RMSEA (root mean square error of approximation). Because some variables remained non-normal after standard transformations and sample size was relatively small (30 samples per model), the

discrepancy function used to fit the models was GLS (generalized least squares) and parameter significance was estimated by 95% bootstrap confidence intervals.

We used generalized linear models (GLZ) to analyze the effect of decline on regeneration patterns (seedlings and saplings) of Scots pine and *Quercus* spp. in the four studied populations. As decline of canopy species opens gaps in the stand, where establishment of new individuals may take place, we calculated the defoliation of Scots pines in each plot (including dead trees) measured in the initial inventory (2007 and 2008) as follows:

$$\text{Weighted Decline}_i = \frac{\sum_j \text{Defoliation}_{i(j)} \times \text{Basal area}_{i(j)}}{\text{Basal area}_i}$$

where dead pines were considered to have 100% defoliation, i is the index for plot and $i(j)$ is the index for tree in plot. The number of seedlings and saplings of Scots pine and *Quercus* spp. were modeled as a negative binomial distribution with log link-function. The four statistical models to analyze the abundance of seedlings and saplings of Scots pine and *Quercus* spp. were build separately using Weighted decline as covariate and Population as factor. To test whether the effect of Weighted decline was similar across the four populations, we also included in the models the interaction term Weighted decline x Population. We used the AICc to compare the fit between the models with and without the interaction term. If the difference between the AICcs of these models was less than two units, we considered the models to be equivalent in terms of fit, and the simpler model (i.e., the one without the interaction) was selected.

The GLM, GLZ and GLMM were carried out with R software (R Development Core Team 2011; Packages *nlme*, *MASS* and *MuMin*). All SEM analyses were performed using the package AMOS 18 (Arbuckle 2009). In all cases, parameter significance was accepted at $\alpha = 0.05$.

RESULTS

Mortality and defoliation patterns

Higher levels of standing dead trees were found in the two unmanaged populations (Prades and Arcalís) and in the wet managed population (Falgars), with values around 10-12%, whereas the dry managed population (Ports) presented significantly lower standing mortality (GLZ, $p < 0.001$; Figure 2; Table 2). Mean crown defoliation of living trees was again similar in Prades, Arcalís and Falgars, with percentages around 45-50%, while Ports had the lowest value, $37.3 \pm 1.0\%$ (GLM, $p < 0.001$; Figure 2; Table 2). Mortality and crown defoliation were positively associated ($\beta = 0.070$, $p < 0.001$, reference level Arcalís), indicative of higher levels of defoliation of living Scots pine in plots with higher mortality levels (Figure 3). The interaction defoliation $\times$ population was significant, indicating that the slope of the relationship between mortality and defoliation was shallower in Prades ($\beta = -0.056$, $p < 0.05$) than in the other populations (Figure 3).

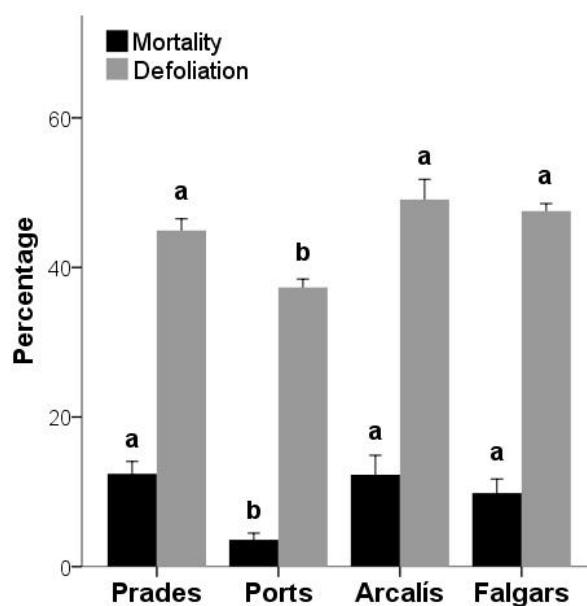


Figure 2. Percentage (mean $\pm$ SE) of standing mortality and crown defoliation of living Scots pines in each population. Different letters correspond to significant differences between populations.

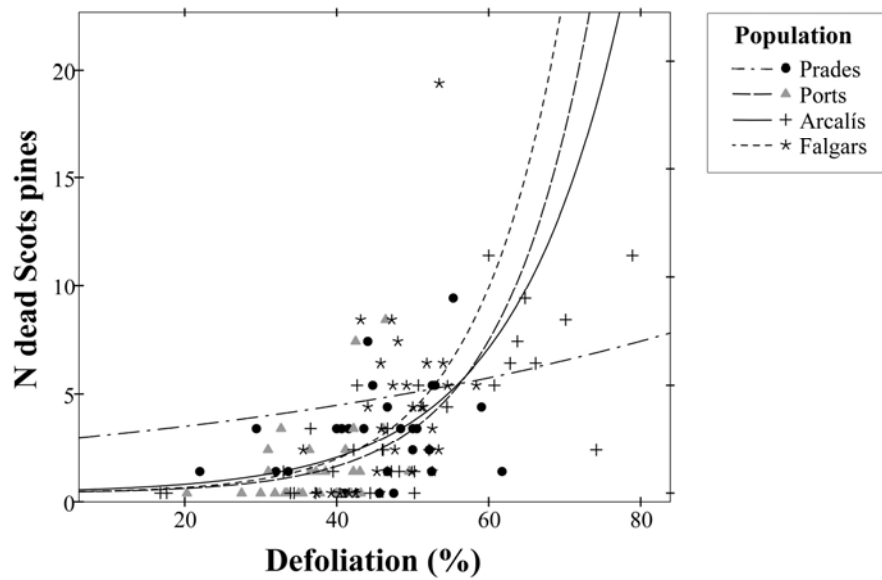


Figure 3. Predicted relationship between mortality and crown defoliation across the four Scots pine populations studied. See *statistical analyses* in the material and methods section for details.

Diameter distributions in the four populations were roughly bell-shaped with a dominance of intermediate size classes (17.5, 22.5, 27.5, 32.5 and 37.5 cm dbh classes; Figure 4). Dead trees were concentrated in smaller size classes (7.5 and 12.5 cm dbh classes; Figure 4), but in intermediate and even in larger size classes (> 37.5 cm dbh class) they were also present (Figure 4). The distribution of percentage mortality across size classes varied among populations. While in the dry managed population (Ports) mortality in the smaller size classes remained around 10%, in the other three populations achieved values around 20%. Regarding intermediate and large size classes, the dry unmanaged population (Prades) showed percentages of mortality up to 40% in the 17.5 cm dbh class, with values around 10-20% in classes of larger size. The wet populations, Arcalís (unmanaged) and Falgars (managed), showed mortality levels of 10% and 4-8%, respectively, in intermediate and larger classes. Crown defoliation showed a similar trend across size classes in the four populations (Figure 5). The higher levels of crown defoliation were concentrated in smaller size classes (around 60%) but larger size classes also showed relatively high levels of defoliation (around 30-40%; Figure 5).

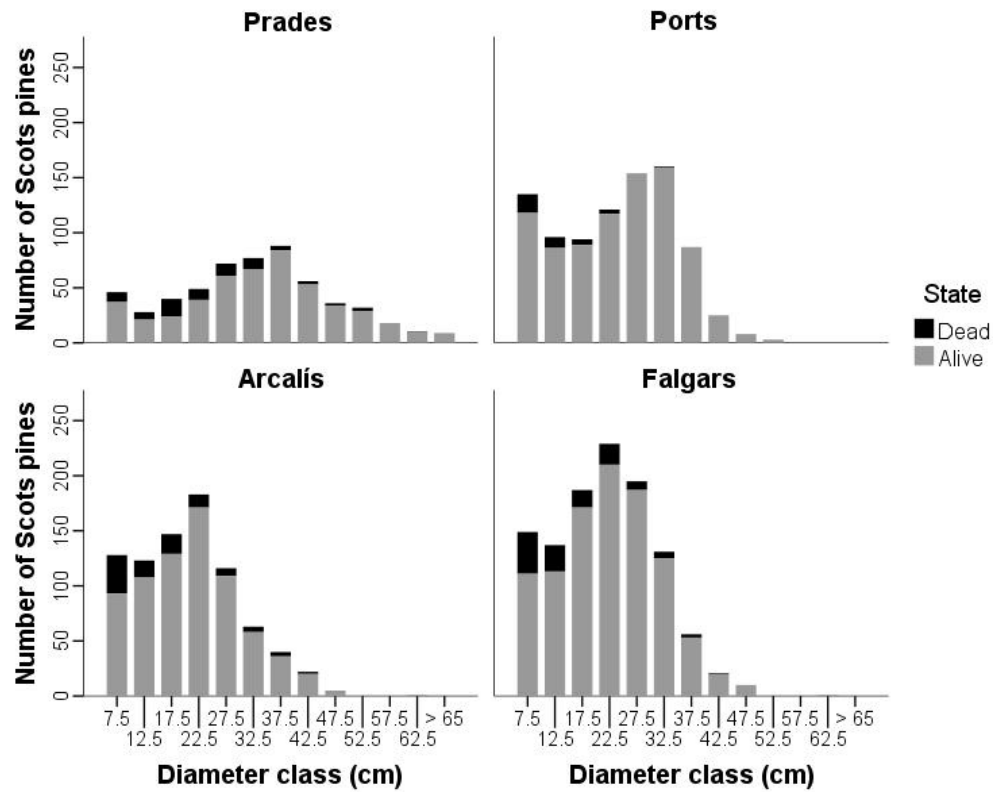


Figure 4. Diameter distributions of dead and living adult Scots pine trees for each population. X-axis labels correspond to the central value of each 5 cm diameter class.

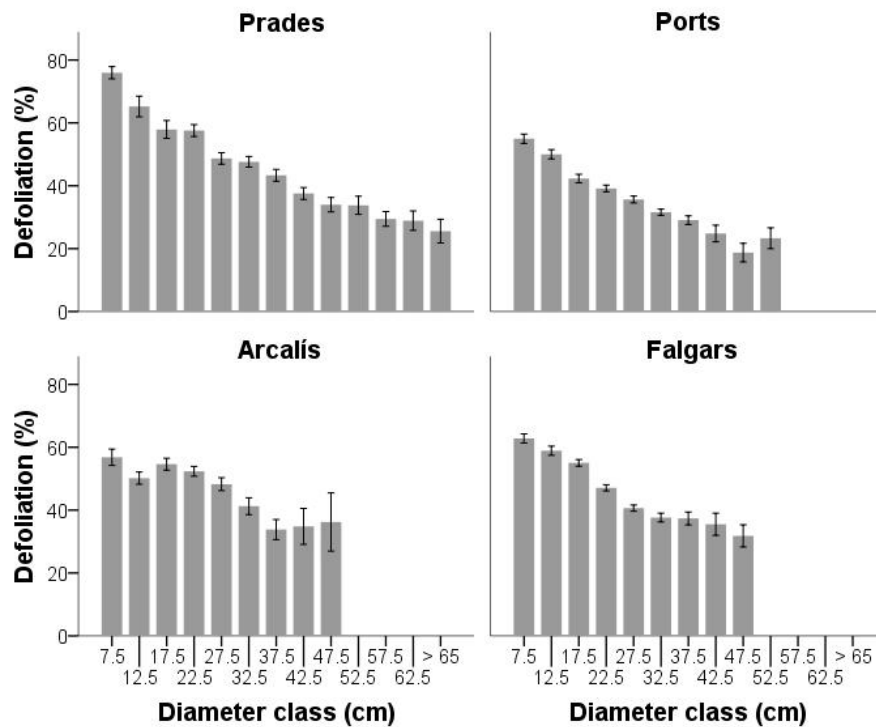


Figure 5. Mean crown defoliation of adult Scots pines as a function of diameter class for each population. X-axis labels correspond to the central value of each 5 cm diameter class.

Determinants of decline across populations

Only one GLMM across populations was selected, i.e. it had the lowest AICc, and there was no other model within two AICc units. This model included the effects of several interactions between Tree density, % Stumps, Summer P/PET, Soil depth and Top index (Appendix 2). Across populations, the decline patterns showed a clear trend throughout the gradient of Summer P/PET (Appendix 2 and 3), showing that plots located in drier sites had higher levels of Scots pine decline. However, this effect varied according to the following interaction effects: (1) Summer P/PET x Stand density, in the sense that climatic dryness only had effect under low stand densities (or plots with many large trees), (2) Summer P/PET x % Stumps, showing that in dry sites more intensive management had a negative effect on decline, and (3) Summer P/PET x Soil depth or Top index, indicating that when soil conditions were poor (low Soil depth and Top index) climatic dryness did not have any effect on decline (Appendix 2 and 3). Moreover, similar interaction effects were found between Stand density and Soil depth, between % Stumps and Soil depth and between Soil depth and Top index (Appendix 2 and 3). Finally, the intra-class correlation coefficient (ICC) was 12.4 %, i.e. the % of the total variation derived from the heterogeneity between the Population levels, suggesting that most of the variability in decline was within populations.

Determinants of decline within populations

The structural equation models provided a good overall fit to the data sets for each population studied (Figure 6). The four models had a non significant χ^2 , indicating that the covariance structure specified by the model could not be rejected given the covariance structure of the data. The model GFI was > 0.9 and CFI > 0.9 in all cases, and the model RSMEA was < 0.001 (with the exception of Arcalís; RMSEA = 0.160), indicating an overall adequate fit (Figure 6).

The SEM results indicated significant direct and indirect effects of the studied variables on *Scots pine Decline*, and complex relationships among the different components involved, which overall captured a substantial proportion of the variance in Decline (50-62 %; Figure 6). The relationships most consistent across populations were the effects of Tree density and Soil depth on Decline. In the four populations, stands with higher densities showed higher levels of Decline, while deeper soils (mediated by Tree density in Prades, the dry unmanaged population) were related to lower Decline (Figure 6). The

effect of Summer P/PET was found to be different from zero with a marginally negative effect on Decline in the wet unmanaged population (Arcalís, Figure 6c) and also had a negative effect, but mediated by Tree density, in the dry unmanaged population (Prades, Figure 6a) and in the wet managed population (Falgars, Figure 6d). An opposite, positive effect of Summer P/PET was found also in the wet managed population (Falgars, Figure 6d) and in the dry managed population, in this latter case mediated by Tree density (Ports, Figure 6b). Finally, Top index had a marginally positive effect mediated by Tree density in the wet unmanaged population (Arcalís, Figure 6c).

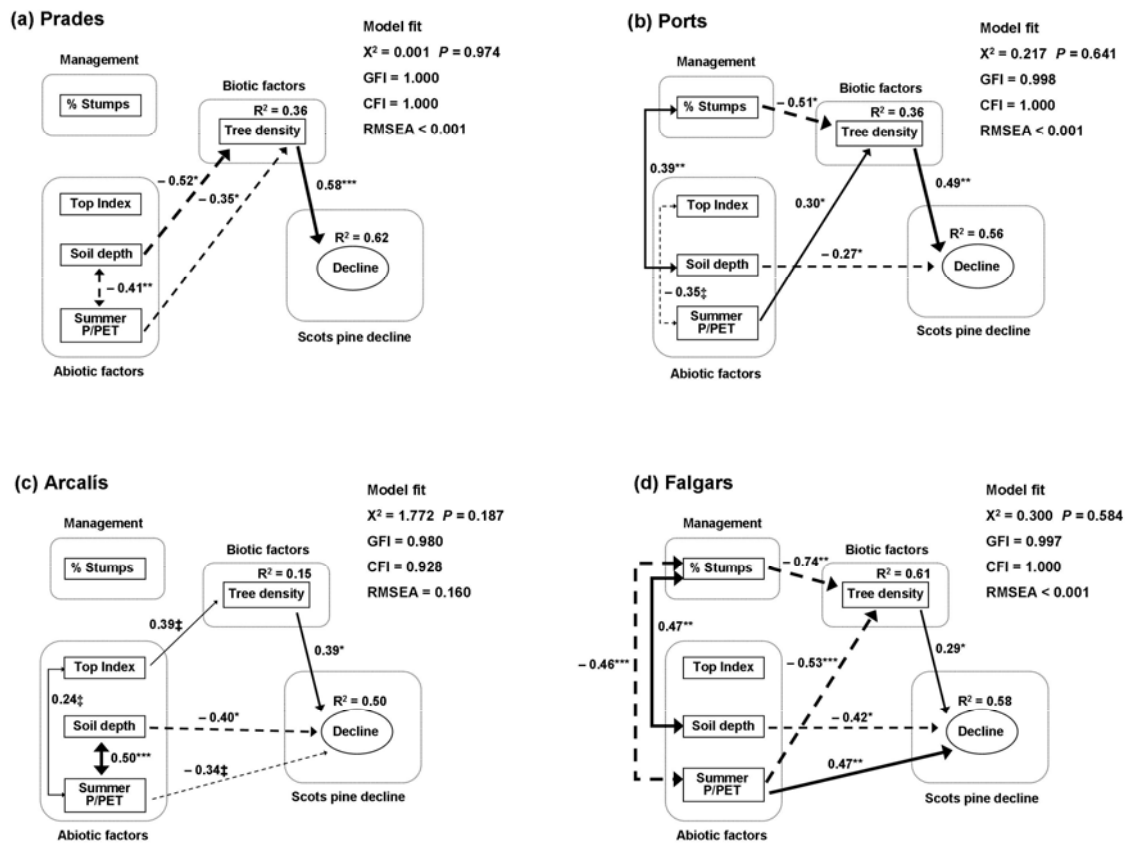


Figure 6. Results of the structural equation models relating *Scots pine Decline* with three groups of variables representing *Biotic factors*, *Abiotic factors* and *Management* (dotted lines) for the studied Scots pine populations: (a) Prades, (b) Ports, (c) Arcalís and (d) Falgars. Rectangles correspond to measured variables representing each group. Only the path values that were significant in the models are shown in their standardized form next to their corresponding arrow. Arrows represent the proposed links between variables (single headed: directional paths, double headed: covariances). Positive effects are indicated by solid lines and negative effects by broken lines. Arrow thickness is proportional to the strength of the effect in terms of the absolute value of the standardized coefficients (> 0.45 and $p < 0.05$; < 0.45 and $p < 0.05$; < 0.45 and $p < 0.1$). The values above the response variables indicate the explained variance (R^2). Significance: ‡, $p < 0.1$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

Management was an important factor only in the two populations that had been more intensively managed (Ports and Falgars), where Decline was affected negatively by the % of stumps, an effect that was mediated by Tree density (Figure 6b and 6d). This effect was not found in the other two populations. The SEMs also identified significant covariations between *Management* and *Abiotic factors* or between components within *Abiotic factors* (Figure 6), highlighting the complexity of each system.

Regeneration patterns

Similar patterns of the abundance of Scots pine seedlings and saplings were found between contrasted populations in terms of climate and management. In the dry managed (Ports) and the wet unmanaged (Arcalís) populations the abundance of regeneration was higher than in the dry unmanaged and in the wet managed populations (Prades and Falgars, respectively; Table 3). In contrast, the two unmanaged populations (Prades and Arcalís) showed the highest abundances of *Quercus* spp. seedlings, while the two managed populations showed noticeably lower values (Table 3). The abundance of *Quercus* spp. saplings was much higher in Prades than in the other three populations (Table 3).

Table 3. Mean abundance $\pm$ SE (individuals ha⁻¹) of seedlings and saplings of Scots pine and *Quercus* spp. for each population studied. Different letters correspond to significant differences between populations according to the GLZ.

