Impactes del canvi global sobre els boscos de la Península Ibèrica: estocs, creixement i regeneració

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per optar al grau de doctor

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A la meva família... i, en particular, a la Gemma

El bosc és l'ecosistema terrestre d'estructura més complexa.
La peça cabdal n'és l'arbre,
i cal un poeta per descriure apropiadament la complexitat de l'arbre.

Ramon Margalef

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Ara ve aquella part tan complicada on, sobretot, cal no oblidar-se de ningú important.

En primer lloc m'agradaria agrair molt sincerament als meus directors de tesi, en Marc i en Javi, per la seva dedicació permanent al bon desenllaç d'aquesta tesi. La veritat és que amb ells tot ha estat molt fàcil perquè sempre rebia l'ajuda necessària i a temps per avançar ràpidament tot i dels alts i baixos inevitables, imagino, de la majoria de tesis. Després d'un llarg procés previ que em va servir per anar madurant la situació, recordo molt bé el dia que en Javi em va proposar de fer la tesi amb ell i en Marc. Tot i que ja m'esperava que em faria aquesta proposta, va ser sobretot el seu optimisme desbordant el que em va fer acabar de decidir sense a penes dubtar. Semblava tot tan fàcil com m'ho plantejava que era impossible que m'hi pogués negar.

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En fi.... que això no s'acabaria mai!

Índex

Capítol 1

Introducció general

Situació actual dels boscos en el context del canvi global

Els boscos juguen un paper clau en el cicle global del carboni (C) perquè són els responsables de capturar el 30% de les emissions de CO_2 d'origen antropogènic (Canadell et al. 2007; Pan et al. 2011). També són globalment valuosos per molts altres serveis indispensables pel benestar de la societat incloent valors i serveis ecològics, econòmics, socials, estètics i recreatius (Bonan, 2008, Pan et al. 2011). Els boscos tenen un efecte significatiu sobre el clima a través de processos físics químics i biològics afectant el cicle d'energia, el cicle hidrològic i la composició atmosfèrica a escala planetària. Per la seva banda, el clima a gran escala és el principal factor determinant de la distribució i dinàmica de la vegetació (Woodward 1987; Ellenberg 1988). Aquestes interaccions bosc-atmosfera són complexes i no lineals i poden amplificar o esmorteir el canvi climàtic (Bonan 2008).

Els treballs per determinar els estocs i els embornals de C a escala continental i mundial han estat recurrents en les darreres dècades des del ja clàssic estudi de Dixon *et al.* (1994) passant pel treball de Goodale et al. (2002), per citar-ne alguns. Ara bé, el més recent i exhaustiu que s'ha dut a terme a escala mundial per Pan *et al.* (2011) (majoritàriament amb dades d'inventaris forestals) conclou que l'estoc actual de C dels boscos és de 861 ± 66 Pg C (1 Pg = 10^9 Mg = 10^{15} g), amb 383 ± 30 Pg C (44%) en el sòl (fins a 1 m de profunditat), 363 ± 28 Pg C (42%) en la biomassa viva (aèria i subterrània), 73 ± 6 Pg C (8%) en la fusta morta i 43 ± 3 Pg C (5%) a la virosta. Geogràficament, 471 ± 93 Pg C (55%) estan emmagatzemats als boscos tropicals, 272 ± 23 Pg C (32%) als boreals i 119 ± 6 Pg C (14%) als boscos temperats. L'estoc de C per hectàrea en els boscos tropicals i boreals és comparable (242 *versus* 239 Mg C ha^{-1}), mentre que els boscos temperats és aproximadament un 60% dels altres dos biomes (155 Mg C ha^{-1}). Encara que els boscos tropicals i els boreals emmagatzemen la major part del C, hi ha una diferència fonamental en com es distribueix en els diferents compartiments de l'ecosistema: els boscos tropicals tenen el 56% del C emmagatzemat a la biomassa i el 32% en el sòl, mentre que en els boscos boreals només un 20% es troba a la biomassa i un 60% en el sòl. Aquest mateix estudi ha estimat que l'embornal net de C a escala mundial dels boscos ha passat del 1.04 ± 0.79 Pg C any^{-1} a la dècada 1990-1999 a 1.20 ± 0.85 a la 2000-07. Les enormes incerteses que encara s'arrosseguen són degudes sobretot a una escassa i sovint poc precisa informació a les zones tropicals.

A escala Europea els boscos també estan actualment acumulant C i la majoria d'estudis apunten que encara tenen un important potencial per segrestar C a mig termini (Nabuurs *et al.;* 2003; Ciais *et al.*, 2008; Nabuurs *et al.* 2010). La tendència a l'increment de la capacitat d'embornal dels boscos a escala mundial però sobretot dels boscos de l'hemisferi nord (Goodale *et al.* 2002) i en particular dels Europeus (Ciais *et al.* 2008) s'atribueix a una combinació de factors que han actuat de manera sinèrgica durant les darreres dècades : 1) bona part dels boscos Europeus han estat durant molt de temps intensament explotats de manera que la majoria són boscos joves en fase de recuperació i acumulant C (Ciais *et al.* 2008); 2) la fracció de l'increment que s'aprofita cada any ha anat disminuint del prop del 90-95% en la dècada dels cinquanta del segle passat a menys del 50% actual, augmentant l'embornal de C de la biomassa forestal (Nabuurs *et al.* 2003; Ciais *et al.* 2008); 3) l'impacte favorable de la deposició de nitrogen, actuant com a fertilitzant, en l'acumulació de C (Aber *et al.* 1998); 4) l'efecte fertilitzant de l'augment atmosfèric de CO_2 combinat amb l'efecte positiu de l'augment de la temperatura (Oren *et al.* 2001); i 5) millora del creixement dels boscos temperats i boreals degut a l'allargament del període de creixement (Saxe *et al.* 2001). La magnitud de l'efecte d'aquests dos darrers factors ha estat objecte de molts estudis i els seus efectes a mitjà i llarg termini encara són incerts (Nabuurs *et al.* 2003; McMahon *et al.* 2010), particularment en els ecosistemes limitats per l'aigua, com els boscos de la conca Mediterrània, on el potencial efecte positiu de la fertilització per CO_2 i l'augment de la temperatura interacciona amb la disponibilitat d'aigua (Barber *et al.* 2000; Martínez-Vilalta *et al.* 2008).

Principals factors de canvi: biòtics i abiòtics

Els arbres poden ser especialment sensibles al clima perquè són organismes sèssils i de vida llarga, dos trets que no els permet adaptar-se de manera ràpida als canvis ambientals (Lindner *et al.* 2010; Lenoir *et al.* 2008). Entendre com els factors ambiental, globals i locals, i les pertorbacions interaccionen per controlar els patrons de distribució espacials de les espècies i la dinàmica de les comunitats és un tema recorrent en ecologia (Woodward 1987; Ellenberg 1988; Huston 1994; Thuiller *et al.* 2003). Predir els patrons de distribució des estocs i els canvis en la capacitat d'embornal dels boscos i els canvis demogràfics subjacents és fonamental per entendre el paper actual dels boscos en el cicle del C i fer projeccions de la seva evolució futura, de la seva capacitat d'adaptació i del seu possible paper mitigador del canvi climàtic. A gran escala, és ben conegut que la distribució de les espècies i la seva dinàmica estan controlades pel clima, principalment per l'aigua i l'energia (i.e., particularment la temperatura) (Woodward 1987; Ellenberg 1988; Houghton, 2005; Zhao & Zhou 2006). No obstant, en els ecosistemes semiàrids, la precipitació i l'evapotranspiració potencial juguen un paper clau (Kerkhoff *et al.* 2004; Sankaran *et al.* 2005; Huang *et al.* 2009). A escala més local, les propietats del sòl (p.e.., textura, quantitat de matèria orgànica, pedregositat, profunditat) modulen el contingut d'aigua al sòl, mentre que l'orografia actua de manera indirecta modificant els patrons climàtics a escala local (Zhao & Zhou 2006; Huang *et al.* 2009). Les pertorbacions naturals (p.e., incendis, ventades, nevades i d'altres) i les pertorbacions directament induïdes per l'home com la gestió forestal (p.e., aclarides, estassades, aprofitament comercials...) són també factors de canvi de l'estructura, de la composició específica i de la diversitat dels boscos (Merino *et al.* 2007; Nabuurs *et al.* 2008) i, en definitiva, del funcionament dels ecosistemes forestals.

Si bé pels arbres adults la distribució actual de les espècies arbòries és conseqüència de les condicions del passat (i.e., clima, gestió i pertorbacions), l'èxit en l'establiment i supervivència en les fases juvenils (ja sigui plàntules o plançons) és la resposta a condicions que sovint actuen a una escala espacial i temporal molt més petita (Marañón *et al.* 2004; Gravel *et al.* 2010; Urbieta *et al.* 2011). La importància dels diferents determinant biòtics i abiòtics de la regeneració de les diferents espècies varia al llarg de gradients ambientals, de la història recent de pertorbacions (Gazol & Ibáñez 2010) i que varia en les diferents etapes de l'ontogènesi (Messier *et al.* 2000). Està àmpliament acceptat que l'abundància del regenerat depèn directament de l'abundància d'arbres adults que conformen el vol perquè són la primera font de reclutament natural, però també, encara que indirectament, perquè modifiquen les condicions ambientals (reduint la radiació solar i mantenint la humitat del sòl), i els factors biòtics com la competència (Grace & Tilman 2003) o la facilitació (Gómez-Aparicio *et al.*, 2004; Pulido & Díaz 2005; Gómez-Aparicio *et al.*, 2008). El sotabosc també pot afectar la regeneració de dues maneres: tenint un efecte positiu protegint els individus d'agents biòtics (principalment herbivoria) o abiòtics (Plieninger *et al.* 2004; Gómez-Aparicio *et al.* 2008; Pausas *et al.* 2009; Plieninger *et al.* 2010), o negatiu competint pels mateixos recursos limitants, llum i aigua principalment (Maestre *et al.* 2005). Finalment, l'efecte de les pertorbacions pot ser particularment significatiu, especialment en el cas dels incendis forestals (Rodrigo *et al.* 2004; Urbieta *et al.* 2011) i l'herbivoria (Plieninger *et al.* 2004, 2010). En molts països desenvolupats l'abandonament de la gestió forestal ha esdevingut un procés clau que ha accelerat el tancament de les capçades impedint la regeneració de les espècies intolerants a l'ombra. Per tant, a escala regional, les restriccions pel reclutament (transició des d'arbres joves a arbres adults) podrien ser la resposta a unes condicions completament diferents a les dels adults, de manera que conèixer-la és essencial per predir la resposta futura de la dinàmica forestal sota eventuals canvis de clima i de gestió forestal (Bravo *et al.* 2008).

Impactes recents del canvi global en els boscos

(a) Impactes del canvi climàtic

El ràpid escalfament a escala global ja experimentat a finals del segle XX i l'augment de la temperatura amb l'increment de la freqüència d'esdeveniments climàtics extrems (IPCC 2007), que tots els escenaris de canvi climàtic projecten pel segle XXI, són una amenaça molt seriosa pels boscos d'arreu del món. Donat el paper clau del clima en la determinació de la distribució i composició de les espècies i dels estocs i embornals de C, sembla inevitable que el canvi climàtic dispararà aquests processos com de fet ja s'ha anat observant arreu (Ciais *et al.* 2005, Lenoir *et al.* 2008; Allen *et al.* 2010). Exemple recents i molt coneguts a la literatura són els que s'han observat i quantificat en moltes zones del planeta on s'han produït reduccions significatives del creixement dels boscos i episodis de declivi i de mortalitat massius afectant, en definitiva, a la capacitat d'embornal dels boscos (Ciais *et al.* 2005; van Mantgem *et al.* 2009; Allen *et al.* 2010). Aquests episodis poden ser directament induïts per esdeveniments climàtics extrems (p.e. sequeres, onades de calor, ventades...) (Ciais *et al*. 2005; Bigler 2007; Allen *et al*. 2010; Lewis *et al.* 2011) i indirectament debilitant els arbres i amb el conseqüent increment de plagues (Kurz *et.al.* 2008a). En qualsevol dels casos, la conseqüència més immediata ha estat des d'una reducció significativa de l'absorció de CO_2 i, en alguns casos fins i tot, a convertir-se, encara que de manera temporal, en una font neta d'emissió de CO_2, en alguns casos de gran abast territorial (Kurz *et al.* 2008b). Des del moment en què aquest fenòmens han afectat a extenses zones del planeta i diferents regions del món, alguns estudis suggereixen que ja estan afectant la producció primària neta dels ecosistemes terrestres i, per tant, el balanç de C a escala global (Zhao & Running 2010).

Una altra de les conseqüències del canvi climàtic, que nombrosos estudis ja han constatat, són els canvis en la distribució de les espècies vegetals seguint principalment els canvis en la temperatura (Jump *et al.* 2009). Aquests canvis s'han observat freqüentment a les zones de muntanya, amb desplaçaments a més altitud (Kelly & Goulden 2008; Lenoir *et al.* 2008, 2009, Chen *et al.* 2011, Pauli *et al.* 2012). Molts menys estudis documenten desplaçament latitudinals en direcció als pols (Jump *et al.* 2009, Zhu *et al.* 2012). Per a què es produeixin aquests canvis en els boscos cal que la mortalitat i el reclutament no estiguin en equilibri en el temps (cf. Lloret *et al.* 2012), bé degut a un increment de la mortalitat en el límit geogràfic desfavorable per l'espècie (*trailing edge*) portant a l'extinció local, bé a una colonització més enllà del rang actual de la seva distribució (*leading edge*), o les dues situacions a la vegada (Breashears *et al.* 2008).

(b) Impactes de la gestió forestal i les pertorbacions

En general, un factor clau a tenir en compte en la producció és la gestió forestal, que ha demostrat tenir major influència en els boscos temperats Europeus que el clima o els canvis d'usos del sòl (Schröter *et al.* 2005). La gestió és un tipus de pertorbació controlada per l'home que converteix el bosc en una font neta d'emissió de CO_2 de curta durada (Law *et al.* 2003) però que com permet augmentar la productivitat perquè es redueix significativament la competència pels recursos (Westoby 1984), es reverteix la situació a mig termini. Ben al contrari, la manca de gestió porta a un increment de les interaccions competitives, la qual cosa acaba desembocant en un menor creixement i en un augment de la mortalitat. Aquest mecanisme de supressió 'natural' afecta preferentment els arbres més joves i/o més petits, perquè tenen menys capacitat per competir (Lutz & Halpern 2006). Tenint en compte que la fracció que s'aprofita del bosc cada vegada és més reduïda, alguns estudis preveuen que els boscos europeus encara poden multiplicar per dos les seves actuals reserves de carboni durant el segle XXI (mirar, Ciais *et al.* 2008) malgrat que la sequera, l'escalfament i els fenòmens meteorològics extrems augmentin la incertesa sobre la seva capacitat d'embornal a llarg termini (Nabuurs *et al.* 2003; Ciais *et al.* 2008). De nou, si la disponibilitat hídrica és baixa, l'efecte d'una major densificació pot ser especialment perjudicial en boscos amb importants limitacions perquè es redueix significativament l'aigua disponible per cada arbre amb una reducció del seu creixement i l'aparició d'episodis de mortalitat induïts per la sequera (Bigler *et al.* 2006, 2007; Linares *et al.* 2009; Vilà-Cabrera *et al.* 2011). És molt probable que l'escalfament agreugi encara més la capacitat d'acumulació de C degut a l'efecte directe en la disponibilitat hídrica, i que aquest efecte negatiu sigui encara més perjudicial en els boscos no gestionats on la densitat d'arbres i la competència és més elevada.

La majoria d'estudis que analitzen els canvis en la distribució de les espècies els atribueixen al canvi climàtic, principalment a la temperatura, i no consideren altres possibles factors de canvi (Chen *et al.* 2011). Alguns estudis han mostrat que aquests desplaçaments geogràfics no sempre es donen en la direcció esperada (Crimmins *et al.* 2011, Lenoir *et al*. 2008, 2010) probablement perquè les espècies no estan responent únicament al canvi climàtic sinó a tot un conjunt de factors que actuen en contraposició o sinèrgicament. Així, les respostes aparentment inconsistents poden atribuir-se, en alguns casos, a condicions locals, com ara canvis en el recobriment de la vegetació, bé augmentant la seva presència com a conseqüència de l'abandonament de la gestió, o disminuint de sobte degut a pertorbacions (Lenoir *et al.* 2010). Com a conseqüència de la multitud de factors que poden actuar a la vegada, hi ha hagut avenços limitats en entendre quins són els principals factors de canvi en la distribució de les espècies arbòries (Lenoir *et al.* 2010). Són necessaris estudis integrats que identifiquin les causes subjacents als processos de colonització i extinció de les espècies arbòries tenint en compte tots els possibles factor biòtics i abiòtics, especialment els que són conseqüència directa de les activitats humanes.

El canvi climàtic en el context de la Mediterrània: la Península Ibèrica com a cas d'estudi

Està previst que els efectes del canvi global siguin particularment significatius en els ecosistemes mediterranis on es preveu que el canvi climàtic serà particularment sever implicant, a la vegada que un ràpid escalfament, una reducció significativa de la precipitació (Schröter *et al.* 2005). Les projeccions climàtiques per la conca Mediterrània prediuen un escalfament de 3-4ºC de mitjana anual i una reducció de la precipitació d'estiu d'almenys un 50% abans de finals del 2100 (EEA 2008). En aquestes condicions és molt probable que els boscos de la península Ibèrica no només pateixin forts canvis en el balanç de carboni (reclutament, creixement i mortalitat) sinó que, com a conseqüència d'aquests canvis, també es produeixin canvis en la composició específica, amb desplaçaments significatius (colonitzacions i extincions) d'abast regional (Iverson *et al.* 2004; Lenoir *et al.* 2008; Jump *et al.* 2009). Tenint en compte que hi ha pocs estudis que abordin els efectes del canvi global a escala regional en boscos situats en clima Mediterrani, la Península Ibèrica ofereix una oportunitat única d'estudi per avaluar, no només els canvis associats a les tendències climàtiques recents, sinó també, els efectes de les pertorbacions i de la gestió forestal (o la no gestió, és a dir, l'abandonament). En primer lloc, molts boscos estan al seu límit més meridional (i sec), la qual cosa els fa particularment vulnerables al canvi climàtic (Hampe & Petit 2005; Allen *et al*. 2010), En segon lloc algunes espècies de distribució boreal també troben a la Península Ibèrica el seu límit més meridional de distribució. En tercer lloc, la península cobreix un ampli espectre de gradients ambientals de disponibilitat hídrica i de temperatura, des de zones humides i relativament fredes del nord i de la majoria de zones de muntanya, a zones seques i càlides del sud i del sud-est. En quart lloc, tot i que els boscos de la península Ibèrica van ser intensament explotats durant segles principalment per a la obtenció de fusta i llenya, en les darreres tres dècades, com a conseqüència d'importants canvis socio-econòmics, hi ha hagut una forta expansió del bosc fruit de l'abandonament progressiu dels terrenys agrícoles marginals i menys productius que, combinat amb un abandonament de la gestió forestal sobretot dels boscos menys productius, ha portat a un augment sostingut dels estocs de C als boscos (Houghton 2003; Friedlingstein *et al.* 2010; Lindner *et al*. 2010; SEFC 2011). En definitiva, aquest ampli espectre de condicions que representa la península Ibèrica fa que els resultats que se'n puguin derivar puguin ser parcialment traslladats a moltes altres parts del món (Lavorel *et al.* 1998).

Trets funcionals i ecològics que distingeix a les espècies i els tipus funcionals

Les espècies de port arbori es poden classificar segons les estratègies de regeneració, dispersió i supervivència i creixement que els confereixen diferents habilitats per enfrontar l'estrès biòtic i abiòtic al llarg de la seva llarga vida (Zavala *et al.* 2000, Gazol & Ibáñez 2010, Messier *et al.* 2000). Com a conseqüència, al llarg dels diferents estadis de desenvolupament (de plàntula a plançó i de planço a adult) cada espècie o tipus funcional (conífera o planifoli) pot tenir respostes molt diferents davant del canvi climàtic que, analitzades a escala regional, poden servir per definir diferents estratègies de gestió forestal adaptativa per fer front al canvi climàtic. D'acord amb molts estudis empírics de diferenciació de nínxols ecològics, les espècies es poden classificar segons el compromís entre créixer ràpidament amb molta llum (*high-light growth*) o créixer lentament però tenir elevada capacitat de supervivència amb poca llum (*low-light survival*). El primer grup es considera intolerant a l'ombra i s'associa amb els primer estadis de successió (estratègia de la r o colonitzadors), el segon grup d'espècies es considera tolerant a l'ombra i s'associa amb etapes avançades de la successió (Messier *et al.* 1999; Gravel *et al.* 2010). Les espècies també es poden classificar d'acord amb els principals mecanismes de regeneració com a germinadores si només es poden reproduir a partir de llavor, o rebrotadores, si a més es poden regenerar per rebrot (Retana *et al.* 1992). Finalment, les espècies arbòries es poden classificar segons la mida de la llavor i el principal agent de dispersió en: anemòcores (i.e., dispersades pel vent) o zoòcores (i.e., dispersades per animals) (McEuen & Curran 2004; Montoya *et al.* 2008). Tots aquests trets s'associen habitualment amb dues síndromes ben contrastades. Els pins són exemples de la primera, perquè solen ser de creixement ràpid, espècies pioneres que regeneren per llavors normalment petites i dispersades pel vent (Lanner 1998). Aquestes espècies poden facilitar l'establiment de les espècies del segon grup, que són de creixement més lent i d'etapes avançades de la successió, com moltes espècies de caducifolis (Barbéro *et al.* 1998; Pausas *et al.* 2004) o esclerofil·les (Espelta *et al.* 1995; Urbieta *et al.* 2011), la majoria d'elles caracteritzades per la seva capacitat de rebrotar i de tenir llavors de mida gran dispersades per animals.

A la Península Ibèrica, el canvi climàtic recent i l'augment progressiu dels estocs en peu han portat a un increment significatiu de la competència pels recursos i es pot constatar que s'ha produït un increment significatiu dels planifolis enfront de les coníferes. L'anàlisi del pes dels diferents factors biòtics (competència, gestió forestal, foc...) i abiòtics (clima, qualitat del lloc...) en cada espècie o grups funcional –d'acord amb les diferents estratègies de regeneració i supervivència segons els trets funcionals i ecològics que els diferencien– pot ajudar a interpretar el perquè dels canvis recents en la composició d'espècies i grups funcionals i, anant més enllà, el perquè dels canvis en la distribució geogràfica que s'han produït en els boscos recentment. En resum, per poder tenir una visió conjunta dels patrons de canvi cal tenir en compte no només els efectes del canvi global sinó cal situar-los en un context més ampli considerant l'efecte complementari de la resta de possibles factors influents i de les seves possibles interaccions, remarcant les diferències en els trets funcionals de les espècies o grups funcionals.

Inventaris forestals nacionals una eina imprescindible per estudis a gran escala

Molt abans que el cicle del C formés part de l'agenda de recerca, en el seu inici els inventaris forestals nacionals es van concebre estrictament per estimar el valor comercial de la fusta (Ciais *et al.* 2008). Els inventaris forestals nacionals, en contra de la majoria d'estudis a escala més local, proporcionen una informació sistemàtica, estadísticament no esbiaixada, regularment actualitzada que dóna un visió general dels conjunt de boscos a gran escala representant la variació temporal i espacial al llarg de gradients ambientals (Kauppi *et al.* 2006; Charru *et al.* 2010). Avui en dia, juntament amb els sensors remots i els sensors LiDAR areotransportats (airborne laser scanning sensors) (Magnussen *et al.* 2010; Mc Roberts *et al.* 2010), s'han acabat convertint en una font d'informació imprescindible per quantificar i entendre la distribució geogràfica i temporal dels estocs i els embornals de C a escala global (Goodale 2002; Körner *et al.* 2003, Liski *et al.* 2003, Ciais *et al.* 2008, Pan *et al.* 2011) i a escala regional (Caspersen *et al.* 2000, Charru *et al.* 2010). Això és degut, d'una banda, als llargs temps de residència del C en els boscos però també a l'enorme potencial de processos destructius que, encara que de baixa freqüència, poden produir en poc temps canvis molt significatius en els estocs i en el balanç de C (Pretzsch 1996; Goodale *et al*. 2002).

Els inventaris forestals nacionals a Espanya constitueixen una base de dades d'aproximadament 90.000 parcel·les de mostreig monitoritzades periòdicament (aproximadament cada 10 anys) i sistemàticament distribuïdes per tota la superfície forestal arbrada d'Espanya (Villaescusa & Díaz, 1998; Villanueva 2005). Aquests IFNs es basen en una xarxa regular de parcel·les circulars a una densitat d'aproximadament una parcel·la per cada 200 hectàrees. La informació recollida ha permès una caracterització exhaustiva de la composició específica i de l'estructura de l'estrat arbori i del sotabosc (incloent l'estrat arbustiu i la regeneració de les espècies arbòries). El caràcter continu dels IFNs es va iniciar amb els segon inventari forestal nacional (IFN2) que es va dur a terme entre 1986 i 1996, i va continuar amb el tercer (IFN3), entre 1997 i 2008. Actualment s'està duent a terme el quart inventari (IFN4) les dades del quals encara no estan disponibles. A cada parcel·la, cada peu individual d'almenys 7,5 cm de diàmetre normal mostrejat a l'IFN2 es va tornar a mesurar a l'IFN3. D'aquesta manera es va obtenir informació precisa i per espècies de la incorporació de nous individus, del creixement dels arbres supervivents i de la desaparició de peus (morts o desapareguts).

Objectius i estructura de la tesi

Els impactes recents que tots aquests factors han pogut tenir sobre els boscos a escala regional es poden analitzar des de molts punts de vista però dos d'ells ens han semblat particularment rellevants per les enormes implicacions que podrien tenir en el futur i que ja hem apuntat en aquesta introducció. D'una banda analitzar els efectes sobre els estocs i els canvis en els estocs de C i per tant l'efecte en la capacitat d'embornal de C dels boscos. D'altra banda, abordar la qüestió des del punt de vista dels canvis demogràfics en relació a les diferents estratègies de regeneració i de supervivència de les diferents espècies o grups funcionals, per determinar qüestions relacionades amb canvis en la composició i distribució a escala regional i canvis en el funcionament dels ecosistemes forestals (Fig. 1).

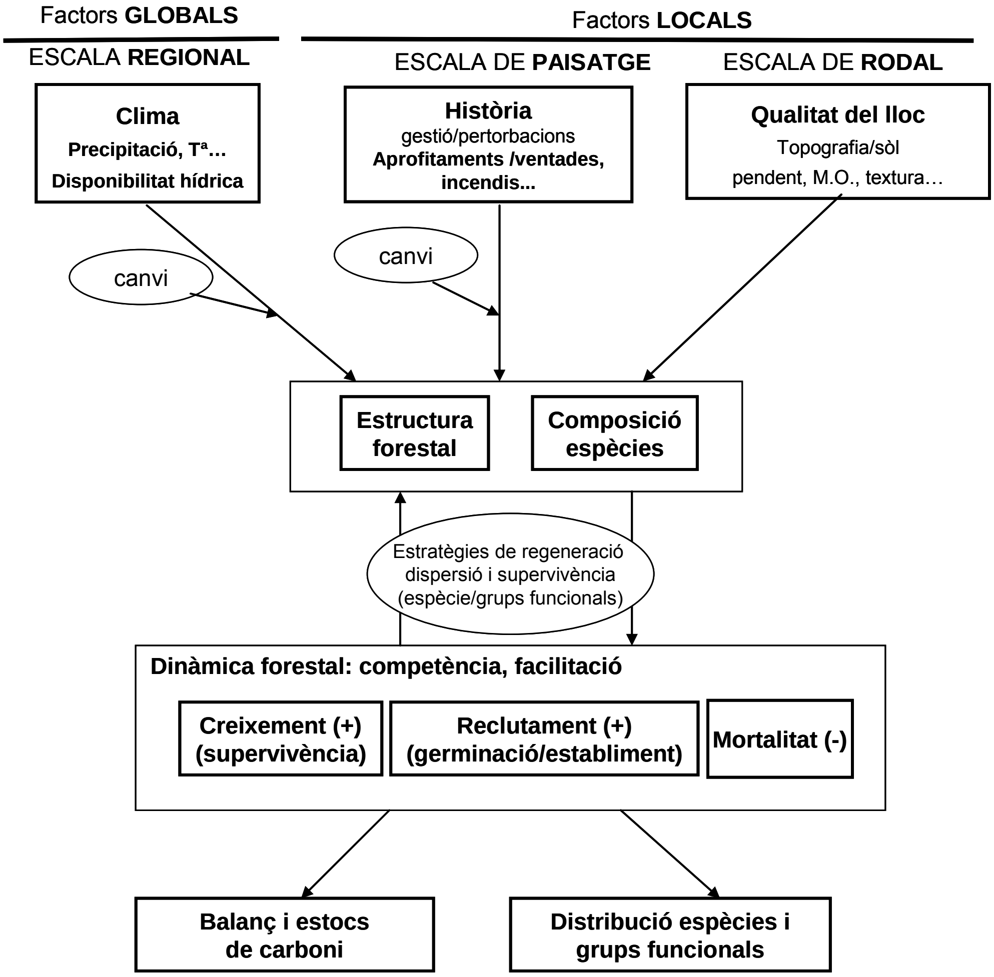

Figura 1. Esquema general dels principals factors de canvi i els processos implicats en la dinàmica dels boscos de la Península Ibèrica considerats en els diferents capítols de la tesi doctoral.

Concretament, els objectius de la tesi han estat els següents: (i) analitzar els principals factors que han determinat els patrons espacials actuals dels estocs de C dels boscos de l'Espanya peninsular, (ii) analitzar els canvis recents en aquests estocs i, per tant, la capacitat d'embornal dels boscos espanyols, (iii) establir les conseqüències que han tingut aquests canvis del punt de vista demogràfic, analitzant els patrons de reclutament per espècies i grups funcionals, i (iv) analitzar els patrons d'extinció i colonització i els conseqüents canvis en la distribució geogràfica de les espècies i grups funcionals. Tots els anàlisis s'han dut a terme per intentar desglossar i a la vegada determinar la importància de l'efecte dels diferents factors de canvi (*drivers*): estructura, gestió/pertorbació, clima i canvis recents en el clima i en la gestió. Aquest efectes s'han analitzat a escala regional i, segons els casos, per espècies i grups funcionals de l'Espanya peninsular, utilitzant, com a informació principal, la base de dades dels dos darrers inventaris forestals nacionals l'IFN2 i l'IFN3. A més d'aquesta introducció general i d'un apartat final amb les conclusions més destacades, aquesta tesi consta de quatre capítols amb els següents objectius específics:

Capítol 1. ***Patrons espacials i predictors dels estocs de carboni a l'oest del Mediterrani.***

En aquest capítol hem mirat d'entendre a gran escala les relacions entre l'estoc de carboni dels boscos de l'Espanya peninsular i les condicions ambientals i la diversitat estructural i específica per predir l'impacte del canvi global, definir possibles estratègies de gestió que permetin maximitzar els estocs de carboni i potenciar el paper del bosc com a reservori de C. En primer lloc s'analitzen els patrons espacials dels estocs de C de la biomassa aèria i subterrània dels diferents compartiments, espècies i grups funcionals. En segon lloc, es determinen les principals variables predictives dels patrons de distribució dels estocs de C distingint coníferes i planifolis, posant l'èmfasi en el paper de la riquesa estructural i específica separant l'efecte de la resta de factors determinants que actuen o bé a escala global com el clima (temperatura i disponibilitat hídrica) o bé a escala més local com les pertorbacions prèvies (foc i aprofitaments forestals) i altre factors com el sòl i la topografia.

Capítol 2. ***El canvi climàtic recent interactua amb l'estructura del bosc i la gestió forestal per determinar els canvis en els estocs de C dels boscos espanyols.***

Si bé és cert que la majoria de boscos temperats estan acumulant C essencialment per l'efecte positiu de l'augment de la temperatura i la fertilització pel CO_2 atmosfèric, la situació podria ser molt diferent en els ecosistemes Mediterranis limitats per l'aigua. En aquest capítol, en primer lloc, s'identifiquen els factors que determinen la variació espacial dels embornals de C dels boscos espanyols (canvis en els estocs de carboni de la biomassa aèria i subterrània) i dels seus dos components (creixement i mortalitat). En segon lloc es posa l'èmfasi en el paper de les tendències climàtiques recents (escalfament i sequera) i com varia al llarg del gradient geogràfic de disponibilitat hídrica. En tercer lloc s'analitza fins a quin punt la gestió forestal recent ha permès mitigar l'efecte negatiu de l'escalfament recent.

Capítol 3. ***Patrons i factors de canvi que determinen la regeneració de les espècies de coníferes i planifolis en els boscos de l'Espanya peninsular***

En aquest capítol s'identifiquen els principals factors que determinen a gran escala el reclutament dels arbres en la fase de transició clau de joves (*saplings*) a adults per les diferents espècies, posant l'èmfasi en les diferents estratègies de regeneració que les distingeix a fi i efecte de poder predir la distribució de les espècies en el futur davant del canvi global. En les condicions actuals, on s'ha produït un abandonament força generalitzat de la gestió forestal, però que ha anat acompanyat d'un escalfament global, cal tenir en compte el conjunt de factors que potencialment poden influir sobre la regeneració en termes d'abundància de regenerat (en l'estadi previ a la fase adulta) i en la taxa de reclutament. En primer lloc al capítol s'identifiquen els factors clau: estructura, règim de pertorbacions, clima i canvis recent en el clima que determinen els patrons de regeneració. En segon lloc, l'estudi discuteix fins a quin punt les estratègies de regeneració que diferencia els planifolis de les coníferes permeten explicar els patrons actuals de regeneració.

Capítol 4. ***Canvis ràpids i direccionals en la distribució geogràfica de les espècies d'arbres porten a una dominància creixent dels planifolis***

En aquest capítol es documenten els canvis recents (9-12 anys) que s'han produït en la distribució geogràfica de les principals espècies arbòries autòctones de l'Espanya peninsular (inclou espècies de distribució alpina, temperada i mediterrània) i també a nivell de grans grups funcionals: coníferes i planifolis. Per determinar si els canvis direccionals observats podrien ser atribuïbles a factors principalment climàtics, aquest capítol analitza l'efecte conjunt dels diferents factors de canvi: clima, canvis recents en el clima i canvis en les condicions de l'hàbitat (pertorbacions recents com el foc i l'abandonament de la gestió forestal). En particular, s'examina si les diferències en els trets funcionals entre coníferes i planifolis pel que fa a la capacitat de resistir a factors biòtics o abiòtics permeten explicar la ràpida expansió dels planifolis en relació a les coníferes

Els quatre capítols centrals estan escrits en anglès perquè estan pensats en format article científic per ser enviats directament a revistes científiques internacionals. A data d'avui un dels capítols ja ha estat publicat, un segon està acceptat per publicació i la resta han estat enviats i estan pendents de revisió.

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Capítol 1

Spatial patterns and predictors of forest carbon stocks in western Mediterranean

A modified version of this chapter is in press in *Ecosystems;*

Jordi Vayreda, Marc Gracia, Josep G. Canadell & Javier Retana (in press)

Abstract

Mediterranean semi-arid forest ecosystems are especially sensitive to external forcing. An understanding of the relationship between forest carbon (C) stock, and environmental conditions and forest structure enable to predict the impacts of climate change on C stocks and to define management strategies that maximize the value of forests for carbon mitigation. Based on the national forest inventory of Spain (1997-2008 with 70,912 plots), we estimated the forest C stock and its spatial variability in Peninsular Spain and, we determined the extent to which the observed patterns of stand C stock can be explained by structural and species richness, climate and disturbances. Spain has an average stand C stock of 45.1 Mg C/ha. Total C stock in living biomass is 621 Tg C (7.8% of the C stock of European forests). The statistical models show that structural richness, which is driven by past land-use and life forest history including age, development stage, management activities and disturbance regime, is the main predictor of stand tree C stock with larger C stocks in structurally richer stands. Richness of broadleaf species has a positive effect on both conifer and broadleaf forests, while richness of conifer species shows no significant or even negative effect on C stock. Climate variables have mainly an indirect effect through structural richness but a smaller direct predictive ability when all predictors are considered. To achieve a greater standing C stock, our results suggest the need for promoting high structural richness by managing for uneven-aged stands and favoring broadleaf over conifer species.

Key words: Tree carbon stock; Understory carbon stock; National forest inventory; Conifer and broadleaf forests; Structural richness; Tree species richness; Water availability; Forest management; Fire disturbance; Peninsular Spain.

Introduction

Knowledge on the patterns and ways to predict forest carbon (C) stocks are needed to determine the role of forests in the C cycle and in the provision of multiple ecosystem services which the wellbeing of societies depends upon. The current estimate of the world's forests C stocks is 861 ± 66 Pg C (1 Pg = 10^9 Mg = 10^{15} g) with 363 ± 28 Pg C (42%) in above- and below-ground live biomass (Pan *et al.* 2011). The same forests were a net C sink of 1.2 ± 0.9 Pg C yr^{-1} over the past decade (Pan *et al.* 2011). On a global scale, forests dominate the terrestrial C sink which is responsible for removing 30% of all anthropogenic C emissions (Canadell *et al.* 2007). However, uncertainty of these estimates and those of regional fluxes is large and the accurate quantification of forest C stocks is one of the main sources (Houghton *et al.* 2009). The uncertainty also affects the calculations of the potential capacity for C mitigation of forests and forestry, and the reporting commitments to the Ministerial Conference on the Protection of Forests in Europe, United Nations Convention on Climate Change, the Kyoto Protocol, and the Forest Resource Assessment with important management implications.

At large scales, the most influential drivers in determining stand C stocks are climatic variables, particularly temperature (Brown *et al.* 1999; Houghton 2005; Zhao & Zhou 2006). However, in semiarid ecosystems, precipitation and potential evapotranspiration also play a key role (Kerkhoff *et al.* 2004; Sankaran *et al.* 2005; Huang *et al.* 2009). At a local scale, soil properties (e.g., texture, amount of organic matter, stoniness, soil depth) modulate soil water content and affect C stock, while topographic factors act in an indirect way by modifying local climatic patterns (Zhao & Zhou 2006; Huang *et al.* 2009). Natural disturbances (e.g., wildfires, wind, storms) and human-induced disturbances by means of management practices (e.g., clearing, thinning, reforestation) are also important determinants of stand C stock due to changes in stand structure and diversity (Merino *et al.* 2007; Nabuurs *et al.* 2008). Temperate and Mediterranean forests were intensively managed for timber production over the last century. However, during the last decades there has been a process of forest expansion after agricultural abandonment and reduction in forest management now thought to be responsible for the increment of C stock in many forested areas (Houghton 2003; Friedlingstein *et al.* 2010).

The above external factors lead to a particular forest structure and composition such as structural diversity (i.e., the variation in tree size and height), and species and functional richness (McElhinny *et al.* 2005; Lexerød & Eid 2006) which can also be used to predict C accumulation (Kueppers & Harte 2005). Under similar environmental conditions different stand structures and species composition have different growth and mortality rates and these differences eventually lead to differences in stand C stocks. A positive relationship between structural diversity and stand C stock may be due to the fact that different horizontal and vertical layers enhances niche complementarities of resource use reducing competition among trees (Lei et al. 2009). Additionally, there is evidence that forests with high species diversity may promote a more efficient use of resources and higher rate of C sequestration (Vandermeer 1989; Vilà *et al.* 2007) compared with sites with a lower number of species or poor structural diversity. As a direct consequence, these stands can maintain higher living C stock.

Moreover, some authors (e.g., Lei *et al.* 2009) recommend uneven-aged stand management in conjunction with selective or partial cutting to maintain high structural and species diversity.

There has been much attention to assess C stocks of forests at the global scale (Goodale *et al.* 2002; Nabuurs *et al.* 2008; Pan *et al.* 2011) as well as at regional scales (e.g., Brown *et al.* 1999; Dieter & Elsasser 2002; Kueppers & Harte 2005; Zhao & Zhou 2006; de Castilho *et al.* 2006; Risch *et al.* 2008) with little or no attention to semi-arid and Mediterranean regions. In this context, forest woodlands in Spain (Iberian Peninsula, SW Europe) represent well the influence of environmental and disturbance factors that have been dominant in semi-arid forest ecosystems of Southern Europe. Most of the region is under the influence of Mediterranean climate, with strong gradients in temperature and precipitation, it has high structural and tree species diversity that, combined with a long history of disturbances and human management, influence the current patterns of C stocks.

The objective of this study is to estimate the total forest C stock and its spatial distribution, and to determine the main predictive variables of the observed patterns of C stocks in conifer and broadleaf forests in Peninsular Spain. Our main hypothesis is that structural and species richness variables, rather than factors such as climate and local site variables are better predictors of C accumulation, because they integrate many of the above factors.

Material and methods

Study Area

The study area comprises the forested areas of Spain (SW of Europe, situated between 9º 2’W and 3º 2’E and 36º 0’N and 43º 5’N) excluding the Canary and Balearic Islands (ca. 49.35 million has). The climate is highly variable due to topographic and continental gradients. Mean minimum temperature ranges from -2 to 14ºC and mean maximum temperature from 9 to 25ºC. Annual precipitation ranges from 100 to 2500 mm. There are two major climatic domains (Capel Molina 2000): the Mediterranean , which covers most part of the Iberian Peninsula (except in the northwest and mountain regions) which is characterized by mild winters and hot and dry summers, and the temperate-oceanic, which covers the northwest of the Spain and is characterized by a relatively wet and cold climate. According to the Forest Map of Spain (MFE50, MARM 2007), the forested area has 18.4 million ha or 37.3% of the whole area. Forests are mainly concentrated in the steeper areas, from 0 to 2500 m above-sea-level. Flat and low regions are mainly covered with croplands and urban areas. Forests are distributed in Mediterranean, sub-Mediterranean, Eurosiberian and Boreoalpine areas. The national definition of forest in Spain also includes dehesas, a particular forest (ca. 2.2 million ha) of low tree cover (between 5 and 20%) and very low tree density (20-200 trees/ha), which allows the presence of pastures that maintain extensive livestock of either pigs or cows and having a high socioeconomic importance.

Dataset: the Third National Forest Inventory of Spain (IFN3)

In this study, the main data set used for computing stand C stock (Mg/ha) was the third National Forest Inventory of Spain (IFN3, Villanueva 2005), which was conducted from 1997 to 2008. The IFN is an extensive national database of forest surveys distributed systematically across the forested area of Spain. The IFN is based on a network of circular plots at a density of 1 plot per 200 ha, which allows forest characterization and includes exhaustive information on the structure and composition of canopy and understory woody species. There were 89,369 plots in the IFN3 and, from those, 70,912 had at least one adult tree (diameter at breast height, DBH≥7.5 cm) (i.e. 15.2 million ha, 30.8% of the whole area). According to data of IFN3, the ten most abundant species depending on the area occupied were: *Quercus ilex* (22.8%), *Pinus pinaster* (11.9%), *Pinus halepensis* (11.8%), *Pinus sylvestris* (9.1%), *Pinus nigra* (7.0%), *Quercus pyrenaica* (5.3%), *Pinus pinea* (3.9%), *Quercus suber* (3.8%) *Fagus sylvatica* (3.1%) and *Quercus faginea* (2.9%). These ten species represented 81.5% of all Peninsular Spain forests.

Tree sampling followed a nested design with plot size depending on tree DBH to guarantee the representative of tree size distribution. 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 also considered within 10–15 m and 15–25 m around the centre of the plots, respectively. Species identity, DBH, and height of all living were recorded. In a radius of 5 m from the center of the plot, the number of small trees (from 2.5 to 7.5 cm DBH) and their mean height was recorded. Understory was sampled by identifying each species present in a radius of 10 m within the plot and annotating its fraction cover and mean height.

Calculations of stand C stock

We established and defined two different compartments to compute stand C stock (Mg/ha) for each plot: (1) *Tree biomass.* This compartment included the living biomass, both aboveground (trunks, branches and leaves) and belowground (large roots and stumps) of individuals with DBH≥7.5 cm sampled in each plot and; (2) *Understory biomass.* This component included the living biomass, both aboveground (trunks, branches and leaves) and belowground (large roots and stumps) of the shrub stratum and of living small tree individuals with DBH between 2.5 and 7.5 cm sampled in each plot.

To compute stand C stock of tree biomass we applied the equations obtained in different studies (Gracia *et al.* 2004 a, b; Montero *et al.* 2005) to the data of each IFN3 plot. Aboveground biomass (AGB) of each living tree with DBH≥7.5 cm was computed using specific equations as a function of DBH and height (H) developed in the Ecological Forest Inventory of Catalonia (IEFC, Gracia *et al.* 2004a):

$$AGB = a \cdot DBH^{b} \cdot H^{c} \qquad \text{(Eq. 1)}$$

where a, b and c were specific coefficients for the different species. For the least common species we applied the coefficients of general equations obtained for the different functional groups (conifer, deciduous and sclerophyllous species).

Tree belowground biomass (BGB) was computed using the equations developed by Montero *et al.* (2005) from dried samples of the different fractions for the most abundant tree species in the Iberian Peninsula. For each species, Montero *et al.* (2005) computed AGB and BGB as a function of DBH:

$$AGB = a \cdot DBH^{b} \qquad \text{(Eq. 2)}$$

$$BGB = a \cdot DBH^{b} \qquad \text{(Eq. 3)}$$

where a and b were specific coefficients for the different species. For the least common species we applied the coefficients of general equations obtained for the different functional groups (conifer, deciduous and sclerophyllous species). From this information the proportion of BGB (%BGB) as a function of AGB was estimated as:

$$\%BGB = a \cdot AGB^{b} \qquad \text{(Eq. 4)}$$

where a and b were specific coefficients for the different species. This equation was used to compute % root biomass in relation to AGB.

C amount of each living tree was determined by multiplying biomass values of each fraction, AGB and BGB, by the specific C content of the species obtained in the IEFC (Gracia *et al.* 2004b) from oven-dried samples. Overall stand C stock per fraction (aboveground and belowground) in each plot was obtained by summing up the values of all trees present in the plot.

The stand C stock of living understory biomass was the sum of the biomass of shrubs and trees smaller than 7.5 cm in DBH. Biomass of shrubs in each plot was obtained from the information of the understory in each IFN3 plot and the equations described by Armand *et al.* (1993). We computed AGB of each shrub species in each plot as a function of apparent volume (AV, computed as $AV = S \cdot H$, where S was the area occupied by this shrub species in the plot and H its mean height):

$$AGB = a \cdot AV^{b} \qquad \text{(Eq. 5)}$$

where a and b were specific coefficients for the different species that were available in Armand *et al.* (1993). Consistent with Armand et al. four different morphologies of shrub species, we classified the species that were not present in their study in one of the four morphologies and applied the general equation of corresponding category. BGB was computed as a constant proportion of 25% of AGB. Living understory biomass was computed as the sum of the two fractions, AGB and BGB, of all shrub species present in the plot. We then obtained C density (Mg/ha) by multiplying this sum by 0.5, a standard value used for shrub species (IPCC 2003).

Biomass of small trees (from 2.5 to 7.5 cm of DBH) for each species was estimate applying the Eq. 1 by multiplying a mean DBH value of 4 cm (because there were smaller than large individuals within this class) by the mean height of these small trees. BGB of small trees for each species present in the plot were computed using Eq. 4. We multiplied the sum of the values of AGB and BGB of single small trees for each species by their plot densities to obtain the biomass. Carbon stock of small trees for each species was calculated by multiplying living biomass in the plot by the specific C content of the species. We summed up the values of small trees of all species to obtain the overall C density for small trees in the plot.

To upscale stand C stock (Mg/ha) to total C stock (Tg) we chose a very simple and direct method consisting in computing for each province (corresponding to the main administrative division in Spain) the ratio between the forest area (MFE50, MARM 2007) and the number of sampled plots. This factor is a measurement of the sampling effort and is equivalent to the forest area represented by each plot**.** The absolute C stock at the province scale was obtained as the sum of the C stock of each plot multiplied by the corresponding province factor. Finally, the sum of all values obtained at the province level was the absolute C stock for the whole peninsular Spain.

We produced stand C stock maps (tree + understory) (Mg C/ha) for conifers, broadleaf forests and forests as a whole (conifers + broadleaves) using MiraMon GIS software (Pons 2008). The map was obtained by dividing the territory of Spain in polygons of 10’x10’ resolution. For each of these polygons with forest area of at least 10% we computed the mean stand C stock of all plots included in the polygon. The polygons with forest surface below this threshold were included in the map as N/A (not available).

Predictors of stand tree C stock

We analyzed the relationship between stand tree C stock (above and underground biomass) and structural and species richness, climate variables, local site characteristics, and recent disturbances. In these analyses we include the five main broadleaf species (*F. sylvatica*, *Q. faginea*, *Q.ilex*, *Q. pyrenaica* and *Q. suber*) and the five main conifer species (*P. halepensis*, *P. nigra*, *P. pinaster*, *P. pinea* and *P. sylvestris*). The dominant tree species of each plot (DBH ≥ 7.5 cm) was determined using basal area as criteria. We also exclude forest plantations and dehesas (open woodland forests). For each plot we obtained the following groups of predictor variables:

(a) Climate. This information was obtained from the Digital Climatic Atlas of the Iberian peninsula (Ninyerola *et al.* 2005) a collection of digital maps of 200x200 m resolution with annual and monthly information for cumulative rainfall, and maximum, mean and minimum temperatures. Based on the geographic coordinates of each IFN3 plot we determined three climatic variables: (1) *Mean annual temperature* (MT, ºC); (2) *Mean annual thermal amplitude* (or temperature range, TR) obtained from the annual difference between maximal and minimal temperature (ºC); and (3) *Annual water availability index* (WAI) obtained at monthly level according to:

$$WAI = ((P - PET) / PET) \cdot 100 \qquad \text{(Eq. 6)}$$

where P is rainfall (mm/month) and PET is potential evapotranspiration (in mm/month) following the Samani & Hargreaves approach (1982). Annual WAI was obtained as a sum of the WAI of twelve months. Negative values of WAI correspond to dry sites, and positive values to wet sites. The map of

WAI (Fig. 1.1) indicates that 85% of the overall area of Spain has water deficit and only 15% of the area has water surplus throughout the year. The WAI values indicate a clear latitudinal gradient and a slight gradient from west to east.

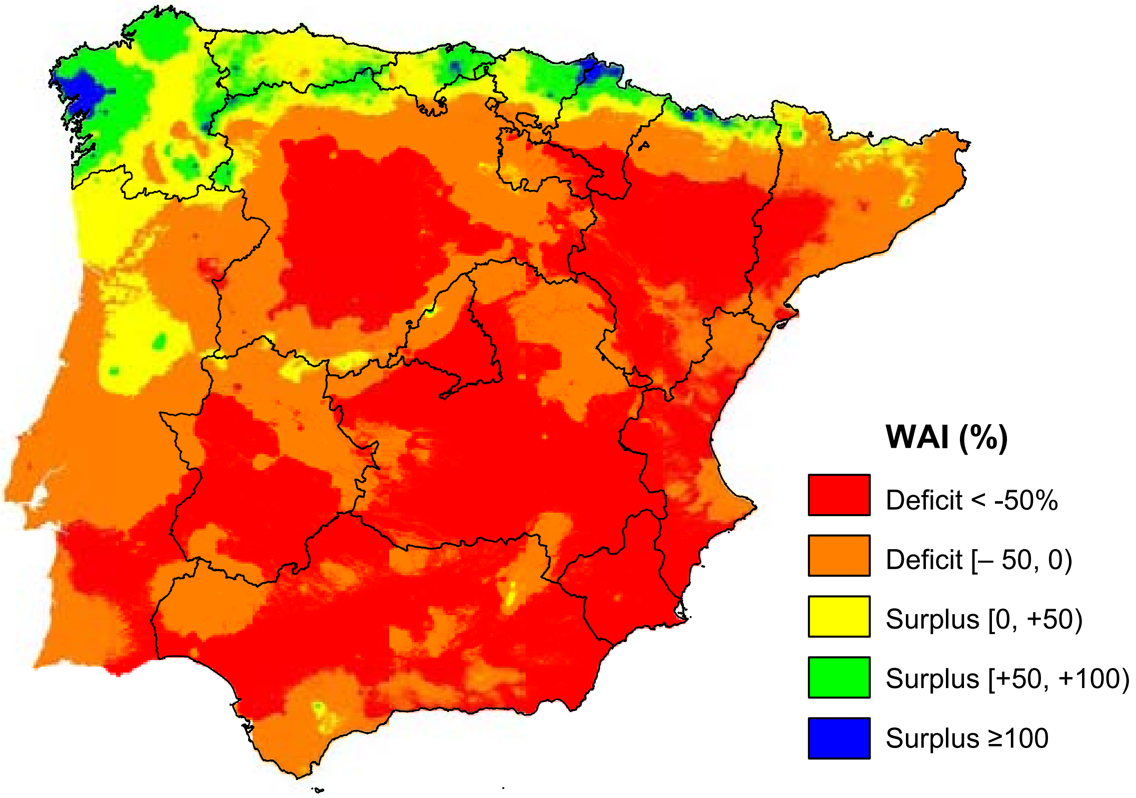


Figure 1.1. Map of the annual water availability index (WAI) in the Iberian Peninsula.

(b) Local site characteristics. We used four local site variables: (4) *Soil type*: it had two categories based on the reaction of mineral soil to the hydrochloric acid: limestone (those that reacted with the acid) or siliceous (those that did not show any chemical reaction with the acid); (5) *Soil texture*: in each plot soil texture was estimated following a granulometric classification of three categories: sandy, loam and clay; (6) *Stoniness*: surface soil stoniness was estimated following a four-level ordinal classification: 0%, 1-25%, 26-50% and 51-75% of stones on the surface of the soil; (7) *Slope*: the only topographical variable considered was slope which was estimated as the maximum slope (°) in the centre of the plot.

(c) Recent forest disturbances. We used two categorical variables related to forest disturbances and included in the IFN3 dataset: (8) *Forest management* (Yes/No): we considered that there had been recent exploitation when there was any evidence of cutting or thinning in the plots; (9) *Fire* (Yes/No): evidence of severe damage caused by fire in the recent past.

(d) Structural and species richness. These predictor variables were obtained from the living trees with DBH≥7.5 cm: (10) *Structural richness*: number of diameter classes present in the plot for any species (each class was 5 cm of DBH wide); (11) *Conifer species richness*: number of conifer species present

in the plot and; (12) *Broadleaf species richness*: number of broadleaf species present in the plot. To avoid the bias that could be produced in these variables due to low numbers of trees per plot, we only included plots with at least six trees sampled (that is, the threshold of the first quartile of the number of trees sampled in all plots).

Statistical analyses

The total number of plots used in statistical analyses was 33,827. From those, 12,642 plots were dominated by one of the five broadleaf species and 21,185 plots were dominated by one of the five conifer species. We fitted separate models, using general linear model (GLM), for conifers and for broadleaves (see above) with stand tree C stock as response variable (previous log-transformation to satisfy the normality assumption). Species identity was included in each model as a fixed factor. The other predictor variables were described in the previous section. Stepwise model selection was applied starting from the saturated model (using all variables) and removing the least significant term until there was no further decrease in the Bayesian Information Criterion (BIC). We considered all models within 2 BIC units as equivalent in terms of fit. Given the large sample size, significance was accepted at $p<0.01$. We checked if residuals of the models did show any spatial pattern using spherical spatial correlation structure by using generalized least squares (GLS). These models were similar in terms of the fitted coefficients to the equivalent general linear models (GLM). Given that the two types of models did not significantly differ (BIC values < 2 units) in the results we only included the models without spatial autocorrelation. Statistical analyses were carried out with the R software (package nmle, R 2.10.0, The R Foundation for Statistical Computing).

Structural equation modeling (SEM) was used to analyze the complex effects of the three groups of variables: climate, local site characteristics and richness, on stand tree C stock. We carried out different models with conifers and broadleaves and also in the plots affected or not by disturbances (both management and fire), that is, we carried out four models for the combinations of forest type and presence or not of disturbances. We tested a common conceptual model to explain the patterns of stand C stocks in these four combinations. This general model considered that climate and local site characteristics have indirect effects on response variable through richness variables but also direct effects on stand C stocks. We fitted each “saturated” model including all possible directional relationships plus covariation between the climate variables and between the richness variables. Each model was simplified stepwise removing the least significant term until there was no further decrease in the Bayesian Information Criterion (BIC). We considered all models within 2 BIC units as equivalent in terms of fit. All SEM analyses were performed using the package AMOS 18 (Arbuckle 2009). In all cases, parameter significance was accepted at $\alpha = 0.05$.

Results

Patterns of Total C stocks

The total C stock of forests in Peninsular Spain was 621 Tg (1 Tg = 10^{12} g) of which 547 Tg (88.1%) were in trees and 74 Tg (11.9%) in the understory. A significant fraction of this stock was belowground, with 29.5% for trees and 37.6% for the understory (Table 1.1). The mean stand C stock was 45.1±0.16 Mg/ha, with 39.8±0.15 Mg/ha (88.4%) for trees and 5.2±0.002 Mg/ha for the understory (11.6%). Total C stock of broadleaf forests (trees + understory) was 330 Tg, while that of conifer forests was 291 Tg. Conifers had lower value of stand C stock (41.8±0.185 Mg/ha) than broadleaves (48.6±0.254 Mg/ha). The mean stand C stock stored belowground on broadleaf forest was higher (36.5%) than on conifer forests (23.8%).

Table 1.1. Mean and standard error (SE) of stand C stock (Mg/ha) by fractions (aboveground and belowground) and total, percent of each compartment related to overall stand C stock and absolute C stock (Tg, 1Tg =10^{12} g) in: A) compartments (trees and understory) and B) broadleaf and conifer forests (trees + understory). Total number of plots: 70,912; broadleaf forest: 34,334 and conifer forests: 36,578.

A) **Compartment**	**Fraction**	**Stand C stock (Mg/ha)**	**SE**	**% fraction**	**C stock (Tg)**
Trees	Aboveground	28.1	0.109	70.5	385
	Belowground	11.8	0.049	29.5	161
	Total	**39.8**	**0.152**	**100.0**	**547**
Understory	Aboveground	3.3	0.012	62.5	47
	Belowground	2.0	0.008	37.5	28
	Total	**5.2**	**0.018**	**100.0**	**74**
Total (Trees + understory)	Aboveground	31.3	0.109	69.5	432
	Belowground	13.7	0.052	30.5	189
	Total	**45.1**	**0.156**	**100.0**	**621**
B)					
Broadleaves (Trees + understory)	Aboveground	30.8	0.166	63.5	210
	Belowground	17.7	0.092	36.5	120
	Total	**48.5**	**0.254**	**100.0**	**330**
Conifers (Trees + understory)	Aboveground	31.9	0.143	76.2	222
	Belowground	10.0	0.044	23.8	69
	Total	**41.8**	**0.185**	**100.0**	**291**

The spatial distribution of stand C stock in Peninsular Spain showed that forests with the highest values (>80 Mg/ha) were mostly concentrated in the north and the northwest regions by the Atlantic Ocean, Pyrenees, and other mountain regions (Fig. 1.2A). Forests in the south and the east had the lowest stand C stocks, especially along the southern Mediterranean coast. The spatial distribution of broadleaf and conifer forests showed similar pattern (Fig. 1.2B and 1.2C). Broadleaf forests were mostly concentrated in the north, again with the highest values. The lowest values (<35 Mg/ha) were in the south-west where there are the major concentration of dehesas (mainly *Q. ilex* and *Q. suber*).

Similarly, the highest values of conifer forests were in the north but the major concentration, and also de lowest values, were located in the south-east (coinciding mainly to the forests of *P. halepensis*).