Population	<i>Pinus sylvestris</i>		<i>Quercus</i> spp.	
	Seedlings	Saplings	Seedlings	Saplings
Prades	6.67 $\pm$ 6.67 a	51.59 $\pm$ 20.15 a	6773.33 $\pm$ 828.00 a	982.35 $\pm$ 84.22 a
Ports	1480.00 $\pm$ 445.32 b	142.57 $\pm$ 42.45 b	173.33 $\pm$ 68.97 b	13.58 $\pm$ 11.11 b
Arcalís	740.00 $\pm$ 450.61 b	148.68 $\pm$ 37.96 b	4146.67 $\pm$ 713.67 a	16.29 $\pm$ 7.33 b
Falgars	153.33 $\pm$ 81.19 c	61.10 $\pm$ 17.55 a	713.33 $\pm$ 154.82 c	15.61 $\pm$ 7.29 b

The results of the regeneration models showed that the effect of Weighted decline was marginally negative on Scots pine seedlings and significantly negative on Scots pine saplings, and that this relationship did not vary among populations (Table 4). In contrast, model results indicated that the relationship between Weighted decline and

regeneration of *Quercus* spp. varied across populations, i.e. the best model included the interaction term Weighted decline x Population (Table 4). For *Quercus* spp. seedlings, the effect of Weighted decline was positive in the wet unmanaged population (Arcalís) and in the dry managed population (Ports), but it was negative in the wet managed population (Falgars) (Table 4). Finally, Weighted decline showed a marginal positive effect on *Quercus* spp. saplings only in the wet unmanaged population, whereas it had a significant negative effect in the dry managed population (Table 4).

Table 4. Summary of parameter estimates (mean $\pm$ SE) of the regeneration models for seedlings and saplings of Scots pine and *Quercus* species.

	<i>Pinus sylvestris</i>		<i>Quercus</i> spp.	
	Seedlings	Saplings	Seedlings	Saplings
Intercept	3.02 $\pm$ 0.95 **	3.38 $\pm$ 0.63 ***	0.07 $\pm$ 0.55	– 1.63 $\pm$ 0.92 ‡
Weighted decline	– 0.03 $\pm$ 0.02 ‡	– 0.03 $\pm$ 0.01 **	0.05 $\pm$ 0.01 ***	0.03 $\pm$ 0.02 ‡
Prades	– 5.06 $\pm$ 1.17 ***	– 1.19 $\pm$ 0.40 **	3.19 $\pm$ 0.99 **	5.99 $\pm$ 1.32 ***
Ports	0.03 $\pm$ 0.60	– 0.43 $\pm$ 0.42	– 2.45 $\pm$ 1.82	26.63 $\pm$ 6.15 ***
Falgars	– 1.91 $\pm$ 0.58 ***	– 0.87 $\pm$ 0.39 *	2.12 $\pm$ 1.24 ‡	1.54 $\pm$ 1.83
Weighted decline x Prades	n.i	n.i	– 0.05 $\pm$ 0.02 *	– 0.04 $\pm$ 0.03
Weighted decline x Ports	n.i	n.i	0.01 $\pm$ 0.05	– 0.97 $\pm$ 0.24 ***
Weighted decline x Falgars	n.i	n.i	– 0.08 $\pm$ 0.03 **	– 0.03 $\pm$ 0.04

Note: Arcalís was considered the reference level. Abbreviations and symbols: n.i, not included; ‡, $p < 0.1$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$

Discussion

When considering all plots, a clear climatic signal was detected, suggesting that Scots pine stands located in drier sites could suffer higher levels of water stress (Vilà-Cabrera *et al.*, 2011). However, this process seems to be result of interactions of climatic dryness with the biotic and abiotic forest factors as well as with the past management, specific components of each population. Overall, the most relevant results at the

regional scale suggest that (1) processes of stand development and competition are driving forest decline in younger stands (i.e. higher tree densities), while dryness or poor quality sites are the triggering factors of decline in more mature stands, (2) unfavorable site conditions are related to higher forest decline independently of climatic dryness, and (3) past logging practices could have beneficial effects on forest stands in drier or in poor quality sites. Thus, climatic dryness seems to play at the regional scale but, ultimately, within-population environments, i.e. forest structure, local site conditions and past human legacies, could be the main underlying drivers of Scots pine decline (Gitlitz *et al.*, 2006).

Intra-population determinants of Scots pine decline

The SEM models applied in this study described satisfactorily the decline patterns within each Scots pine population studied, underscoring the importance of considering forest decline as a non-random process. The models allowed us to identify a first process related to stand structure and past forest history operating directly on the decline in a consistent way across populations. Biotic factors, represented by stand density, had a strong positive effect on decline, suggesting that stand development resulted in intense intra-specific competition and density-dependent tree mortality and defoliation (Appendix 4 and 5; Peet & Christensen 1987; Oliver & Larson 1990). The bell-shaped diameter distribution and the fact that higher mortality and defoliation concentrated in small size classes is consistent with this interpretation and implies asymmetric competition, where smaller trees are more likely to die by stagnation. The current structural attributes of Scots pine populations reflect the decreasing use of fuelwood and timber during the last century after the abandonment of rural areas (Poyatos *et al.*, 2003; Améztegui *et al.*, 2010), resulting in a densification and development of forests where competition for space and resources is at present amplified.

The separation of causality of biotic vs. abiotic factors on forest decline is often difficult (Suarez *et al.*, 2004). However, our design allowed the identification of a second, abiotic, factor related to soil depth that had a direct influence on the level of decline in our systems. Site moisture conditions are strongly influenced by topography and soil characteristics (Stephenson, 1990). Soil depth likely acted as a long-term predisposing factor in our populations, as Scots pine in Mediterranean mountains strongly relies on soil water stores to meet summer evaporative demand (Llorens *et al.*, 2010). Concerning

the direct effects of Summer P/PET on decline, we can not generalize a detrimental effect of climatic dryness within each population as has been shown in a previous study (Galiano *et al.*, 2010). Thus, this could be result of the gridded climate data set used (Summer P/PET) that, within populations, only could reflect the altitudinal gradient beyond to describe adequately the variation of water availability, and the results obtained should be taken with caution. However, this inconsistency among populations may arise on the complexity and singularity of each system that depends on how forest dynamics responds to the interactions between the different components in a given stand.

Overall, our results provide evidence of complex structures of causation involving indirect effects, which highlight important differences among populations. The SEMs identified effects of abiotic factors and management on decline mediated by biotic factors. These interactive effects among components likely relate to the key role of soil water availability during summer in Mediterranean ecosystems (Reichstein *et al.*, 2002). Previous logging practices have reduced stand density, inducing competition release and lower decline. This is particularly apparent in the two recently managed populations, showing that past and recent forest history is a relevant factor differentiating between-population decline patterns. The differential effect of local measures of water availability (i.e. Summer P/PET, Soil depth, Top index) on decline mediated by tree density or covarying with biotic and management factors in the different populations (Figure 6) highlights again the dominant role of forest structural attributes and past management in our systems. These differential effects are likely related to the stand forest structure and to the specific configuration of site conditions, which together determine the differential responses of trees under environmental stress (Greenwood & Weisberg 2008).

Our results illustrate the relative influence of biotic vs. abiotic controls on population decline and how competition for resources interacts with past history and microsite conditions that constrain resource availability. Thus, this study indicates that the spatial patterns of decline are the result of processes acting at the plot level that modulate forest responses to local environmental stress (Linares *et al.*, 2010; Vilà-Cabrera *et al.*, 2011), and highlights the importance of accounting for forest history. These findings have relevant implications for the use of management to mitigate future changes in forest

ecosystems. In contrast with recent work by Camarero *et al.* (2011), who have found that past intense logging practices increased the vulnerability of silver fir under water deficit, our results support the idea that moderate and planned logging could improve the capacity of Scots pine to cope with stress conditions.

Potential vegetation shifts

Our results showed overall low abundances of Scots pine seedlings and saplings related to higher decline. Scots pine is a shade-intolerant species with high requirements of light to regenerate and develop (Castro *et al.*, 2004). However, these conditions are unavailable in the current stand structure of the studied populations, and open gaps created by forest decline do not appear to enhance the emergence and development of new recruits, either due to their small size or to their excessively dry conditions. If the lack of replacement of dead pines by new recruits persists over time, it may have major implications for the long-term persistence of Scots pine in the studied communities, particularly if other potentially dominant species, such as *Quercus* spp., are favoured by the new conditions. However, our GLZs did not provide widespread support to the previous expectation, as the abundances of *Quercus* spp. in the different populations studied did not show a common response but tended to react idiosyncratically to Scots pine decline (Table 4).

Although we can not generalize an expanding niche of co-occurring *Quercus* species under declining Scots pines in all the study areas, an interesting pattern emerged at the regional scale: the abundance of *Quercus* species was higher in the two populations with higher decline, which also correspond to the unmanaged populations. Land use history and past management regimes in southern Spain have been documented as drivers of shift in species composition (Urbieto *et al.*, 2008). Similar processes are probably occurring in Swiss Scots pine forests, where drought-induced Scots pine decline is concomitant with a spread of deciduous trees as a result of land-use changes (Gimmi *et al.*, 2010), as they are likely occurring in our unmanaged populations after cessation of traditional logging practices (Garcia-Ruiz *et al.*, 1996; Gracia *et al.*, 2011).

Conclusions

The difference in overall decline among populations was relatively small despite large differences in climate and past management. However, considering the four populations

together (i.e., across all plots) there was a large spatial variability in the levels of decline, which was explained by the interactive effects of local water availability, forest structure, site conditions and past management. This implies that progressive Scots pine decline appears to be patchy related to local environmental constraints mediated by structural attributes as a result of past and recent management history. In that respect, our results provide improved understanding of the ecological processes behind forest decline in regard not only to climate but to local components of forests and past human legacies. Moreover, decline of adult Scots pine trees seems not to be compensated by self-recruitment so that the future dynamics of these forest ecosystems is uncertain.

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LITERATURE CITED

- Allen, C.D., Makalady, A.K., Chenchouni H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J-H., Allard, G., Running, S.W., Semerci, A. & Cobb, N. (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, 259: 660-84.
- Améztegui, A., Brotons, L. & Coll, L. (2010) Land-use changes as major drivers of mountain pine (*Pinus uncinata* Ram.) expansion in the Pyrenees. *Global Ecology and Biogeography*, 19: 632-641.
- Arbuckle, J.L. (2009) Amos 18 user's guide. Chicago, IL, USA: SPSS Inc.
- Beven, K. & Kirkb, M.J. (1979) A physically based variable contributing area model of basin hydrology. *Hydrological Sciences Journal*, 24: 43-69.
- Bréda, N., Huc, R., Granier, A. & Dreyer, E. (2006) Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. *Annals of Forest Science*, 63: 625-644.

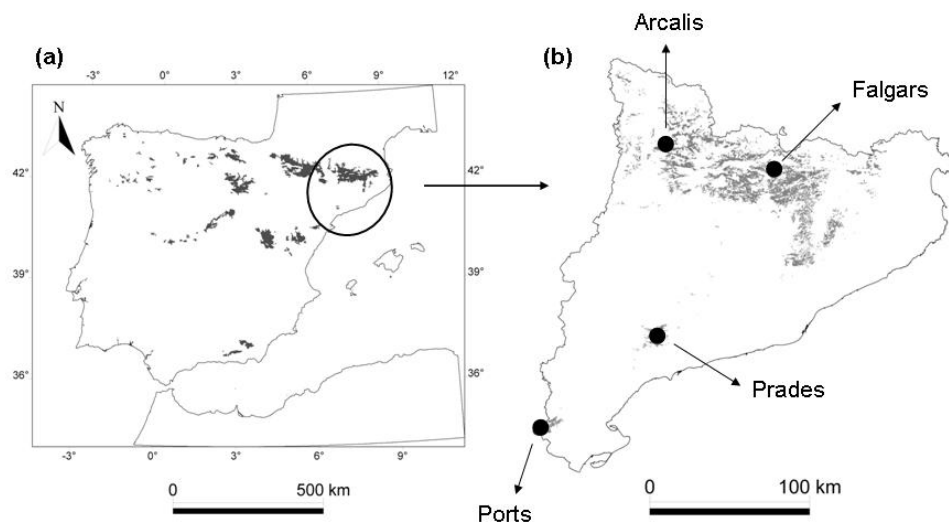
- Burriel, J.A., Gracia, C., Ibáñez, J.J., Mata, T. & Vayreda, J. (2000-2004)** Inventari ecològic i forestal de Catalunya. Catalunya, 10 Volumes. CREA, Bellaterra (Catalunya).
- Camarero, J.J., Bigler, C., Linares, J.C. & Gil-Pelegrín, E. (2011)** Synergistic effects of past historical logging and drought on the decline of Pyrenean silver fir forests. *Forest Ecology and Management*, 262: 759-769.
- Carnicer, J., Coll, M., Ninyerola, M., Pons, X., Sánchez, G. & Peñuelas, J. (2011)** Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought. *Proceedings of the National Academy of Sciences, USA*, 108: 1474-1478.
- Castro, J., Zamora, R., Hódar, J.A. & Gómez, J.M. (2004)** Seedling establishment of a boreal tree species (*Pinus sylvestris*) at the southernmost distribution limit: consequences of being in a marginal Mediterranean habitat. *Journal of Ecology*, 92: 266-277.
- Chauchard, S., Carcaillet, C. & Guibal, F. (2007)** Patterns of land-use abandonment control tree-recruitment and forest dynamics in Mediterranean mountains. *Ecosystems*, 10: 936-948.
- Dale, V.H., Joyce, L.A., McNulty, S., Neilson, R.P., Ayres, M.P., Flannigan, M.D., Hanson, P.J., Irland, L.C., Lugo, A.E., Peterson, C.J., Simberloff, D., Swanson, F.J., Stocks, B.J. & Wotton, B.M. (2001)** Climate change and forest disturbances. *BioScience*, 51: 723-34.
- Franklin, J.D., Shugart, H.H. & Harmon, M.E. (1987)** Tree death as an ecological process. *Bioscience*, 37: 550-556.
- Galiano, L., Martínez-Vilalta, J. & Lloret, F. (2010)** Drought induced multi-factor decline of Scots pine in the Pyrenees and potential vegetation change by the expansion of co-occurring oak species. *Ecosystems*, 7: 978-991.
- García-Ruiz, J.M., Lasanta, T., Ruiz-Flaño, P., Ortigosa, L., White, S., González, C. & Martí, C. (1996)** Land-use changes and sustainable development in mountain areas: A case study in the Spanish Pyrenees. *Landscape Ecology*, 11: 267-277.
- Gimmi, U., Wohlgemuth, T., Rigling, A., Hoffmann, C.W. & Bürgi, M. (2010)** Land-use and climate change effects in forest compositional trajectories in a dry Central-Alpine valley. *Annals of forest Science*, 67: 701.
- Gitlin, A.R., Sthultz, C.M., Bowker, M.A., Stumpf, S., Paxton, K.L., Kennedy, K., Muñoz, A., Bailey, J.K. & Witham, T.G. (2006)** Mortality gradients within and among dominant plant populations as barometers of ecosystem change during extreme drought. *Conservation Biology*, 20: 1477-1486.
- Gonzalez, P., Neilson, R.P., Lenihan, J.M. & Drapek, R.J. (2010)** Global patterns in the vulnerability of ecosystems to vegetation shifts due to climate change. *Global Ecology and Biogeography*, 19: 755-768.
- Grace, J.B. (2006)** Structural equation modelling and natural systems. Cambridge University Press, Cambridge, UK.
- Gracia, M., Meghelli, N., Comas, L. & Retana, J. (2011)** Land-cover changes in and around a National Park in a mountain landscape in the Pyrenees. *Regional Environmental Change*, 11: 349-358.
- Greenwood, D.L. & Weisberg, P.J. (2008)** Density-dependent tree mortality in pinyon-juniper woodlands. *Forest Ecology and Management*, 255: 2129-2137.

- Grove, A.T. & Rackham, O. (2001) The nature of Mediterranean Europe: an ecological history. Yale University Press, New Haven.
- Hampe, A. & Petit, R.J. (2005) Conserving biodiversity under climate change: the rear edge matters. *Ecology Letters*, 8: 461-467.
- Hargreaves, G.H. & Samani, Z.A. (1982) Estimating potential evapotranspiration. *Journal of the Irrigation and Drainage Division*, 108: 225-230.
- Hódar, J.A., Castro, J. & Zamora, R. (2003) Pine processionary caterpillar *Thaumetopoea pityocampa* as a new threat for relict Mediterranean Scots pine forests under climatic warming. *Biological Conservation*, 110: 123-129.
- Houghton, R.A.. (1994) The worldwide extent of land-use change. *BioScience*, 44: 305-313.
- Ibáñez, I., Clark, J.S., LaDeau, S. & Hille Ris Lambers, J. (2007) Exploiting temporal variability to understand tree recruitment response to climate change. *Ecological Monographs*, 77: 163-177.
- IPCC (2007) Climate change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge
- Laurance, W.F. (1999) Reflections on the tropical deforestation crisis. *Biological Conservation*, 91: 109-117.
- Lertzman, K.P. (1992) Patterns of gap-phase replacement in a subalpine, old-growth forest. *Ecology*, 73: 657-669.
- Linares, J.C., Camarero, J.J. & Carreira, J.A. (2010) Competition modulates the adaptation capacity of forests to climatic stress: insights from recent growth decline and death in relict stands of the Mediterranean fir *Abies pinsapo*. *Journal of Ecology*, 98: 592-603.
- Llorens, P., Poyatos, R., Latron, J., Delgado, J., Oliveras, I. & Gallart, F. (2010) A multi-year study of rainfall and soil water controls on Scots pine transpiration under Mediterranean mountain conditions. *Hydrological Processes*, 24: 3053-3064.
- Lloret, F., Siscart, D. & Dalmases, C. (2004) Canopy recovery after drought dieback in holm-oak Mediterranean forests of Catalonia (NE Spain). *Global Change Biology*, 10: 2092-2099.
- MacDonald, D., Crabtree, J.R., Wiesinger, G., Dax, T., Stamou, N., Fleury, P., Gutierrez Lazpita, J. & Gibon, A. (2000) Agricultural abandonment in mountain areas of Europe: Environmental consequences and policy response. *Journal of Environmental Management*, 59: 47-69.
- Malhi, Y., Roberts, J.T., Betts, R.A., Killeen, T.J., Li, W. & Nobr, C.A. (2008) Climate change, deforestation, and the fate of the Amazon. *Science*, 319: 169-172.
- Martínez-García, F. (1999) Los bosques de *Pinus sylvestris* L. del Sistema Central español. Distribución, historia, composición florística y tipología. PhD dissertation, Universidad Complutense de Madrid, Madrid, Spain.
- Martínez-Vilalta, J. & Piñol, J. (2002) Drought-induced mortality and hydraulic architecture in pine populations of the NE Iberian Peninsula. *Forest Ecology and Management*, 161: 247-256.
- Ninyerola, M., Pons, X. & Roure, J.M. (2000) A methodological approach of climatological modelling of air temperature and precipitation through GIS techniques. *International Journal of Climatology*, 20: 1823-1841.