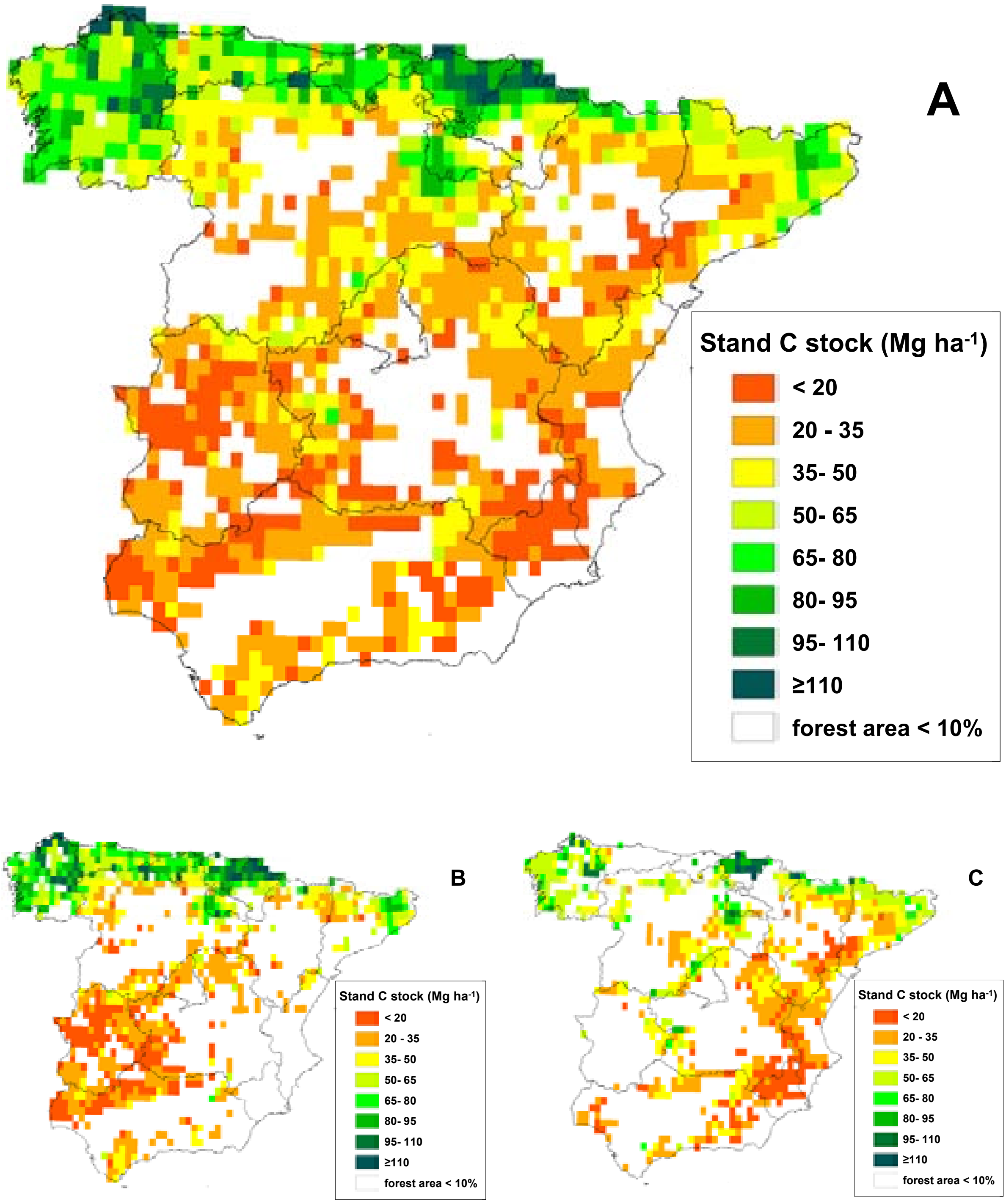


Figure 1.2. Map of mean stand C stock (sum of the two compartments –trees and understory– Mg/ha) in cells of 10'x10' resolution in forests of peninsular Spain for (A) all species (number of plots=70,912); (B) forests dominated by broadleaf species (number of plots =34,334); and (C) conifer forests (number of plots = 36,578).

The lowest values of stand tree C stock (both above- and belowground) (Fig. 1.3A) among broadleaf species corresponded to *Q. suber* (20.3±0.37 Mg/ha), *Q. faginea* (22.9.0±0.52 Mg/ha) and *Q. ilex*

(26.2±0.22 Mg/ha). Intermediate values are found for *Q. pyrenaica* (41.0±0.67 Mg/ha) and very high values for *F. sylvatica* (105.4±1.09 Mg/ha). Among conifers, the lowest values were for *P. halepensis* (19.2±0.17 Mg/ha), followed by *P. pinea* (23.8±0.36 Mg/ha) and *P. nigra* (32.7±0.37 Mg/ha), while the highest mean values were those of *P. pinaster* and *P. sylvestris*, with 44.8±0.38 and 48.7±0.42 Mg/ha respectively. The patterns of stand C stock for understory were opposite to those found for trees: as stand tree C stock decreased, understory stand C stock increased and vice versa (Fig. 1.4A and 1.4B). Hence, the highest proportion values in relation to the total stand C stock were in Mediterranean forests of *Q. suber* (24.7%), *P. halepensis* (23.2%), *Q. faginea* (20.2%) and of *Q. ilex* (16.7%). The mean values of stand C stock for conifers (mean of five conifer species) of the two compartments (trees and understory) were slightly lower than for broadleaves because conifer forests stored less biomass belowground (Fig. 1.4A and 1.4B). The highest values of stand C stocks in natural forests in relation to reforestations was mainly due to the higher biomass stored in their understory (Fig. 1.4B). The significant lower stand C stock found in dehesas was due to the fact that they stored less C in the two compartment (trees and understory) but, unlike the other forest types, the proportion of biomass stored belowground increased (Fig. 1.4A and 1.4B).

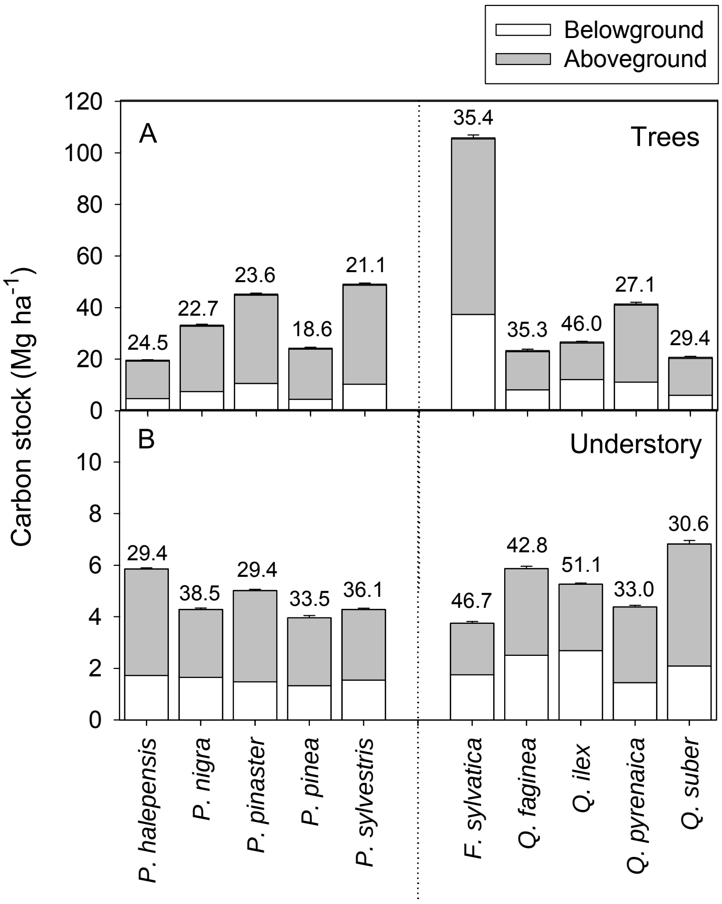


Figure 1.3. Mean (±standard error) of stand C stock (Mg/ha) for the five conifer species and for the five broadleaf species in: (A) tree compartment (above- and belowground) and; (B) understory (above- and belowground). Values indicated the percent of the total stand C stock of the compartment corresponding to belowground.

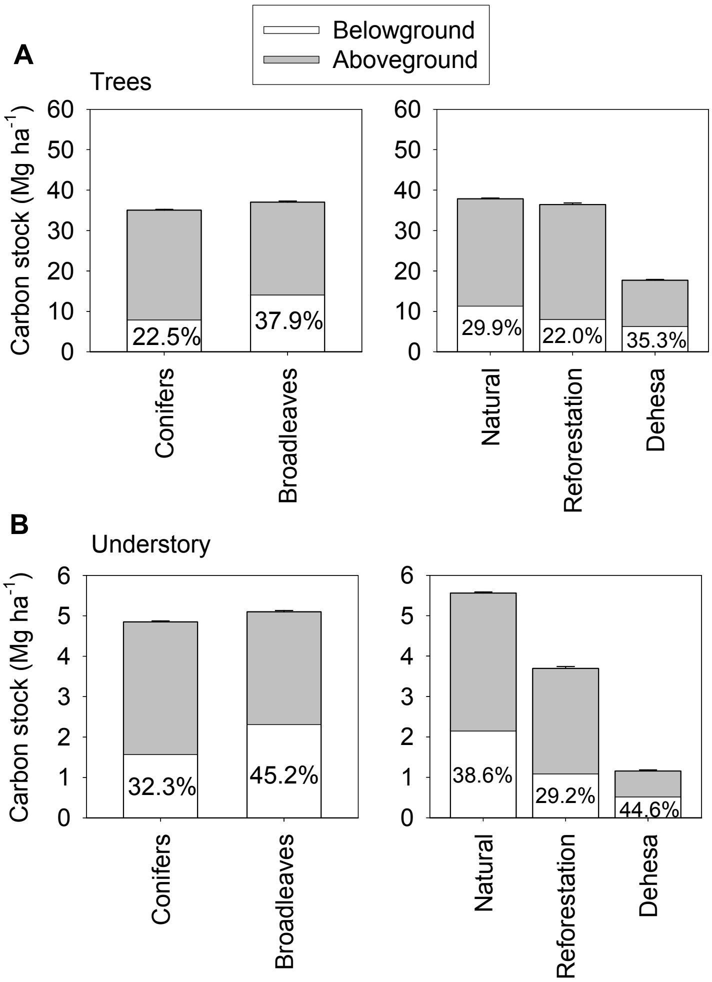


Figure 1.4. Mean (±standard error) of aboveground and belowground stand C stock (Mg/ha) by compartment (average of ten species analyzed) for: (A) Tree compartment (left panel by: conifer and broadleaf species; right panel by forest history: natural forests, reforestations or dehesas) and; (B) Understory compartment. Values indicated the percent of the stand C stock corresponding to belowground.

Predictors of stand tree C stock of conifer and broadleaf forests

The two GLM proposed determining stand tree C stock explained 62% of variance for broadleaf species (Table 1.2A) and 53% for conifer species (Table 1.2B). The decomposition of explained variability (%) of stand tree C stocks (Mg/ha) to the different group of variables showed that richness variables (both structural and species richness) showed the greatest effect in conifer and broadleaf forests (Fig. 1.5).

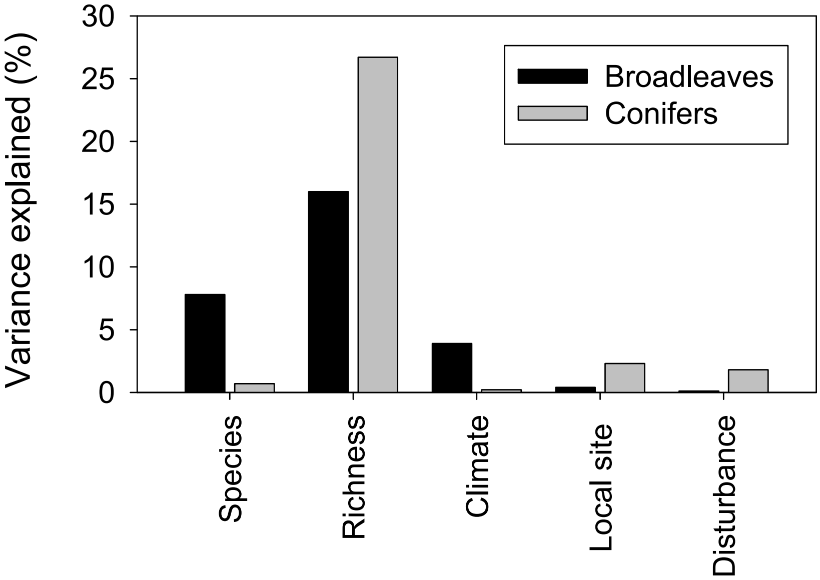


Figure 1.5. Decomposition of the explained variability (%) of tree C stock (Mg/ha) of the different group of variables for the models of broadleaves and conifers. The values indicate the percent of variance explained by each group of variables in the model.

The effect of local site characteristics and variables concerning forest disturbances was lower than that of climatic variables. The highest effect was the strong and exponential positive effect of the number of diameter classes on stand C stock (Tables 1.2A and 1.2B, Fig. 1.6). In broadleaf forests, the number of broadleaf species had a positive effect on stand tree C stock, while the presence of conifer species had a negative effect on it. In conifer forests, only the presence of broadleaf species had a positive effect on stand C stock while the presence of other conifers was not significant. Among climate variables, in the two groups of species WAI had a small and positive effect on stand tree C stock whereas mean annual temperature had a negative effect, stronger in broadleaf species. Finally, temperature range also showed a strong and negative effect on broadleaves, while in conifers was not significant (Tables 1.2A and 1.2B). Among local site variables, stoniness had the most significant negative effect. Soil type showed opposite patterns: stand tree C stock in conifers was highest in siliceous soils while broadleaves showed the highest C accumulation in limestone soils. Soil texture had a low effect, while on conifer forests showed the highest C accumulation on loam, intermediate on clay and the lowest on sandy soils; on broadleaves showed the highest values on clay and the lowest in sandy and loam. Slope had a positive effect on broadleaf species; in conifers it had not a significant effect. Managed conifer forest had higher stand C stock than unmanaged ones; in broadleaf forests this factor was not significant. Finally, fire disturbance leaded broadleaf forests to accumulate less C.

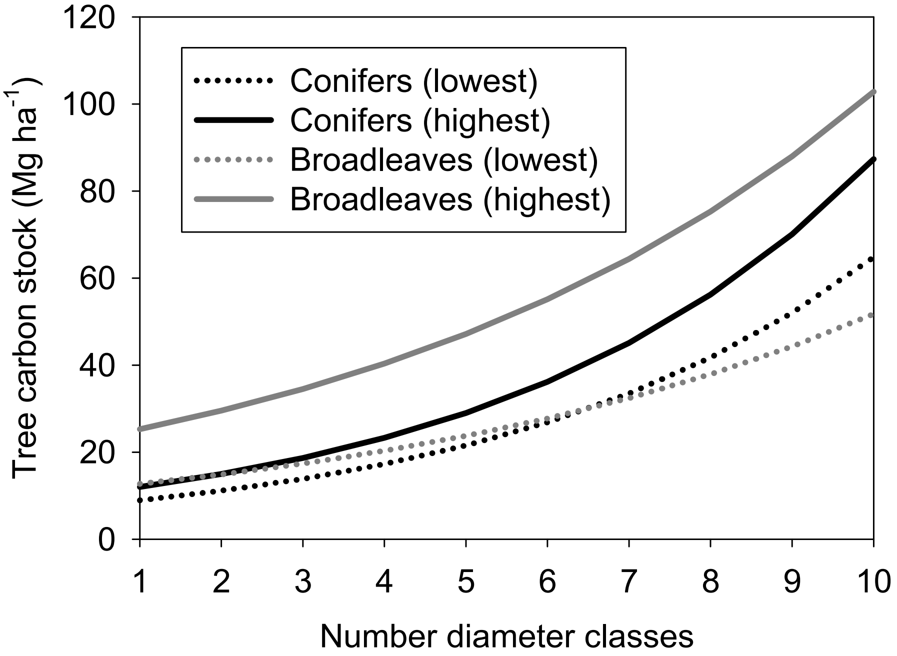


Figure 1.6. Predicted effects of structural richness, measured as the number of diameter classes, on stand tree C stock (Mg/ha) for conifers and broadleaves. Black lines represent the extremes of the effects predicted for the five studied conifers, whereas grey lines indicate the corresponding range for broadleaves (solid lines show the highest effect and dotted lines the lowest effect in each case).

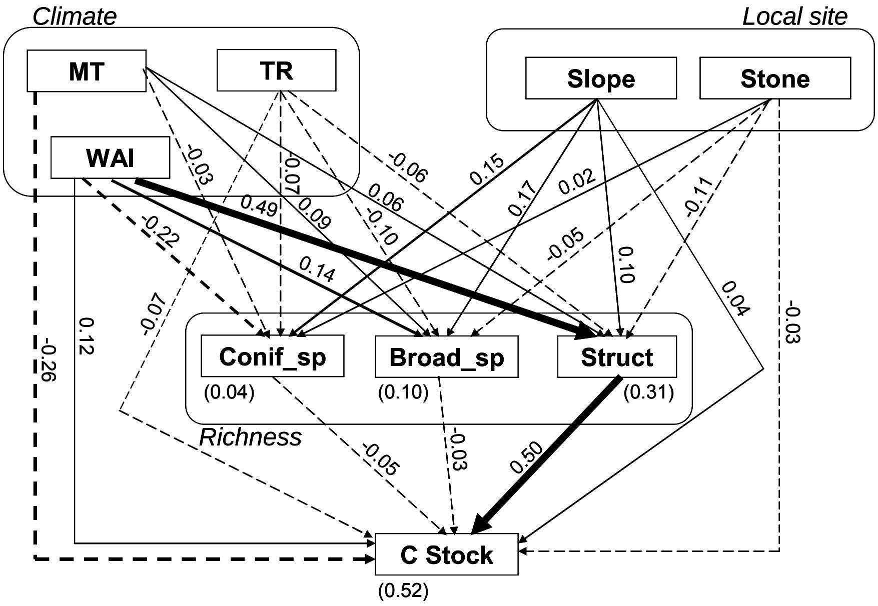
The results of the path analyses for the different forest types without disturbances (Fig 1.7) and with disturbances (Fig. 1.8) were essentially identical. All final four path models provided a good fit to the data indicated with a non significant chi-squared value. The models captured a substantial proportion of the variance in stand C stocks, ranging from 42.3% to 47.6% for conifers and from 52.2% to 54.6% for broadleaves. The resulting models differed not much from the saturated models, especially in the models of undisturbed forests, suggesting a complex network of direct and indirect relationships affecting stand C stocks. Structural richness was again the variable with a highest direct effect on stand C stock. The models indicated a higher effect of WAI on stand C stock to that shown in the GLM models, with a significant direct effect and an indirect effect through structural richness. Local site variables also showed both direct and indirect effects (through richness variables) on stand C stocks, although lower than those of climatic variables.

Table 1.2. Summary of stand tree C stock (Mg/ha) models (A) for broadleaves and; (B) for conifers. All values shown are significant at p<0.01 (indicated with **) or p<0.001 (***).

A) Broadleaves	Estimate	t-value		**B) Conifers**	Estimate	t-value	
(Intercept)	4.924 ± 0.071	69.0	***	(Intercept)	2.811 ± 0.0309	90.9	***
SP (*Q. pyrenaica*)			n.s.	SP (*P. nigra*)	-0.047 ± 0.0126	-3.7	***
SP (*Q. faginea*)	-0.423 ± 0.021	-20.2	***	SP (*P. pinaster*)	-0.058 ± 0.0135	-4.3	***
SP (*Q. ilex*)	0.070 ± 0.019	3.6	***	SP (*P. pinea*)	-0.269 ± 0.0208	-12.9	***
SP (*Q. suber*)	-0.667 ± 0.025	-26.8	***	SP (*P. halepensis*)	-0.202 ± 0.0157	-12.9	***
WAI (%)	0.001 ± 0.0002	5.1	***	WAI (%)	0.001 ± 0.0001	7.5	***
MT (ºC)	-0.066 ± 0.003	-24.8	***	MT (ºC)	-0.016 ± 0.0025	-6.5	***
TR (ºC)	-0.101 ± 0.005	-20.4	***	TR (ºC)			n.s.
Soil type (Limestone)	0.032 ± 0.011	2.9	**	Soil type (Limestone)	-0.119 ± 0.0093	-12.8	***
Texture (Loam)			n.s.	Texture (Loam)	0.043 ± 0.0104	4.1	***
Texture (Clay)	0.042 ± 0.016	2.6	**	Texture (Clay)			n.s.
Slope	0.004 ± 0.0004	8.7	***	Slope			n.s.
Stoniness	-0.042 ± 0.004	-9.5	***	Stoniness	-0.104 ± 0.0038	-27.2	***
Fire (=yes)	-0.164 ± 0.030	-5.5	***	Fire (=yes)			n.s.
Management (=yes)			n.s.	Management (=yes)	0.079 ± 0.0074	10.7	***
# coniferous species	-0.038 ± 0.008	-4.5	***	# coniferous species			n.s.
# broadleaved species	0.035 ± 0.005	7.2	***	# broadleaved species	0.032 ± 0.0050	6.5	***
# diameter classes	0.156 ± 0.002	70.7	***	# diameter classes	0.220 ± 0.0019	115.7	***
degree of freedom	12625			degree of freedom	21167		
adjusted -r^2	0.62			adjusted -r^2	0.53		
F-value	<0.001			F-value	<0.001		

SP, species factor; WAI (%), water availability index; MT, (ºC) annual mean temperature; TR (ºC), temperature range.

A) Broadleaves



B) Conifers

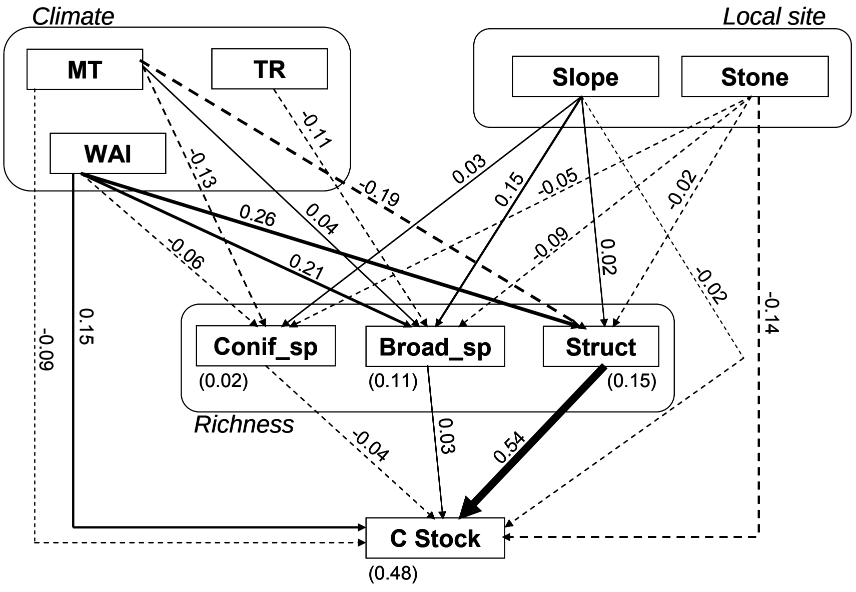
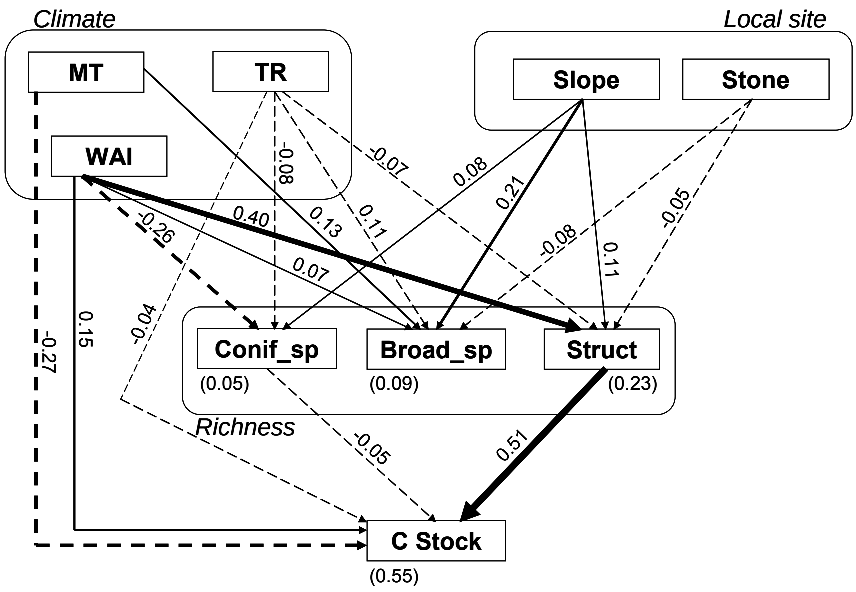


Figure 1.7. Path models relating tree C stock of natural forests (without recent disturbances) with groups of variables representing climate, local site characteristics and richness variables for: (A) Broadleaves and (B) Conifers. Only single headed arrows (directional paths) that are significant in the models are shown indicating the proposed links between variables. Double-headed arrows indicating covariances are not showed for clarity. Positive effects are indicated by solid lines and negative ones by dashed lines. Arrow thickness is proportional to the strength of the effect in terms of the absolute value of the standardized coefficients, indicated by the value close to each arrow. The number in brackets over a given endogenous variable corresponds to the R^2 value indicating the percentage of the variance in that variable that is accounted for by the model. Significance is accepted at $p < 0.01$. WAI (%), water availability index; MT (ºC) annual mean temperature; TR (ºC), temperature range; Stone, surface soil stoniness (%); Conif_sp, conifer species richness; Broad_sp, broadleaf species richness; Struct, structural richness; C_stock, tree C stock (Mg/ha).

A) Broadleaves (with recent disturbances)



B) Conifers (with recent disturbances)

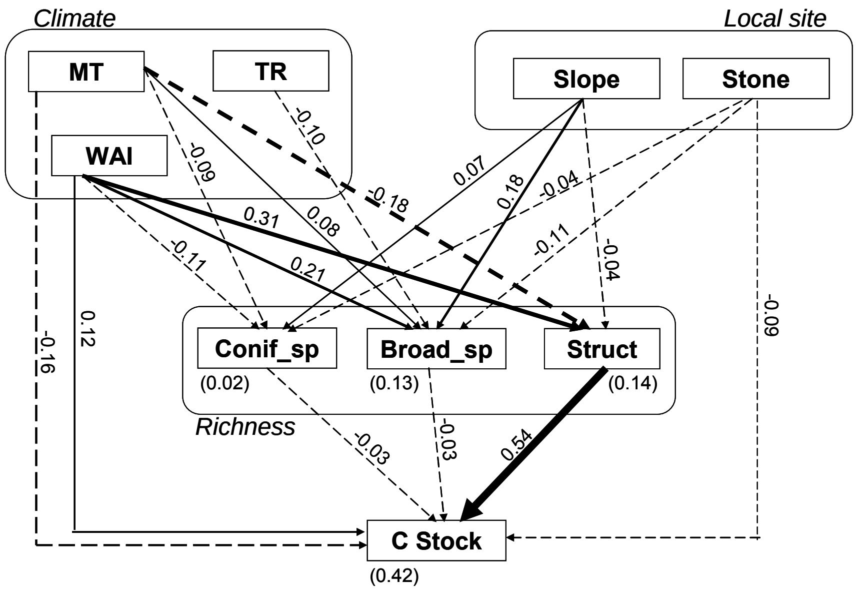


Figure 1.8. Path models relating tree C stock natural forests (with recent disturbances) with groups of variables representing climate, local site characteristics and richness variables for: (A) Broadleaves and (B) Conifers. Only single headed arrows (directional paths) that are significant in the models are shown indicating the proposed links between variables. Double-headed Arrows indicating covariances are not showed for clarity. Positive effects are indicated by solid lines and negative ones by dashed lines. Arrow thickness is proportional to the strength of the effect in terms of the absolute value of the standardized coefficients, indicated by the value close to each arrow. The number in brackets over a given endogenous variable in the path diagram corresponds to the R^2 value indicating the percentage of the variance in that variable that is accounted for by the model. Significance is accepted at $p < 0.01$. WAI (%), water availability index; MT (ºC) annual mean temperature; TR (ºC), temperature range; Stone, surface soil stoniness (%); Conif_sp, conifer species richness; Broad_sp, broadleaf species richness; Struct, structural richness; C_stock, stand tree C stock (Mg/ha).

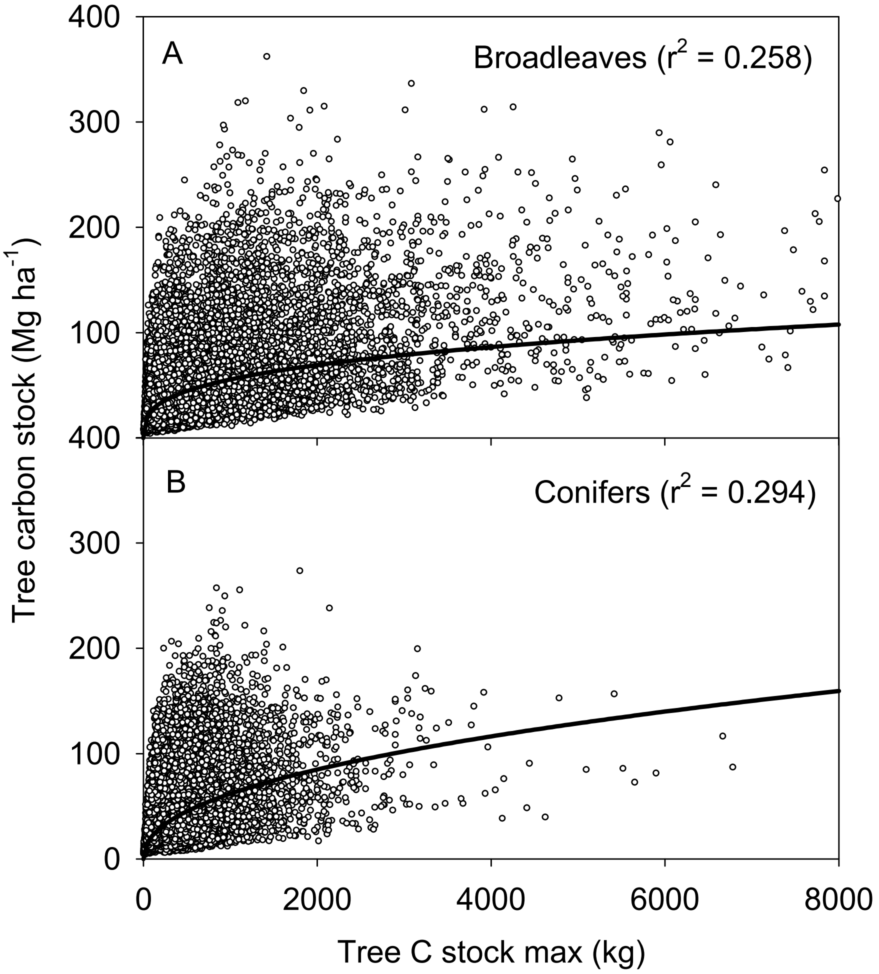


Figure 1.9. Relationship between tree C stock of the highest tree in the plot (kg) and stand tree C stock (Mg/ha) for (A) forests dominated by any of the five broadleaf species analyzed (number of plots =13,911); and (B) forest dominated by any of the five conifer forests analyzed (number of plots = 25,907).

Discussion

Patterns of Total C stocks in peninsular Spain

The total forest C stock (trees + understory) in Peninsular Spain was 621 Tg C, representing 8% of the C stock in Europe (Goodale *et al.* 2002) and 0.17% of the world's C stocks. The use of ancillary data as topographic and climate variables to improve the upscaling of stand C stock to total C stock (Tg) (Table 1.1) and the maps of stand C stock (Figure 1.2) (Raupack *et al.* 2005; Keith *et al.* 2010) would have had a low improvement of the accuracy of these estimates as a consequence of the low direct effect of topography (slope) and climate variable (mean annual temperature and WAI) on stand C stock (Figures 1.5 and 1.7 and Table 1.2). The spatial pattern of stand C stock (trees + understory) in Peninsular Spain follows a north-south gradient from high to low C accumulation (Fig. 1.2A), This is especially true in the most arid areas of the Peninsula, where the severe climate prevents canopy closure and limits C accumulation (Sankaran *et al.* 2005). The patterns obtained for the two groups of species were similar (Fig. 1.2B and 1.2C). Mean stand C stocks (trees + understory) in forest of Peninsular Spain was low with an average of 45.1±0.16 Mg/ha, or 40±0.15 Mg/ha considering only the tree compartment. This stand C stock was less than half of the one observed for more productive forest regions, such as tropical Amazonia (de Castilho et al. 2006) or temperate regions (Brown *et al.* 1999, Dieter & Elsasser, 2002) where mean stand C stock is usually over 100 Mg/ha.

In contrast to the abundant information on stand tree C stock in Europe, estimates of forest understory are scarce (Risch *et al.* 2008). This study presents extensive values of the understory of forests in Peninsular Spain. The understory stand C stock across all forests represents 11.9% of the C stock of the woody vegetation (Table 1.1). However, the fraction represented by the understory of the most Mediterranean forests is particularly high, 17 and 23% of the stand C stock (trees+understory) for *Q. ilex* and *P. halepensis* forests, respectively (Fig. 1.3A and 1.3B). Conifer and broadleaf forests maintained similar understory stand C stocks (Fig. 1.4B). Understory stand C stock of reforested forests was two thirds to that of natural forests and in dehesas this value was reduced to one fifth of natural forests (Fig. 1.4B). In the two cases, and when the main purpose is to maximize wood production (reforestation) or pastureland and acorn production for livestock (dehesas; Linares 2007), the understory is periodically eliminated from these forests.

Predictors of Stand Tree C Stock Patterns

The results of the GLM were robust and roughly similar among groups of species, both in terms of their overall significance and the sign of the main effects (Tables 1.2A and 1.2B). However, there were large differences in the magnitude of the effects of these predictive variables (Fig. 1.5). Structural and species richness were the dominant predictors of stand C stocks in both forest types because these variables result from a number of important forest characteristics such as age, development stage, composition and forest history (eg, management activities, disturbance regime) (Lei *et al.* 2009; Keith *et al.* 2009). The effect of species identity was high only in broadleaves, probably because, unlike conifers (all belonging to the genus *Pinus*), they show higher differences in architecture such as the branches:stem ratio (Keith *et al.* 2009, Zhang *et al.* 2011), root:shoot ratio (Montero *et al.* 2005) and wood density (Baroloto *et al.* 2011). Climatic variables had an important effect modifying spatial patterns, especially in broadleaf species, while they had almost no effect in conifers. In contrast, local scale factors – site characteristics and disturbances– had more effects in conifers. These differences between conifers and broadleaves suggest a different history of natural disturbances and human management, more intense in conifers, which lead to shorter time for the climate to influence stand C stocks (Sankaran *et al.* 2005; Raich *et al.* 2006; Keith *et al.* 2009; Stegen *et al.* 2011). The results obtained in the path analyses indicate that the effects of climate on stand C stocks are mainly through modifying species and structural richness (Fig. 1.7).

Stand structure is a consequence of both autogenic development processes (i.e., successional stage with regeneration, competition, and the consequent self-thinning effect) and past events such as forest management and disturbances (Lei *et al.* 2009). In our study, the higher is the number of classes, the higher the stand C stock (Table 1.2A and 1.2B, Fig. 1.6). This result is not necessarily obvious, because as forests grow, competition for resources also increases and this may favor the elimination of suppressed individuals (usually small ones) and, thus, reduce the number of diametric classes (Keddy, 2005; Healy *et al.* 2008; Vance-Chalkraft *et al.* 2010). The positive effect of the number of diametric classes on C accumulation for both conifers and broadleaves suggests that when trees occupy different horizontal and vertical layers, they can maximize the resources, while homogenous stand structure may reduce complementary effects (Lei *et al.* 2009). Moreover, the almost exponential relationship between the number of diametric classes and stand C stock (Fig. 1.6) is consistent with the idea that stand tree C stock increases with stand age and with the presence of larger trees (Fig. 1.9) and highlights the important contribution of these trees on C storage in forests, such it has been suggested in other studies (Vanninen *et al.* 1996; Baraloto *et al.* 2011; Stegen *et al.* 2011; Zhang *et al.* 2011).

In mixed forests, there can be differences between the species in diametric classes when one species grows first and another is incorporated later. This can make that structural richness incorporates in part the effect of species richness, explaining why the relationship between stand C stock and species richness is weaker than expected, but still significant in some cases. In this study, stand C stock of forests dominated by a conifer species increased if additional species were broadleaves, but not if they were conifers. These results agree with the niche complementarity hypothesis (Vandermeer, 1989; Lei *et al.* 2009) which stems from the different functional traits of the two groups of species. Thus, broadleaf species add new functional variation that enhances stand C stock when they share the plot with conifers and are able to access and utilize additional resources. This is particularly import for light, because they are more shade-tolerant species (Gravel *et al.* 2010) and, for water, because they have more developed root systems than conifers (Montero *et al.* 2005). It is also possible, as suggested by Caspersen & Pacala (2001) that causality runs in the opposite direction, i.e., more productive stands may simply permit the coexistence of more species. If this was the case, then any increment in the number of species would have been positive. However, in our study only certain combinations of species are complementary in their patterns of resource-use and can accumulate higher stand C stock by increasing the rate of productivity and nutrient retention or maintaining during more time stand C stock. In forests dominated by broadleaf species, the relationship with broadleaf species richness was also positive, but conifer richness had a negative effect, suggesting that stand C stock was also determined by the morphologic characteristics of the accompanying species (Zhang *et al.* 2011). These results are analogous to those obtained in experimental biodiversity studies where particular species are better predictors for stand C stocks than overall species richness (Kahmen *et al.* 2005). Several studies (Keddy, 2005; Healy *et al.* 2008) describe a potential decrease in species richness due to competition as biomass continues to slowly increase and resulting in a few dominant species excluding the others. But taking into account that many of the forests considered are still young, it has not been possible to determine the long-term trends of species richness.

Although with a weak direct effect, water availability had a positive effect on both groups of species. Interestingly, the results of path analysis revealed a strong and mainly positive indirect effect through richness variables. This result is relevant taking into account that 85% of Peninsular Spain is water deficit (Fig. 1.1). That water scarcity limits biomass in dry ecosystems is not surprising (Sankaran *et al.* 2005; Kerkhoff *et al.* 2004; Hicke *et al.* 2007; Huang *et al.* 2009), but may be relevant for understanding forest biomass dynamics in the context of changing precipitation regimes and increasing frequency of extreme droughts (e.g. Goswami *et al.* 2006; Stegen *et al.* 2011). Temperature had also a weak direct negative effect on both groups of species, limiting stand C stock at high temperatures and exacerbating the adverse effect of water scarcity.

Among local site characteristics variables, different studies have described the effects of soil on trees and concluded that soil characteristics are among the most important factors describing stand C stock patterns al local scale (e.g. Clark *et al.* 1999, de Castilho *et al.* 2006). In our study, stoniness had the most strong and negative effect on stand C stock (Tables 1.2A and 1.2B). This is an expected result because a higher amount of surface soil stones could be associated to low soil availability for plants, high erosion and loss of fertile soil in the past. Unfortunately, the precision of the other soil variables considered was poor, reducing their potential effect in the full model. The unexpected, mainly indirect, positive effect of slope on stand C stocks of broadleaf forests (high slope has been traditionally associated with more stressed conditions –e.g., shallow soils, high soil moisture variation, and pronounced soil erosion) (e.g., Huang *et al.* 2009) could be the result of the interaction with time since disturbance as suggested by Merino *et al.* (2007). Stands confined to steep slopes, where access is difficult, have been maintained with little or no active management; in fact, this agreed with no effect of recent management in these forests. In contrast, recent management had a positive effect on stand C stocks of conifer forests, probably because managed forests occupy areas with higher site quality.

Implications for the Future

The low values of stand C stocks observed in Spain are due to a complex set of local and regional factors considered in this study, and particularly of legacy of land use and land cover change, and past management practices and disturbances. A better understanding of the relationship between forest stand C stock, environmental conditions and forest structure is important to predict the impacts of climate change on C stocks and maximize the role of forests for C mitigation. This includes increasing the rate of carbon uptake, maintaining high stand C stocks and avoiding C loss through increasing their resilience. In this context, a comprehensive management approach is required that includes changes in the rotation length of harvest and the intensity of logging. Replacement of present species by others less vulnerable to climate change is another option that could be considered. In our study we have showed that structural richness is the main predictor of stand C being a good indicator of past and recent land-use and life forest history. We have also showed that a significant proportion of stand C stocks was stored in the larger trees and, while broadleaf species richness had a positive effect, conifer species richness showed no significant or even negative effect on stand C stock. Thus, if the aim is to maximize stand C stocks, the first forest management option is to not log and allow the forest to regrow and reach the maturity. The second management option is to lead forests to uneven-age stands combining selective or partial cutting to maintain high structural diversity and always favoring the maintenance of the larger trees. In all cases, favoring late successional species, such as broadleaf species over conifers, with lower turnover rates will lead to more stable and longer residence times for stand C stocks.

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Capítol 2

Recent climate changes interact with stand structure and management to determine changes in tree carbon stocks in Spanish forests

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Abstract

Most temperate forests are accumulating carbon (C) and may continue to do so in the near future. However, the situation may be different in water-limited ecosystems, where the potentially positive effects of C and N fertilization and rising temperatures interact with water availability. In this study we use the extensive network of plots of two consecutive Spanish national forest inventories to identify the factors that determine the spatial variation of the C stock change, growth and mortality rate of forests in Peninsular Spain (below- and aboveground). We fitted general linear models to assess the response of C stock change and its components to the spatial variability of climate (in terms of water availability), forest structure (tree density and C stock), previous forest management, and the recent warming trend. Our results show that undisturbed forests in Peninsular Spain are accumulating C at a rate of ~1.4 Mg C ha^{-1} yr^{-1}, and that forest structural variables are the main determinants of forest growth and C stock change. Water availability was positively related to growth and C accumulation. On the other hand, recent warming has reduced growth rate and C accumulation, especially in wet areas. Spatial variation in mortality (in terms of C loss) was mostly driven by differences in growth rate across plots, and was consistent with 'natural', self-thinning dynamics related to the recent abandonment of forest management over large areas of Spain, with the consequent increase in tree density and competition. Interestingly, the negative effect of warming on forest C accumulation disappears if only managed stands are considered, emphasizing the potential of forest management to mitigate the effects of climate change. However, the effect of forest management was weak and, in some cases, not significant, implying the need of further research on its impact.

Keywords: Tree Carbon stock, Tree Carbon stock change, Water availability, Forest Inventory of Spain, Mortality rate, Growth rate, Mortality occurrence, Warming, Water stress, Forest management

Introduction

Forests and their soils contain most of the earth's terrestrial carbon stocks (Dixon 1994; McMahon *et al.* 2010) and also control the major terrestrial fluxes of C between the atmosphere and the biosphere. During the 1990s the estimated amount of carbon stored in terrestrial ecosystems increased by about 0.7 Pg C yr^{-1}, corresponding to the net difference between emissions of about 1.6 Pg C yr^{-1} and a total uptake of about 2.3 Pg C yr^{-1} (Goodale *et al.* 2002; Houghton 2003). However, in the recent years reductions in forest growth and episodes of forest decline have been observed in many region of the world (Allen *et al.* 2010). These episodes can be directly induced by extreme climatic events (e.g. drought, heat waves, frosts, windstorms) (Ciais *et al*. 2005; Bigler 2007; Allen *et al*. 2010) or indirectly by causing tree weakness and the consequent increase of pest outbreaks (Kurz *et.al.* 2008). In both cases, the immediate consequence is a significant reduction in forest carbon sequestration. As these phenomena have affected large areas in different regions of the Earth, some studies suggest that they are already affecting terrestrial net primary production and, thus, the global carbon balance (Zhao & Running 2010).

European forests are currently accumulating carbon and have a large potential for carbon sequestration in the mid-term (Nabuurs *et al.;* 2003; Ciais *et al.*, 2008; Nabuurs *et al.* 2010). The increasing trend in the European forest carbon sink may be the result of a combination of factors: 1) forests in Europe had been largely managed in the past, thus they mostly correspond to young forests in the vegetation rebound phase, which typically accumulate carbon (Ciais *et al.* 2008); 2) the fraction of the increment that is harvested every year has decreased from around 90-95% in 1950 to less than 50% at present, increasing the carbon sink in forest biomass (Nabuurs *et al.* 2003; Ciais *et al.* 2008); 3) the favorable impact of N–deposition on carbon accumulation (Aber *et al.* 1998); 4) the increasing atmospheric CO_2–fertilization combined with positive recent climate warming (Oren *et al.* 2001); 5) enhanced plant growth in temperate and boreal ecosystems due to an extended growing season (Saxe *et al.* 2001). The magnitude of the effect of the two latter factors has been the objective of many studies, but their effects in the mid- and long-term are still uncertain (Nabuurs *et al.* 2003; McMahon *et al.* 2010), particularly in water-limited ecosystems, where the potentially positive effects of CO_2–fertilization and rising temperatures interact with water availability (Barber *et al.* 2000; Martínez-Vilalta *et al.* 2008).

In general, management has been shown to have greater influence on wood production in Europe than climate or land-use change (Schröter *et al.* 2005). Management is a man-controlled disturbance that turns forests into short-term sources of CO_2 (Law *et al.* 2003) but that allows high stand productivity in the mid-term by reducing competition for resources (Ciais *et al.* 2008). The abandonment of management increases competitive interactions, which typically result in lower growth and increased mortality rates. This 'natural' suppression mechanism affects preferentially the youngest and smallest trees, which have lower competitive ability (Westoby 1984; Lutz & Halpern 2006). Until now the reduction of forest exploitation in many areas of the northern hemisphere has resulted in increased forest density, which may lead to an increase in growing stocks and thus temporally enhance the carbon sink, but the longer-term effects remain uncertain (Nabuurs *et al.* 2003; Ciais *et al.* 2008). Again, the effect of this forest densification may be particularly detrimental in water-limited forests, as it causes a reduction in water availability on a tree basis that could predispose to subsequent drought-induced growth declines and mortality episodes (Bigler *et al.* 2006, 2007; Linares *et al.* 2009; Vilà-Cabrera *et al.* 2011).

Regional studies of the combined effects of climatic change and land use changes on forest growth and mortality at the stand level are relatively scarce (Charru *et al.* 2010). This is particularly so in Mediterranean ecosystems, where climate change is forecasted to be particularly severe, involving rapid warming and reduced precipitation (Schröter *et al.* 2005). Many studies on forest productivity and carbon stock change have been derived from samples of restricted size (e.g. Bigler *et al.* 2006, Linares *et al.* 2009), whose representativeness at the regional scale is questionable. Moreover, many of these assessments are based on dendrochronological analyses that use radial growth as a proxy for productivity (e.g. Barber *et al.* 2000), something that is problematic owing to its dependence on stand density (Charru *et al.* 2010). National forest inventories, in contrast with local studies, provide a systematic and unbiased statistical information and a regularly updated overview of the forested area at a large scale representing the variation along wide environmental gradients (Charru *et al.* 2010) Thus, they are a promising, but relatively unused, tool for regional scale assessments of carbon balance trends (but see Charru *et al*. 2010). In fact, forest inventories are, together with remote sensing, the best available tool to asses long-term changes in forest carbon dynamics (Körner et al 2003). This is due to the relatively long residence times of carbon in forests and to the potentially large disruptive effects of low-frequency (Pretzsch 1996; Goodale *et al*. 2002).

In this study we use the network of > 50,000 forest plots that have been re-sampled across Spain over successive national forest inventories to identify the factors that determine the spatial variation of the C stock change in trees of Spanish forests, both above- and belowground. This carbon pool represents less than half of the total C pool of the ecosystem but it is the main component of NPP at the mid term. The study area offers a unique opportunity to evaluate such changes in relation to recent climatic and management trends. Firstly, many of the forests in Spain are at the southern (and dry) limit of their range, which makes them particularly vulnerable to climate changes (Hampe & Petit 2005; Allen *et al*. 2010). Secondly, Spain covers a large gradient in water availability and temperature, from humid and cool areas in the north to dry and hot areas in the southeast (Fig. 2.1). Finally, abandonment of forest management has been particularly intense, due to low potential for wood production and a combination of socioeconomic factors (Lindner *et al*. 2010). Our main objectives are: (1) to analyze which factors determine the spatial patterns of forest C stock changes and its components (i.e., growth and mortality); (2) to evaluate how the recent trends in climate have affected C stock changes along a water availability gradient, and (3) to determine whether or not forest management has contributed to mitigate the effects of recent warming. Our main hypothesis is that warming will have a negative effect on forest C accumulation due to its effect on water availability, and that this negative effect will be enhanced in unmanaged forests, where tree density and competition are greater.

Material and methods

Study area

The studied area comprises the forested areas of Spain excluding the Canary and Balearic Islands (ca. 18.4 million ha or 37.3% of the total area; MARM 2007a) located between 9º 2'W and 3º 2'E and 36º 0'N and 43º 5'N). 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 N of the area, and is characterized to be relatively wet and cold (wet Spain, with mean temperature of 12.7ºC and annual precipitation of 1500 mm). The rest of Spain falls within the Mediterranean climate, which is characterized by mild winters and hot and dry summers (dry Spain, with mean temperature of 15.3 ºC and annual precipitation of 650 mm). Mean annual temperature and annual precipitation in forest areas in Spain are highly variable, due to topographic gradients of orography and continentality. Mean temperature ranges from 4 to 18ºC (Fig. 2.1A), and annual precipitation ranges from 200 to 2500 mm (Fig. 2.1B).

Forests occur mainly in steep areas, from 0 to 2500 m a.s.l. Vegetation types include: Atlantic, sub-Atlantic and sub-Mediterranean deciduous forests; montane, sub-Alpine, and Mediterranean coniferous forests; sclerophyllous, and evergreen shrublands and forests (Rivas Martínez, 1987). Coniferous forests are the most abundant forest type (48% of the total forest area), followed by sclerophyllous (32%) and deciduous forests (20%). Flat zones are mainly occupied by crops, urban areas and open woodlands (=dehesas). This latter forest type, characteristic of some areas of the inland of the Iberian Peninsula, has very low tree density (20-200 stems ha^{-1}) and canopy cover (5-20%), which allows the presence of a pasture that maintains extensive livestock. The area of new reforestations with productive or protective objectives in Spain has ranged between 40,000 and 120,000 ha per year since 1952. Most recent reforestations projects use autochthonous species, are concentrated in arid areas, and aim at reducing erosion (MARM 2007b).

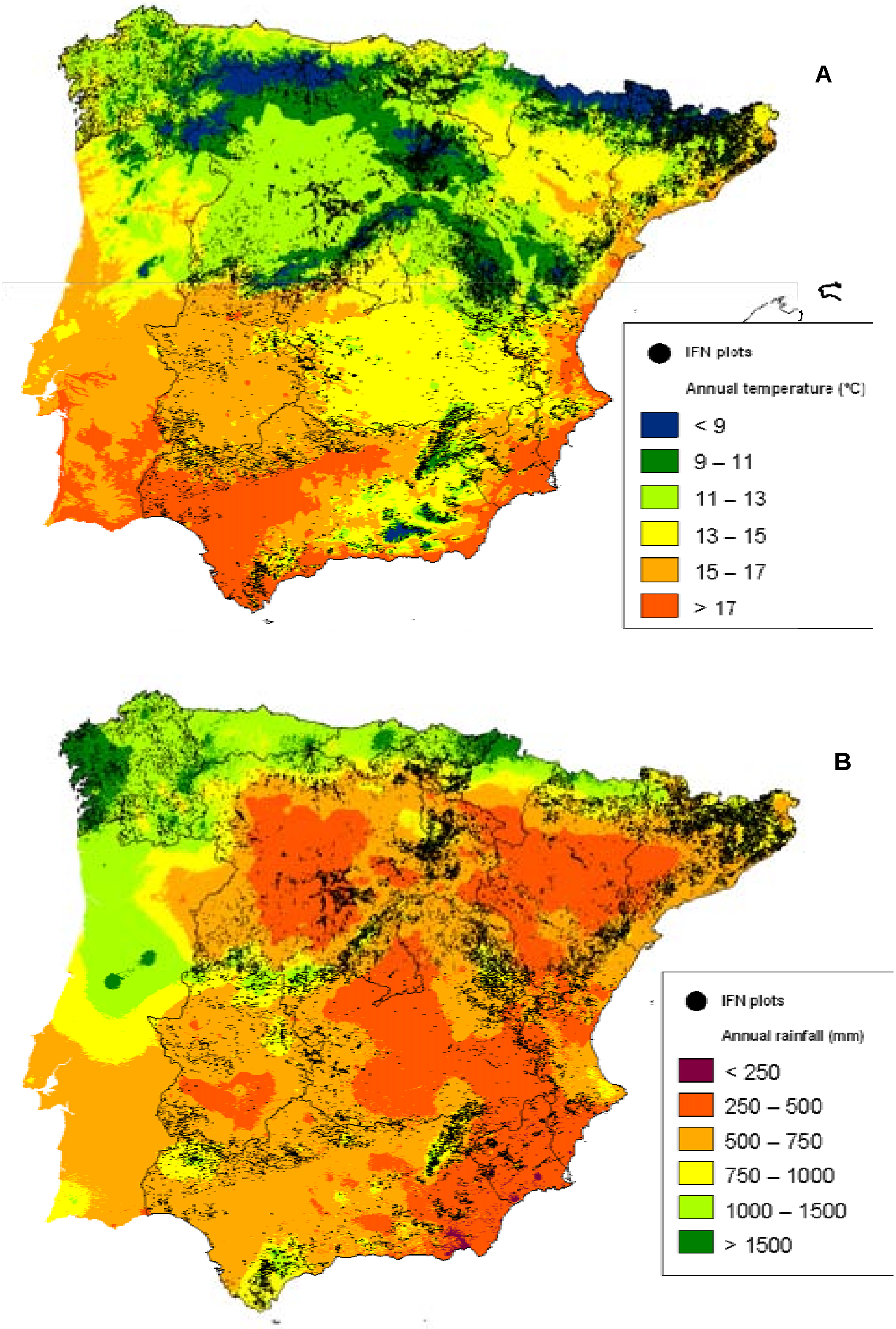

Figure 2.1. Distribution of (A) mean annual temperature (ºC) and (B) annual rainfall (mm/yr) in the Iberian Peninsula. The black dots represent the 22,477 plots of the two IFN inventories (IFN2 and IFN3) used in this study.

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

The IFN is an extensive national database of periodical forest surveys distributed systematically across the forested area of Spain (Villaescusa & Díaz, 1998; Villanueva 2005). The IFN is based on a network of circular plots at a density of 1 plot per 200 ha, 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. Tree sampling followed a nested design, that is, plot size depends on the diameter at breast height (DBH) of the measured trees to guarantee a representative sampling of the tree size distribution. Thus, all trees with DBH ≥ 7.5 cm were measured within 5 m of the centre of the plots, trees with DBH ≥ 12.5 cm were also measured between 5 and 10 m around the centre of the plots, whereas trees with DBH ≥ 22.5 cm and DBH ≥ 42.5 cm were also considered within 10–15 m and 15–25 m around the centre of the plots, respectively. Species identity of all living and standing dead trees was recorded and its height (H) and DBH were measured

The continuous character of the IFN project started with the second inventory (IFN2), which was conducted from 1986 to 1996, and continued with the third one (IFN3), from 1997 to 2008. Plots and individual trees surveyed in the IFN2 were revisited again in the IFN3. The information of the IFN2 for three regions (i.e. autonomous communities) in the north of Spain (Navarra, Cantabria and Asturias) was not available (ca. 1.13 million ha, 6.15% of forests in Peninsular Spain), and for this reason they have not been included in our analyses. Dead trees were recorded in IFN3, but they were not measured again (i.e., their DBH and H were assumed to be the same as in IFN2).

In the present study we selected plots according to two criteria. Firstly, we only included plots with at least five sampled trees belonging to tree species that form natural forests in the study area; that is, we have excluded the species that are used exclusively in plantations for wood production (*Eucalyptus* spp, *Pinus radiata*, *Pseudotsuga menziesii…*) or for agriculture (*Olea europaea*, *Ceratonia siliqua*…). Secondly, we selected only plots without evident signs of disturbances (i.e. fires, windstorms) or management between the two surveys, according to the information recorded by IFN3 surveyors. After following these criteria, the total number of plots used in this study was 22,477.

C stock change and its components

To compute carbon content per tree we applied allometric equations obtained in different studies to the data of each IFN2 and IFN3 plot. Aboveground biomass (AGB) of each living tree with DBH≥7.5 cm was computed using specific equations as a function of DBH and H developed in the Ecological Forest Inventory of Catalonia (IEFC, Gracia *et al.* 2004a): $AGB = a \cdot DBH^{b} \cdot H^{c}$, where a, b and c are specific coefficients for the different species. For the least common species we applied the coefficients of generalized equations obtained for the different functional groups (coniferous, deciduous and sclerophyllous species). For computing AGB of standing dead trees with DBH≥7.5 cm we only considered trunk biomass. We first determined volume over bark (VOB) of each dead tree following a geometric equation determining its volume as: $VOB = \pi \cdot (DBH/2)^{2} \cdot H \cdot f$, where f is the form factor varying by species. AGB was then obtained as: $AGB = VOB \cdot WD$, where WD is wood density of the species obtained from the IEFC (Gracia *et al.* 2004b). Belowground biomass (BGB) of both dead and living trees was computed using the equations developed by Montero *et al.* (2005) from dried samples of each fraction (stem wood, stem bark, thick roots, branches and leaves) for the most abundant tree species in the Iberian Peninsula. For each species, Montero *et al.* (2005) computed AGB and BGB as a function of DBH. From this information, the proportion of BGB as a function of AGB was estimated as: $\%BGB = e \cdot AGB^{f}$, where e and f are specific coefficients for the different species. This equation was used to compute BGB from AGB. Again, for the least common species we applied the coefficients of generalized equations obtained for the different functional groups.

Total C amount of each living or dead tree was determined by multiplying biomass values of each fraction, AGB and BGB, by the specific C content of the species obtained in the IEFC from oven-dried samples (Gracia *et al.* 2004b). Mean values C content of the species were obtained in the IEFC from oven-dried samples (Gracia *et al.* 2004b). Mean values per species vary between 0.472 and 0.486 g C/g d.m. (i.e., dry matter) in deciduous species, and between 0.497 and 0.510 g C/g d.m in conifers, similar to the values published by the IPCC for temperate and boreal forests (IPCC 2003).

Three variables were used to describe C stock change and its main components at the plot level: (1) *Increment of C amount due to tree growth* (Growth rate, in Mg C ha^{-1} yr^{-1}), defined as the sum of the C increment due to growth of surviving trees and the C of the ingrowth to the canopy (i.e., new trees with DBH ≥ 7.5 cm). (2) *Decrease of C amount due to mortality* (Mortality rate in Mg C ha^{-1} yr^{-1}). Mortality included those trees that were alive at the IFN2 and either remained as standing dead trees or had disappeared by the IFN3 sampling (5994 plots showed mortality occurrence, 30% of the total number of plots). (3) *C stock change* (in Mg C ha^{-1} yr^{-1}), calculated as the difference between the two former variables, that is, the increment of C amount due to growth of surviving trees and the incorporation of new trees minus the decrease due to tree mortality. In all three cases the values obtained were divided by the number of years elapsed between the two inventories to obtain rates per year.

Generation of maps of C stock change and its components

We generated maps of growth rate, mortality rate and C stock change using the MiraMon GIS software (Pons 2008). Each map was obtained by dividing the territory of Spain in cells of 10’x10’ resolution (Figure 2.4A, 2.4B and 2.4C). This leads to similar but not exactly equivalent area across cells (range of polygon areas between 277.8 km^2 in the south and 249.4 km^2 in the north). For each of these cells with at least 10% of forest area we computed the mean of the corresponding variable of all IFN plots included in each area. The polygons with forest surface below the 10% threshold, according to Forest Map of Spain (MFE50, MARM 2007a), were excluded and are specified in the map as N/A (not available). To display these maps we have used the Universal Transverse Mercator reference grid corresponding to the zone 30 of the northern hemisphere (UTM-30N), with Datum ED50 (parameters of the Spanish National Geographic Institute).