- Oliver, C.D. & Larson, B.C. (1990)** Forest stand dynamics. McGraw-Hill, New York, NY.
- Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A., Phillips, O.L., Shvidenko, A., Lewis, S.L., Canadell, J.G., Ciais, P., Jackson, R.B., Pacala, S.W., McGuire, A.D., Piao, S., Rautiainen, A., Sitch, S. & Hayes, D. (2011)** A large and persistent carbon sink in the World's forests. *Science*, 333: 988-993.
- Peet, R.K. & Christensen, N.L. (1987)** Competition and tree death. *Bioscience*, 37: 586-595.
- Plieninger, T., Rolo, V. & Moreno, G. (2010)** Large-scale patterns of *Quercus ilex*, *Quercus suber*, and *Quercus pyrenaica* regeneration in central-western Spain. *Ecosystems*, 13: 644-660.
- Poyatos, R., Latron, L. & Llorens, P. (2003)** Land use and land cover change after agricultural abandonment. The case of a Mediterranean mountain Area (Catalan Pre-Pyrenees). *Mountain Research and Development*, 23: 362-368.
- R Development Core Team. (2009)** R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. URL www.r-project.org/.
- Reichstein, M., Tenhunen, J.D., Rouspard, O., Ourcival, J.M., Rambal, S., Miglietta, F., Peressotti, A., Pecchiari, M., Tirone, G. & Valentini, R. (2002)** Severe drought effects on ecosystem CO₂ and H₂O fluxes at three Mediterranean evergreen sites: revision of current hypotheses? *Global Change Biology*, 8: 999-1017.
- Stephenson, N.L. (1990)** Climatic control of vegetation distribution: the role of water balance. *American Naturalist*, 135: 649-670.
- Suarez, M.L., Chermandi, L. & Kitzberger, T. (2004)** Factors predisposing drought-induced tree mortality in *Nothofagus*-site, climatic sensitivity and growth trends. *Journal of Ecology*, 92: 954-966.
- Sugden, A., Smith, J. & Pennisi, E. (2008)** The future of forests. *Science*, 320: 1435.
- Urbieto, I.R., Zavala, M.A. & Marañón, T. (2008)** Human and non-human determinants of forest composition in southern Spain: evidence of shifts towards cork oak dominance as a result of management over the past century. *Journal of Biogeography*, 35: 1688-1700.
- Vilà-Cabrera, A., Martínez-Vilalta, J., Vayreda, J. & Retana, J. (2011)** Structural and climatic determinants of demographic rates of Scots pine forests across the Iberian Peninsula. *Ecological Applications*, 21: 1162-1172.

APPENDIXES

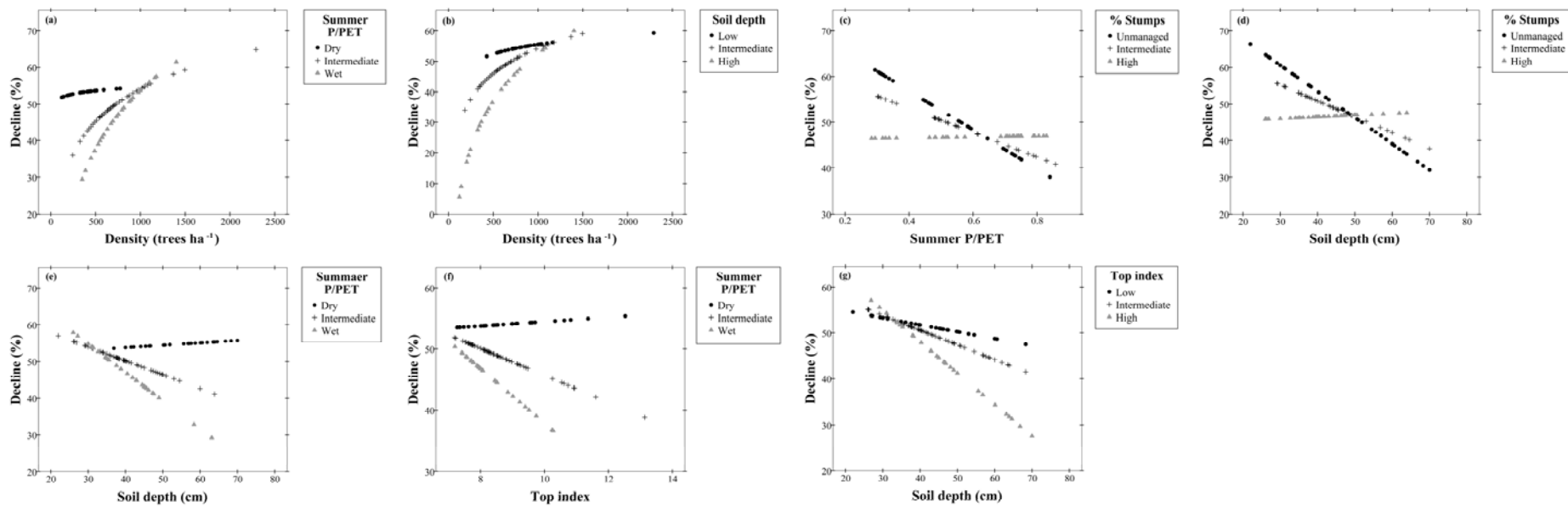
Appendix 1. (a) Scots pine distribution (grey surface) and situation of Catalonia (circle) in Spain. (b) Scots pine distribution in Catalonia (grey surface) and location of the Scots pine populations studied (black dots).



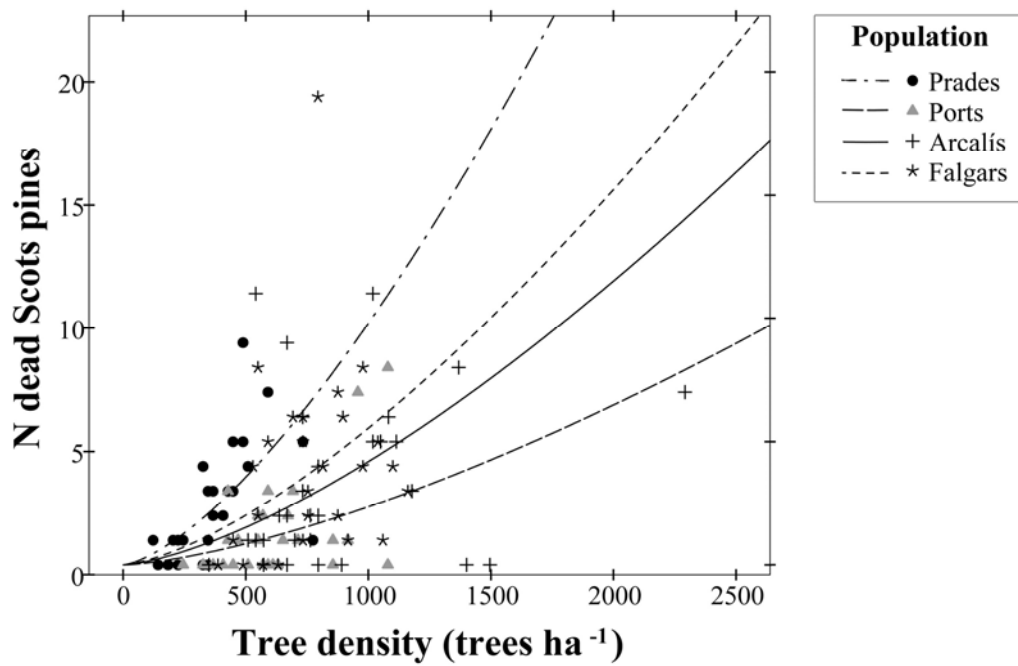
Appendix 2. Summary of parameter estimates (mean $\pm$ SE) of the best GLMM relating patterns of Scots pine decline with biotic factors, abiotic factors and management across populations.

Fixed effect	Estimate $\pm$ SE
Intercept	223.778 $\pm$ 117.421 ‡
ln(Density)	– 41.842 $\pm$ 17.635 *
% Stumps	– 3.007 $\pm$ 0.871 ***
Summer P/PET	– 186.449 $\pm$ 124.650
Soil depth	– 2.004 $\pm$ 1.443
Top index	12.405 $\pm$ 5.587 *
ln(Density) x Summer P/PET	49.499 $\pm$ 17.808 **
ln(Density) x Soil depth	0.618 $\pm$ 0.233 **
Summer P/PET x % Stumps	2.134 $\pm$ 0.751 **
Soil depth x % Stumps	0.037 $\pm$ 0.012 **
Soil depth x Summer P/PET	– 1.887 $\pm$ 0.685 **
Top index x Summer P/PET	– 10.861 $\pm$ 5.244 *
Soil depth x Top index	– 0.195 $\pm$ 0.083 *
R ²	0.53

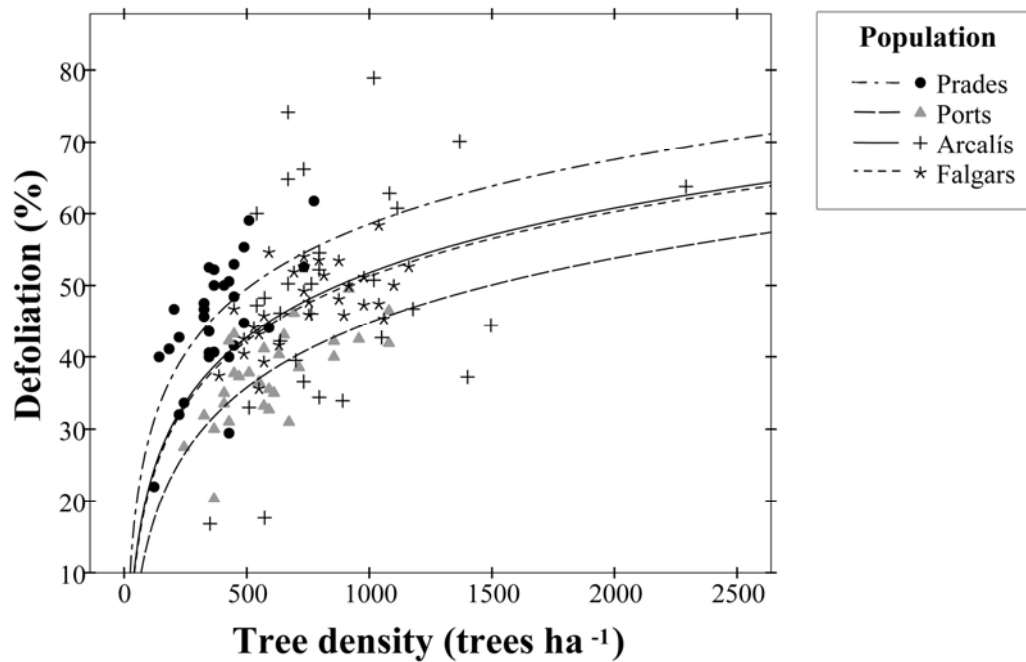
Appendix 3. Predicted effects of Stand density x Summer P/PET (a), Stand density x Soil depth (b), Summer P/PET x % Stumps (c), Soil depth x % Stumps (d), Soil depth x Summer P/PET (e), Top index x Summer P/PET (f), and Soil depth x Top index (g) on Scots pine decline across populations. The levels of categorized variables were considered according to their quartile distribution (lower, interquartilic and upper). Regression coefficients are based on the fixed effects of the model shown in Appendix 2.



Appendix 4. Predicted effect of tree density on standing mortality in each Scots pine population studied. To evaluate the relationship between mortality and tree density (ln transformed) we fitted a negative binomial GLZ with log-link function with the number of dead Scots pines as dependent variable, population as factor and $\ln[\text{tree density}]$ as covariate. The interaction population $\times \ln[\text{tree density}]$ was not significant.



Appendix 5. Predicted effect of tree density on defoliation in each Scots pine population studied. To evaluate the relationship between defoliation and tree density (ln transformed) we fitted a general linear model with defoliation as dependent variable, population as factor and $\ln[\text{tree density}]$ as covariate. The interaction population $\times \ln[\text{tree density}]$ was not significant.



Appendix 6. Standardized and unstandardized estimates of SEM models. (a) Prades, (b) Ports, (c) Arcalís and (d) Falgars. Lower and upper confidence intervals are shown with the associated p-value.

(a) Prades

Pathway		Std. estimates	Estimates	Lower	Upper	P
Tree density $\leftarrow$ Soil depth	–	0.524	– 8.213	– 15.317	– 1.483	0.015
Tree density $\leftarrow$ Summer P/PET	–	0.346	– 2580.384	– 5102.463	– 93.804	0.042
Tree density $\leftarrow$ Top Index	–	0.301	– 35.894	– 70.143	15.526	0.147
Tree density $\leftarrow$ % Stumps	–	0.085	– 1.798	– 10.525	4.182	0.561
Decline $\leftarrow$ Summer P/PET		0.218	100.318	– 49.750	253.585	0.183
Decline $\leftarrow$ Soil depth	–	0.199	– 0.192	– 0.488	0.054	0.107
Decline $\leftarrow$ Tree density		0.578	0.036	0.020	0.061	< 0.001
Decline $\leftarrow$ Top Index	–	0.159	– 1.168	– 3.092	0.727	0.205
Soil depth $\leftrightarrow$ Top Index		0.101	1.184	– 2.881	4.605	0.568
Summer P/PET $\leftrightarrow$ % Stumps		0.075	0.010	– 0.038	0.055	0.674
Soil depth $\leftrightarrow$ Summer P/PET	–	0.406	– 0.076	– 0.142	– 0.022	0.006
Summer P/PET $\leftrightarrow$ Top Index	–	0.051	– 0.001	– 0.008	0.007	0.763
Soil depth $\leftrightarrow$ % Stumps	–	0.109	– 7.192	– 25.347	11.319	0.423
Top Index $\leftrightarrow$ % Stumps		0.051	0.447	– 2.582	4.553	0.753

(b) Ports

Pathway		Std. estimates	Estimates	Lower	Upper	P
Tree density $\leftarrow$ Soil depth	–	0.005	– 0.161	– 10.844	11.471	0.968
Tree density $\leftarrow$ Summer P/PET		0.303	2366.408	168.647	5134.002	0.037
Tree density $\leftarrow$ Top Index		0.063	13.453	– 121.574	106.777	0.714
Tree density $\leftarrow$ % Stumps	–	0.513	– 16.351	– 27.820	– 2.562	0.020
Decline $\leftarrow$ Summer P/PET		0.040	12.100	– 104.347	85.603	0.803
Decline $\leftarrow$ Soil depth	–	0.274	– 0.346	– 0.666	– 0.028	0.036
Decline $\leftarrow$ Tree density		0.490	0.019	0.007	0.030	0.002
Decline $\leftarrow$ Top Index	–	0.264	– 2.173	– 4.227	3.585	0.374
Soil depth $\leftrightarrow$ Top Index		0.283	1.850	– 0.252	5.699	0.102
Summer P/PET $\leftrightarrow$ % Stumps	–	0.096	– 0.018	– 0.083	0.039	0.549
Soil depth $\leftrightarrow$ Summer P/PET	–	0.107	– 0.019	– 0.084	0.048	0.570
Summer P/PET $\leftrightarrow$ Top Index	–	0.355	– 0.010	– 0.027	0.000	0.056
Soil depth $\leftrightarrow$ % Stumps		0.390	17.048	4.030	6.765	0.009
Top Index $\leftrightarrow$ % Stumps		0.308	2.068	– 0.570	6.765	0.199

(c) Arcalís

Pathway	Std. estimates	Estimates	Lower	Upper	P
Tree density $\leftarrow$ Soil depth	0.114	3.707	– 12.080	15.895	0.673
Tree density $\leftarrow$ Summer P/PET	– 0.055	– 214.263	– 1509.853	1407.722	0.862
Tree density $\leftarrow$ Top Index	0.391	118.187	– 8.460	252.459	0.065
Tree density $\leftarrow$ % Stumps	0.179	25.567	– 21.897	235.600	0.371
Decline $\leftarrow$ Summer P/PET	– 0.337	– 58.810	– 145.886	5.689	0.070
Decline $\leftarrow$ Soil depth	– 0.396	– 0.577	– 0.970	– 0.053	0.034
Decline $\leftarrow$ Tree density	0.386	0.017	0.004	0.038	0.016
Decline $\leftarrow$ Top Index	– 0.240	– 3.233	– 7.251	– 1.004	0.125
Soil depth $\leftrightarrow$ Top Index	– 0.213	– 3.130	– 7.797	1.704	0.193
Summer P/PET $\leftrightarrow$ % Stumps	0.222	0.058	– 0.009	0.173	0.124
Soil depth $\leftrightarrow$ Summer P/PET	0.498	0.567	0.271	0.909	< 0.001
Summer P/PET $\leftrightarrow$ Top Index	0.241	0.030	– 0.003	0.068	0.079
Soil depth $\leftrightarrow$ % Stumps	0.242	7.547	– 2.510	24.823	0.188
Top Index $\leftrightarrow$ % Stumps	– 0.120	– 0.402	– 1.832	0.710	0.447

(d) Falgars

Pathway	Std. estimates	Estimates	Lower	Upper	P
Tree density $\leftarrow$ Soil depth	– 0.155	– 4.985	– 14.971	5.120	0.280
Tree density $\leftarrow$ Summer P/PET	– 0.528	– 2389.535	– 3894.595	– 1071.968	< 0.001
Tree density $\leftarrow$ Top Index	0.181	58.172	– 36.106	128.578	0.176
Tree density $\leftarrow$ % Stumps	– 0.737	– 13.835	– 19.110	– 7.064	0.002
Decline $\leftarrow$ Summer P/PET	0.471	83.838	27.986	137.883	0.004
Decline $\leftarrow$ Soil depth	– 0.416	– 0.525	– 0.901	– 0.114	0.010
Decline $\leftarrow$ Tree density	0.295	0.012	0.000	0.023	0.049
Decline $\leftarrow$ Top Index	0.130	1.652	– 1.208	5.140	0.288
Soil depth $\leftrightarrow$ Top Index	0.178	0.761	– 0.507	2.473	0.243
Summer P/PET $\leftrightarrow$ % Stumps	– 0.458	– 0.238	– 0.433	– 0.112	< 0.001
Soil depth $\leftrightarrow$ Summer P/PET	– 0.051	– 0.016	– 0.107	0.078	0.726
Summer P/PET $\leftrightarrow$ Top Index	0.050	0.002	– 0.008	0.015	0.719
Soil depth $\leftrightarrow$ % Stumps	0.472	34.568	14.334	62.013	0.001
Top Index $\leftrightarrow$ % Stumps	– 0.021	– 0.151	– 2.414	1.748	0.844

**V. REPRODUCTIVE VS. VEGETATIVE ALLOCATION IN DECLINING
SCOTS PINE POPULATIONS**

ABSTRACT

Aim Processes involved on how plants allocate resources to different functions is a fundamental aspect of life history theory. Because reproduction is costly, the allocation of resources to reproduction should occur at the expense of vegetative growth. Although it is known that reproductive allocation is an allometric process and that environmental conditions can influence life-history traits, patterns of resource allocation between vegetative and reproductive functions across and within individuals of long-lived tree species suffering drought-induced decline have not been documented. In this study we use Scots pine (*Pinus sylvestris* L.), a widely distributed temperate tree, as a model species to explore patterns and dynamics of reproduction and growth in two declining populations.

Location Catalonia (NE Iberian Peninsula): the southern edge of Scots pine distribution.

Methods General linear mixed models were used to assess patterns of resource allocation between reproductive and vegetative functions in response to drought stress between individuals from an allometric perspective, and within individuals across years to capture evidences of costs of reproduction on growth.

Results From the allometric view, allocation of resources increased with increasing tree size but in the case of reproduction stabilized in larger trees and, consequently, the reproductive effort maximized in intermediated tree sizes. Drought stress at the individual level affected negatively both vegetative and reproductive allocation but, at the stand level, the vegetative allocation increased with increasing drought stress, while the reproductive allocation decreased. These effects varied according to differences in tree size, being this variation more pronounced for larger individuals. At the intra-individual level, there was a negative relationship between growth and reproduction suggestive of a trade-off (cost of reproduction), being stronger under stress conditions.