Climatic and forest structural data

Climatic variables

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 recent climatic trends occurred during the time interval between the two inventories. The first data set was obtained from the Digital Climatic Atlas of the Iberian Peninsula (Ninyerola *et al*., 2005), a collection of digital maps at 200x200 m resolution with average annual and monthly data for total rainfall and maximum, mean and minimum temperatures (period 1950–1999). Based on the geographic coordinates of the IFN3 plots we determined an integrative index of water availability (WAI), which integrates temperature and rainfall at each plot. The average values of annual WAI over the 1950-1999 period were calculated for each IFN plot as:

$$WAI = ((P - PET) / PET) \cdot 100$$

where P is average rainfall (mm yr^{-1}) and PET is average potential evapotranspiration (in mm yr^{-1}) obtained from monthly values according to the Hargreaves & Samani (1982) method.

The second data source consisted of monthly temperature and precipitation per year with a spatial resolution of 0.5x0.5 degree of latitude/longitude grid (201 cells). This information was downloaded from http://climate.geog.udel.edu/~climate (Center for Climatic Research, Department of Geography, University of Delaware; Matsuura & Willmott 2009). This data source allowed us to obtain the climatic trends in temperature and precipitation. Yearly averages were computed using monthly values from March to August each year; that is, with a month ahead in relation to the mean growing season of the vegetation in the Iberian Peninsula (Orshan, 1989).

An absolute temperature trend was defined as the difference between the mean value of temperature for the study period and the mean value for a reference period. A relative precipitation trend was defined as the ratio between the equivalent difference for precipitation and the mean value of precipitation for a reference period. The study period comprised the years between the two surveys plus two extra years before the IFN2 sampling to include lagged climatic effects on growth and mortality. The reference period corresponded to the 30 years before the IFN2 sampling. Absolute (March-August) temperature trends across the Iberian Peninsula ranged from -0.15 ºC to 2ºC (Fig. 2.2A), with an average increment of +1 ºC. Regarding precipitation, the relative trend along the Iberian Peninsula varied between -22% and +8.9% in relation to the reference period (Fig. 2.2B), with a mean value of -6% (average decline of -19 mm). As the temporal trend for precipitation was significant in less than 5% of the 201 cells studied, this variable was not included in our final statistical models (see “Statistical analyses” section below). In contrast, the temporal trend for temperature was significant in 92% of cells.

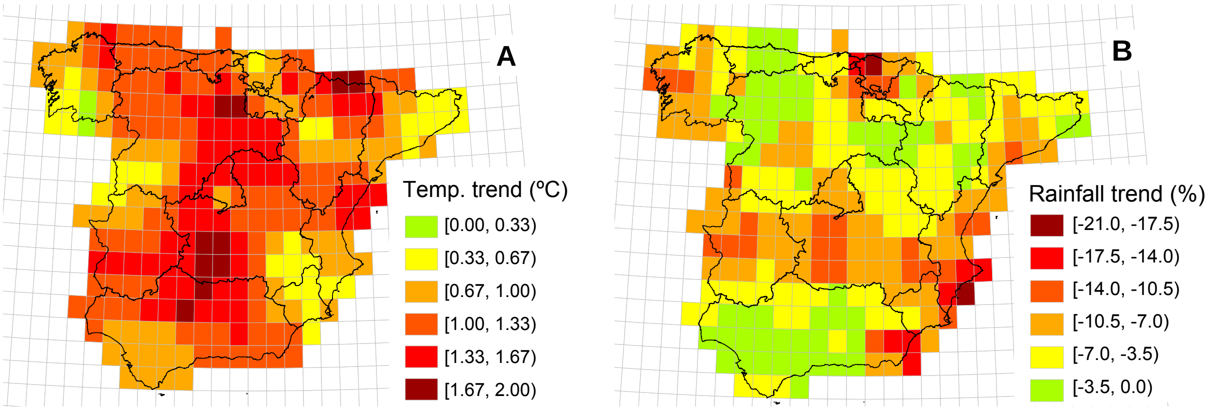

Figure 2.2. Distribution of (A) the absolute temperature trend (ºC) and (B) the relative precipitation trend (%) in Peninsular Spain at a grid resolution of 0.5x0.5 degrees.

Forest characteristics

The following characteristics were determined for each IFN plot using data recorded during the IFN surveys: (1) Forest type. We distinguished three categories: natural forest, reforestation and open woodland (= dehesa). (2) Forest management. With this variable we evaluated the effect of forest management previous to the period between inventories (6411 plots were affected by forest management, 28.5% of the total number of plots). We considered that a forest had been managed when there was indication of commercial cutting or thinning at the IFN2 sampling. We excluded from the analysis all plots that had been managed in the period between two surveys to avoid the confusing effect of recent forest management.

Forest structure and site properties

The variables related to forest structure corresponded to the values at the beginning of the study period, that is, those of the IFN2. These values were included for evaluating the role of initial forest structure in subsequent carbon accumulation. The forest structure variables included were: C stock (above and belowground, in Mg C ha^{-1}) of living trees (DBH≥7.5 cm), mean DBH (cm) of living trees, density of living trees (trees ha^{-1}), and mean height (m) of the three tallest trees per plot, as a measure of site index. Concerning site properties, two variables were considered: surface stoniness, estimated following a four-level ordinal classification: 0%, 1-25%, 26-50% and 51-75% of stones on the soil surface; and slope (in degrees), estimated as the maximum slope at the centre of the plot.

Statistical analyses

To reduce the number of explicative variables related to forest structure and site properties in the models and avoid multicollineality problems, we carried out a principal component analysis (PCA) (see supplementary information Fig. 2.S1). The variance explained by the first principal component of this PCA was 32%, and it was considered an indicator of site quality. The variance explained by the second principal component of this PCA was 28%, and it was considered as an indicator of stand development. As the variables that showed the highest correlation with the first and second PCA axes were C stock and tree density, respectively, these two variables were used in all further analyses instead of the six original ones.

Statistical models to analyze C stock change and its components (growth rate and mortality rate) were constructed using the same set of predictor variables. In each case we fitted a general statistical model that included all plots and models restricted to each forest type (natural forest, reforestation and open woodland). The selected predictor variables were: C stock (as an indicator of site quality), Tree density (as an indicator of stand development), Water availability (WAI), Relative temperature trend, and Forest management (as a dichotomous variable). The following interactions were also considered, based on our initial hypotheses: C stock x Tree density, Water availability x Recent temperature trend, and Management x Recent temperature trend.

We used general linear models (GLM) to analyze the effect of the different explanatory variables and their interactions on the C stock change and growth. Growth was log-transformed to satisfy the normality assumption. In the case of mortality, and given the large proportion of zeros (that is, plots without dead trees), this variable was analyzed in two steps. First, we transformed the variable to a dichotomous one, indicating the presence/absence of mortality (mortality occurrence) in each plot. We used generalized linear models (GLZ) with a binomial distribution and a logit link function to analyze this variable. In a second step, we used GLM to model mortality rate (Mg C ha^{-1} yr^{-1}) in plots with at least one dead tree (after log-transformation of mortality rate to satisfy the normality assumption). Stepwise model selection was applied starting from the saturated model and removing the least significant term until there was no further decrease in the Bayesian Information Criterion (BIC). We considered all models within 2 BIC units as equivalent in terms of fit. Given the large sample size, significance was accepted at $P=0.01$. Statistical analyses were carried out with the R software (package nmle, R 2.10.0, The R Foundation for Statistical Computing). The residuals of the models did not show any pattern and were not spatially autocorrelated (package nmle, R 2.10.0, GLS using a spherical spatial correlation structure).

Results

Overall distribution of C stock change and its components

Comparing the different forest types (Fig. 2.3), the highest growth was observed for reforestations, followed by natural forests and dehesas. The highest decrease due to mortality was for reforestations and natural forests, followed by dehesas. Overall, the highest increase in C stock was for reforestations. On average, Spanish forests accumulated 1.40±0.01 Mg C ha^{-1} yr^{-1} during the period between the two surveys.

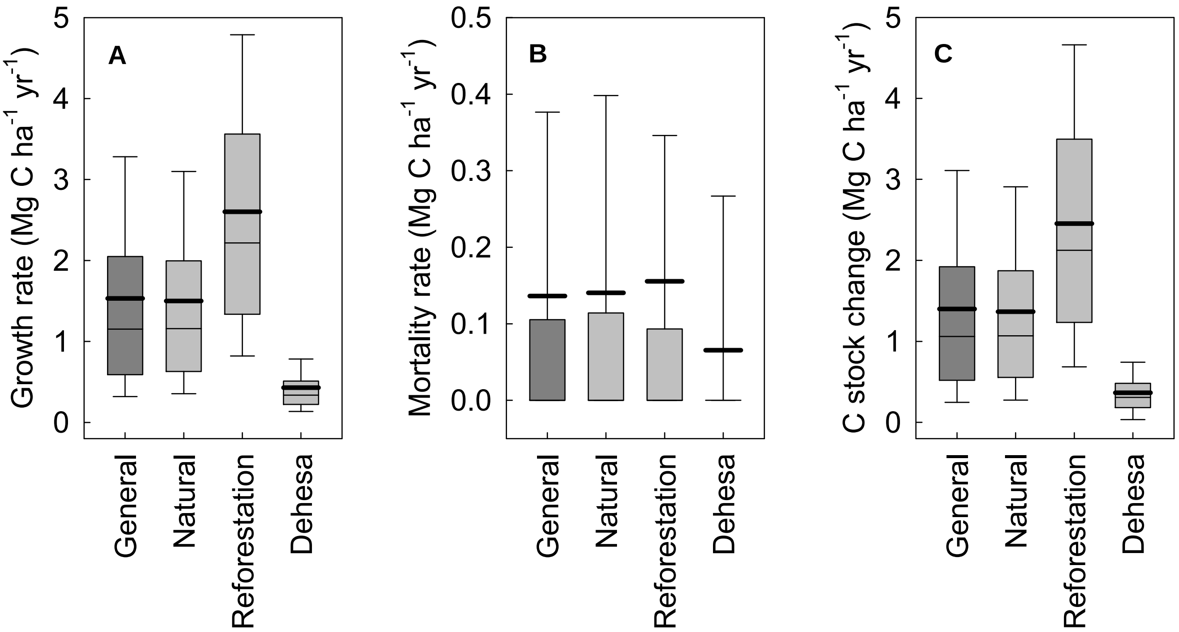

Figure 2.3. Box-whisker plots of (A) growth rate (Mg C ha^{-1} yr^{-1}), (B) mortality rate (Mg C ha^{-1} yr^{-1}) and (C) C stock change (Mg C ha^{-1} yr^{-1}) in natural forests, reforestations, dehesas and all plots combined. Boxes indicate the lower and upper quartile, the horizontal bands are the mean (in bold) and the median, and whiskers extend to lower 5% percentile and upper 95% percentile.

Forests with the highest growth rates (>2 Mg C ha^{-1} yr^{-1}; Fig. 2.4A) and highest increase in C stock (>1 Mg C ha^{-1} yr^{-1}; Fig. 2.4C) were mostly concentrated in the north and, particularly, in the northwest regions facing the Atlantic Ocean. Forests in the south, east and inner plains of the Iberian Peninsula had the lowest values, especially in the southwestern inland and along the southern Mediterranean coast. There was a close correspondence between areas showing high growth rates (Fig. 2.4A) and areas with high mortality rates in terms of C loss (Fig. 2.4B), as shown by the positive relationship between mean growth rate and mean mortality rate in the 10'X 10' cells (R^2 = 0.30, P<0.001; Fig. 2.S2).

Factors affecting C accumulation due to growth

The variance explained of the general growth model was 62.2%, while for the different forest types it ranged from 27.8% for dehesas, to 58.9% and 59.7% for natural forests and reforestations, respectively. In the general model, the direct effect of all explanatory variables, except Management, was significant (Table 2.1). The three interactions considered were significant in the general model (Table 2.1) but only two or one out of three interactions were significant for natural forests and plantations respectively (no interaction was significant in dehesas). However, when significant, they showed the same pattern (Supplementary information, Table 2.S1). The variable with greater effect on growth was Tree density, followed by C stock and Water availability. The interaction between Tree density and C stock indicated that growth was lowest in areas with low tree density and C stock, but it increased rapidly as these two variables increased (Fig. 2.5A). Water availability had a positive effect on forest growth. The interaction Water availability x Temperature trend was significant in the general and natural forests models, with similar patterns (Fig. 2.5B): the negative effect of warming was particularly marked at sites with high water availability. The interaction Management x Temperature trend was again significant in the general and natural forests models, indicating that, as warming increased, C stock increased in managed stands but declined in unmanaged ones (Fig. 2.6A).

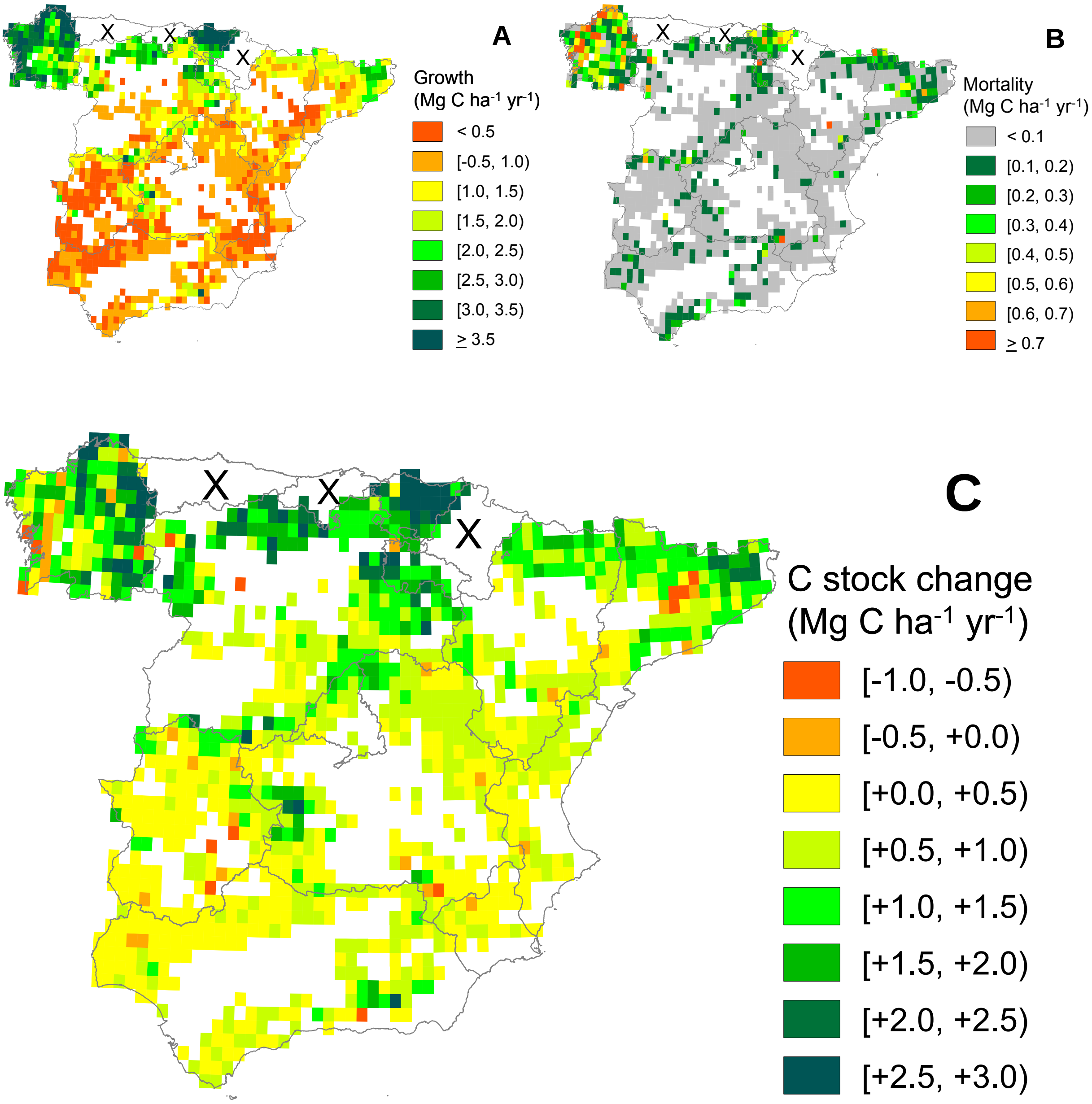

Figure 2.4. Distribution of (A) growth rate (Mg C ha^{-1} yr^{-1}), (B) mortality rate (Mg C ha^{-1} yr^{-1}) and (C) C stock change (Mg C ha^{-1} yr^{-1}) in Peninsular Spain at a spatial resolution of 10'x10' degrees. Plotted values are the mean of the corresponding variable from all IFN plots included in the cell. Black crosses indicate regions without data available.

Table 2.1. Summary of the best model (in terms of BIC) of growth rate (Mg C ha^{-1} yr^{-1}; log transformed) as a function of plot variables (all forest types combined)

Effects	**Estimate**			**t-value**	**Pr(>|t|)**	**Sign.**
Intercept	-6.29E+00	±	1.26E-01	-49.840	<0.001	***
Management(= true)	-		-	-	-	n.s.
ln(C stock (Mg C ha-1))	1.07E+00	±	3.68E-02	28.956	<0.001	***
ln(Tree density (trees ha^{-1})	8.80E-01	±	2.06E-02	42.655	<0.001	***
Water availability	1.00E-02	±	3.80E-04	26.354	<0.001	***
Temperature trend (ºC)	-1.90E-01	±	1.64E-02	-11.575	<0.001	***
ln(C stock) X ln(Tree density)	-1.12E-01	±	5.90E-03	-19.004	<0.001	***
Water availability X Temperature trend	-5.21E-03	±	3.64E-04	-14.329	<0.001	***
Management (=true) X Temperature trend	9.88E-02	±	2.29E-02	4.314	<0.001	***
Degrees of freedom	22468					
BIC	37794					
Adjusted-R²	0.622					
F-value	4627					
p-value	<0.001					

Significant. codes: '***' 0.001; '**' 0.01; n.s. not significant.

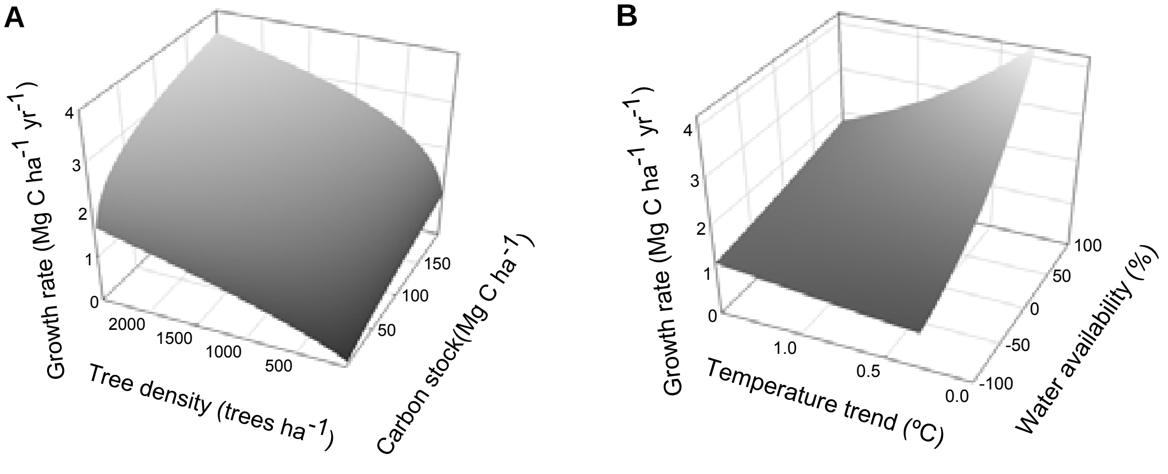

Figure 2.5. Tridimensional mesh plot showing the predicted effects of the significant interactions of the general model on forest growth rate (Mg C ha^{-1} yr^{-1}): (A) C stock (Mg C ha^{-1}) x Tree density (Trees ha^{-1}) and (B) Water availability (%) x Temperature trend (ºC).

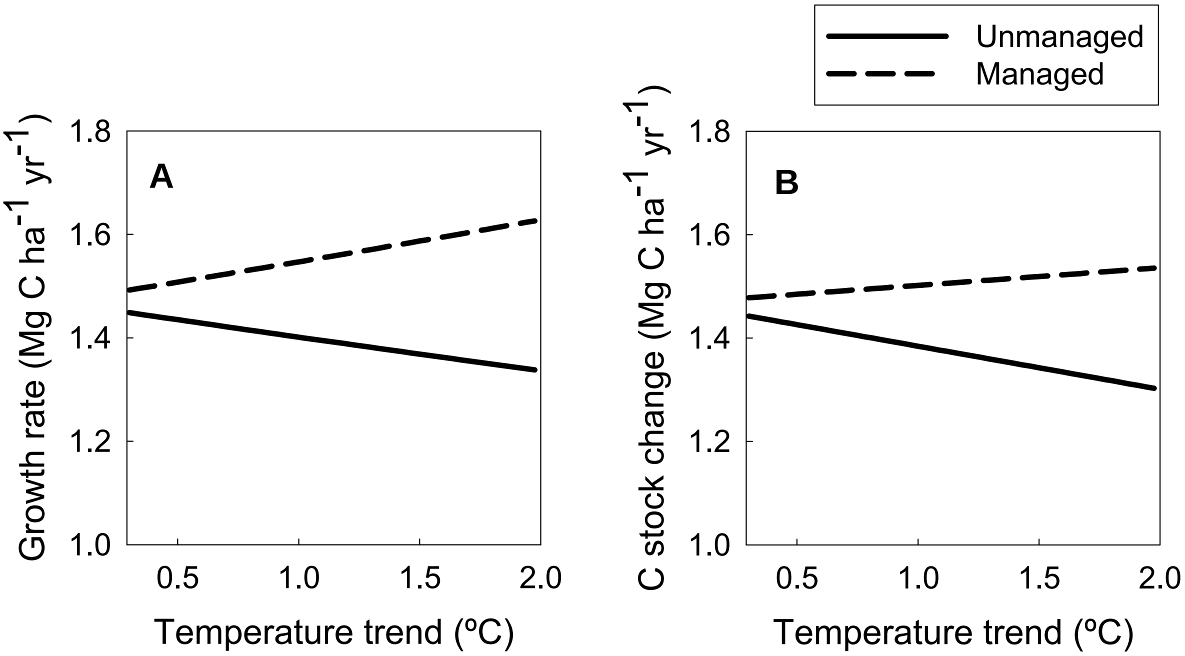

Figure 2.6. Predicted effects on (A) growth rate (Mg C ha^{-1} yr^{-1}) and (B) C stock change (Mg C ha^{-1} yr^{-1}) of the interaction Management (dichotomic) x Temperature trend (ºC).

Factors affecting C loss due to mortality

Regarding mortality occurrence (dichotomous variable), the deviance explained by the GLZ models was relatively low: 10.2% for the general model, 13.7% for reforestations, 10.3% for natural forests and 2.2% for dehesas. In general, mortality occurrence increased with the C stock in all models and also increased with Tree density except for dehesas (Table 2.2A and Supplementary Information, Table 2.S2A). The effect of Water availability was less strong but in all cases except reforestations the probability of finding dead trees increased with water availability. The effect of the temperature trend on the presence of dead trees was significant but relatively low, showing an unexpected decrease of mortality with warming. Forest management did not have a significant effect in any of the four models. Finally, none of the three interactions analyzed affected the presence of dead trees (Table 2.2A) except for the C stock x Tree density interaction in reforestations (Supplementary Material, Table 2.S2A).

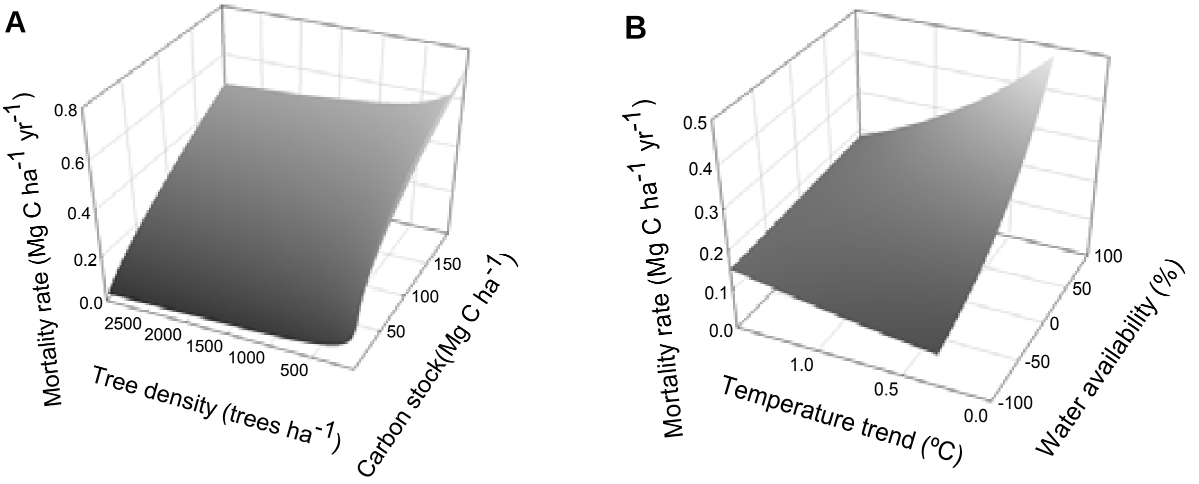

Figure 2.7. Tridimensional mesh plot showing the predicted effects of the significant interactions of the general model on forest mortality rate (Mg C ha^{-1} yr^{-1}): (A) C stock (Mg C ha^{-1}) x Tree density (Trees ha^{-1}) and (B) Water availability (%) x Temperature trend (ºC).

Concerning the mortality rate for sites where mortality was recorded (5994 plots, 30% of the total number of plots), the R^2 of the general model was 25.3%, while for the different forest types it ranged from 24.2% for reforestations to 24.8% for dehesas and 25.5% for natural forests. The variable with strongest effect on mortality rate was Water availability, with higher mortality rates in wet than in dry areas (Table 2.2B). Regarding the two structural variables, Tree density interacted with the C stock in the general and in the natural forest models, with a similar pattern: mortality rate increased with C stock, particularly at low tree density (Fig. 2.7A). The interaction Water availability x Temperature trend was significant in all models except for dehesas (Table 2.2B and Supplementary Material, Table 2.S2A). The effect of warming on mortality rate was negative at sites with high Water availability, whereas it was slightly positive at sites with low water availability (Fig 2.7B). Finally, the direct effect of Management or its interaction with Temperature trend was not significant in any of the models (Table 2.2B and Supplementary Material, Table 2.S2A).

Table 2.2. Summary of the best models (in terms of BIC) of (A) mortality occurrence (dichotomic) and (B) mortality rate (Mg C ha^{-1} yr^{-1}; log transformed) as a function of plot variables (all forest types combined).

A) mortality ocurrence

Effects	**Estimate**			**Z-value**	**Pr(>|t|)**	**Sign.**
Intercept	-1.44E+00	±	5.99E-02	-24.088	<0.001	***
Management(= true)	-		-	-	-	n.s.
C stock (Mg C ha-1)	1.81E-02	±	6.63E-04	27.288	<0.001	***
Tree density (trees ha^{-1})	3.01E-04	±	2.92E-05	10.286	<0.001	***
Water availability	6.91E-03	±	5.49E-04	12.584	<0.001	***
Temperature trend (ºC)	-1.83E-01	±	4.74E-02	-3.854	<0.001	***
C stock X Tree density	-		-	-	-	n.s.
Water availability X Temperature trend	-		-	-	-	n.s.
Management (=true) X Temperature trend	-		-	-	-	n.s.
Degrees of freedom	20020					
BIC	22001					
AIC	21969					
Deviance explained	0.102					

B) mortality rate

Effects	**Estimate**			**t-value**	**Pr(>|t|)**	**Sign.**
Intercept	-		-	-	-	n.s.
Management(= true)	-		-	-	-	n.s.
ln(C stock (Mg C ha-1))	-		-	-	-	n.s.
ln(Tree density (trees ha^{-1}))	-5.75E-01	±	0.064	-9.049	<0.001	***
Water availability	1.10E-02	±	0.001	12.174	<0.001	***
Temperature trend (ºC)	-1.26E-01	±	0.036	-3.546	<0.001	***
ln(C stock) X ln(Tree density)	9.10E-02	±	0.017	5.373	<0.001	***
Water availability X Temperature trend	-6.74E-03	±	0.001	-7.621	<0.001	***
Management (=true) X Temperature trend	-		-	-	-	n.s.
Degrees of freedom	5987					
BIC	14739					
Adjusted-R²	0.253					
F-value	339.4					
p-value	<0.001					

Significant. codes: '***' 0.001; '**' 0.01; n.s. not significant.

Factors affecting C stock change

The R^2 of the general C stock change model was 40.6%, while for the different forest types it ranged from 32.4% for dehesas and 32.6% for reforestations to 37.8% for natural forests. All direct effects of the variables considered in the general model were significant except Management (Table 2.3). The variables with the highest effect on C stock change were Tree density and C stock, except in dehesas, where the effect of C stock was not significant (Table 2.3 and Supplementary information, Table 2.S3). The interaction Tree density x C stock was significant in all four models: C accumulation increased markedly with Tree density at sites with low C stock but barely changed with Tree density when C stock was high (Fig. 2.8A). Water availability was significant in the four models, with a positive effect on C accumulation in all cases. The interaction Water availability x Relative temperature trend was significant in all except the reforestations model: the effect of warming on C accumulation was negative at sites with high Water availability, whereas it became positive at sites with low water availability (Fig. 2.8B). Finally, the interaction Management x Temperature trend was only significant in the general model, with a similar pattern to that found for growth; that is, as warming increases C accumulation remains approximately constant in managed stands but declines in unmanaged ones (Fig. 2.6B) .

Table 2.3. Summary of the best model (in terms of BIC) of C stock change (Mg C ha^{-1} yr^{-1}) as a function of plot variables (all forest types combined).