Main conclusions Drought-induced forest decline is associated with differences in biomass allocation between growth and reproduction in Scots pine, both at the plot- and

individual levels. These differential responses suggest variation in resource allocation strategies of trees according to their size and to the variation of stressful conditions.

Keywords: allometry; biomass allocation; decline; drought; growth; *Pinus sylvestris*; reproduction; trade-off

INTRODUCTION

An axiom of evolutionary biology is that the investment in reproduction involves costs and, therefore, organisms face trade-offs between reproduction and other life-history traits (Reznick, 1985). This topic deserves special attention for trees because of their long lifespans and the fact that their fecundity often increases continuously with increasing size, inducing a compromise in resource distribution between current reproduction and other functions such as growth or maintenance (Petit & Hampe, 2006). Numerous studies have reported negative correlations between reproduction and growth in trees, suggesting ecological conflicts between these functions (Harper, 1977; El Kassaby & Barklay, 1992; Silvertown & Dodd, 1999; Climent *et al.*, 2008). However, responses to investment in reproduction are extremely variable both within and between individuals or populations due to the effects of individual size or population size class distributions (Bazzaz *et al.*, 2000), stored resources in trees (Yusumura *et al.*, 2006) and/or variations at different hierarchical levels within individuals (Sánchez-Humanes *et al.*, 2011).

Demographic trade-offs arise from genetic, morphological and functional constraints within individuals, reflecting the allocation of resources between different functions (Stearns, 1992). However, resource availability affects individual performance. In the face of stressful conditions, reproductive reduction and failure are frequent (García *et al.*, 2000; Zlotin & Parmenter, 2008) and growth is largely restricted (Aber *et al.*, 2001; Adams & Kolb, 2005). Thus, variation in the environmental conditions can determine resource allocation, and may give rise to trade-offs between different functions. For instance, trees can match their reproductive output with the fluctuations of resource availability, particularly in unfavorable environments (Monks & Kelly, 2006), and it has been suggested that the occurrence of individuals trading off reproduction and growth

may be more apparent in low-resource situations, while both functions may respond concomitantly when conditions are favorable (Despland & Houle, 1997). Moreover, several studies have shown that the steepness of trade-offs between life-history traits may vary among trees along different sites or environments between and within species (Kobe, 1996; Russo *et al.*, 2008).

Plant allocation is mainly an allometric process, i.e., it changes with size and, consequently, characterizing size-dependent allocation is a first step in understanding plant reproductive behavior and life-history strategies (Niklas & Enquist, 2003). However, little is known about the allometry of reproduction in long-lived tree species, but it is predicted a decrease of the reproductive effort with increasing size due to the amount of structural dead tissue (Wiener *et al.*, 2009). Moreover, the omission of allometric constraints imposed by plant size can lead to erroneous conclusions about the direct effect of the environment on reproductive traits. If allocation is allometric, an environmental factor that influences growth (i.e., changes size) will also affect reproduction, and this effect should be accounted for when comparing plants under different environmental conditions (Weiner *et al.*, 2009). According to the allometric perspective, only a change in the allometric trajectory between size and reproductive output through an environmental gradient can be interpreted as a differential response between individuals of a species in terms of reproductive allocation (Weiner, 2004).

Drought is a common disturbance in Mediterranean ecosystems and several recent studies have reported drought-induced forest decline in terms of tree mortality, canopy defoliation (Lloret *et al.*, 2004; Galiano *et al.*, 2010; Carnicer *et al.*, 2011; Di Filippo *et al.*, 2012), decrease and abrupt reductions of growth rates (Gómez-Aparicio *et al.*, 2011; Linares & Camarero, 2012; Sánchez-Salguero *et al.*, 2012; Martínez-Vilalta *et al.*, 2012), and reproduction restriction or failure (Mutke *et al.*, 2005; Espelta *et al.*, 2008, 2011; Pérez-Ramos *et al.*, 2010). In this sense, it can be expected that in water-limited environments such as Mediterranean forests, resource allocation to different functions can be constrained for individuals growing under stress, and intra-individual trade-offs between reproduction and growth could become stronger when resources are scarcer. However, though apparent trade-offs can be exhibited, patterns are often variable and sometimes vary throughout resource gradients in unexpected ways, as it has been shown recently for Californian oaks (Barringer *et al.*, 2012).

To our knowledge, patterns of resource allocation between vegetative and reproductive functions across and within individuals of long-lived tree species suffering different levels of drought-induced decline have not been documented. In this regard, variation in resource allocation across individuals or between year variability within individuals may respond to the spatial and temporal variation of stress conditions, inducing trade-offs (Hulshof *et al.*, 2012). In this study we use Scots pine (*Pinus sylvestris* L.), a widely distributed temperate tree, as a model species to explore patterns and dynamics of reproduction and growth in two declining populations at the southern edge of its distribution. In both populations Scots pine regeneration is very poor and oak species (*Quercus* spp.) appear to be gaining dominance in the forest (Galiano *et al.*, 2010; Vilà-Cabrera *et al.*, in press). Three main hypotheses are addressed: (1) Larger Scots pines allocate proportionally less resources to reproduction than smaller individuals; (2) Scots pines with higher levels of defoliation or located in high decline stands have lower reproductive effort, due to different allometric relationships between tree size and growth and reproduction; (3) There is a negative relationship between yearly growth and reproduction within individuals, suggestive of a trade-off (cost of reproduction for growth), and this relationship is steeper with increasing size and when trees suffer high defoliation.

MATERIAL AND METHODS

Study area

The study was carried out in Catalonia (NE Iberian Peninsula; Fig. 1a) where Scots pine is the second most abundant tree species covering 219,754 ha (18.4% of the total forested area, Burriel *et al.*, 2004). It occupies large areas in the Pyrenees and some residual locations in the center and south of the region (Fig. 1b). The species is present from 200 to 2100 m a.s.l., but it is mainly distributed between 800 and 1600 m a.s.l.. Throughout the species distribution area, annual precipitation ranges from 520 to 1330 mm and average annual temperature between 3.6 and 14.3 °C.

Two Scots pine populations were selected (Fig. 1b), one located in the center of the region (Prades) and another one in the Central Pyrenees (Arcalís). Drought-induced forest decline has been related to severe summer droughts in Prades during 1994 and

1998 (Martínez-Vilalta & Piñol 2002) and in Arcalís during 2005 (Galiano *et al.*, 2010); see also Hereş *et al.* (2012). Previous studies have reported that current patterns of Scots pine decline are the result of interactions between forest structural attributes and local site conditions that modulate forest responses to environmental stress (Galiano *et al.*, 2010; Vilà-Cabrera *et al.*, in press).

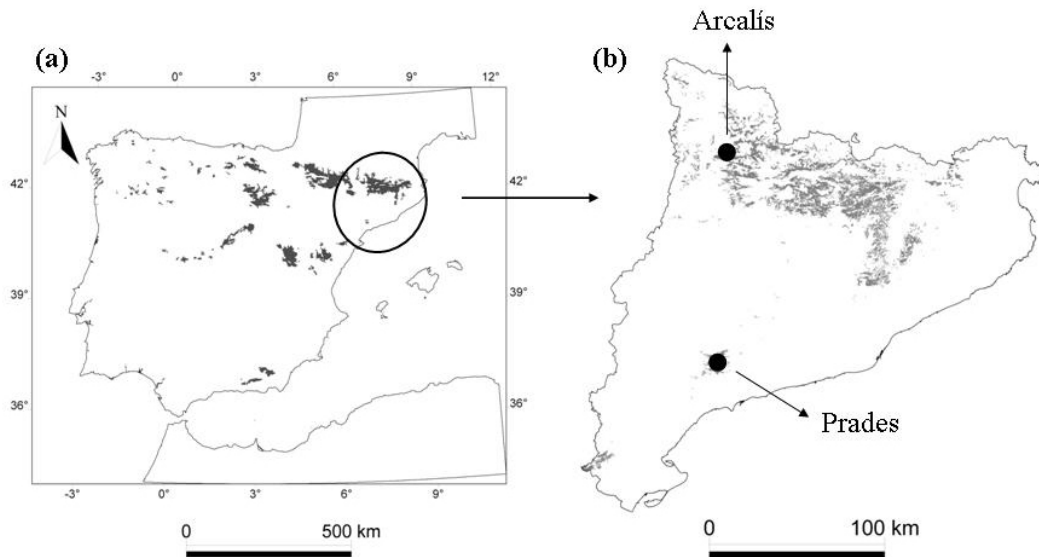


Figure 1. (a) Scots pine distribution (grey surface) and situation of Catalonia (circle) in the Iberian Peninsula; (b) Scots pine distribution in Catalonia (grey surface) and location of the two Scots pine populations studied (black dots).

Field sampling

During 2007 and 2008, 30 circular plots were established along an altitudinal gradient at each of the two studied Scots pine populations (Galiano *et al.*, 2010; Vilà-Cabrera *et al.*, in press). Plot size in Arcalís was 314 m² (10 m radius) while in Prades was 491 m² (12.5 m radius). Within each plot, all adult Scots pines (diameter at breast height [dbh] ≥ 5 cm) were measured for dbh, censused for mortality and estimated for the percentage of green needles relative to a healthy canopy of a similar sized tree in the same population. During spring 2009, 2010 and 2011 we monitored the percentage of green needles and the number of mature cones (with binoculars) in the canopy of each individual in 54 plots (27 plots at each population). During spring 2011 a hand increment borer (5 mm diameter; Suunto, Vantaa, Finland) was used to obtain a sample core to the pith at 1.35 m above the ground and perpendicular to the slope from 5-7 trees per plot in each population. Trees were selected at random taking into account the

following criteria: (1) $\text{dbh} \geq$ than the size threshold required to achieve a 50% of probability to produce cones. This size threshold was computed separately for each population using a binomial model of cone production as a function of dbh; (2) distance to the plot edge $\geq$ than 5 m to avoid edge effects in the calculation of the competition index (see the “Tree size, competition and decline” section). The final number of trees sampled was 309, 160 in Arcalís ($\text{dbh} \geq 15$ cm; Table 1) and 149 in Prades ($\text{dbh} \geq 20$ cm; Table 1).

Tree size, competition, stand development and decline

We used the following tree and stand-level variables on the basis that they could explain growth, reproduction and reproductive effort patterns: tree size, inter-individual competition, tree defoliation, plot basal area and decline level. We used vegetative biomass (obtained from allometric equations; IEF, Burriel *et al.*, 2000-2004) as a measure of tree size and the Hegyi competition index (Hegyi, 1974) as an estimate of the intensity of competition with all living Scots pine neighbors within a 5-m radius of each tree. We calculated the mean annual crown defoliation for each Scots pine during the period 2009-2011 as an indicator of tree condition. We used the total Scots pine basal area per plot as a measure of stand development. As a measure of decline at the plot level, we calculated the defoliation of Scots pines in each plot (including dead trees) measured in the initial inventory as follows:

$$\text{Decline}_i = \frac{\sum_j \text{Defoliation}_{i(j)} \times \text{Basal area}_{i(j)}}{\text{Basal area}_i}$$

where dead pines were considered to have 100% defoliation, i is the index for plot and $i(j)$ is the index for tree in plot.

Growth and reproduction data

Wood cores were air dried and sanded progressively until growth rings could be recognized. The last 3 ring widths of each core, i.e., those corresponding to 2008, 2009 and 2010, were measured to a precision of 0.01 mm using the CDendro software (CDendro 7.3 & Coorecorder 7.3; Cybis Elektronik & Data AB. Sweden). Basal area

increment (BAI, cm² year⁻¹) was used as a measure of tree growth according to the formula:

$$BAI = \pi \cdot (R_t^2 - R_{t-1}^2)$$

where R is the radius of the tree and t is the year of tree ring formation. We computed the mean annual BAI for the years 2008-2010 to characterize the growth rate during the period considered. We computed the corresponding biomass increment during the study period applying allometric equations obtained in previous studies (IEFC, Burriel *et al.*, 2000-2004).

Scots pine is a monoecious, wind-pollinated species, and female cones take two years to develop. The flowering period occurs during spring (April-June) and cone formation lasts until spring of the next year when fecundation occurs. The investment in resources on cone formation occurs mainly during this second year (April-November), and cone maturation and seed dispersal start at late autumn until spring of the following year (Cousens, 1988; Gracia & Ordóñez, 2011). According to the phenology of the species, we considered that the mature cone count in a given year was the tree cone production (or resource investment to reproduction) throughout the previous year. Thus, we obtained the annual cone production for each monitored tree. We calculated the mean annual cone production for the years 2008, 2009 and 2010 to obtain a measure of reproduction for each Scots pine during the period studied. For comparative purposes, we estimated mean cone biomass (g year⁻¹) produced per tree during the three years of measurement by multiplying the total number of cones per tree by a representative mean cone weight (7.46 g), obtained for a nearby Scots pine population in a previous study (Agundez *et al.*, 1992).

Finally we calculated for each tree the mean percentage of biomass allocated to reproduction (% year⁻¹) with respect to the total biomass invested in reproduction and growth, as a measure of reproductive effort during the study period (2008-2010).

Statistical analyses

We used linear mixed models to study the effects of tree size (vegetative biomass), competition (Hegyi competition index), tree condition (individual defoliation), plot-

level Scots pine basal area and decline on growth (mean BAI 2008-2010), reproduction (mean cone biomass production 2008-2010) and mean reproductive effort (mean % cone biomass 2008-2010). Population (Prades or Arcalís) was also included as a factor in the models. Because preliminary analyses indicated hump-shaped relationships between reproductive variables and vegetative biomass, both vegetative biomass and $\ln(\text{vegetative biomass})$ were included in the models (cf., Davies, 2001). To check if the relationship between response variables and covariates varied between populations we included the corresponding interaction terms in the models. To explore shifts in the relationship between tree size and response variables through the covariate gradients (competition, plot basal area, defoliation and decline) we also included the corresponding interaction terms in the models. Plot was introduced in the models as a random factor to account for spatial autocorrelation within populations. The response and competition variables were normalized applying natural logarithms and square root transformations, respectively. Starting from the saturated model, we created the fully crossed set of models and ranked them from lowest to highest AICc (second-order Akaike information criterion). From all best models (lowest AICc) within 2 AICc units we selected the simplest model, i.e. that with the lowest number of parameters. We decided to use biomass to quantify reproductive output and tree size to aid interpretation. However, we also fitted the models using the measured variables (N cones year^{-1} and dbh) and the results were essentially similar.

We used a mixed linear model to explore if there was a relationship between growth and reproduction within trees across the three years of measurement and to check if this relationship was modified by yearly vegetative biomass, changes in canopy defoliation or whether it varied between populations. To remove inter-individual differences in reproduction and defoliation, these two variables were centered around the mean value for each tree over the three years before including them in the model. Positive values of these centered variables in a given year indicated that the cone production (or defoliation) of the corresponding tree was above its average, while negative values indicated the opposite. As our main goal was to explore the existence of relationships modified by tree condition we recoded the centered defoliation variable as a dichotomic measure of defoliation change, with two levels: defoliation increase and defoliation decrease. Thus, the tree yearly BAI (cm^2 , $\ln$ transformed) was the response variable, centered cone production and vegetative biomass the covariates, and defoliation change

and population the factors. To check if the relationship between tree yearly BAI and centered cone production varied with inter-individual differences in vegetative biomass, defoliation change or population, the corresponding interaction terms were introduced in the model. Finally, we also included the interaction terms between vegetative biomass and defoliation change, between vegetative biomass and population, and between defoliation change and population. Tree nested within plot was introduced in the model as a random factor to account for the repeated measures across years and the spatial autocorrelation among trees within plots. Model selection was conducted based on AICc as explained before.

All model parameters were estimated by maximum likelihood and significance was accepted at $\alpha = 0.05$. The R^2 was estimated using a likelihood ratio statistic (Nagelkerke, 1991). Regarding model selection, all models within 2 AICc units of the selected one (and thus equivalent in terms of statistical explanatory power) are given in Appendix 1. In the results we only discuss the effects that were consistent across models. Statistical analyses were carried out with R software version 2.13.0 (R Development Core Team, 2011). Throughout the manuscript all values are given as mean $\pm$ SE.

Results

Decline at the plot level recorded in the first inventory was similar between the two populations with values around 45-50 %, standing mortality was around 12-14 % and defoliation of living individuals was around 50 % (Table 1a). At the individual level, mean defoliation of sampled Scots pines was around 40 % in the two populations, but Arcalís showed a marginally higher value (Table 1b). Growth rate was not significantly different between populations (Table 1b), whereas cone production was significantly higher in Prades than in Arcalís (Table 1b). Biomass allocated to growth was much higher than biomass allocated to reproduction, and Prades showed a significantly higher % of biomass allocated to reproduction than Arcalís (Table 1b). Cone production of sampled trees declined through time while growth increased in Arcalís, whereas the opposite trend was observed in Prades, suggesting an overall trade-off between growth and reproduction in the two populations (Figure 2).

Table 1. Main characteristics of the studied Scots pine stands (a) and of sampled Scots pines individuals (b). Mean $\pm$ SE values are shown.

(a) Plot characteristics	Arcalís	Prades
Number of plots	27	27
Altitude (m)	645 – 1383	849 – 1050
Annual precipitation (mm)	922	699
Annual temperature (°C)	9.6	11.6
Density of living trees (trees ha ⁻¹)	766 $\pm$ 74 a	337 $\pm$ 25 b
Basal area of living trees (m ² ha ⁻¹)	30.3 $\pm$ 2.5 a	35.0 $\pm$ 2.2 a
Mortality (%; 1st inventory)	12.4 $\pm$ 2.9 a	13.8 $\pm$ 1.6 a
Defoliation (%; 1st inventory)	49.6 $\pm$ 3.0 a	52.5 $\pm$ 1.8 a
Decline	49.5 $\pm$ 3.8 a	44.3 $\pm$ 2.0 a
(b) Sampled Scots pine characteristics		
Number of Scots pines	160	149
Vegetative biomass (Mg)	0.19 $\pm$ 0.01 a	0.56 $\pm$ 0.03 b
Defoliation 2008-2010 (%)	43.6 $\pm$ 1.3 a	37.7 $\pm$ 1.1 b
Cone production 2008 - 2010 (N Cones year ⁻¹)	17 $\pm$ 2 a	30 $\pm$ 2 b
Cone biomass production (g year ⁻¹)	129 $\pm$ 18 a	224 $\pm$ 17 b
Growth 2008 - 2010 (BAI [cm ² year ⁻¹])	5.97 $\pm$ 0.36 a	4.94 $\pm$ 0.27 a
Vegetative biomass production (Mg year ⁻¹)	0.0030 $\pm$ 0.0002 a	0.0042 $\pm$ 0.0003 b
Reproductive allocation (% year ⁻¹)	4.8 $\pm$ 0.6 a	6.7 $\pm$ 0.6 b
Growth allocation (% year ⁻¹)	95.2 $\pm$ 0.6 a	93.3 $\pm$ 0.6 b

Note: Different letters (*a* or *b*) between populations correspond to significant differences on the corresponding variable according to the statistical test indicated below. Plot level: general linear model for tree density, basal area, defoliation and decline; negative binomial-generalized linear model for the number of dead trees per plot including an offset of the total number of trees in the plot (very similar to modeling percentage of mortality). Individual level: general linear mixed model in all cases.

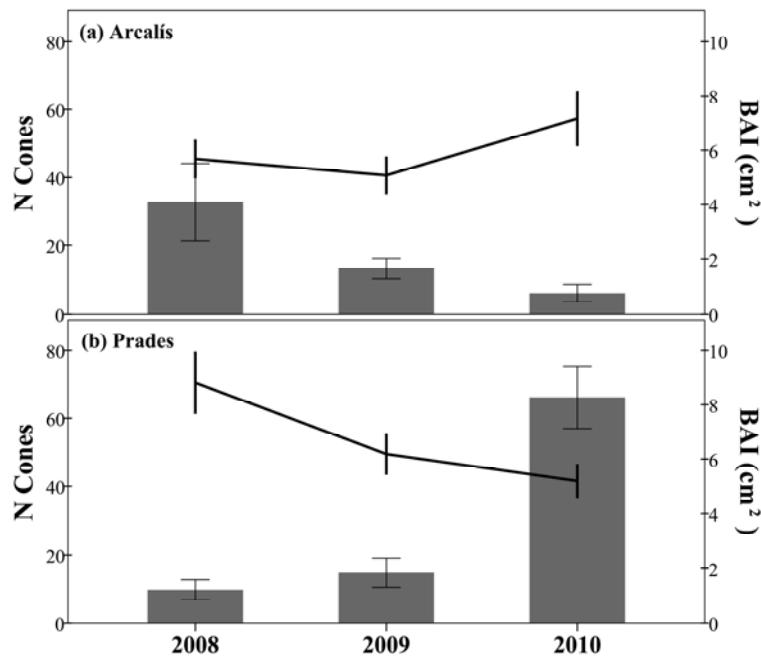


Figure 2. Annual cone production (mean $\pm$ SE; grey bars) and annual basal area increment (mean $\pm$ SE; solid lines) for the sampled Scots pines in Arcalís (a) and Prades (b).

Growth, cone biomass production and reproductive effort

The final growth model included the effect of vegetative biomass, basal area, defoliation, decline and population (Table 2). The variance explained by the growth model was 37% (Table 2). Growth rate was higher in Arcalís than in Prades (Table 2; Figure 3a-d). Growth increased less than linearly with tree size, meaning that the relative increase of BAI was lower for larger trees (Table 2; Figure 3a). Plot basal area had an opposite effect on BAI in the two populations: while in Arcalís the effect of basal area on growth was negative, this effect was positive in Prades (Table 2; Figure 3b). Tree defoliation and plot decline had an effect on growth rate but with opposite trends: defoliation had a negative effect on BAI and decline had a positive effect (Table 2; Figure 3c and Figure 3d).

Table 2. Summary of the growth, cone biomass production and reproductive effort models.

Fixed effect	Growth (BAI)	Cone biomass production	Cone biomass (%)
	Estimate $\pm$ SE	Estimate $\pm$ SE	Estimate $\pm$ SE
Intercept	0.011 $\pm$ 0.851	– 8.702 $\pm$ 4.473 ‡	– 10.086 $\pm$ 3.615 **
ln(Vegetative biomass)	0.222 $\pm$ 0.066 ***	1.225 $\pm$ 0.366 ***	1.024 $\pm$ 0.300 ***
Vegetative biomass	n.i	– 0.872 $\cdot 10^{-6} \pm 0.00$ ‡	– 0.144 $\cdot 10^{-5} \pm 0.00$ ***
sqrt(Competition)	n.i	– 0.428 $\pm$ 0.211 *	n.i
Basal area	– 0.014 $\pm$ 0.005 *	n.i	n.i
Defoliation	– 0.029 $\pm$ 0.004 ***	– 0.010 $\pm$ 0.005 ‡	n.i
Decline	0.011 $\pm$ 0.004 **	0.123 $\pm$ 0.072 ‡	0.112 $\pm$ 0.009 ‡
Prades	– 1.754 $\pm$ 0.362 ***	n.i	0.326 $\pm$ 0.164 ‡
Basal area x Prades	0.026 $\pm$ 0.008 **	n.i	n.i
Defoliation x Prades	0.012 $\pm$ 0.005 **	n.i	n.i
ln(Vegetative biomass) x Decline	n.i	– 0.012 $\pm$ 0.006 *	– 0.011 $\pm$ 0.005 *
R ²	0.37	0.39	0.26

Note: Arcalís was considered the reference level. Bold characters indicate significant ($p < 0.05$) or marginal ($p < 0.1$) effects. Abbreviations and symbols: n.i, not included; ‡, $p < 0.1$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

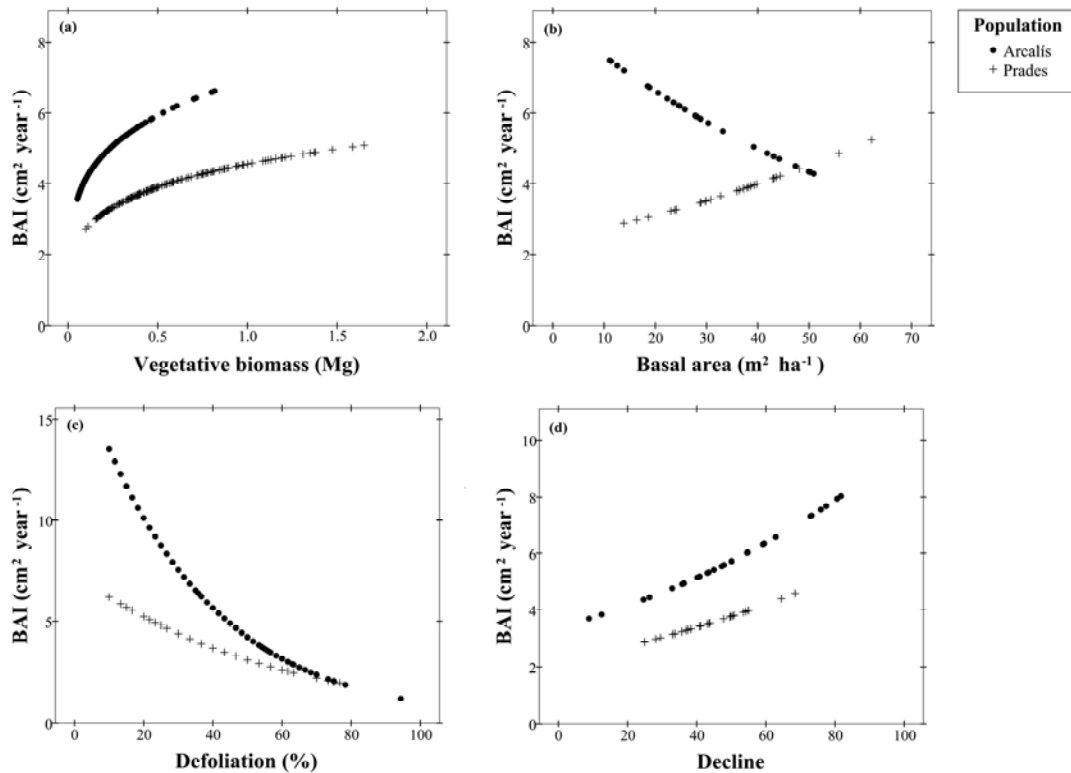


Figure 3. Predicted effects of vegetative biomass (a), basal area (b), defoliation (c) and decline (d) on annual basal area increment (BAI, growth model) in the two Scots pine populations. Regression coefficients are based on the fixed effects of the models shown in Table 2.

The variance explained by the final reproduction model (cone biomass production) was 39% (Table 2). Cone biomass production increased more than linearly with size (slope of $\ln(\text{reproductive to vegetative biomass}) > 1$ for small trees, but for larger trees it increased at a lower rate and eventually stabilized (Figure 4a). The allometry between cone biomass production and vegetative size varied through the gradient of decline (interaction $\ln[\text{vegetative biomass}] \times \text{decline}$; Table 2; Figure 4a). For small trees, the reproductive output was similar through the gradient of decline but, with increasing size, cone biomass production was lower in plots with higher levels of decline. Maximum biomass production occurred at smaller tree sizes under higher levels of decline (Table 2; Figure 4a). Finally, cone biomass production decreased with competition and defoliation (Table 2).

The final reproductive effort model (% cone biomass) included the effect of $\ln(\text{vegetative biomass})$, vegetative biomass, decline, population and the interaction $\ln(\text{vegetative biomass}) \times \text{decline}$, and explained 26 % of the variability in the response

variable (Table 2). At the population level, Prades showed a slightly higher % of cone biomass (Table 2). Consistent with the allometric relationships reported in the cone biomass production model, the percentage of cone biomass increased with vegetative biomass in smaller trees, reached a maximum at intermediate tree sizes and declined abruptly in larger trees (Figure 4b). There was a significant interaction between the effect of $\ln[\text{vegetative size}]$ and decline, so that the negative effect of decline on the % of cone biomass was greater on medium and large trees (Figure 4b). In addition, maximum allocation to cone biomass appeared to occur at smaller tree sizes under higher levels of decline (Figure 4b).

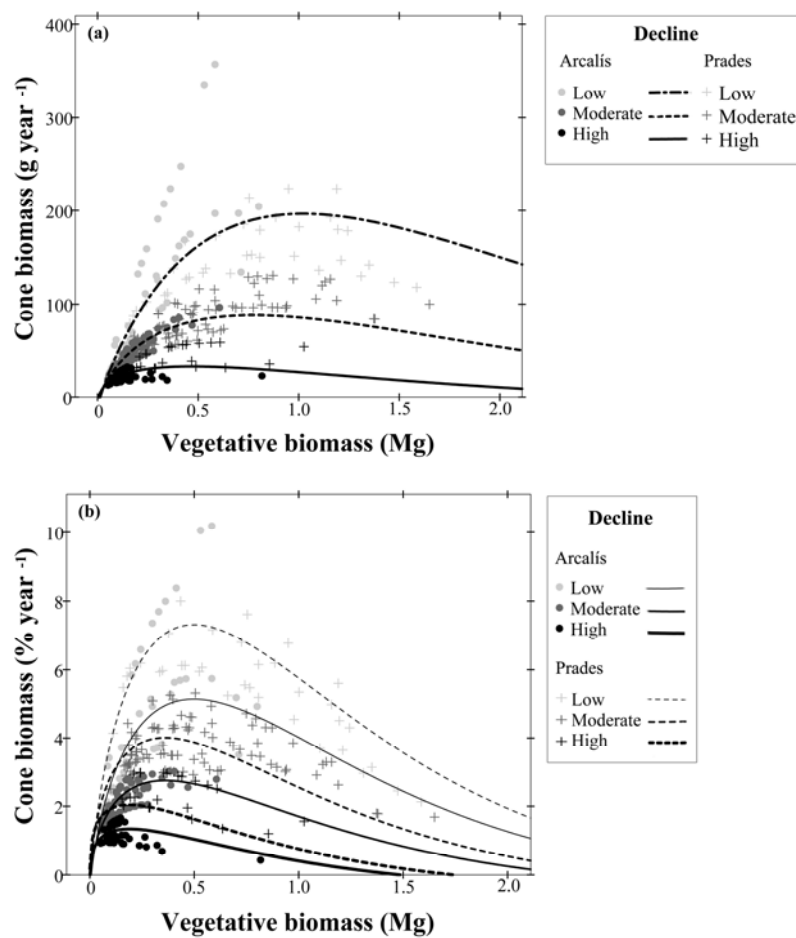


Figure 4. Predicted effects of vegetative biomass on cone biomass production (a), and on the percentage of cone biomass (b). The interaction between vegetative biomass and Decline is illustrated by categorizing the latter variable. The following levels of Decline were considered: low, including the plots belonging to the lower quartile (Decline < 36.80, N=13); high, including those plots in the upper quartile (Decline > 54.76, N=13); and moderate (the rest; N=28). Regression coefficients are based on the fixed effects of the models shown in Table 2.

Relationship between growth and reproduction within individuals

The best model of the relationship between growth and reproduction included the effect of vegetative biomass, centered cone production, defoliation change and population (Table 3). This model explained 65 % of the variance in BAI (Table 3). Consistent with previous models, Scots pines growth was higher in Arcalís than in Prades (Table 3; Figure 5) and vegetative biomass had a positive effect on BAI (Table 3). The model indicated that a higher than average cone production in a given year implied a lower BAI, suggesting a reproduction cost for growth (Table 3; Figure 5). Besides, the cost of reproduction was modified by population and defoliation change: the cost of reproduction was more pronounced in Prades (Table 3; Figure 5) and also was more noticeable when the tree experienced a higher defoliation with respect to the mean (defoliation change [increase]), both in Arcalís and Prades (Table 3; Figure 5).

Table 3. Summary of the model of the relationship between growth and reproduction within individuals. Basal area increment (BAI) is the response variable of the model.

Fixed effect	Estimate $\pm$ SE
Intercept	2.1084 $\pm$ 0.1431 ***
ln(Vegetative biomass)	0.3851 $\pm$ 0.0651 ***
Centered cone production	– 0.0029 $\pm$ 0.0008 ***
Centered defoliation [Decrease]	0.1438 $\pm$ 0.0337 ***
Prades	– 0.1692 $\pm$ 0.1311
Centered cone production x Prades	– 0.0014 $\pm$ 0.0007 *
Centered defoliation [Decrease] x Prades	– 0.1685 $\pm$ 0.0496 ***
Centered cone production x Centered defoliation [Decrease]	0.0024 $\pm$ 0.0010 *
R ²	0.65

Note: Arcalís (for population factor) and Increase (for Centered defoliation factor) were considered the reference levels. Bold characters indicate significant effects ($p < 0.05$). Abbreviations and symbols: *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$

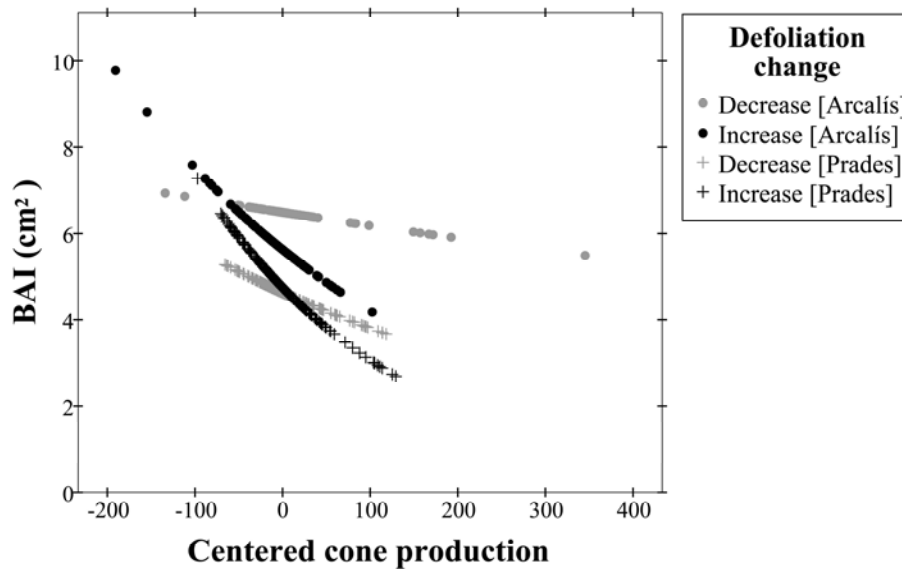


Figure 5. Predicted effect of centered cone production on basal area increment (BAI) in the model of the relationship between BAI and centered cone production. Regression coefficients are based on the fixed effects of the model shown in Table 3.

DISCUSSION

Variation in the efficiency to convert assimilation into reproductive biomass across plant sizes through environmental gradients is rarely documented (Weiner *et al.*, 2009; but see Guo *et al.*, 2012) and has been rarely evidenced in long-lived tree species (but see Climent *et al.*, 2008; Hulshof *et al.*, 2012). In this study we report that Scots pines show different patterns of size-dependent resource allocation and reproduction costs across individuals, and that these differences are associated with drought effects at the individual and plot levels.

Patterns of size-dependent vegetative and reproductive allocation

Our results highlight the importance of tree size to explain patterns of resource allocation to vegetative or reproductive functions among individuals. Although we found an increase of cone biomass production with size for the Scots pines studied, the reproductive output reached a maximum and stabilized at larger sizes (Figure 4a). This trend, together with the relative increase of growth with tree size (Figure 3a), resulted in a maximization of the reproductive effort (allocation to reproductive structures) at intermediate tree sizes and a decline at larger sizes (Figure 4b). This pattern has seldom

been reported (but see Climent *et al.*, 2008) and implies that the efficiency of the conversion of biomass production to reproductive output decreased for larger trees. The achievement of large sizes normally incurs in high costs for maintenance and transport (Mencuccini *et al.*, 2005), and the results reported here suggest that these costs could be proportionally higher for reproductive functions than for growth. In this sense, such costs may suggest conflicts in resource allocation with increasing size, because larger individuals could preferentially allocate the remaining resources to vegetative growth at the expense of reproduction.

Effects of defoliation and decline on reproductive allocation

Our results show that environmental constraints reflected at the tree level induce detrimental effects on Scots pine growth and reproduction. In this study crown defoliation was taken as a measure of tree-level stress, showing that stressed Scots pines had lower rates of growth (Figure 3c) and cone biomass production (Table 2). From an allometric perspective, the observed effects of defoliation on the intercept of the size-growth and size-cone biomass production trajectories suggests that healthy trees have higher efficiency in converting resources into growth and reproductive biomass than defoliated trees of the same size. Such patterns are consistent with many studies reporting growth reductions and reproductive failures under drought stress conditions (Montserrat-Martí *et al.*, 2009; Sánchez-Humanes & Espelta, 2011; Girard *et al.*, 2012), including Scots pines (Thabeet *et al.*, 2009; Hereş *et al.*, 2012; Martínez-Vilalta *et al.*, 2012). Drought-induced leaf-shedding leads to reduced photosynthetic area and has been related to carbon reserve depletion in one of the studied populations (Galiano *et al.*, 2011). In this context, lower growth and reproduction investment in more defoliated trees may reflect a lower availability of carbon or a higher investment to refill the decimated stores (cf., Sala *et al.*, 2012). It should be noted, however, that resource depletion associated with reproductive effort may be as important for nutrients such as N and P as for carbon, as reproductive structures tend to be nutrient enriched relative to vegetative biomass (Sala *et al.*, 2012b).

Forest decline at the plot level induced differential responses between Scots pine growth and reproductive biomass production. An overall increase of growth rates was detected under more pronounced decline conditions (Figure 3d). This can result from stabilizing processes after forest decline events, as drought-induced Scots pine mortality could be

compensated by a release of competition, enhancing growth and future survival (Lloret *et al.*, 2012). However, the opposite pattern was observed for the reproductive biomass production (Figure 4a), indicating that trees in declining plots invested preferentially in growth at the expense of reproduction, which could be an strategy to reduce the reproductive cost and gain access to further resources for their long-term survival (Sakai *et al.*, 2006). Furthermore, we found a change in the allometric intercept and slope between reproductive biomass and vegetative biomass through the gradient of decline (Table 2). Therefore, reproductive investment and effort were lower overall under decline but the divergence was more pronounced for larger trees (Figure 4). Although we must be cautious, such patterns of allometric resource allocation to vegetative and reproductive functions should be interpreted together, and under a context of forest decline related with stressful conditions in these populations (Vilà-Cabrera *et al.*, in press). In this sense, it can be suggest that the larger the individual, the higher is the proportional investment in vegetative growth under stressful conditions (high decline), constraining the rate of resource conversion to reproductive biomass. Conversely, when conditions are favorable (low decline), the larger the individual, the higher is the investment of resources into reproductive biomass at the expense of vegetative growth. The previous explained variation in reproductive allometry across the gradient of decline, and the fact that this variation was lower at small sizes may be related to the “reproductive economy” concept (Aarssen, 2008) in populations under stress conditions such as droughts in our study. If larger trees allocate limited resources to vegetative growth under constrained conditions (i.e. high levels of decline) at the expense of reproduction, then smaller (or intermediate sized) trees could be more efficient than larger ones in the use of space and resources. In this sense, a change in the reproduction-size trajectory through the gradient of decline represents a change in resource allocation strategies between individuals according to its size (small vs. large) and to the level of decline (low vs. high).