Effects	**Estimate**			**t-value**	**Pr(>|t|)**	**Sign.**
Intercept	6.55E-01	±	3.51E-02	18.644	<0.001	***
Management(= true)	-		-	-	-	n.s.
C stock (Mg C ha-1)	1.15E-02	±	3.78E-04	30.499	<0.001	***
Tree density (trees ha^{-1})	1.39E-03	±	2.24E-05	61.920	<0.001	***
Water availability	1.48E-02	±	6.82E-04	21.781	<0.001	***
Temperature trend (ºC)	-2.91E-01	±	2.96E-02	-9.823	<0.001	***
C stock X Tree density	-6.18E-06	±	3.41E-07	-18.146	<0.001	***
Water availability X Temperature trend	-7.59E-03	±	6.54E-04	-11.600	<0.001	***
Management (=true) X Temperature trend	1.18E-01	±	4.13E-02	2.847	<0.01	**
Degrees of freedom	22468					
BIC	64326					
Adjusted-R²	0.4062					
F-value	1923					
p-value	<0.001					

Significant. codes: '***' 0.001; '**' 0.01; n.s. not significant.

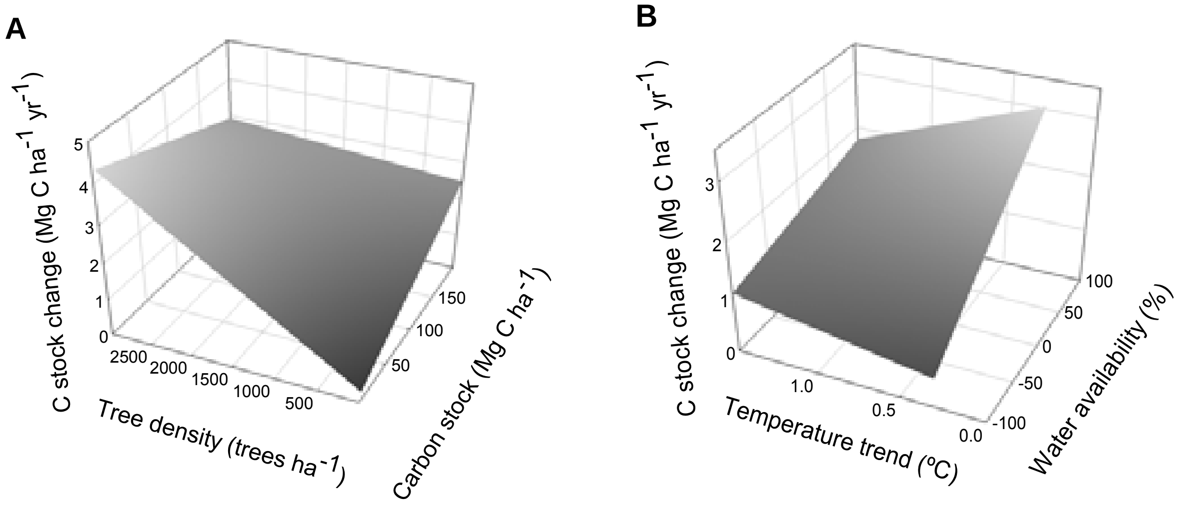

Figure 2.8. Tridimensional mesh plot showing the predicted effects of the significant interactions of the general model on forest C stock change (Mg C ha^{-1} yr^{-1}): (A) C stock (Mg C ha^{-1}) x Tree density (Trees ha^{-1}) and (B) Water availability (%) x Temperature trend (ºC).

Discussion

Overall, forests of Peninsular Spain had a positive C balance over the period between the early 1990s and early 2000s, as observed in the forests of other European countries (Nabuurs *et al.* 2003, Ciais *et al.* 2008) and of the northern hemisphere (Goodale *et al.* 2002, Zhao & Running 2010). The spatial pattern of growth rate (Fig. 2.4A) and C stock change (Fig. 2.4C) for the whole territory of Peninsular Spain agreed with the pattern found for annual precipitation (Fig. 2.1B) and was inverse to that of mean temperature (Fig. 2.1A). This suggests a key role of water availability, as confirmed by our GLM models (Tables 2.1-2.3). The spatial pattern of mortality was also similar (Figs. 2.4B and 2.S2). This is not surprising if one considers that we measured mortality in terms of absolute C loss, and in any case it suggests that a high growth rate could accelerate suppression-mechanisms leading to an increase of background mortality (Westoby 1984).

Structural and climatic factors determining C stock change and its components

The variance explained by our statistical models was especially high for growth rate (ca. 60%) and considerably lower for mortality occurrence (ca. 10%) and mortality rate (ca. 25%), whereas it was intermediate for C stock change (ca. 40%). In all cases the results of statistical models were robust and roughly homogeneous among forest types, both in terms of their overall significance and the sign of the main effects (Tables 2.1-2.3 and Supplementary information, Tables 2.S1-2.S3). The low variance explained by mortality occurrence models is probably due to the relative rareness of mortality (in >14,000 plots, almost 70%, no dead tree was recorded) and its stochastic and episodic nature (McMahon *et al*. 2010). These characteristics determine the difficulty in obtaining accurate estimates of tree mortality from national forest inventories (Stokland *et al.* 2005).

Although different studies identify age as a determinant factor in even aged forests (Böttcher *et al.* 2008), in our study, and given that most forests (>85% of plots) are natural and uneven aged, we have considered other structural variables instead of stand age. The two variables describing forest structure (Tree density and C stock), which can be considered a reflection of past disturbances (logging history, wildfire…), showed the highest effect on both C stock change and growth rate (Tables 2.1, 2.3). These results are consistent with other recent studies based on forest inventories (Charru *et al.* 2010; Vilà-Cabrera *et al.* 2011). The positive relationship between growth and C stock and of the interaction Tree density x C stock (Fig. 2.5A) indicates that these forests are still young and thus far from their maximum stock capacity, that is, they still have a high sink potential that will probably be maintained at short- and mid-term (Karjalainen *et al.* 2003; Nabuurs *et al.* 2003, Böttcher *et al.* 2008, Pan *et al.* 2011). Many Spanish forests are still recovering from the overexploitation occurred during the 1950s and 1960s, so that they are still young, similar to what happens in the rest of Europe (Nabuurs *et al.* 2003; Ciais *et al.* 2008). The water availability index used here, although it is a simplification of the actual amount of available water (i.e., it does not consider soil characteristics, run on/run off or ground percolation), also showed a positive effect on both C stock change and growth rate. This is an expected result, given that most of Peninsular Spain has a Mediterranean climate and many forests reduce or stop their growth during the summer drought, which also reduces their sink capacity (Sabaté *et al.* 2002).

Mortality occurrence increased with tree density while mortality rate decreased with this structural variable (Table 2.2). This result reflects the fact that denser plots, where mortality is more likely, tend to contain smaller trees (Fig. 2.S1), and suggests again a suppression mechanism whereby competition for resources has mainly affected small and suppressed trees that cannot compete efficiently for resources (Westoby 1984; Lutz & Halpern 2006). As a consequence, at sites with high tree density the increase in mortality occurrence and rate with the C stock resulted in lower C accumulation. Mortality could also affect trees smaller than those considered here (i.e., DBH< 7.5 cm) but, unfortunately, this information was not available. On the other hand, at low tree densities and high C stock, which corresponds to forests with old and large trees, the low occurrence of mortality (the death of an only large tree occurs at very low probability but has a large impact on mortality rate) allowed higher C accumulation with increasing C stock (Figs. 2.7A and 2.8A). Surprisingly, but in a robust and consistent way, the pattern of mortality (both mortality occurrence and mortality rate) also showed a positive relationship with water availability (Table 2.2). Once more, this result suggests that water availability, is a good indicator of favorable conditions for growth, leading to a quicker differentiation of tree sizes and a consequent increase of the mortality of small and suppressed trees.

Effect of warming on C stock change and its components along the water availability gradient

In the time period between the two inventories, March to August temperature experienced a mean increment of 1ºC compared to the mean value of the thirty previous years (Fig. 2.2A). However, warming had a low statistical weight in the models compared to other climatic and structural factors. In many areas, especially in temperate and boreal ones where water is not a limiting factor, rising temperatures have had a positive effect on forest growth, mainly by increasing the length of the vegetative period (Saxe *et al*. 2001; Houghton 2007). But more recently warming has been related to an increase of drought stress that affects negatively forest productivity (Ciais *et al*. 2005; Chhin *et al.* 2008; Zhao & Running 2010). Our results support this latter view in a (mostly) water limited system, as warming reduced both C accumulation and growth rate (Tables 2.1, 2.3). This negative effect could be magnified in the Mediterranean basin if rainfall declines as predicted by most climate change projections (Bates *et al.* 2008). In our study, the negative effect of warming was especially important in wet areas located in the north and the north-west and in mountain areas such as the Pyrenees (Fig. 2.5B and 2.8B), where forests are dominated by Eurosiberian species located at the southern limit of their distribution. This species are known to be particularly sensitive to climate change (Andreu *et al.* 2007; Macias *et al.* 2006; Linares *et al.* 2009). On the other hand, warming had almost no effect on growth and C stock change in the drier areas of Peninsular Spain (Fig. 2.5B and 2.8B). Under these climatic conditions forests are dominated by Mediterranean species, presumably more adapted to long dry periods (Montero *et al.* 2005, Bréda *et al.* 2006).

Many recent studies carried out in different regions of the world have documented episodes of forest decline and mortality induced by water stress and/or high temperatures (summarized by Allen *et al.* 2010). In our study, the highest mortality occurrence and rate (in terms of C loss) occurred in areas with low temperature increment (Tables 2.2A, 2.2B). Surprisingly, in wet areas where warming was lowest mortality rate was highest (Fig. 2.7B). This result highlights again the link between the spatial patterns of mortality and growth (Fig. 2.5B and 2.7B), and suggests that the present tree mortality in Spanish forests can hardly be attributed to climate change. On the other hand, in dry areas (ca. 85% of the territory considered in this study) tree mortality showed the expected pattern, with a slight increase with warming (Fig. 2.7B). Apparently, the warming levels registered so far in Peninsular Spain are not enough to affect the overall C balance of forests through increased mortality. However, there is evidence that increased warming and drought are increasing defoliation in Spanish forests (Carnicer *et al.* 2011) and, if warming continues, the possibility of widespread mortality episodes can not be ruled out (Allen *et al.* 2010).

The contribution of forest management to mitigate the effects of recent warming

Forest management, besides generating tangible benefits from forest products such as wood, also has the objective of reducing competition by cutting trees and releasing resources to surviving ones, thus stimulating their growth and reducing subsequent mortality (Olano & Palmer 2003; Ciais *et al.* 2008; Linares *et al.* 2009). In Spain, there has been a progressive abandonment of forest management over the last decades, which could have increased competition for resources (mainly water) and enhanced the consequences of climate warming (Vilà-Cabrera *et al.* 2011). Surprisingly, in our study, the expected benefit of forest management, prior to the study period, did not have a direct effect on C stock change or its components (Tables 2.1-2.3). However, there was a significant interaction between warming and forest management (Fig. 2.6A and 2.6B), which supports, at least partially, our hypothesis that warming and abandonment of forest management have a synergistic effect on forest C balance. This effect has resulted in a reduced sink capacity with warming in unmanaged forests, likely due to reduced water availability. Other studies have also found that under low water availability conditions the effect of drought can be intensified in unmanaged forests (Linares *et al.* 2009; Vilà-Cabrera *et al.* 2011), so that their role as carbon sinks could be compromised. Interestingly, our results suggest that forest management can even reverse the effect of warming (Fig. 2.6A and 2.6B), so that managed forests may respond positively to moderate increases in temperature by increasing their growth and maintaining or even slightly increasing their sink capacity. However, we should be cautious because the mitigating effect of management was only detected when we considered all forests and its effect on C stock change and on growth rate was small compared to other variables (Tables 2.1 and 2.3). According to the results obtained, we could suggest some general orientations. Thus, the role of forests as carbon sinks at high C stocks and high tree densities could be considered optimal because it allows maintaining high carbon stocks and high forest production. But additional studies should be carried out to complete this general conclusion.

Conclusions

We have observed that warming and forest management have produced changes in carbon stocks at the mid-term (~10 years) in two forest compartments (living and dead trees). It is not clear whether these changes will be transient or they will persist through time (*cf.*, Thompson *et al.* 2009) or whether they will affect the total C pool of the ecosystem, because we have not been able to include the soil C pool. Soil carbon is dynamically linked to the tree stratum (Hall *et al.* 2006). During the study period temperature has increased 1ºC on average in Peninsular Spain (up to 2ºC in some areas), while rainfall has declined slightly (6% on average). Despite that fact, and the fact that most forests in Spain grow under Mediterranean conditions and are limited by water availability, Spanish forests are accumulating carbon, similar to temperate European forests (Ciais *et al.*, 2008; Nabuurs *et al.* 2003). However, our results show that warming is already affecting the forest carbon balance of Spanish forests by reducing forest growth. On the other hand, no consistent mortality increase has been found in connection with increased drought stress. At present, overall mortality patterns are consistent with ‘natural’ dynamics of self-thinning, whereas drought-induced mortality episodes seem to occur at a local scale and are hardly noticeable at the scale of the Spanish national inventory. Given that climate projections for the Mediterranean Basin predict warming by 3-4ºC and a reduction of summer precipitation by almost 50% before 2100 (EEA 2008), it is very likely that the growth of Spanish forests will slow down further. Our results show that relatively humid sites may be particularly vulnerable to this effect. Additionally, widespread mortality episodes are likely if drought conditions intensify according to predictions. Overall, these trends could imply that a significant proportion of Spanish forest become net sources of CO_2 during the current century. We have shown that forest management could be, in some cases, an efficient tool to mitigate the impact of climate change on the forest carbon balance, at least under current conditions. But as its effect was weak and not always significant, further work is required to establish the strength and generality of this effect. Despite this, we consider that this result should encourage public administrations to favor forest policies and management practices directed towards mitigating the effects of climatic change.

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Supplementary information

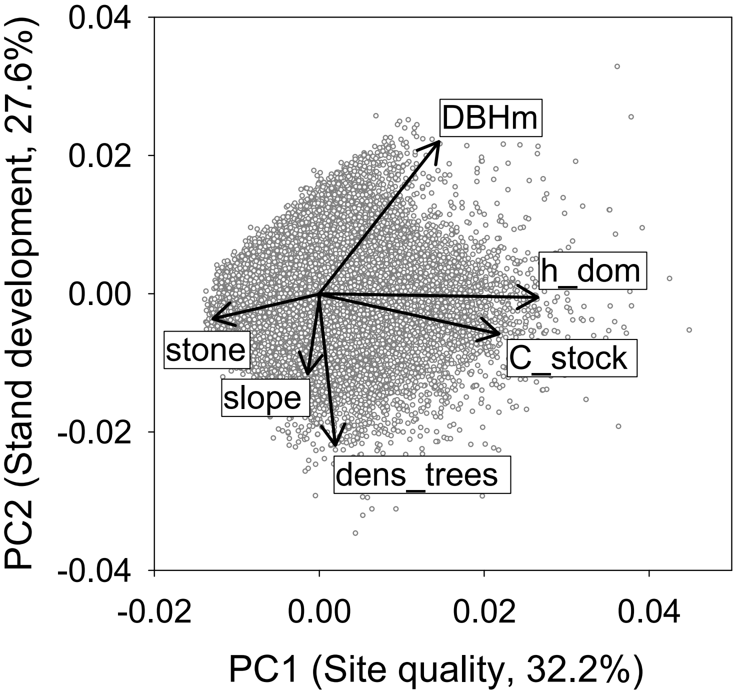

Figure 2.S1. Principal components analysis of plot structural and topographic variables. C_stock, Carbon stock of living trees at the IFN2 (Mg C ha^{-1} yr^{-1}); DBHm, mean DBH (cm) of living trees at the IFN2; dens_trees, density of living trees (trees ha^{-1}) at the IFN2; h_dom, dominant height (mean height (m) of the three tallest trees per plot); stone, surface stoniness; slope, maximum slope at the centre of the plot (in degrees).

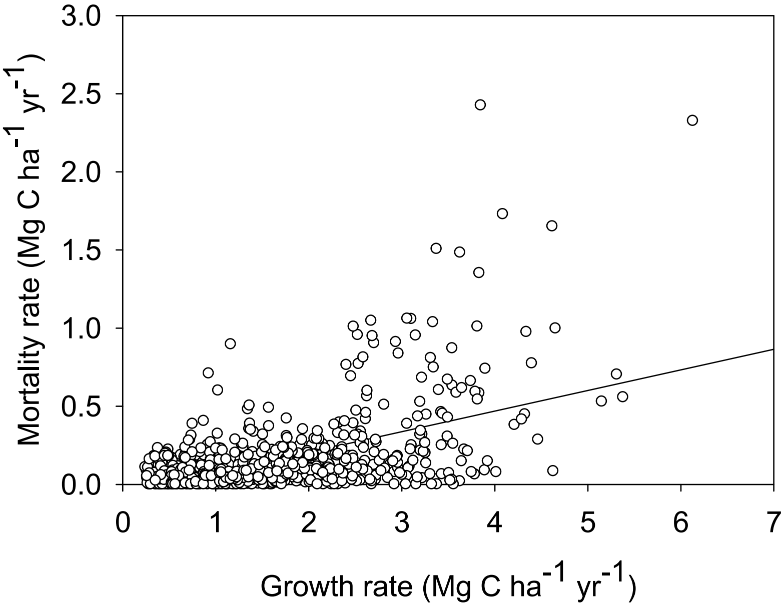

Figure 2.S2. Relationship between growth rate (Mg C ha^{-1} yr^{-1}) and mortality rate (Mg C ha^{-1} yr^{-1}) in 10’x10’ cells across forests in Peninsular Spain (cf. Figure 2.4).

Table 2.S1. Summary of the best models (in terms of BIC) of Growth rate (Mg C ha^{-1} yr^{-1}; log transformed) as a function of plot variables, split by forest type.

	Natural forest						**Plantation**						**Open woodland "Dehesa"**					
Effects	**Estimate**			**T-value**	**Pr(>|t|)**	**Sign.**	**Estimate**			**T-value**	**Pr(>|t|)**	**Sign.**	**Estimate**			**T-value**	**Pr(>|t|)**	**Sign.**
Intercept	-5.81E+00	±	1.42E-01	-40.932	<0.001	***	-5.82E+00	±	4.36E-01	-13.349	<0.001	***	-4.75E+00	±	1.70E-01	-27.980	<0.001	***
Management(= true)	-		-	-	-	n.s.	-		-	-	-	n.s.	-		-	-	-	n.s.
ln(C stock (Mg C ha-1))	1.04E+00	±	4.08E-02	25.528	<0.001	***	9.57E-01	±	1.24E-01	7.706	<0.001	***	5.14E-01	±	4.01E-02	12.810	<0.001	***
ln(Tree density (trees ha^{-1})	7.84E-01	±	2.34E-02	33.548	<0.001	***	8.18E-01	±	6.62E-02	12.365	<0.001	***	4.62E-01	±	2.61E-02	17.680	<0.001	***
Water availability - WAI	9.43E-03	±	3.97E-04	23.736	<0.001	***	5.28E-03	±	3.56E-04	14.851	<0.001	***	-		-	-	-	n.s.
Temperature trend (ºC)	-2.49E-01	±	1.69E-02	-14.718	<0.001	***	1.18E-01	±	3.63E-02	3.261	<0.01	**	-		-	-	-	n.s.
ln(C stock) X ln(Tree density)	-1.02E-01	±	6.56E-03	-15.524	<0.001	***	-9.61E-02	±	1.86E-02	-5.163	<0.001	***	-		-	-	-	n.s.
WAI X Temperature trend	-4.81E-03	±	3.81E-04	-12.623	<0.001	***	-		-	-	-	n.s.	-		-	-	-	n.s.
Management (=true) X T. trend	1.11E-01	±	2.42E-02	4.587	<0.001	***	-		-	-	-	n.s.	-		-	-	-	n.s.
Degrees of freedom	19072						1978						1261					
BIC	31396						2500						2484					
Adjusted-R²	0.589						0.597						0.276					
F-value	3414						588.4						241.3					
p-value	<0.001						<0.001						<0.001					

Significant. codes: ‘***’ 0.001; ‘**’ 0.01; ‘*’ 0.05; n.s. not significant.

Table 2.S2. Summary of the best models (in terms of BIC) of (A) mortality occurrence (dichotomic) and (B) mortality rate (Mg C ha^{-1} yr^{-1}; log transformed) as a function of plot variables, split by forest type.

A	**Natural forest**						**Plantation**						**Open woodland "Dehesa"**					
Effects	**Estimate**			**Z-value**	**Pr(>|t|)**	**Sign.**	**Estimate**			**Z-value**	**Pr(>|t|)**	**Sign.**	**Estimate**			**Z-value**	**Pr(>|t|)**	**Sign.**
Intercept	-1.35E+00	±	6.39E-02	-21.201	<0.001	***	-1.13E+00	±	1.99E-01	-5.666	<0.001	***	-8.68E-01	±	3.54E-01	-2.454	0.014	*
Management(= true)	-		-	-	-	n.s.	-		-	-	-	n.s.	-		-	-	-	n.s.
C stock (Mg C ha-1)	1.71E-02	±	6.96E-04	24.520	<0.001	***	1.12E-02	±	4.45E-03	2.517	0.012	*	1.37E-02	±	5.64E-03	2.427	0.015	*
Tree density (trees ha^{-1})	3.12E-04	±	3.40E-05	9.178	<0.001	***	-9.88E-04	±	1.97E-04	-5.014	<0.001	***	-		-	-	-	n.s.
Water availability - WAI	7.40E-03	±	5.84E-04	12.667	<0.001	***	-		-	-	-	n.s.	2.34E-02	±	6.33E-03	3.703	<0.001	***
Temperature trend (ºC)	-2.26E-01	±	5.13E-02	-4.400	<0.001	***	-		-	-	-	n.s.	-		-	-	-	n.s.
C stock X Tree density	-		-	-	-	n.s.	2.19E-05	±	3.90E-06	5.605	<0.001	***	-		-	-	-	n.s.
WAI X Temperature trend	-		-	-	-	n.s.	-		-	-	-	n.s.	-		-	-	-	n.s.
Management (=true) X T trend	-		-	-	-	n.s.	-		-	-	-	n.s.	-		-	-	-	n.s.
Degrees of freedom	16936						1668						1261					
BIC	18814						1834						1159					
AIC	18783						1813						1149					
Deviance explained	0.103						0.137						0.022					

Significant. codes: '***' 0.001; '**' 0.01; '*' 0.05; n.s. not significant.

B	Natural forest						Plantation						Open woodland "Dehesa"					
Effects	Estimate			T-value	Pr(>|t|)	Sign.	Estimate			T-value	Pr(>|t|)	Sign.	Estimate			T-value	Pr(>|t|)	Sign.
Intercept	-		-	-	-	n.s.	-1.70E+00	±	4.01E-01	-4.234	<0.001	***	-2.54E+00	±	3.64E-01	-6.968	<0.001	***
Management(= true)	-		-	-	-	n.s.	-		-	-	-	n.s.	6.33E-01	±	7.78E-02	8.131	<0.001	***
ln(C stock (Mg C ha-1))	-		-	-	-	n.s.	6.03E-01	±	7.32E-02	8.236	<0.001	***	-1.56E-01	±	5.80E-02	-2.694	<0.01	**
ln(Tree density (trees ha^{-1}))	-6.32E-01	±	0.0743	-8.509	<0.001	***	-2.70E-01	±	6.43E-02	-4.205	<0.001	***	-		-	-	-	n.s.
Water availability -WAI	1.05E-02	±	0.0010	10.963	<0.001	***	2.36E-02	±	3.85E-03	6.135	<0.001	***	-		-	-	-	n.s.
Temperature trend (ºC)	-1.17E-01		0.0370	-3.155	<0.01	**	-		-	-	-	n.s.	-		-	-	-	n.s.
ln(C stock) X ln(Tree density)	1.07E-01	±	0.0193	5.526	<0.001	***	-		-	-	-	n.s.	-		-	-	-	n.s.
WAI X Temperature trend	-6.33E-03	±	0.0009	-6.682	<0.001	***	-1.67E-02	±	3.62E-03	-4.626	<0.001	***	-		-	-	-	n.s.
Management (=true) X T trend	-		-	-	-	n.s.	-		-	-	-	n.s.	-		-	-	-	n.s.
Degrees of freedom	5208						526						217					
BIC	12803						1465						413					
Adjusted-R²	0.255						0.242						0.248					
F-value	297.8						34.9						37.1					
p-value	<0.001						<0.001						<0.001					

Significant. codes: ‘***’ 0.001; ‘**’ 0.01; ‘*’ 0.05; n.s. not significant.

Table 2.S3. Summary of the best models (in terms of BIC) of C stock change (Mg C ha^{-1} yr^{-1}) as a function of plot variables, split by forest type.

	Natural forest						**Plantation**						**Open woodland "Dehesa"**					
Effects	**Estimate**			**T-value**	**Pr(>|t|)**	**Sign.**	**Estimate**			**T-value**	**Pr(>|t|)**	**Sign.**	**Estimate**			**T-value**	**Pr(>|t|)**	**Sign.**
Intercept	7.84E-01	±	3.32E-02	23.610	<0.001	***	8.64E-01	±	1.14E-01	7.572	<0.001	***	6.00E-01	±	1.43E-01	4.194	<0.001	***
Management(= true)	1.63E-01		1.53E-02	10.640	<0.001	***	-		-	-	-	n.s.	-		-	-	-	n.s.
C stock (Mg C ha-1)	1.13E-02	±	3.80E-04	29.690	<0.001	***	1.70E-02	±	2.24E-03	7.608	<0.001	***	-		-	-	-	n.s.
Tree density (trees ha^{-1})	1.12E-03	±	2.52E-05	44.510	<0.001	***	1.47E-03	±	8.83E-05	16.630	<0.001	***	6.93E-04	±	2.32E-04	2.988	<0.01	**
Water availability -WAI	1.41E-02	±	6.88E-04	20.460	<0.001	***	1.06E-02	±	1.09E-03	9.762	<0.001	***	8.97E-03	±	3.03E-03	2.965	<0.01	**
Temperature trend (ºC)	-3.54E-01	±	2.71E-02	-13.050	<0.001	***	-		-	-	-	n.s.	-4.20E-01	±	1.36E-01	-3.079	<0.01	**
C stock X Tree density	-4.28E-06	±	3.58E-07	-11.940	<0.001	***	-7.86E-06	±	1.50E-06	-5.251	<0.001	***	4.57E-05	±	7.75E-06	5.891	<0.001	***
WAI X Temperature trend	-7.33E-03	±	6.64E-04	-11.040	<0.001	***	-		-	-	-	n.s.	-7.62E-03	±	2.78E-03	-2.743	<0.01	**
Management (=true) X T trend	-		-	-	-	n.s.	-		-	-	-	n.s.	-		-	-	-	n.s.
Degrees of freedom	19073						1979						1257					
BIC	52817						7134						1028					
Adjusted-R^2	0.3775						0.3259						0.3237					
F-value	1449						240.7						101.7					
p-value	<0.001						<0.001						<0.001					

Significant. codes: ‘***’ 0.001; ‘**’ 0.01; ‘*’ 0.05; n.s. not significant.

Capítol 3

Patterns and drivers of regeneration of conifer and broadleaf species in forests of peninsular Spain

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Abstract

Aim Understanding the main factors that determine tree recruitment of species at regional scale in Mediterranean ecosystems with contrasted life history attributes is essential for predicting future tree species distribution in face of recent environmental changes.

Location The forests of peninsular Spain

Methods We use the extensive network of plots of two consecutive Spanish national forest inventories (> 30,000 plots) to identify the factors that determine regeneration patterns of the ten most abundant forest species of Spain at large temporal (~10 years) and spatial scales (across peninsular Spain), focusing on the key transition phase from saplings to adult trees. We fitted separate generalized linear models for conifers and broadleaves (based on their different regeneration strategies) to assess the response of sapling abundance and ingrowth rate to the spatial variability of climate (temperature, water availability and recent warming), forest structure (tree density, under and overstory canopy cover and basal area change) and disturbances (previous forest management, wildfires and grazing).

Results Mean sapling abundance was four times higher for broadleaves than for conifers while mean annual ingrowth was twice as high. The higher values of ingrowth rate of broadleaves can be explained because of their ability to maintain a higher sapling bank due to their higher shade-tolerance. Sapling abundance and ingrowth rate were mainly determined by stand structure, both in conifers and broadleaves, whereas the direct effects of disturbances and climate were relative small and there was no detectable effect of recent warming.

Main conclusions The differential response of conifers and broadleaves to canopy closure suggests a likely increment of broadleaves at the expense of conifers. This transition could occur earlier in stands with faster canopy closure dynamics. Further inventories and spatially explicit mixed-species demographic models incorporating the ingrowth component will be needed for predicting the composition of future forests.

Key words: Sapling abundance, Ingrowth rate, Stand structure, Water availability, National Forest Inventory, Warming, Disturbances, Conifers and broadleaves, Shade-tolerance, Seeder-Sprouter, Seed size.

Introduction

Understanding how broad environmental drivers, local site factors and disturbances interact to control spatial patterns and dynamics of biological communities is a recurrent topic in ecology (Woodward, 1987). At a large scale, it is well known that the distribution of species is controlled by climate, mainly water and energy (Woodward, 1987). However, at a local scale, climatic factors are likely to be overridden by local factors determining demographic processes (e.g., reproduction, seed dispersal, germination and establishment, growth and mortality) and by natural or human-induced disturbances (e.g., wildfire, windstorm logging…) (Gomez Aparicio *et al.* 2009). The current distribution of adult trees is mainly a response to past conditions (i.e., climate, management, etc.), while the occurrence and success of tree species at young life stages (either seedlings or saplings) is a response to more recent and local environmental conditions, such as soil characteristics or light availability (Gravel *et al.* 2010; Urbieta *et al.* 2011). Constraints on the last regeneration stage (transition from sapling to adult trees) remain poorly studied, but they are essential for predicting future responses of stand dynamics under eventual changes in climate or management (Bravo *et al.* 2008).