Trade-off expression: the cost of reproduction

Our results showed a clear negative relationship between BAI and centered cone production within individuals (Figure 5), suggesting a trade-off expression and a reproduction cost for growth. The existence of a trade-off is consistent with the switching hypothesis that postulates the diversion of resources to reproduction in some years, and investment to vegetative growth in other years (Norton & Kelly, 1988).

Larger trees showed higher BAI values, but the steepness (i.e. slope) of the trade-off did not vary according to inter-individual differences in size and, consequently, the relative cost of reproduction within individuals across years appeared to be similar between trees. Conversely, the cost of reproduction shifted with the defoliation change (centered defoliation) implying a stronger trade-off under more stressful conditions. Since canopy defoliation incurs in reductions of carbon assimilation and nutrient acquisition in general, available resources become scarcer and trade-offs could emerge suggesting physiological constraints in resource allocation among functions.

Conclusions

In conclusion, our results show that drought-induced forest decline is associated with differences in biomass allocation between growth and reproduction in Scots pine, both at the plot- and individual levels. Cone production is lower in declining plots and, within them, it is even lower in defoliated trees. These results support the notion that stressful conditions are constraining resource allocation to reproduction even more than growth. At the same time, they may contribute to explain the low regeneration of Scots pine in drought-affected populations (Galiano *et al.*, 2010; Vilà-Cabrera *et al.*, in press), in contrast to recent studies reporting that a limited seedling establishment under ecological constraints may be offset by an increase of seed production (Silva *et al.*, 2012). Taken together with the high mortality rates observed in several Scots pine populations in the Mediterranean region (Martínez-Vilalta *et al.*, 2002; Galiano *et al.*, 2010; Vilà-Cabrera *et al.*, in press), these results suggest that the long-term maintenance of some of these populations may be compromised.

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LITERATURE CITED

- Aarssen, L.W. (2008)** Death without sex – the ‘problem of the small’ and selection for reproductive economy in flowering plants. *Evolutionary Ecology*, 22: 279-298.
- Aber, J., Neilson, R.P., McNulty, S., Lenham, J.M., Bachelet, D. & Drapek, R.J. (2001)** Forest processes and global environmental change: the effects of individual and multiple stressors on forests. *BioScience*, 51: 735-751.
- Adams, H.D. & Kolb, T.E. (2005)** Tree growth response to drought and temperature in a mountain landscape in northern Arizona, USA. *Journal of Biogeography*, 32: 1629-1640.
- Agundez, D., Alía, R., Diez, R., Gil, L. & Pardos, J.A. (1992)** Variación de *Pinus sylvestris* L. en España: características de piñas y piñones. *Investigación agraria. Sistemas y recursos forestales*, 1: 151-162.
- Barringer, B.C., Koeing, W.D. & Knops, J.M.H. (2012)** Interrelationships among life-history traits in three California oaks. *Oecologia*, DOI 10.1007/s00442-012-2386-9.
- Bazzaz, F.A., Ackerly, D.D. & Reekie, E.G. (2000)** Reproductive allocation in plants. - In: Fenner, M. (ed.), *Seeds: the ecology of regeneration in plant communities*. CAB International, pp. 1-29.
- Burriel, J.A., Gracia, C., Ibáñez, J.J., Mata, T. & Vayreda, J. (2000-2004)** Inventari ecològic i forestal de Catalunya. Catalunya, 10 Volumes. CREAF, Bellaterra (Catalunya).
- Carnicer, J., Coll, M., Ninyerola, M., Pons, X., Sánchez, G. & Peñuelas, J. (2011)** Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought. *Proceedings of the National Academy of Sciences, USA*, 108: 1474-1478.
- Climent, J., Prada, M.A., Calama, R., Chambel, M.R., Sánchez de Ron, D. & Alía, R. (2008)** To grow or to seed: ecotypic variation in reproductive by young female Aleppo pine (*Pinus halepensis*, Pinaceae). *American Journal of Botany*, 95: 833-842.
- Cousens, J.E. (1988)** Report of a 12-year study of litterfall and productivity in a stand of mature Scots pine. *Forestry*, 61: 255–266.
- Davies, S.J. (2001)** Tree mortality and growth in 11 sympatric *Macaranga* species in Borneo. *Ecology*, 82: 920-932.
- Despland, E. & Houle, G. (1997)** Climate influences on growth and reproduction of *Pinus banksiana* (Pinaceae) at the limit of the species distribution in eastern North America. *American Journal of Botany*, 84: 928–937.
- Di Filippo, A., Biondi, F., Maugeri, M., Schirone, B. & Piovesan, G. (2012)** Bioclimate and growth history affect beech lifespan in the Italian Alps and Apeninnes. *Global Change Biology*, 18: 960-972.
- El Kassaby, Y.A. & Barclay, H.J. (1992)** Cost of reproduction in Douglas fir. *Canadian Journal of Botany*, 70: 1429-1432.
- Espelta, J.M., Cortés, P., Molowny-Horas, R., Sánchez-Humanes, B. & Retana, J. (2008)** Masting mediated by summer drought reduces acorn predation in Mediterranean oak forests. *Ecology*, 89: 805-817.
- Espelta, J.M., Arnan, X. & Rodrigo, A. (2011)** Non-fire induced seed release in a weakly serotinous pine: climatic factors, maintenance costs or both? *Oikos*, 120: 1752-1760.

- Galiano, L., Martínez-Vilalta, J. & Lloret, F. (2010)** Drought-induced multifactor decline of Scots pine in the Pyrenees and potential vegetation change by the expansion of co-occurring oak species. *Ecosystems*, 13: 978–991.
- Galiano, L., Martínez-Vilalta, J. & Lloret, F. (2011)** Carbon reserves and canopy defoliation determine the recovery of Scots pine four years after a drought episode. *New Phytologist*, 190: 750–759.
- García, D., Zamora, R., Gómez, J.M., Jordano, P. & Hódar, J.A. (2000)** Geographical variation in seed production, predation and abortion in *Juniperus communis* throughout its range in Europe. *Journal of Ecology*, 88: 436–446.
- Girard, F., Vennetier, M., Guibal, F. Corona, C., Ouarmim, S. & Herrero, A. (2012)** *Pinus halepensis* Mill. crown development and fruiting declined with repeated drought in Mediterranean France. *European Journal of Forest Research*, 4: 919–931.
- Gómez-Aparicio, L., García-Valdés, R., Ruíz-Benito, P. & Zavala, M.A. (2011)** Disentangling the relative importance of climate, size and competition on tree growth in Iberian forests: implications for forest management under global change. *Global Change Biology*, 17: 2400–2414.
- Gràcia, M. & Ordóñez, J.L. (2011)** Les pinesdes de pi roig. Manuals de gestió d'hàbitats. Diputació de Barcelona.
- Guo, H., Weiner, J., Mazer, S.J., Zhao, Z., Du, G. & Li, B. (2012)** Reproductive allometry in *Pedicularis* species changes with elevation. *Journal of Ecology*, 100: 452–458.
- Harper, J.L. (1977)** Population biology of plants. London, UK: Academic press.
- Hegyi, F. (1974)** A simulation model for managing jackpine stands. In: Fries J, Ed. Growth models for tree and stand simulation. Stockholm: Royal College of Forestry. p 74–90.
- Hereş, A.M., Martínez-Vilalta, J. & López, J.C. (2012)** Growth patterns in relation to drought induced mortality at two Scots pine (*Pinus sylvestris* L.) sites in NE Iberian Peninsula. *Trees*, 26: 621–630.
- Hulshof, C.M., Stegen, J.C., Swenson, N.G., Enquist, C.A.F. & Enquist, B.J. (2012)** Interannual variability of growth and reproduction in *Bursera simaruba*: the role of allometry and resource variability. *Ecology*, 93: 180–190.
- Kobe, R.K. (1996)** Intraspecific variation in sapling mortality and growth predicts geographic variation in forest composition. *Ecological Monographs*, 66: 181–201.
- Lloret, F., Siscart, D. & Dalmases, C. (2004)** Canopy recovery after drought dieback in holm oak Mediterranean forests of Catalonia (NE Spain). *Global Change Biology*, 10: 2092–2099.
- Lloret, F., Escudero, A., Iriondo, J.M., Martínez-Vilalta, J. & Valladares, F. (2012)** Extreme climatic events and vegetation: the role of stabilizing processes. *Global Change Biology*, 18: 797–805.
- Linares, J.C. & Camarero, J.J. (2011)** From pattern to process: linking intrinsic water-use efficiency to drought induced forest decline. *Global Change Biology*, 18: 1000–1015.
- Martínez-Vilalta, J. & Piñol, J. (2002)** Drought-induced mortality and hydraulic architecture in pine populations of the NE Iberian Peninsula. *Forest Ecology and Management*, 161: 247–256.
- Martínez-Vilalta, J., López, B.C., Loepfe, L. & Lloret, F. (2012)** Stand- and tree-level determinants of the drought response of Scots pine radial growth. *Oecologia*, 168: 877–888.
- Mencuccini, M., Martínez-Vilalta, J., Vanderklein, D., Hamid, H.A., Korakaki, E., Lee, S. & Michiels, B. (2005)** Size-mediated ageing reduces vigour in trees. *Ecology Letters*, 8: 1183–1190.

- Monks, A. & Kelly, D. (2006)** Testing the resource-matching hypothesis in the mast seeding tree *Nothofagus truncata* (Fagaceae). *Austral Ecology*, 31: 366-375.
- Monserat-Martí, G., Camarero, J.J., Palacio, S., Pérez-Rontomé, C., Milla, R., Albuixech, J. & Maestro, M. (2009)** Summer-drought constrains the phenology and growth of two co existing Mediterranean oaks with contrasting leaf habit: implications for their persistence and reproduction. *Trees*, 23: 787-799.
- Mutke, S., Gordo, J. & Gil, L. (2005)** Variability of Mediterranean Stone pine cone production: yield loss as response to climate change. *Agricultural Forest Meteorology*, 132: 263-72.
- Nagelkerke, N.J.D. (1991)** A note on a general definition of the coefficient of determination. *Biometrika*, 78: 691-692.
- Niklas, K.J. & Enquist, B.J. (2003)** An allometric model for seed plant reproduction. *Evolutionary Ecology Research*, 5: 79-88.
- Norton, D.A. & Kelly, D. (1988)** Mast seeding over 33 years by *Dacrydium cupressinum* Lamb (rimu) (Podocarpaceae) in New Zealand: the importance of economies of scale. *Functional Ecology*, 2: 399-408.
- Pérez-Ramos, I.M., Ourcival, J.M., Limousin, J.M., Rambal, S. (2010)** Mast seeding under increasing drought: results from a long-term dataset and from a rainfall exclusion experiment. *Ecology*, 91: 3057-3068.
- Petit, R.J. & Hampe, A. (2006)** Some evolutionary consequences of being a tree. *The Annual Review of Ecology, Evolution, and Systematics*, 37: 187-214.
- R Development Core Team. (2009)** R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. URL www.r-project.org/.
- Reznick, D. (1985)** Costs of reproduction: An evaluation of the empirical evidence. *Oikos*, 44: 257-267.
- Russo, S.E., Brown, P., Tan, S. & Davies, S.J. (2008)** Interspecific demographic trade-offs and soil-related habitat associations of tree species along resource gradients. *Journal of Ecology*, 96: 192-203.
- Sakai, A., Sasa, A. & Sakai, S. (2006)** Do sexual dimorphisms in reproductive allocation and new shoot biomass increase with an increase of altitude? A case of the shrub willow *Salix reinii* (Salicaceae). *American Journal of Botany*, 93: 988-992.
- Sala, A., Woodruff, D.R., Meinzer & F.C. (2012)** Carbon dynamics in trees: feast or famine? *Tree Physiology*, 32: 764-775.
- Sala, A., Hopping, K., McIntire, E.J.B., Delzon, S. & Crone, E.E. (2012b)** Mast seeding in whitebark pine (*Pinus albicaulis*) depletes stored nutrients. *New Phytologist*, 196: 189-199.
- Sánchez-Humanes, B., Sork, V.L. & Espelta, J.M. (2010)** Trade-offs between vegetative growth and acorn production in *Quercus lobata* during a mast year: the relevance of crop size and hierarchical level within the canopy. *Oecologia*, 166: 101-110.
- Sánchez-Humanes, B. & Espelta, J.M. (2011)** Increased drought reduces acorn production in *Quercus ilex* coppices: forest management mitigates this effect but only in the short term. *Forestry*, 84: 73-82.
- Sánchez-Salguero, R., Navarro-Cerrillo, R.M., Camarero, J.J., Fernández-Cancio, A. (2012)** Selective drought-induced decline of pine species in southeastern Spain. *Climatic Change*, 113: 767-785.

- Silva, D.E., Mazzella, P.R., Legay, M., Corcket, E. & Dupouey, J.L. (2012)** Does natural regeneration determine the limit of European beech distribution under climatic stress? *Forest Ecology and Management*, 266: 263-272.
- Silvertown, J. & Dodd, M. (1999)** The demographic cost of reproduction and its consequences in Balsam fir. *American Naturalist*, 29: 321-332.
- Stearns, S.C. (1992)** The Evolution of Life Histories. Oxford University Press, Oxford.
- Thabeet, A., Vennetier, M., Gadbin-Henry, C., Denelle, N., Roux, M., Caraglio, Y. & Vila, B. (2009)** Response of *Pinus sylvestris* L. to recent climatic events in the French Mediterranean region. *Trees*, 23: 843-853.
- Vilà-Cabrera, A., Martínez-Vilalta, J., Galiano, L. & Retana, J. (2012)** Patterns of forest decline and regeneration across Scots pine populations. *Ecosystems*, in press.
- Weiner, J. (2004)** Allocation, plasticity and allometry in plants. *Perspectives in Plant Ecology Evolution and Systematics*, 6: 207-215.
- Weiner, J., Campbell, L.G., Pino, J. & Echarte, L. (2009)** The allometry of reproduction within plant populations. *Journal of Ecology*, 97: 1220-1233.
- Yasumura, Y. (2006)** Resource allocation to vegetative and reproductive growth in relation to mast seeding in *Fagus crenata*. *Forest Ecology and Management*, 229: 228-233.
- Zlotin, R.I. & Parmeter, R.R. (2008)** Patterns of mast production in pinyon and juniper woodlands along a precipitation gradient in central New Mexico (Seville National Wildlife Refuge). *Journal of Arid Environment*, 72: 1562-72.

APPENDIXES

Appendix 1. Fully set of all best models (lowest AICc) within 2 AIC and ranked them from lowest to highest AICc (second-order Akaike information criterion).

Table Appendix 1a. Growth models. The direction of the predictor effects is shown. Significant effects are in orange and marginal effects in grey. Symbols: +, positive effect; –, negative effect; n.i, not included.

Growth models	M1	M2	M3	M4	M5	M6	M7	M8
N parameters	9	10	10	10	8	10	11	9
AICc	589.6	590.3	590.8	590.9	591.1	591.4	591.5	591.5
R ²	0.37	0.38	0.38	0.38	0.37	0.38	0.38	0.38
Intercept	+	+	–	+	+	+	+	+
ln(Vegetative biomass)	+	–	+	+	+	+	–	+
sqrt(Competition)	n.i	n.i	n.i	n.i	n.i	n.i	n.i	–
Basal area	–	–	+	–	–	–	–	–
Defoliation	–	–	–	–	–	–	–	–
Decline	+	+	+	+	+	–	+	+
Prades	–	–	–	–	–	–	–	–
ln(Vegetative biomass) x Prades	+	+	+	+	n.i	+	+	+
Basal area x Prades	+	+	+	+	+	+	+	+
Defoliation x Prades	+	+	+	+	+	+	+	+
Decline x Prades	n.i	n.i	n.i	–	n.i	n.i	–	n.i
ln(Vegetative biomass) x Basal area	n.i	n.i	–	n.i	n.i	n.i	n.i	n.i
ln(Vegetative biomass) x Defoliation	n.i	+	n.i	n.i	n.i	n.i	+	n.i
ln(Vegetative biomass) x Decline	n.i	n.i	n.i	n.i	n.i	+	n.i	n.i

Table Appendix 1b. Reproduction models (cone biomass production). The direction of the predictor effects is shown. Significant effects are in orange and marginal effects in grey. Symbols: +, positive effect; –, negative effect; n.i., not included.

Reproduction models	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12	M13	M14	M15	M16	M17	M18	M19
N parameters	11	10	11	12	12	7	12	8	10	10	11	12	12	11	11	9	12	7	12
AICc	912.9	913.3	913.3	914.0	914.1	914.1	914.4	914.5	914.5	914.6	914.6	914.7	914.7	914.7	914.7	914.8	914.8	914.9	914.9
R²	0.41	0.41	0.41	0.42	0.42	0.39	0.42	0.40	0.40	0.41	0.41	0.42	0.41	0.41	0.41	0.40	0.41	0.39	0.41
Intercept	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ln(Vegetative biomass)	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Vegetative biomass	n.i.	n.i.	n.i.	+	n.i.	–	n.i.	–	+	n.i.	–	+	–	+	n.i.	n.i.	n.i.	+	+
sqrt(Competition)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Basal area	+	+	+	+	+	n.i.	+	n.i.	+	+	+	+	+	+	+	+	+	n.i.	+
Defoliation	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Decline	+	+	+	–	+	+	+	+	–	+	+	+	+	+	+	+	+	–	–
Prades	–	–	–	–	–	n.i.	–	+	+	–	–	–	–	–	–	+	–	n.i.	–
Basal area x Prades	+	+	+	+	+	n.i.	+	n.i.	n.i.	n.i.	+	+	+	+	+	n.i.	+	n.i.	+
Defoliation x Prades	n.i.	n.i.	+	n.i.	+	n.i.	n.i.	n.i.	n.i.	+	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.
Decline x Prades	+	n.i.	n.i.	+	+	n.i.	+	n.i.	n.i.	n.i.	n.i.	+	+	n.i.	n.i.	n.i.	+	n.i.	+
ln(Vegetative biomass) x sqrt(Competition)	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	+	n.i.	n.i.
ln(Vegetative biomass) x Basal area	–	–	–	n.i.	–	n.i.	–	n.i.	n.i.	–	–	n.i.	–	n.i.	–	–	–	n.i.	–
Vegetative biomass x Basal area	n.i.	n.i.	n.i.	–	n.i.	n.i.	n.i.	n.i.	–	n.i.	n.i.	–	n.i.	–	n.i.	n.i.	n.i.	n.i.	n.i.
ln(Vegetative biomass) x Defoliation	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	+	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	+	n.i.	n.i.	n.i.	n.i.
ln(Vegetative biomass) x Decline	–	–	–	n.i.	–	–	–	–	n.i.	–	–	–	–	–	–	–	–	n.i.	n.i.
Vegetative biomass x Decline	n.i.	n.i.	n.i.	–	n.i.	n.i.	n.i.	n.i.	–	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	–	–

Table Appendix 1c. Reproductive effort models (% cone biomass). The direction of the predictor effects is shown. Significant effects are in orange and marginal effects in grey. Symbols: +, positive effect; –, negative effect; n.i., not included.