Tree species have different regeneration and dispersal strategies and show different abilities to colonize, establish and cope with biotic and abiotic stresses at different life stages (Gazol & Ibáñez 2010). According to many empirical studies on niche differentiation, species can be classified following the trade-off between high-light growth and low-light survival. A first group is considered shade-intolerant and is associated to early-successional stages (r-strategy or colonizers), while the second group of species is considered shade-tolerant and typical of late-successional stages (Gravel *et al.* 2010). Species can also be classified according to their main regeneration mechanism as seeders, if they only regenerate by seeds, or resprouters, if they also regenerate by sprouts after disturbances (Retana *et al.* 1992). Finally, tree species can also be located in a gradient between wind-dispersed species with small seeds and animal-dispersed species with large seeds (Montoya *et al.* 2008). All these traits are commonly associated in two contrasting syndromes. In the Mediterranean, pines (and conifers examples) are examples of the first syndrome, as they tend to be fast-growing, pioneer species that mainly regenerate by seeds and that usually have small, wind dispersed seeds. These species can facilitate the establishment of the species of the second group, which are low growth, late-successional species, such as deciduous (Pausas *et al.* 2004a) or evergreen oaks (Espelta *et al.* 1995; Urbieta *et al.* 2011), most of them characterized by their resprouting ability and their large seeds dispersed by animals.

Studies aimed at understanding the combined role of environmental conditions and stand structure on regeneration strategies at large spatial scale are rare (Ribbens *et al.* 1994). Recently, studies on seedling-sapling abundance have been carried out using national (Bravo *et al.* 2008; Adame *et al.* 2010; Plieninger *et al.* 2010) or local forest inventories (Gomez Aparicio *et al.* 2009; Urbieta *et al.* 2011) but usually considering one or few species at a relatively small regional scale (geographically restricted). The strength of different biotic and abiotic determinants of the regeneration of different tree species varies along environmental gradients and by disturbances history (Gazol & Ibáñez 2010). It is widely accepted that the abundance of regeneration depends directly on adult trees (overstory), which make up the stands and are the primary source of natural recruits but also indirectly through abiotic effects (reducing solar radiation or increasing soil moisture), and biotic interactions such as competition (Grace & Tilman, 2003) or facilitation (Gómez-Aparicio *et al.* 2004; Pulido & Díaz 2005; Gómez-Aparicio *et al.* 2008). Woody understory might also affect tree regeneration in two ways: positively by protecting recruits against biotic (mainly herbivory) or abiotic stresses (Plieninger *et al.* 2004; Gómez-Aparicio *et al.* 2008; Pausas *et al.* 2009; Plieninger *et al.* 2010), and negatively by competing for water, light and other resources (Maestre *et al.* 2005). Finally, the effect of disturbances can be particularly important, especially in the case of wildfires (Rodrigo *et al.* 2004; Urbieta *et al.* 2011) and grazing (Plieninger *et al.* 2004, 2010). In many developed countries the abandonement of forest management has also become a key process, as it accelerates canopy closure and hampers regeneration of shade-intolerant tree species.

In most mediterranean forests regeneration is scarce, probably due to the low establishment ability of species under low water availability (Pulido & Díaz, 2005; Acácio *et al.* 2008). Peninsular Spain offers a unique opportunity to evaluate patterns and changes in recruitment under a wide range of environmental and disturbance situations. Firstly, many of the forests in Spain are at the southern limit of their biogeographical range, which makes them particularly responsive to climate and vulnerable to climate changes (Gomez Aparicio *et al.* 2008; Gazol & Ibáñez, 2010). Secondly, Spain covers a large gradient of water availability and temperature, from humid and cool areas in the north to dry and hot areas in the southeast (Vayreda *et al.* 2012). And finally, in the last decades there has been a progressive increment of stocks in Spanish forests, especially as a consequence of the abandonment of forest management, which has increased canopy closure.

In this study, we use the extensive network of > 30,000 forest plots that have been re-sampled across peninsular Spain over two successive national forest inventories to analyze the patterns of regeneration of the dominant tree species in Spanish forests. Our main objective is to determine whether broadleaves or conifers, the two main groups of species according to their regeneration strategy, are favoured under current conditions Our main hypothesis is that, in the current situation of increased canopy closure, the regeneration strategy of broadleaf species is favoured compared to that of conifers. However, many other recent changes in Spanish forests may influence the previous outcome and, thus, we need to test this hypothesis accounting for the rest of factors potentially influencing tree regeneration. Our specific objectives were: 1) to determine the spatial and temporal regeneration patterns of conifer and broadleaved species in natural forests of Peninsular Spain, in terms of sapling abundance (as the latest regeneration stage controlling future stand dynamics) and ingrowth rate (i.e., the rate of incorporation of saplings to the tree stage); and 2) to identify the main factors (stand structure, disturbances, climate and recent climate trends) determining the regeneration patterns of these groups of species with different regeneration strategy.

Material and methods

Study area

The study area comprises the forested areas of Spain excluding the Canary and Balearic Islands (ca. 18.4 million ha, 37.3% of the total land area; MARM 2007a) located between 9º 2'W and 3º 2'E and 36º 0'N and 43º 5'N). Forests occur mainly in steep areas, from 0 to 2500 m a.s.l. Vegetation types include: Atlantic, sub-Atlantic and sub-Mediterranean deciduous forests; montane, sub-alpine, and Mediterranean coniferous forests; sclerophyllous, and evergreen shrublands and forests (Rivas Martínez, 1987). Flat zones are mainly occupied by crops and urban areas. 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 N of the area, and is relatively wet and cold (wet Spain). The rest of Spain falls within the Mediterranean climate, which is characterized by mild winters and hot and dry summers (dry Spain). Mean annual temperature and annual precipitation in forest areas in Spain are highly variable, due to topographic gradients of orography and continentality. Mean temperature ranges from 4 to 18ºC, and annual precipitation ranges from 200 to 2500 mm. The coincidence during the summer months of high temperatures and low precipitation leads to a strong decrease of water availability during this season in most parts of the Iberian Peninsula.

The dataset: 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; Villanueva, 2005). The IFN is based on a regular network with a sampling intensity of approximately one plot per two km^2 of forest. This network allows forest characterization and includes exhaustive information on the composition of canopy and understory woody species, as well as on stand structure and tree regeneration. The continuous character of the IFN project started with the second inventory (IFN2), which was conducted from 1986 to 1996, and continued with the third one (IFN3), conducted from 1997 to 2008. The information of the IFN2 for three regions (autonomous communities) in the north of Spain (Navarra, Cantabria and Asturias) was not available, and has not been included in our analyses.

Tree sampling (diameter at breast height, DBH ≥ 7.5 cm) followed a nested design, that is, plot size depended on the DBH of the measured trees to guarantee a representative sampling of the tree size distribution. Thus, all trees with DBH ≥ 7.5 cm were measured within 5 m of the centre of the plots, trees with DBH ≥ 12.5 cm were also measured between 5 and 10 m around the centre of the plots, whereas trees with DBH ≥ 22.5 cm and DBH ≥ 42.5 cm were also considered within 10–15 m and 15–25 m around the centre of the plots, respectively. Species identity of all living and standing dead trees was recorded and its height (H) and DBH were measured. In the circular plot of 5 m radius, the number of saplings per species (2.5 ≤ DBH < 7.5 cm) and their mean height were also recorded. Finally, woody understory vegetation was sampled by identifying each species present within the circular plot of 10 m radius and recording its corresponding canopy cover and mean height.

In the present study we only considered plots of tree species that form natural forests in the study area; that is, we excluded the species that are used exclusively in plantations for wood production (*Eucalyptus* spp, *Pinus radiata*, *Pseudotsuga menziesii…*) or for agriculture (*Olea europaea*, *Ceratonia siliqua*…). From those, we selected the plots where the dominant tree species (DBH ≥ 7.5 cm) according to basal area was one of the ten more frequent autochthonous tree species in Spain: *Pinus halepensis* (19.9% of the plots), *Quercus ilex* (16.4%), *Pinus pinaster* (13.2%), *Pinus sylvestris* (11.4%), *Pinus nigra* (8.6%), *Quercus pyrenaica* (5.4%), *Pinus pinea* (4.0%), *Quercus suber* (3.8%), *Quercus faginea* (3.7%) and *Fagus sylvatica* (2.9%). The ten species considered in our study represented 86% of natural forests in Peninsular Spain. Table 3.1 summarizes the main reproductive attributes of these species that have allowed us to classify them in two groups depending on their life history and regeneration strategy: conifers and broadleaves. There is an almost perfect coincidence of the attributes of the species in each group, with the exception of the medium shade tolerance of *P. nigra* and, to a lesser extent, *Q. suber*, and the intermediate size of *Pinus pinea* seeds, which can be hardly dispersed by wind.

Table 3.1. Functional traits related with the different regeneration strategies of the ten main species grouped in conifers and broadleaves.

	Resprouter	Shade-tolerance	seed size (seed-dispersal)
Conifers			
Pinus halepensis	No	low	Small (wind)
Pinus nigra	No	Intermediate	Small (wind)
Pinus pinaster	No	Low	Small (wind)
Pinus pinea	No	Low	Medium (animal)
Pinus sylvestris	No	Low	Small (wind)
Broadleaves			
Fagus sylvatica	Yes	High	Large (animal)
Quercus faginea	Yes	High	Large (animal)
Quercus ilex	Yes	High	Large (animal)
Quercus pyrenaica	Yes*	High	Large (animal)
Quercus suber	Yes*	Intermediate	Large (animal)

* the two species can resprout from stump and root. *Quercus suber* can also resprout from crown.

We generated maps of sapling abundance and ingrowth rate per plot for conifers and for broadleaves (representing together the five species in each group), and for each species separately (see supplementary on-line information). The maps were produced using the MiraMon GIS software (Pons, 2008). To display these maps we have used the Universal Transverse Mercator reference grid corresponding to the zone 30 of the northern hemisphere (UTM-30N), with Datum ED50 (parameters of the Spanish National Geographic Institute).

Response variables considered: Sapling abundance and Ingrowth rate

The two response variables considered in this study corresponded to the dominant species (in terms of basal area) present in the plot:

Current sapling abundance (number per plot) of the dominant species. It is the number of individuals with DBH between 2.5 and 7.5 cm present in a given 5 m-radius plot at the IFN3 inventory.

Ingrowth rate (number per plot and per decade) of the dominant species. The continuous character of the IFN project allowed identifying which trees (DBH ≥ 7.5 cm) of each species had been incorporated in each 5 m-radius plot between the two inventories (that is, individuals that were considered trees in the IFN3 but that were absent as trees in the IFN2). As the period lapsed between the two inventories was not constant in all plots, we normalized all values to a standard period of ten years.

The total number of plots used in our analyses was 31,524 plots for the response variable ingrowth rate and 31,363 plots for sapling abundance.

Explanatory variables

Species. The dominant species (acording to basal area) in each plot was used as fixed factor. Thus, there were five species in the analises of conifers and five in that of broadleaves.

Stand structure. The stand structural variables included in the analyses were: (1) the density of living trees (DBH ≥ 7.5 cm trees ha^{-1}) of the dominant species (in terms of basal area) as a measure of species abundance, (2) the total basal area (m^2 ha^{-1}, sum of the basal area of all adult tree species present in the plot) as a measure of competition and tree canopy cover and (3) the total understory canopy cover (%). In the analysis of the current sapling abundance we used the values of the variables corresponding to the same forest survey (IFN3), while for explaining ingrowth rate we used the values corresponding to the IFN2 survey including the sapling abundance corresponding of the dominant species in the plot (as number of saplings per plot) and the rate of change of total basal area (m^2 ha^{-1} yr^{-1}) between the two surveys as a measure of forest growth calculated as the difference in terms of basal area between the two inventories divided by the elapsed time to obtain rate per year.

Disturbances. The following disturbance variables registered at the IFN surveys were included in the analyses: (1) evidence of old (previous to IFN2) and recent (between the two surveys) cutting or thinning practices (yes/no), as an indicator of forest management, (2) evidence of herbivory by domestic or wild animals (yes/no), and (3) evidence of damage caused by fire in the recent past (between the two surveys) (yes/no).

Climatic data. Two data sets were used: Climatic data for the period 1950–1999 was obtained from the Digital Climatic Atlas of the Iberian Peninsula (Ninyerola *et al.* 2005). This atlas is a collection of digital maps at 200x200 m resolution with average annual and monthly data for total rainfall and maximum, mean and minimum temperatures, and was used to characterize the spatial variability of climate across the Iberian Peninsula. Based on the geographic coordinates of the IFN plots we determined mean annual temperature (T) and an integrative index of water availability (WAI), which integrates potential evapotranspiration and rainfall in each plot:

$$WAI = ((P - PET) / PET) \cdot 100$$

where P is average rainfall (mm yr^{-1}) and PET is average potential evapotranspiration (in mm yr^{-1}) obtained from monthly values according to the Hargreaves and Samani (1982) method.

The second data set was used to describe recent climatic trends occurred during the time interval between the two inventories. The information was downloaded from http://climate.geog.udel.edu/~climate (Center for Climatic Research, Department of Geography, University of Delaware; Matsuura & Willmott 2009). We used the version 2.01 (June 2009) because it includes interpolated information of real meteorological data until 2008, which was the last year of IFN3 sampling. This data source provided monthly temperature and precipitation per year with a spatial resolution of 0.5x0.5 degrees of latitude/longitude (201 grid cells). Yearly averages of temperature and precipitation were computed using monthly values from March to August each year; that is, with a month ahead in relation to the mean growing season of the vegetation in the Iberian Peninsula. An absolute temperature trend was defined as the difference between the mean value of temperature for the study period and the mean value for a reference period. The study period comprised the years between the two surveys plus two extra years before the IFN2 sampling to include lagged climatic effects on ingrowth rate. The reference period corresponded to the 30 years before the IFN2 sampling. Absolute (March-August) temperature trends across the Iberian Peninsula ranged from -0.15 ºC to 2ºC, with an average increment of +1 ºC.

Statistical analyses

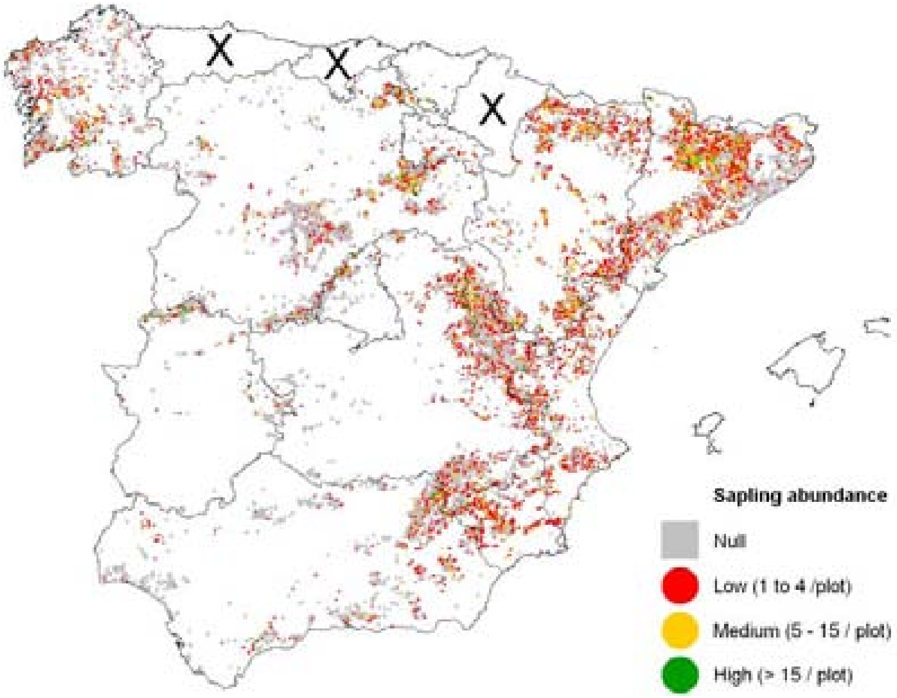
As the two response variables (sapling abundance and ingrowth rate) were counts, we modelled them using a Poisson distribution and a log link function. Whenever the variance of the counts was significantly greater than the mean, indicating overdispersion (Residual deviance/degrees of freedom > 3), we reanalyzed the data using quasi–Poisson models. We fitted separate models for conifers and for broadleaves (see below). Species identity was included in each model as a fixed factor. The predictor variables for the sapling abundance models were: species identity, tree density (DENS_SP), total basal area (BA), understory canopy cover (UCC), water availability (WAI), mean annual temperature (MT), old and recent forest management, grazing and wildfires. The predictor variables for the ingrowth rate models were the same but referred to the IFN2 survey, and adding: mean annual temperature trend between the two surveys (TREND_T), sapling abundance at the IFN2 and total basal area change (CHANGE_BA). Some explanatory variables were transformed to improve the linearity of the relationship (cf. Tables 3.2 and 3.3). The interaction between species identity and total basal area was also considered in all models to account for species specific responses. The interaction between BA and CHANGE_BA was also considered in the ingrowth rate model. Stepwise model selection was applied starting from the saturated model and removing the least significant term (starting by the interactions) until there was no further decrease in the Bayesian Information Criterion (BIC). We considered all models within 2 BIC units as equivalent in terms of fit. Given the large sample size, significance was accepted at □=0.01. Exceptionally, when the fit was carried out with quasi-Poisson model, we could not use the BIC as criterion and we have to used the p-value. Iin this case, we removed stepwise all terms for which P<0.01. Statistical analyses were carried out with the R software (package nmle, R 2.10.0, The R Foundation for Statistical Computing).

Results

Distribution of sapling abundance and ingrowth rate

The spatial pattern of sapling abundance (IFN3, 1997-2008 period) for conifers (Fig. 3.1A) and broadleaves (Fig. 3.1B) in Peninsular Spain showed that the highest values were located at the north and north-east, and the lowest at the south and south-west. This pattern is more evident for broadleaves than for conifers. The spatial pattern of ingrowth rate for conifers (Fig. 3.2A) and broadleaves (Fig. 3.2B) showed patterns similar to those of sapling abundance.

A) Conifers



B) Broadleaves

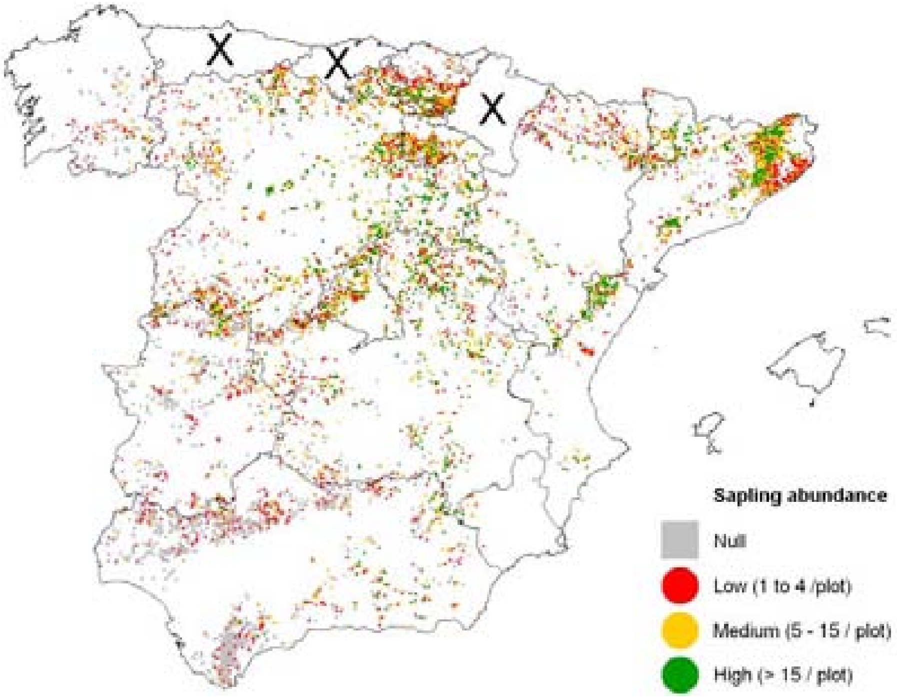
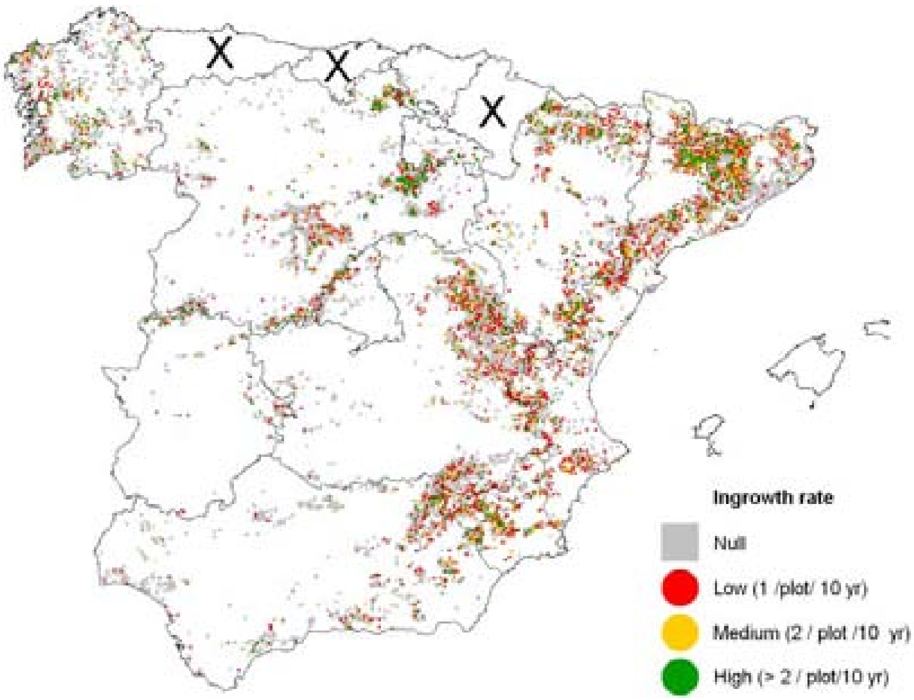


Figure 3.1. (A) Map of sapling abundance (N plot^{-1}) for conifer species (*Pinus halepensis, P. nigra, P.pinaster, P. pinea and P. sylvestris*) and (B) Map of sapling abundance (N/plot) for broadleaved species (*Fagus sylvatica, Quercus faginea, Q. ilex, Q. pyrenaica, Q. suber*). Each point in the map corresponds to a plot where one of the ten studied species is dominant in basal area. Black crosses indicate regions without data available.

A) Conifers



B) Broadleaves

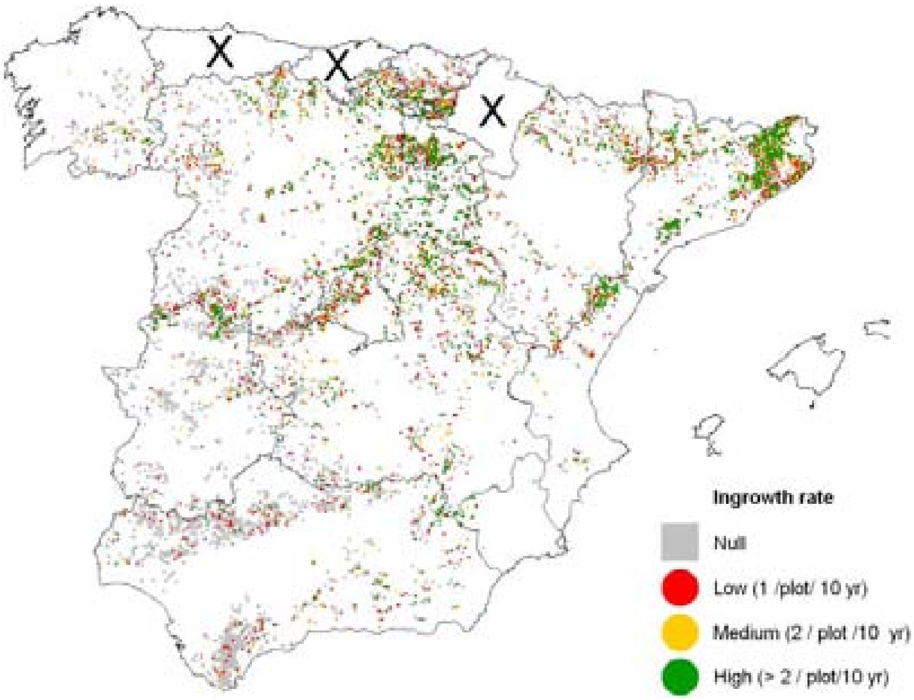


Figure 3.2. (A) Map of ingrowth rate (N plot^{-1} 10 yr^{-1}) for conifer species (*Pinus halepensis, P. nigra, P.pinaster, P. pinea and P. sylvestris*) and (B) Map of ingrowth rate (N plot^{-1} 10 yr^{-1}) for broadleaved species (*Fagus sylvatica, Quercus faginea, Q. ilex, Q. pyrenaica, Q. suber*). Each point in the map corresponds to a plot where one of the ten studied species is dominant in basal area. Black crosses indicate regions without data available.

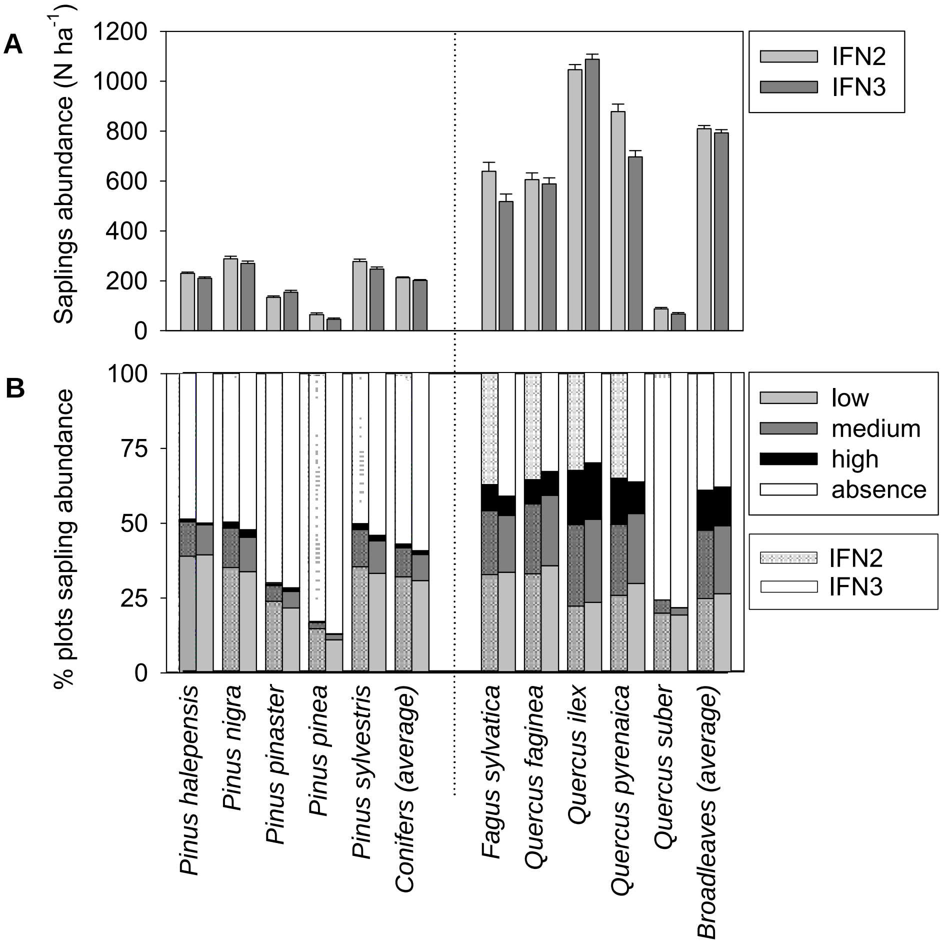


Figure 3.3. (A) Sapling abundance at the IFN2 and IFN3 (N ha^{-1}) for conifer and broadleaved species; for each species the left bar corresponds to the IFN2 and the right bar to the IFN3; and (B) % plots by sapling abundance in IFN2 and IFN3 for conifers and broadleaved species, distinguishing four abundance categories: null in white; low (1-4 saplings per plot) in light grey; medium (5-15 saplings per plot) in dark grey and high (> 15 saplings per plot) in black.

Sapling abundance of the different species in the two inventories was very similar (Fig 3.3A). Mean (± standard error) sapling abundance for broadleaves (mean of five species) was four times higher (~800±12 saplings ha^{-1}) than for conifers (200±3 saplings ha^{-1}). The lowest value of conifers was that of *P. pinea*, while among broadleaves the lowest value was that of *Q. suber*. Overall, 40% of plots where conifers were dominant had saplings of the same dominant species, while for broadleaves this value increased to 62% of plots (Fig. 3.3B). The values of conifers ranged between 20% (*P. pinea*) and 50% of plots (*P. halepensis*) while for broadleaves the values ranged between 29% (*Q. suber*) and 70% (*Q. ilex*).