Reproductive effort models	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12	M13	M14	M15	M16	M17	M18	M19	M20	M21	M22
N parameters	7	6	8	8	7	7	6	7	9	6	9	8	8	8	7	8	9	8	8	8	7	8
AICc	797.2	797.4	797.9	797.9	798.2	798.3	798.3	798.4	798.6	798.7	798.7	798.8	798.8	798.8	798.9	799.0	799.1	799.1	799.2	799	799	799
R²	0.27	0.26	0.27	0.27	0.26	0.26	0.26	0.26	0.27	0.26	0.27	0.27	0.27	0.27	0.26	0.27	0.27	0.27	0.27	0.27	0.26	0.27
Intercept	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ln(Vegetative biomass)	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Vegetative biomass	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+
sqrt(Competition)	n.i.	n.i.	n.i.	–	n.i.	–	n.i.	n.i.	+	n.i.	–	+	–	n.i.	–	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.
Defoliation	+	n.i.	+	+	n.i.	n.i.	+	+	+	n.i.	+	n.i.	+	+	+	+	+	+	+	+	+	+
Decline	+	+	+	+	+	+	+	–	+	–	+	+	–	+	+	+	+	+	+	+	+	–
Prades	+	+	–	+	–	+	n.i.	+	+	+	–	+	+	–	n.i.	+	–	+	+	+	–	n.i.
ln(Vegetative biomass) x Prades	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	+	n.i.	n.i.	+	n.i.	n.i.	n.i.	+	n.i.
Vegetative biomass x Prades	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.
Defoliation x Prades	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	+	n.i.	n.i.	n.i.
Decline x Prades	n.i.	n.i.	+	n.i.	+	n.i.	n.i.	n.i.	n.i.	n.i.	+	n.i.	n.i.	n.i.	n.i.	n.i.	+	n.i.	n.i.	n.i.	n.i.	+
Vegetative biomass x sqrt(Competition)	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	–	n.i.	n.i.	–	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.
ln(Vegetative biomass) x Defoliation	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	–	n.i.	n.i.	n.i.	n.i.
Vegetative biomass x Defoliation	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	–	n.i.	n.i.	n.i.	–	n.i.	n.i.
ln(Vegetative biomass) x Decline	–	–	–	–	–	–	–	n.i.	–	n.i.	–	–	n.i.	–	–	–	–	–	–	–	–	n.i.
Vegetative biomass x Decline	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	–	n.i.	–	n.i.	n.i.	–	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	–

Table Appendix 1d. Models of the relationship between growth and reproduction. The direction of the predictor effects is shown. Significant effects are in orange and marginal effects in grey. Symbols: +, positive effect; –, negative effect; n.i, not included.

Growth–Reproduction relationship models	M1	M2	M3	M4
N parameters	8	9	9	10
AICc	1413.0	1413.1	1413.3	1413.4
R²	0.65	0.65	0.65	0.65
Intercept	+	+	+	+
ln(Vegetative biomass)	+	+	+	+
Centered cone production	–	–	–	–
Centered defolition [decrease]	+	+	+	+
Prades	–	–	+	+
ln(Vegetative biomass) x Prades	n.i	n.i	+	+
Centered cone production x Population	–	–	–	–
Centered defolition [decrease] x Prades	–	–	–	–
ln(Vegetative biomass) x Centered defolition [decrease]	n.i	+	n.i	+
Centered cone production x Centered defolition [decrease]	+	+	+	+

VI. DISCUSSIÓ GENERAL

En aquesta tesi hem estudiat la variació dels principals patrons demogràfics i de declivi del pi roig (*Pinus sylvestris* L.) a diferents escales espacials en funció de l'estructura de les seves poblacions i de les interaccions biòtiques entre els seus individus, així com al llarg de gradients climàtics, de disponibilitat de recursos, d'estrès i de gestió. Aquesta variació l'hem entès com una resposta diferencial dels processos demogràfics i de declivi de l'espècie en un context de post-pertorbació relacionada amb els canvis que estan soffrint els ecosistemes forestals degut a l'alteració dels usos dels territori i del bosc, així com al canvi climàtic i de les pertorbacions que se'n deriven, i.e. els focs i les sequeres. A la introducció hem plantejat un seguit de preguntes que, a partir dels resultats dels quatre capítols anteriors, intentarem respondre.

5. EL PI ROIG I ELS SEUS BOSCOS SÓN VULNERABLES AL FOC? EL FOC POT INDUIR CANVIS EN LA VEGETACIÓ EN ZONES ACTUALMENT DOMINADES PEL PI ROIG?

(1a) VULNERABILITAT AL FOC DELS BOSCOS DE PI ROIG

El pi roig i els seus boscos són especialment vulnerables als focs de capçada. Tot i que *a priori* aquesta afirmació pot semblar molt contundent, tenim el suport de dos resultats importants: l'augment del risc d'incendi dins de l'àrea de distribució de l'espècie a la península Ibèrica i la seva incapacitat de restabliment després d'un incendi. Encara que durant les últimes 3 dècades els focs de capçada han afectat una proporció petita dels boscos dominats per pi roig a Catalunya, la superfície cremada no és negligible donat que l'espècie ocupa zones muntanyoses on els incendis de capçada no hi són freqüents (Pausas *et al.*, 2008). Aquests incendis s'han concentrat en zones àrides i subhúmedes indicant que el clima juga un paper important en el control de l'ocurrència dels incendis (Pausas & Fernández-Muñoz, 2011). D'altra banda, hem pogut veure que el 32% dels boscos espanyols de pi roig són climàticament similars als boscos cremats a Catalunya i que aquest percentatge podria augmentar fins al 66% sota un escenari conservatiu de canvi climàtic. Aquest fet confirma que, sota les condicions climàtiques actuals, una tercera part dels boscos de pi roig al seu límit de distribució sud-oest són climàticament vulnerables al foc i que el canvi climàtic podria modificar-ne substancialment el règim d'incendis en aquestes zones.

En l'escenari actual d'augment de l'ocurrència i mida dels focs de capçada a la conca Mediterrània (Pausas & Fernández-Muñoz, 2011), la capacitat regenerativa de les espècies esdevé clau en l'èxit de recuperació de l'estructura i composició del bosc. En el cas del pi roig, però, aquesta recuperació no es dona ja que hem pogut constatar la seva pràcticament nul·la capacitat de restabliment. Aquest fracàs és el resultat combinat de les característiques pròpies de l'espècie i de l'estacionalitat dels incendis. Donat que el pi roig és una espècie no seròtina (Tapias *et al.*, 2004), els bancs de llavors de l'any en curs presents a les capçades dels pins o al sòl són l'únic recurs que té per regenerar-se dins la zona cremada. Malauradament, a la conca Mediterrània els incendis es produeixen normalment a l'estiu, just després de la dispersió de les llavors de l'espècie, entre finals d'hivern i la primavera (Castro *et al.*, 2004). D'aquesta manera, durant un foc de capçada el banc de llavors de les capçades (i.e. a les pinyes) es destrueix o ja és buit, les plàntules que han germinat i crescut durant la primavera moren cremades i les llavors que han quedat al sòl no sobreviuen a les elevades temperatures (Habrouk *et al.*, 1999). Per tant, existeix un desacoblament entre la fenologia de l'espècie i l'ocurrència dels incendis que anul·la qualsevol recurs de regeneració dins l'àrea afectada, especialment per incendis de grans dimensions (Retana *et al.*, 2002). El fracàs regeneratiu del pi roig dins la zona afectada pel foc porta als límits del bosc no cremats a ser el principal recurs de restabliment per a l'espècie. En aquest treball, però, hem provat que aquest procés és molt lent donat que després de més de 25 anys la majoria dels nous individus establerts en la zona cremada es troben a menys de 25 metres dels marges de l'incendi, distàncies força semblats a les assolides per altres espècies de pins (Nathan *et al.*, 2000; Rodrigo *et al.*, 2007). A més, aquesta lenta taxa de restabliment des dels marges pot veure's encara més limitada pel temps que necessita un nou individu establert per assolir la maduresa sexual, estimada en aquest estudi al voltant de 15 anys.

(1b) CANVIS EN LA VEGETACIÓ

Se'ns dubte s'han produït canvis en la vegetació a les zones ocupades pel pi roig que han patit incendis durant els últims anys i, si l'ocurrència de focs de capçada tendeix a l'augment, se'n produiran més en el futur. Els inventaris que hem realitzat en les zones cremades, a part d'una presència gairebé nul·la de pi roig, indiquen que altres espècies d'arbres i arbustos (majoritàriament rebrotadores) són el nou estrat forestal dominant i, per tant, que s'ha produït un canvi absolut en la composició de la

vegetació. Aquests canvis ja han estat observats en alguns llocs (Espelta *et al.*, 2002) i les nostres projeccions basades en models demogràfics indiquen que després d'un foc de capçada en un bosc de pi roig la comunitat seguirà la mateixa trajectòria. Així doncs, podem esperar que la vulnerabilitat climàtica al foc de l'espècie i el seu fracàs regeneratiu postincendi posaran en risc la persistència de les seves poblacions més meridionals, les quals seran reemplaçades per altres espècies amb una major capacitat regenerativa.

6. COM SÓN ELS PATRONS DEMOGRÀFICS DELS BOSCOS DE PI ROIG DE LA PENÍNSULA IBÈRICA AL LLARG DELS GRADIENTS CLIMÀTICS I ESTRUCTURALS DEL BOSC? HI TENEN ALGUNA COSA A DIR LES SEQUERES? ESTÀ EN DECLIVI EL PI ROIG?

(2a) DETERMINATS ESTRUCTURALS DELS PATRONS DEMOGRÀFICS

Els nostres resultats indiquen que els patrons demogràfics dels boscos de pi roig al conjunt de la península Ibèrica estan regits per l'estructura del bosc i, per tant, pels processos d'autotala i competència que es produeixen en les seves poblacions. Aquest resultat no és sorprenent en el context de la teoria del desenvolupament forestal, ja que molts d'aquests boscos són relativament joves i densos i es trobaven en l'etapa d'exclusió de peus (Oliver & Larsson, 1990), on l'autotala podria ser la principal causa dels patrons emergits en les taxes demogràfiques de mortalitat i creixement (Lutz & Halpern, 2006). Aquests processos també poden explicar l'escassa regeneració que presenta l'espècie. El fet que les taxes de regeneració i mortalitat es relacionin negativament indica que la mort d'alguns arbres no és suficient per originar una obertura de la coberta prou gran que estimuli l'establiment i el desenvolupament de nous individus. Per tant, el reclutament de l'espècie es troba limitat per l'actual estructura del bosc i no sembla existir un mecanisme que compensi la mort dels individus adults.

(2b) L'EFECTE DE LES SEQUERES

En general, hem pogut observar que a l'escala de la península Ibèrica l'efecte de les sequeres és relativament dèbil i condicionat als atributs estructurals del bosc. Per una banda, hem pogut detectar que les taxes de mortalitat més elevades es

concentren en llocs climàticament àrids i en zones que han experimentat períodes de sequera. Tot i això, aquests efectes climàtics són relativament petits i interaccionen amb l'estructura del bosc, concretament en boscos on hi ha arbres grans. Això suggereix que la competència pels recursos té un efecte negatiu per a la supervivència dels arbres en aquests boscos, procés que a més pot veure's exacerbat quan hi ha sequera (Klos *et al.*, 2009, Linares *et al.*, 2009). D'altra banda, els nostres resultats mostren com els boscos situats en zones més seques tenen unes taxes de creixement menors, però que l'efecte dels períodes de sequera és major en boscos humits. Així doncs, a una escala regional els resultats obtinguts suggereixen que l'efecte de les sequeres és secundari (de moment), que els boscos situats en zones climàtiques més idònies (i.e., més humides) podrien ser també vulnerables a l'estrès hídric i posen de manifest el destacat paper dels atributs estructurals del bosc com a moduladors dels processos demogràfics i de l'adaptació i vulnerabilitat del pi roig sota condicions canviants del clima (Linares *et al.*, 2010).

(2c) EL DECLIVI DEL PI ROIG

A una escala regional al llarg de la península Ibèrica, no podem concloure que el pi roig presenti símptomes generals de declivi. En el període de 10 anys entre els dos inventaris forestals nacionals (IFN) la taxa de mortalitat mitjana anual ha estat de 0.45% $\pm$ 0.02%. Malauradament, aquest valor emmascara les diferències entre anys que podrien ser àmplies i no ens ha permès detectar pics puntuals de mortalitat. Aquest valor mitjà, però, duplica la taxa mitjana de mortalitat de boscos francesos de coníferes (Bréda & Badeau, 2008), mentre que es situa molt per sota del 2% anual recentment detectat en boscos de pins a l'oest dels Estats Units (van Mantgem *et al.*, 2009). Aquestes comparacions indiquen que els boscos de pi roig a la Península presenten unes taxes de mortalitat relativament normals donada la seva actual estructura, tot i que evidentment hi ha parcel·les amb mortalitats molt superiors a la mitjana, les quals podrien estar associades a sequeres puntuals (Martínez-Vilalta & Piñol, 2002; Hódar *et al.*, 2003; Galiano *et al.*, 2010). D'altra banda, donat que només tenim dues mesures en el temps (Inventaris Forestals Nacionals, IFN2 i IFN3) i que no coneixem amb precisió quins han estat els canvis en la gestió forestal en cadascuna de les parcel·les, tampoc podem concloure que l'espectacular diferència de pins morts en peu entre els dos inventaris (11 vegades superior a l'IFN3) sigui un increment real i, en aquest cas, tampoc podem saber amb certesa quines en són les causes. Tot i aquestes limitacions, i

que és probable que la gestió de la fusta morta hagi canviat entre el període de mostreig dels dos inventaris, hem de remarcar que només el 27% de les parcel·les havien estat gestionades prèviament a l'IFN2 i que el % de mortalitat mostra un valor semblant entre les parcel·les gestionades i les no gestionades. Així, els nostres resultats suggereixen que els components estructurals i climàtics considerats en aquest estudi i que determinen la variació espacial de la demografia del pi roig, podrien haver contribuït en un suposat augment de la mortalitat de l'espècie a escala regional.

7. COM SÓN ELS PATRONS DE DECLIVI ENTRE POBLACIONS DE PI ROIG? I QUÈ PASSA DINS DE LES POBLACIONS? QUINS FACTORS N'EXPLIQUEN LA VARIABILITAT? QUINS PATRONS DE REGENERACIÓ ES RELACIONEN AMB EL DECLIVI? HI HA INDICIS DE CANVIS EN LA VEGETACIÓ?

Si, com hem vist, a una escala regional les condicions climàtiques condicionen relativament la demografia dels boscos de pi roig, l'ocurrència d'esdeveniments extrems com les sequeres poden originar l'emergència de processos de declivi en determinades poblacions de l'espècie. Per no caure en la redundància, tractarem de discutir conjuntament els resultats per als patrons de declivi obtinguts entre poblacions (o a escala regional) i dins de les poblacions d'estudi a Catalunya.

(3a) DETERMINANTS DELS PATRONS DE DECLIVI ENTRE I DINS DE POBLACIONS DE PI ROIG

El declivi entre i dins les 4 poblacions catalanes de pi roig estudiades presenta uns patrons en mosaic. L'aridesa climàtica sembla jugar un paper a escala regional però, en última instància, les condicions ambientals dins les poblacions, i.e., l'estructura actual del bosc, herència de la gestió del passat, i els components abiòtics locals relacionats amb la disponibilitat d'aigua, podrien ser els principals conductors subjacents del declivi del pi roig. En concordança amb el que hem vist per les taxes demogràfiques dels boscos de pi roig a la Península, un major declivi (mortalitat i defoliació a nivell de parcel·la) es relaciona amb processos de competència i autotala, sobretot en boscos joves o densos. En canvi, a diferència del que hem detectat per a la demografia a escala peninsular, sí que hem trobat una clara senyal climàtica al considerar les parcel·les de les 4 poblacions en conjunt, és a dir, a una escala regional.

No obstant això, aquesta senyal ve condicionada per factors locals tan biòtics (estructura forestal) com abiòtics relacionats amb la disponibilitat hídrica (sòl, topografia). A més a més, al tractar-la més detalladament, hem comprovat que la gestió passada pot haver tingut un efecte beneficiós sobre el bosc pel que fa al declivi, directament reduint la competència.

Conforme amb els patrons demogràfics a la península Ibèrica l'aridesa climàtica i l'estrès hídric local són els factors desencadenants de la defoliació i la mort dels individus en boscos amb presència d'arbres grans. Aquest resultat posa de manifest que els boscos de pi roig amb arbres de gran mida podrien ser més vulnerables davant les sequeres ja que la major mida dels individus pot suposar una major necessitat de recursos, intensificant-se la competència sota condicions desfavorables. A més a més, quan la disponibilitat local d'aigua és escassa (sòls poc profunds i de baixa infiltració) el declivi del bosc és independent de les condicions d'aridesa climàtica. Aquests resultats posen de manifest la importància de les condicions abiòtiques locals donada la dependència que té l'espècie de les reserves d'aigua del sòl per satisfer la demanda evaporativa durant l'estiu (Llorens *et al.*, 2010), i que el declivi causat per sequera podria limitar-se als boscos amb sòls d'escassa capacitat de retenció d'aigua (Peterman *et al.*, 2012).

En aquest treball hem pogut obtenir informació de la prèvia intervenció humana en el bosc, mesurada en un gradient d'intensitat de gestió. És moment, per tant, de discutir la resposta del bosc al llarg dels diferents gradients ambientals segons la intensitat de la gestió. Les pràctiques de tala redueixen la densitat i, en conseqüència, modifiquen la disponibilitat de recursos per càpita i les relacions biòtiques entre els individus. Coherentment, hem observat que els boscos més intensament gestionats presenten nivells menors de declivi i que aquest efecte és major en disminuir la disponibilitat d'aigua. Això ens porta a pensar que la reducció prèvia de la densitat comporta que la competència entre els individus sigui menor durant una sequera o sota condicions d'estrès hídric local. Aquest resultat pensem que aporta informació molt rellevant en dos sentits. En un primer, que la resposta dels boscos a l'estrès ambiental està modulada per processos que actuen a escala local, en els quals la història del bosc i, per tant, la prèvia intervenció humana, hi pot tenir un paper fonamental. En un segon sentit, donada la importància de la història del bosc, certes pràctiques de gestió poc intensa es podrien

considerar com un dels components que aporten al bosc un sistema d'atenuació davant les pertorbacions i una major resiliència posterior (Lloret *et al.*, 2012).

(3b) PATRONS DE REGENERACIÓ I CANVIS EN LA VEGETACIÓ

L'abundància de plàntules i plançons de pi roig es relaciona negativament amb l'augment del declivi, mentre que l'abundància de les espècies de *Quercus* mostra uns patrons idiosincràtics respecte el declivi. D'aquesta manera podem dir que no existeix un mecanisme clar d'auto-substitució però que tampoc hi ha indicis de canvis generalitzats en la composició de les espècies. El pi roig és una espècie intolerant a l'ombra i requereix llum abundant per al seu reclutament i desenvolupament (Castro *et al.*, 2004). El declivi de pins adults, però, no és suficient per canviar prou l'estructura del bosc i aportar les condicions necessàries de llum pel desenvolupament d'individus nous o suprimits al sotabosc. Al contrari, sembla que les condicions d'estrès que es relacionen amb el declivi de l'espècie (competència, estrès hídric) estan també limitant el seu reclutament. En aquest sentit, sembla existir un desajust entre les sortides (mort) i les entrades (establiment) de la població, com s'ha mostrat en altres espècies de pins (Gworek *et al.*, 2007). Si aquesta tendència es manté en el temps la permanència del pi roig a la comunitat pot veure's compromesa a llarg termini, sobretot si altres espècies (*Quercus* spp.) amb la potencialitat de substituir-lo es veuen afavorides per les noves condicions. Encara que aquests canvis en la composició de la comunitat són avui imperceptibles en els boscos estudiats, n'existeixen alguns indicis a petita escala (Galiano *et al.*, 2012) i per al conjunt de boscos a la península Ibèrica (Vayreda *et al.*, 2012, en revisió).

Existeix la idea que el canvi climàtic és i es preveu que sigui la principal causa dels canvis en la distribució de les espècies. Tanmateix, en aquest treball hem detectat un interessant patró entre poblacions que pot aportar valuosa informació: l'abundància de *Quercus* spp. és enormement major en les dues poblacions amb un major declivi que, a més, corresponen a les poblacions que no han estat gestionades, almenys, durant els últims 30 anys. D'aquesta manera, podem suggerir que l'abandonament de les pràctiques de gestió forestal s'estan traduint en canvis de l'estructura i composició d'aquests boscos. Per una banda, el tancament de la coberta per part de l'espècie dominant, el pi roig, no permet l'emergència de nous individus malgrat el declivi dels adults i, per l'altra, aquestes condicions poden afavorir el desenvolupament d'espècies

més tolerants a l'ombra. Malgrat que els nostres resultats no són concloents respecte al procés suggerit pel reduït nombre de poblacions, sí que indiquen que la història de cada bosc és important i que els possibles canvis en la composició de les espècies lligats als canvis en el clima haurien de ser avaluats també en un context d'intervenció humana.

8. SI EL DECLIVI DE LES POBLACIONS VA ASSOCIAT A UN ESTRÈS PER SEQUERA, COM RESPON L'ESFORÇ REPRODUCTIU DELS INDIVIDUS SOTA AQUESTES CONDICIONS?

Hem comprovat com el declivi a nivell poblacional està associat a diferents processos que involucren factors biòtics i abiòtics relacionats amb un estrès ambiental. **En aquesta tesi hem reportat que el pi roig mostra diferents patrons al·lomètrics en l'assignació de recursos entre els individus i variacions en els costos reproductius dins dels individus, i que aquestes diferències i variacions estan associades amb els efectes de la sequera a nivell individual i de parcel·la.**

Com hem indicat a la introducció, la reproducció és costosa i això pot veure's expressat en forma de *trade-offs* amb el creixement. En aquesta tesi n'hem mostrat l'existència a nivell intra-individual, la qual cosa és coherent amb la hipòtesis del *switching*, és a dir, que alguns anys l'individu destina la major part dels recursos per créixer mentre que altres anys prioritza la reproducció (Norton & Kelly 1988). Encara que no hem detectat una variació d'aquest cost reproductiu amb la mida de l'arbre, els nostres resultats mostren que majors nivells d'estrès (i.e. defoliació) estan associats amb un major cost reproductiu per al creixement. Això suggereix limitacions fisiològiques dins dels individus, lligades al fet que la defoliació comporta una reducció en l'adquisició de recursos.

Si l'assignació de recursos pot variar dins dels individus, és obvi que també pot fer-ho a nivell inter-individual. Donat que hem atribuït certa importància als processos al·lomètrics, no està de menys comentar la relació general entre la mida dels arbres i els patrons en l'assignació de recursos. El fet que l'augment de producció de biomassa de pinyes s'estabilitzi en arbres grans i, per tant, que l'esforç reproductiu es maximitzi en mides intermèdies ens porta a pensar que els costos de manteniment associats a

l'assoliment de mides grans (Mencuccini *et al.*, 2005) podrien ser proporcionalment majors per a la reproducció. En aquest sentit, aquests costos poden manifestar un conflicte en l'assignació de recursos a l'augmentar la mida dels individus, ja que els arbres grans podrien assignar proporcionalment més recursos al creixement, en detriment de la reproducció.

Si ens centrem en l'estrès per sequera a nivell individual, entès com a una defoliació de la capçada, els pins que en pateixen mostren una menor eficiència en la conversió dels recursos en biomassa vegetativa i reproductiva en comparació amb pins sans de la mateixa mida. Sabem que en una de les poblacions estudiades l'estrès per sequera causa la caiguda de les fulles donant lloc a una reducció de l'àrea fotosintètica, i això es relaciona amb un esgotament de les reserves de carboni (Galiano *et al.*, 2011). En aquest context, el fet que els arbres defoliats mostrin una menor inversió en el creixement i en la reproducció pot reflectir una menor disponibilitat de carboni o una major inversió per reomplir-ne les reserves (c.f. Sala *et al.*, 2012).

En canvi, al dirigir l'atenció als efectes de la sequera a nivell de parcel·la (i.e. declivi), hem observat que els individus sota un major declivi creixen més però, per contra, es reproduïen menys. Per acabar-ho de complicar, hem detectat que aquesta disminució de la inversió en la reproducció i l'esforç reproductiu amb el declivi s'intensifica notablement a l'augmentar la mida dels individus. És a dir, quan les condicions són desfavorables (i.e. major declivi), com més gran és l'individu sembla que inverteix més recursos en el creixement vegetatiu limitant-ne la inversió a la reproducció. En canvi, quan les condicions són millors (i.e. menor declivi) com més gran és l'individu sembla que inverteix més recursos a reproduir-se, a expenses del creixement vegetatiu. El perquè de tot plegat sembla ser complicat. Per una banda, el fet que els efectes del declivi són menors per arbres de mida petita insinua que, en condicions d'estrès, el “ser petit” podria ser avantatjós en termes d'eficiència en la utilització dels recursos (Aarssen, 2008). D'altra banda, la inversió dels recursos al creixement en individus de mida gran en un ambient d'estrès pot significar una estratègia per reduir el cost reproductiu a curt termini, i així accedir a una major quantitat de recursos que podrien ser importants per a la supervivència a llarg termini (Sakai *et al.*, 2006). D'aquesta manera, aquests patrons diferencials poden representar canvis en les estratègies

d'assignació de recursos entre els individus d'acord amb la seva mida (petit vs. gran) i al nivell de declivi (menor vs. major).

CONCLUSIONS

En referència al marc conceptual exposat a la introducció (veure Fig. 2 de la introducció), en aquesta tesi hem observat que les respostes demogràfiques del pi roig són més o menys dràstiques segons el tipus de pertorbació, que aquestes respostes poden variar al llarg de diferents gradients ambientals i que aquests processos poden desencadenar canvis en la vegetació. Basats en els resultats d'aquesta tesi, intentarem exposar algunes conclusions que ens ajudaran a completar aquesta figura, respondre'n (si podem) els interrogants i obrir-ne, si cal, de nous.

Els boscos de pi roig més meridionals (i.e. més secs) de la península Ibèrica són vulnerables als incendis. L'augment en el risc climàtic d'incendis i l'absència, en aquesta espècie, de mecanismes efectius de regeneració després del foc ens indiquen que els incendis poden provocar canvis en la vegetació en zones actualment dominades pel pi roig. Aquestes prediccions, però, no poden ser del tot concloents donat que no hem considerat explícitament l'estructura del bosc que, juntament amb el clima determinen el règim de focs (Debussche *et al.*, 1999; Badia *et al.*, 2002; Flannigan *et al.*, 2006; Loepfe *et al.*, 2011; Pausas & Fernández-Muñoz, 2012).

El llegat de la intervenció humana en els boscos de pi roig n'expliquen l'estructura actual. Els processos resultants de competència i autotala esdevenen els principals factors que expliquen els patrons demogràfics i de declivi. Per tant, l'abandonament de les activitats agràries i forestals durant el segle XX (Martínez-García, 1999; OSE, 2007) són la principal pertorbació que explica els patrons i processos observats en aquesta tesi. Tanmateix, les sequeres i les limitacions abiòtiques del sistema estan desencadenant processos de declivi, aparentment en boscos amb una estructura més desenvolupada, i.e. major abundància d'arbres grans. Aquestes pertorbacions incideixen directament en els processos demogràfics. El resultat de tot plegat és una variació en mosaic de la dinàmica del bosc, resultat de les estratègies de resposta de cada individu, de les

interaccions de competència i dels factors abiòtics del sistema que incideixen en la disponibilitat d'aigua.

La incertesa sobre el futur d'algunes poblacions és palesa donat que no hi ha un mecanisme d'auto-substitució intraespecífica mitjançant l'establiment de nous individus que compensi la mort dels adults. Això es veu agreujat per l'efecte negatiu que la defoliació causada per la sequera té en l'esforç reproductiu a nivell d'individu (i.e., producció de pinyes). Aquests processos poden estar desencadenant canvis en la vegetació donat que altres espècies amb una major capacitat de regeneració s'estan desenvolupant, aparentment, com a resultat de l'abandonament agrícola i dels canvis recents en els usos forestals (Urbietà *et al.*, 2008; Gimmi *et al.*, 2010; Gracia *et al.*, 2011; Vayreda *et al.*, 2012, en revisió).

Finalment, quin paper pot tenir la gestió forestal en un futur escenari de canvi climàtic? Sens dubte, una gestió de tala moderada pot atenuar els efectes d'una sequera i donar una major capacitat de resiliència al bosc. De la mateixa manera, el control de les densitats pot disminuir l'ocurrència del foc en poblacions meridionals o, almenys, reduir-ne la velocitat de propagació. En aquest sentit, els resultats d'aquesta tesi insinuen en quina direcció cal que vagi la recerca forestal, és a dir, quines estructures s'han d'afavorir en els boscos per tal de mitigar els efectes del canvi climàtic. D'aquesta manera, si els gradients climàtics que hem considerat en aquesta tesi són equivalents a les condicions futures, podem esperar que es produiran canvis importants en la demografia dels boscos de pi roig a la península Ibèrica. La gestió forestal emergeix com una eina important a l'hora de tamponar els canvis previstos en la dinàmica d'aquests boscos, com a mínim allà on els impactes siguin menys extrems.

REFERÈNCIES BIBLIOGRÀFIQUES

- Aarssen, L.W. (2008) Death without sex – the 'problem of the small' and selection for reproductive economy in flowering plants. *Evolutionary Ecology*, 22: 279-298.
- Badia, A., Saurí, D., Cerdan, R. & Llurdés, J.C. (2002) Causality and management of forest fires in Mediterranean environments: an example from Catalonia. *Global Environmental Change Part B: Environmental Hazards*, 4: 23-32.

- Bréda, N. & Badeau, V. (2008)** Forest tree responses to extreme drought and some biotic events: towards a selection according to hazard tolerance? *C.R. Geoscience*, 340: 651-662.
- Castro, J., Zamora, R., Hódar, J.A. & Gómez, J.M. (2004)** Seedling establishment of a boreal tree species (*Pinus sylvestris*) at the southernmost distribution limit: consequences of being in a marginal Mediterranean habitat. *Journal of Ecology*, 92: 266-277.
- Debussche, M., Lepart, J. & Dervieux, A. (1999)** Mediterranean landscape changes: evidence from old postcards. *Global Ecology and Biogeography*, 8: 3-15.
- Espelta, J.M., Rodrigo, A., Habrouk, A., Mighelli, N., Ordóñez, J.L. & Retana, J. (2002)** Land use changes, natural regeneration patterns, and restoration practices after a large wildfire in NE Spain: challenges for fire ecology and landscape restoration. Fire and biological processes (ed. by L. Traubaud and R. Prodon), pp. 315-324. Backhurs Publishers, Leiden.
- Flannigan, M.D., Amiro, B.D., Logan, K.A., Stocks, B.J. & Wotton, B.M. (2006)** Forest fires and climate change in the 21st century. *Mitigation and Adaptation Strategies for Global Change*, 11: 847-859.
- Galiano, L., Martínez-Vilalta, J. & Lloret, F. (2010)** Drought induced multi-factor decline of Scots pine in the Pyrenees and potential vegetation change by the expansion of co-occurring oak species. *Ecosystems*, 7: 978-991.
- Galiano, L., Martínez-Vilalta, J. & Lloret, F. (2011)** Carbon reserves and canopy defoliation determine the recovery of Scots pine four years after a drought episode. *New Phytologist*, 190: 750-759.
- Galiano, L., Martínez-Vilalta, J., Eugenio, M., de la Cerda, I.G. & Lloret, F. (2012)** Seedling emergence and growth of *Quercus* spp. following severe drought effects on a *Pinus sylvestris* canopy. *Submitted*.
- Gimmi, U., Wohlgemuth, T., Rigling, A., Hoffmann, C.W. & Bürgi, M. (2010).** Land-use and climate change effects in forest compositional trajectories in a dry Central-Alpine valley. *Annals of forest Science*, 67: 701.
- Gracia, M., Meghelli, N., Comas, L. & Retana, J. (2011)** Land-cover changes in and around a National Park in a mountain landscape in the Pyrenees. *Regional Environmental Change*, 11: 349-358.
- Gworek, J.R., Vander Wall, S.B. & Brussard, P.F. (2007)** Changes in biotic interactions and climate determine recruitment of Jeffrey pine along an elevation gradient. *Forest Ecology and Management*, 239: 57-68.
- Habrouk, A., Retana, J. & Espelta, J.M. (1999)** Role of heat tolerance and cone protection of seeds in the response of three pine species to wildfires. *Plant Ecology*, 145: 91-99.
- Hódar, J.A., Castro, J. & Zamora, R. (2003)** Pine processionary caterpillar *Thaumetopoea pityocampa* as a new threat for relict Mediterranean Scots pine forests under climatic warming. *Biological Conservation*, 110: 123-129.
- Klos, R.J., Wang, G.G., Bauerle, W.L. & Rieck, J.R. (2009)** Drought impact on forest growth and mortality in the southeast USA: an analysis using Forest Health and Monitoring data. *Ecological Applications*, 19: 699-708.

- Linares, J.C., Camarero, J.J. & Carreira, J.A. (2009)** Interacting effects of changes in climate and forest cover on mortality and growth of the southernmost European fir forests. *Global Ecology and Biogeography*, 18: 485-497.
- Linares, J.C., Camarero, J.J. & Carreira, J.A. (2010)** Competition modulates the adaptation capacity of forests to climatic stress: insights from recent growth decline and death in relict stands of the Mediterranean fir *Abies pinsapo*. *Journal of Ecology*, 98: 592-603.
- Llorens, P., Poyatos, R., Latron, J., Delgado, J., Oliveras, I. & Gallart, F. (2010)** A multi-year study of rainfall and soil water controls on Scots pine transpiration under Mediterranean mountain conditions. *Hydrological Processes*, 24: 3053-3064.
- Lloret, F., Escudero, A., Iriondo, J.M., Martínez-Vilalta, J. & Valladares, F. (2012)** Extreme climatic events and vegetation: the role of stabilizing processes. *Global Change Biology*, 18: 797-805.
- Loepfe, L., Martínez-Vilalta, J., & Piñol J. (2011)** An integrative model of human influenced fire regimes and landscape dynamics. *Environmental Modelling & Software*, 26: 1028-1040.
- Lutz, J.A. & Halpern, C.B. (2006)** Tree mortality during early forest development: A long-term study of rates, causes, and consequences. *Ecological Monographs*, 76: 257-275.
- Martínez-García, F. (1999)** Los bosques de *Pinus sylvestris* L. del Sistema Central español. Distribución, historia, composición florística y tipología. PhD Thesis, Universidad Complutense de Madrid, Madrid, Spain.
- Martínez-Vilalta, J. & Piñol, J. (2002)** Drought-induced mortality and hydraulic architecture in pine populations of the NE Iberian Peninsula. *Forest Ecology and Management*, 161: 247-256.
- Mencuccini, M., Martinez-Vilalta, J., Vanderklein, D., Hamid, H.A., Korakaki, E., Lee, S. & Michiels, B. (2005)** Size-mediated ageing reduces vigour in trees. *Ecology Letters*, 8: 1183-1190.
- Nathan, R., Safriel, U.N., Noy-Meir, I. & Schiller, G. (2000)** Spatiotemporal variation in seed dispersal and recruitment near and far from *Pinus halepensis* trees. *Ecology*, 81: 2156-2169.
- Norton, D.A. & Kelly, D. (1988)** Mast seeding over 33 years by *Dacrydium cupressinum* Lamb (rimu) (Podocarpaceae) in New Zealand: the importance of economies of scale. *Functional Ecology*, 2: 399-408.
- Oliver, C.D. & Larson, B.C. (1990)** Forest stand dynamics. McGraw-Hill, New York, NY.
- OSE (Observatorio de la Sostenibilidad en España) (2007)** *Sostenibilidad en España 2007*. Universidad de Alcalá, Alcalá de Henares (Madrid), Spain.
- Pausas, J.G., Llovet, J., Rodrigo, A. & Vallejo, R. (2008)** Are wildfires a disaster in the Mediterranean basin? – A review. *International Journal of Wildland Fire*, 17: 713-723.
- Pausas, J.G. & Fernández-Muñoz, S. (2012)** Fire regime changes in the Western Mediterranean basin: from fuel-limited to drought-driven fire regime. *Climatic Change*, 110: 215-226.
- Peterman, W., Waring, R.H., Seager, T. & Pollock, W.L. (2012)** Soil properties affect pinyon pine-juniper response to drought. *Ecohydrology*, DOI: 10.1002/eco.1284.
- Retana, J., Espelta, J.M., Habrouk, A., Ordóñez, J.L. & Solà-Morales, F. (2002)** Regeneration patterns of three Mediterranean pines and forest changes after a large wildfire in northeastern Spain. *Écoscience*: 9, 89-97.

- Rodrigo, A., Quintana, V. & Retana, J. (2007)** Fire reduces *Pinus pinea* distribution in the northeastern Iberian Peninsula. *Écoscience*, 14: 23-30.
- Sakai, A., Sasa, A. & Sakai, S. (2006)** Do sexual dimorphisms in reproductive allocation and new shoot biomass increase with an increase of altitude? A case of the shrub willow *Salix reinii* (Salicaceae). *American Journal of Botany*, 93: 988-992.
- Sala, A., Woodruff, D.R., Meinzer & F.C. (2012)** Carbon dynamics in trees: feast or famine? *Tree Physiology*, 32: 764-775.
- Tapias, R., Climent, J., Pardos, J. & Gil, L. (2004)** Life histories of Mediterranean pines. *Plant Ecology*, 171: 53-68.
- Urbietta, I.R., Zavala, M.A. & Marañón, T. (2008)** Human and non-human determinants of forest composition in southern Spain: evidence of shifts towards cork oak dominance as a result of management over the past century. *Journal of Biogeography*, 35: 1688-1700.
- van Mantgem, P.J., Stephenson, N.L., Byrne, J.C., Daniels, L.D., Franklin, J.F., Fulé, P.Z., Harmon, M.E., Larson, A.J., Smith, J.M., Taylor, A.H. & Veblen, T.T. (2009)** Widespread increase of tree mortality rates in the western United States. *Science*, 323: 521-524.
- Vayreda, J., Gràcia, M., Martínez-Vilalta, J. & Retana, J. (2012)** Rapid and directional changes in tree distribution lead to increased dominance of broad leaf species. *In review*.