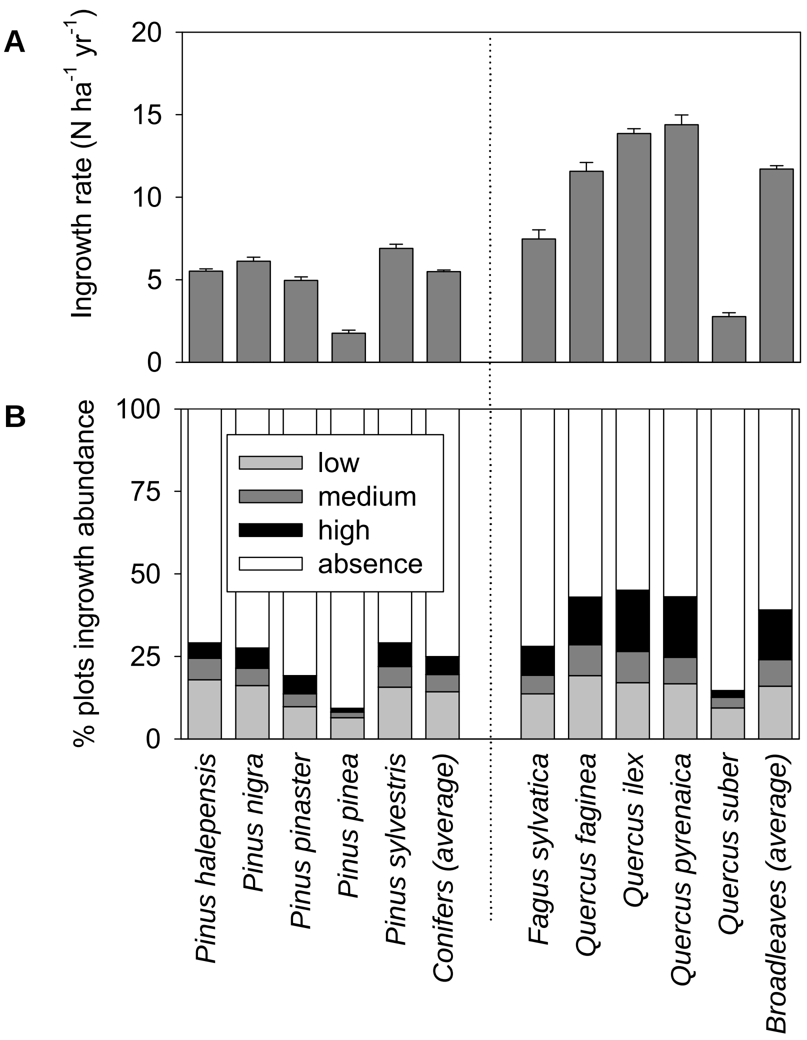


Figure 3.4. (A) Ingrowth rate (N ha^{-1} yr^{-1}) for conifer and broadleaved species and (B) % plots with ingrowth occurrence between IFN2 and IFN3 for conifers and broadleaved species, distinguishing four abundance categories: null in white; low (1 tree incorporated per plot each 10 years) in light grey; medium (2 trees) in dark grey and high (> 2 trees) in black.

Mean annual ingrowth rate between IFN2 and IFN3 (Fig. 3.4A) was two times higher for broadleaves (11±0.2 ha^{-1} yr^{-1}) than for conifers (5.5±0.1 ha^{-1} yr^{-1}). Again, the lowest values were for *P. pinea* (1.8±0.2) among conifers and for *Q. suber* (2.8±0.2) among broadleaves. Overall, only 25% of plots where conifers were dominant had ingrowth of the same species between the two successive surveys, while for broadleaves this value increased to 39% of plots (Fig. 3.4B). The values of conifers ranged between 9% (*P. pinea*) and 30% of plots (*P. halepensis* and *P. sylvestris*) and for broadleaves values ranged between 14% (*Q. suber*) and 45% (*Q. ilex*).

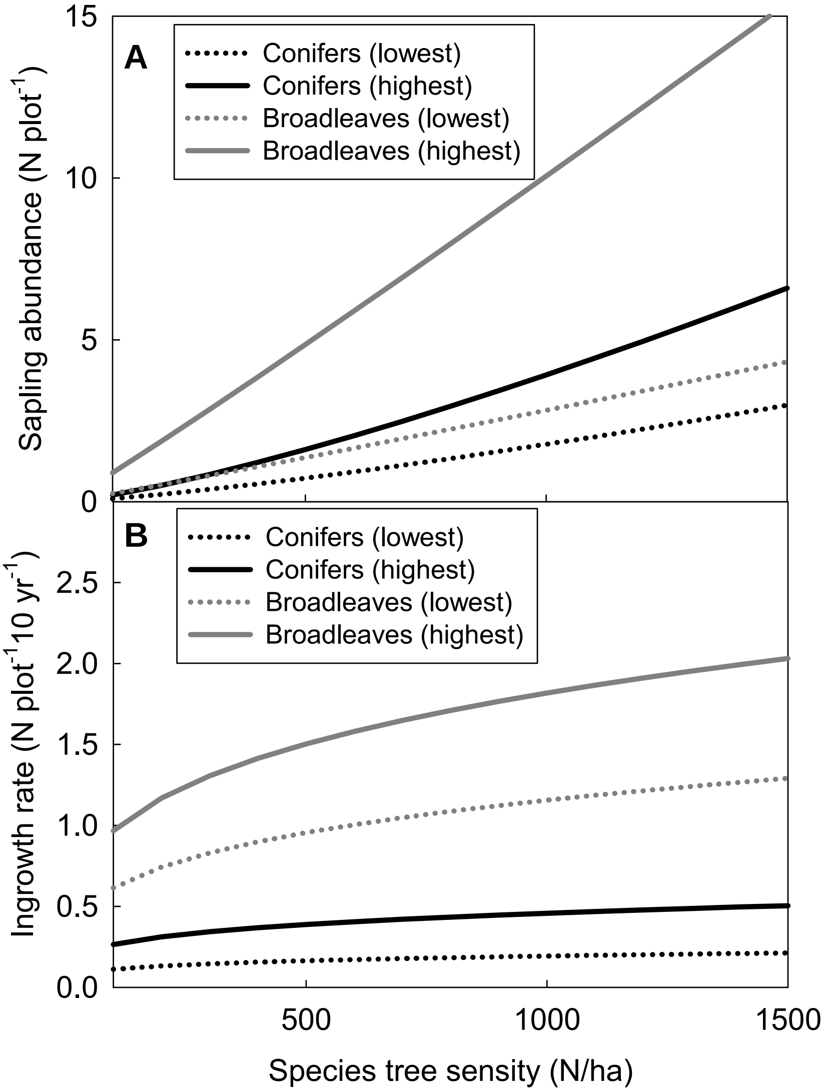


Figure 3.5. Predicted effects of species tree density (N ha^{-1}) on (A) sapling abundance (N $plot^{-1}$) and (B) Ingrowth rate (N $plot^{-1}$ 10 yr^{-1}) for conifers and broadleaves. Black lines represent the extremes of the effects predicted for the five studied conifers, whereas grey lines indicate the corresponding range for broadleaves (solid lines show the highest and dotted lines the lowest effect in each case).

Factors affecting sapling abundance of conifers and broadleaves

The deviance explained by the models of sapling abundance was 30.2% for conifers (Table 3.2A) and 46.9% for broadleaves (Table 3.2B). The variables with greater effect were those related with stand structure. Tree density of the focal species showed the greatest effect, with a strong positive effect on sapling abundance. Values of broadleaves were clearly higher and more sensitive to tree density than those of conifers (Fig. 3.5A). Total basal area always showed a negative effect on sapling abundance for the two groups of species (Table 3.2A, 3.2B and Fig. 3.6A). Whereas for broadleaves there were no differences among species in the relationship between total basal area and sapling abundance, among conifers *P. nigra* showed a less marked decrease of sapling abundance with total basal area. Understory canopy cover had a small and positive effect in conifers (Table 3.2A) and had not effect in broadleaves.

Concerning climate variables, mean annual temperature had a negative effect on sapling abundance in both conifers and broadleaves, although for conifers the effect was smaller (Fig. 3.7A). Water availability (WAI) only had a significant and positive effect on sapling abundance for conifers. Finally, among the different disturbances analysed (Table 3.2A and 3.2B), recent forest management had the highest and negative effect on sapling abundance of the two groups of species, conifers and broadleaves. Old management (previous to the IFN2 survey) only had a positive effect for conifers while wildfire and grazing had a negative effect for conifers but not for broadleaves.

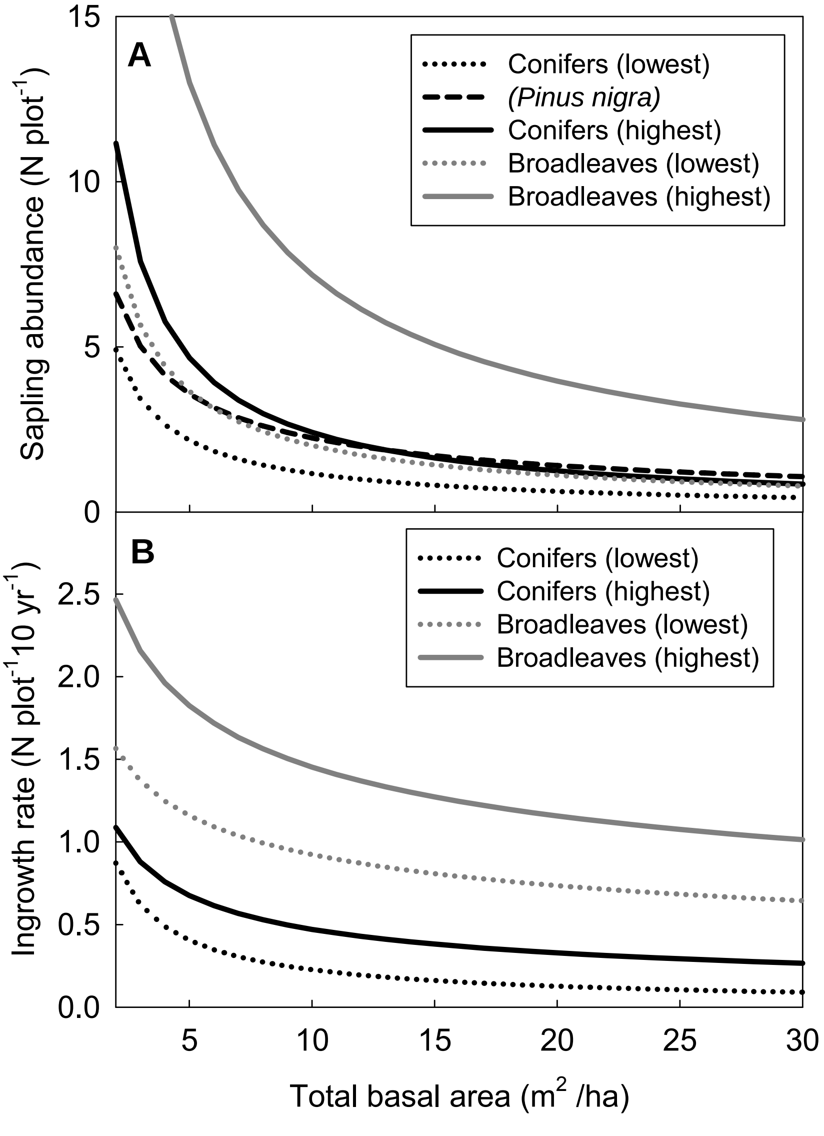


Figure 3.6. Predicted effects of total basal area (m^2 ha^{-1}) on (A) sapling abundance (N plot^{-1}) and (B) Ingrowth rate (N plot^{-1} 10 yr^{-1}) for conifers and broadleaves. Black lines represent the extremes of the effects predicted for the five studied conifers, whereas grey lines indicate the corresponding range for broadleaves (solid lines show the highest and dotted lines the lowest effect in each case; the long dashed line shows the significantly different effect for *P. nigra*).

Table 3.2. Summary of the sapling abundance (N plot^{-1}) models (A) for conifers (Poisson model with log link function) and (B) for broadleaves (quasi-Poisson model, overdispersion >3). All values shown are significant at p<0.001 (indicated with ***). Note that *Pinus pinea* (in a) and *Quercus suber* (in b) are used as the reference species.

A) Conifers	**Estimate**	**SE**	**z-value**	
Intercept (=*Pinus pinea*)	-5.068	0.187	-27.117	***
Pinus sylvestris	0.779	0.180	4.340	***
Pinus halepensis	0.861	0.173	4.978	***
Pinus nigra				n.s.
Pinus pinaster	0.763	0.178	4.293	***
Old management (=true)	0.162	0.022	7.252	***
Recent manag. (=true)	-0.177	0.022	-8.037	***
Grazing (=true)	-0.160	0.047	-3.37	***
Wildfire (=true)	-0.316	0.050	-6.345	***
ln(DENS_SP) (IFN3)	1.284	0.011	116.83	***
ln(BA) (IFN3)	-0.896	0.063	-14.256	***
sqrt(UCC) (IFN3)	0.013	0.005	4.802	***
P. sylvestris X ln(BA)				n.s.
P. halepensis X ln(BA)				n.s.
P. nigra X ln(BA)	0.224	0.065	3.435	***
P. pinaster X ln(BA)				n.s.
WAI	0.003	0.0002	12.99	***
T	-0.049	0.005	-10.42	***
Degrees of freedom	19519			
BIC	47620			
Deviance explained	0.302			
Overdispersion	2.440			

B) Broadleaves	**Estimate**	**SE**	**t-value**	
Intercept (=*Quercus suber*)	-2.754	0.188	-14.646	***
Quercus pyrenaica	0.832	0.113	7.346	***
Quercus faginea	0.696	0.115	6.055	***
Quercus ilex	1.271	0.109	11.682	***
Fagus sylvatica	1.012	0.122	8.278	***
Old management (=true)				n.s.
Recent manag. (=true)	-0.206	0.036	-5.717	***
Grazing (=true)				n.s.
Wildfire (=true)				n.s.
ln(DENS_SP) (IFN3)	1.051	0.021	50.896	***
ln(BA) (IFN3)	-0.857	0.020	-42.315	***
sqrt(UCC) (IFN3)				n.s.
Q. pyrenaica X ln(BA)				n.s.
Q. faginea X ln(BA)				n.s.
Q. ilex X ln(BA)				n.s.
F. sylvatica X ln(BA)				n.s.
WAI				n.s.
T	-0.101	0.008	-13.472	***
Degrees of freedom	11450			
BIC	NA			
Deviance explained	0.469			
Overdispersion	5.179			

ln(DENS_SP) (IFN3): current species density of adult trees (trees ha^{-1}), log transformed; ln(BA) (IFN3): current total basal area (m^{2} ha^{-1}), log transformed; sqrt(UCC) (IFN3): current total understory canopy cover (%), square-root transformed; WAI: water availability index (%); T: mean annual temperature (ºC).

Table 3.3. Summary of the ingrowth rate (N plot^{-1} 10 yr^{-1}) models (A) for conifers, and (B) for broadleaves. In the two cases we applied a Poisson model with log link function. All values shown are significant at $p<0.001$ (indicated with ***) or $p< 0.01$ (indicated with **).

A) Conifers	**Estimate**	**SE**	**z-value**	
Intercept (=*Pinus pinea*)	-2.288	0.119	-19.2	***
Pinus sylvestris				n.s.
Pinus halepensis				n.s.
Pinus nigra				n.s.
Pinus pinaster				n.s.
Old management (=true)	0.329	0.035	9.5	***
Recent manag. (=true)	-0.168	0.034	-5.0	***
Grazing (=true)				n.s.
Wildfire (=true)	-0.528	0.087	-6.1	***
sqrt(N_SAPLING) (IFN2)	0.569	0.008	69.5	***
ln(DENS_SP) (IFN2)	0.239	0.021	11.6	***
ln(BA) (IFN2)	-0.583	0.038	-15.5	***
BA_CHANGE	3.316	0.066	50.5	***
ln(BA) X BA_CHANGE	-0.905	0.021	-43.6	***
sqrt(UCC) (IFN2)				n.s.
P. sylvestris X ln(BA)	0.289	0.035	8.4	***
P.halepensis X ln(BA)	0.251	0.032	7.7	***
P.nigra X ln(BA)	0.252	0.034	7.4	***
P.pinaster X ln(BA)	0.318	0.032	9.8	***
WAI				n.s.
T	-0.026	0.007	-3.9	***
TREND_T				n.s.
Degrees of freedom	20013			
BIC	29332			
Deviance explained	0.470			
Overdispersion	0.87			

B) Broadleaves	**Estimate**	**SE**	**z-value**	
Intercept (=*Quercus suber*)	-2.627	0.139	-18.9	***
Quercus pyrenaica	0.169	0.063	2.7	**
Quercus faginea	0.445	0.064	6.9	***
Quercus ilex	0.454	0.059	7.7	***
Fagus sylvatica				n.s.
Old management (=true)	0.171	0.031	5.6	***
Recent manag. (=true)				n.s.
Grazing (=true)	-0.198	0.041	-4.9	***
Wildfire (=true)	0.322	0.062	5.2	***
sqrt(N_SAPLING) (IFN2)	0.326	0.006	52.2	***
ln(DENS_SP) (IFN2)	0.274	0.017	16.0	***
ln(BA) (IFN2)	-0.211	0.020	-10.6	***
BA_CHANGE	2.471	0.046	53.4	***
ln(BA) X BA_CHANGE	-0.463	0.019	-24.9	***
sqrt(UCC) (IFN2)	0.032	0.004	8.8	***
Q. pyrenaica X ln(BA)				n.s.
Q. faginea X ln(BA)				n.s.
Q. ilex X ln(BA)				n.s.
F. sylvatica X ln(BA)				n.s.
WAI				n.s.
T	-0.040	0.006	-6.3	***
TREND_T				n.s.
Degrees of freedom	11157			
BIC	23165			
Deviance explained	0.614			
Overdispersion	1.04			

sqrt(N_SAPLING) (IFN2): previous sapling abundance (N plot^{-1}), square-root transformed; ln(DENS_SP) (IFN2): previous species density of adult trees (trees ha^{-1}), log transformed; ln(BA) (IFN2): previous total basal area (m^{2} ha^{-1}), log transformed; CHANGE_BA: change in total basal area (m^{2} ha^{-1} yr^{-1}) between the two surveys; sqrt(UCC) (IFN2): previous total understory canopy cover (%), square-root transformed; WAI: water availability index (%); T: mean annual temperature (ºC); TREND_T: recent temperature trend (ºC).

Factors affecting ingrowth rate of conifers and broadleaves

The deviance explained by the ingrowth rate model for conifers was 47.0% (Table 3.3A) while that of broadleaves was 61.4% (Table 3.3B). Again, the variables with highest significant effect were those related with stand structure. As expected, previous sapling abundance had a large positive effect on ingrowth rate in the two groups, although with a steeper effect for conifers than for broadleaves (Fig. 3.8). Basal area change had also a positive impact on ingrowth rate in the two groups, with a steeper effect in broadleaves (Fig. 3.9). Total previous basal area showed a consistent and negative effect on ingrowth rate in the two groups (Fig. 3.6B). The interaction between total basal area and basal area change had a significant effect on the two groups, but it was specially high on conifers. In this group of species, the effect of a positive basal area change was especially steep at low basal areas, while at high basal areas it hardly had any effect on ingrowth rate (Fig. 3.10A). Althouth in broadleaves the pattern was similar (Fig. 3.10B), at high basal areas there was a positive effect of basal area chagne on ingrowth rate. Previous tree density of the focal species also showed a positive effect on ingrowth rate (Fig. 3.5B). Whereas for broadleaves there were no differences among species in the relationship between total basal area and ingrowth rate, among conifers *P. pinea* showed a more marked decrease of ingrowth with total basal area than the other conifer species (Table 3.3A). Finally, understory canopy cover had a slight and positive effect in broadleaves (Table 3.3B) but had no effect in conifers.

Climate variables had a relativelly small effect on ingrowth rate compared to stand structure (Tables 3.3A and 3.3B). Only mean annual temperature had a negative effect on ingrowth rate in the two groups of species (Fig. 3.7B), whereas WAI and warming were never significant. The effect of disturbances, when significant, was always small (Tables 3.3A and 3.3B). Old management had a positive effect on ingrowth rate in the two groups of species; while recent management had a negative effect on conifers. Grazing was only significant in broadleaves with a negative effect. Finally, wildfire had an opposite effect on ingrowth rate for the two groups: negative in conifers and positive in broadleaves.

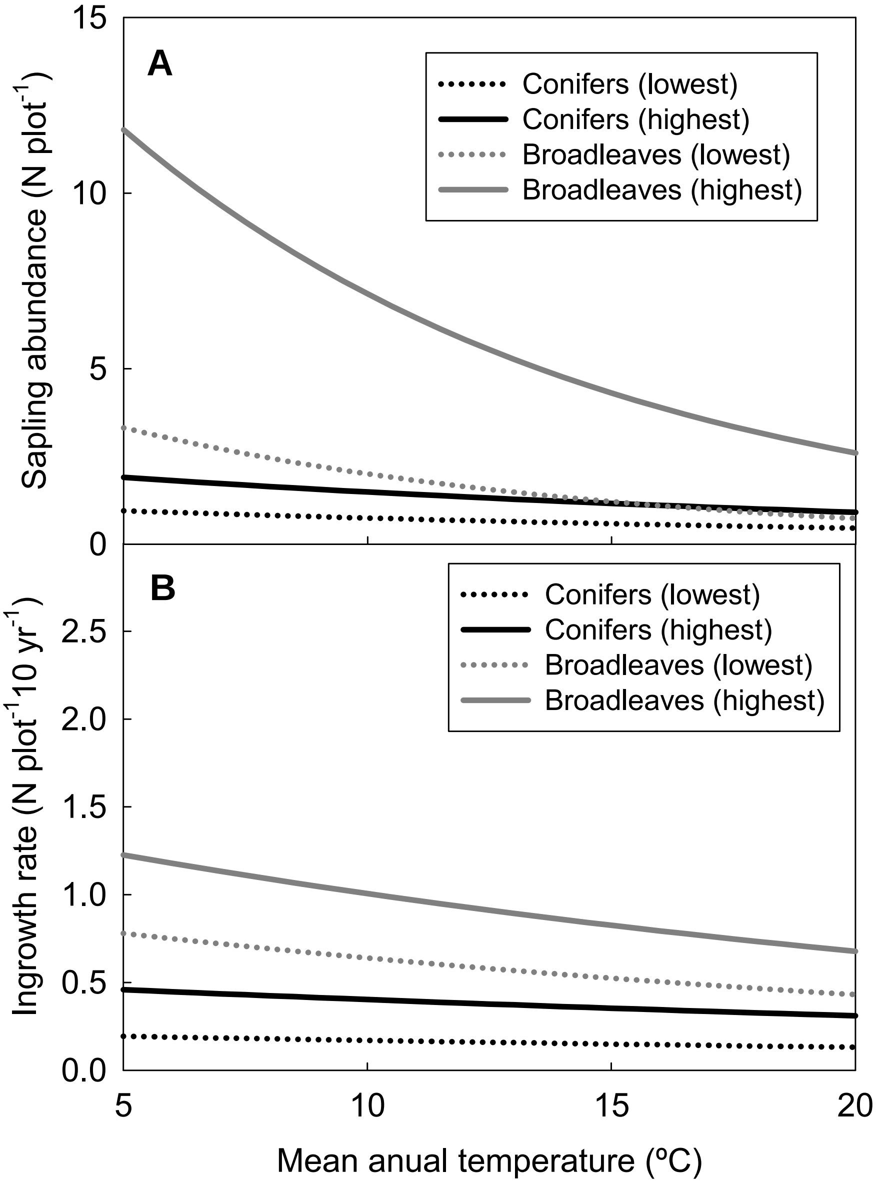


Figure 3.7. Predicted effects of mean annual temperature (ºC) on (A) sapling abundance (N plot^{-1}) and (B) Ingrowth rate (N plot^{-1} 10 yr^{-1}) for conifers and broadleaves. Black lines represent the extremes of the effects predicted for the five studied conifers, whereas grey lines indicate the corresponding range for broadleaves (solid lines show the highest and dotted lines the lowest effect in each case).

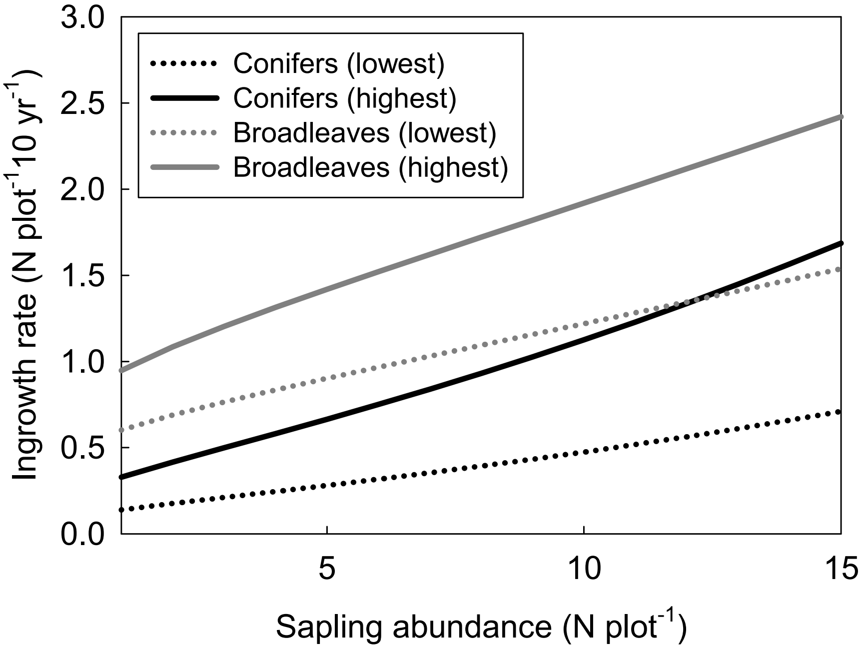


Figure 3.8. Predicted effects of sapling abundance (N plot^{-1}) on Ingrowth rate (N plot^{-1} 10 yr^{-1}) for conifers and broadleaves. Black lines represent the extremes of the effects predicted for the five studied conifers, whereas grey lines indicate the corresponding range for broadleaves (solid lines show the highest and dotted lines the lowest effect in each case).

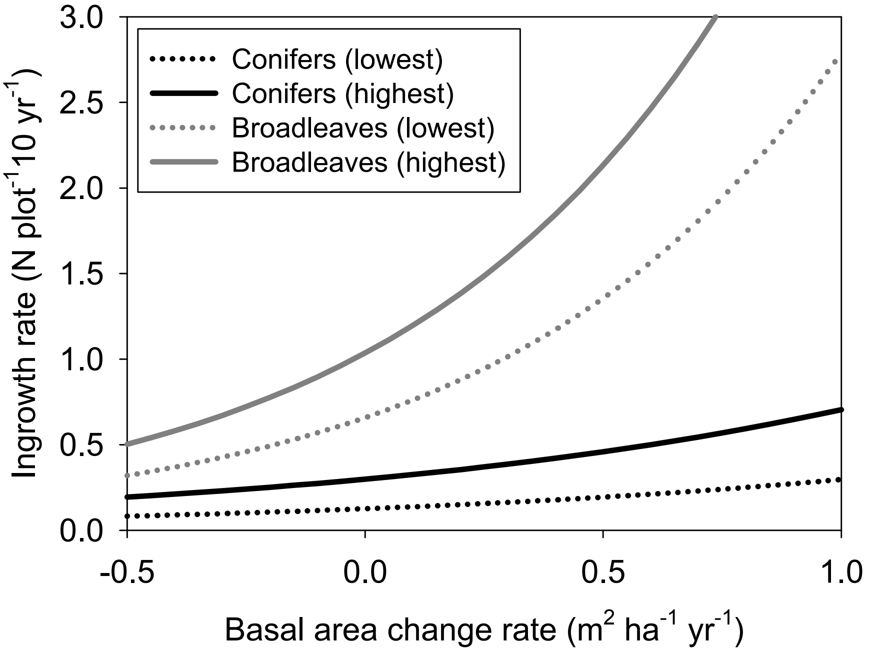


Figure 3.9. Predicted effects of basal area change rate (m^2 ha^{-1} yr^{-1}) on Ingrowth rate (N plot^{-1} 10 yr^{-1}) for conifers and broadleaves. Black lines represent the extremes of the effects predicted for the five studied conifers, whereas grey lines indicate the corresponding range for broadleaves (solid lines show the highest and dotted lines the lowest effect in each case).

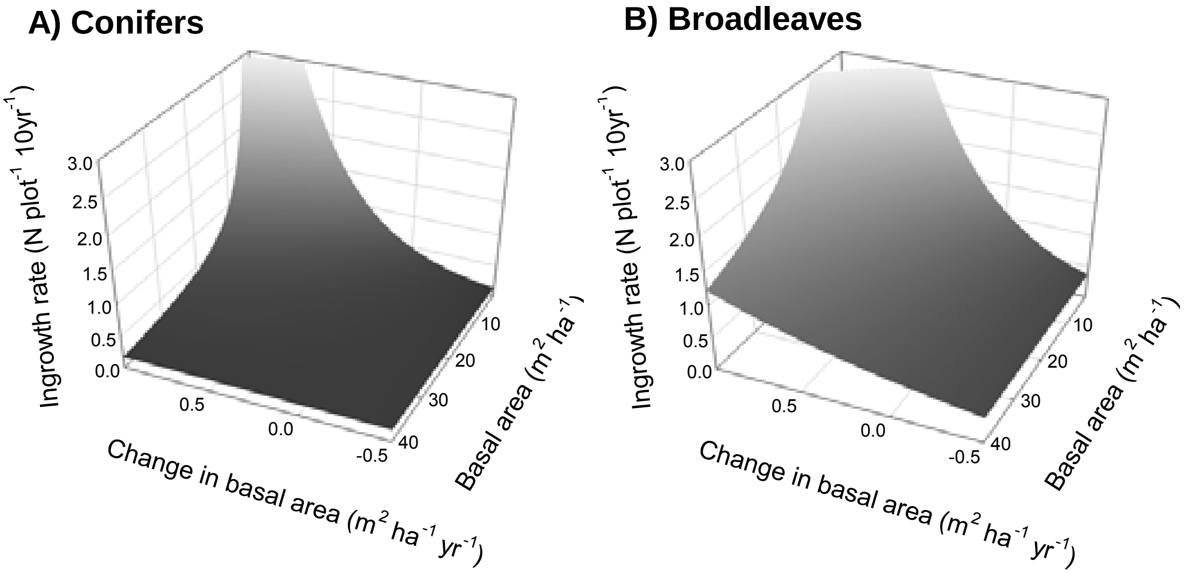


Figure 3.10. Tri-dimensional plot showing the predicted effects on Ingrowth rate (N plot^{-1} 10 yr^{-1}) of the interaction between Basal area (m^2 ha^{-1}) and Basal Area change (m^2 ha^{-1} yr^{-1}) in: (A) conifers and; (B) broadleaves.

Discussion

Regeneration patterns in Peninsular Spain

The results obtained in the present study indicate that, after one decade (the time-lag between surveys), less than 50% of sampled plots had ingrowth occurrence (i.e., the transition rate from saplings to adults) of any of the tree species considered (Fig. 3.4B). These low ingrowth values suggest that new recruitment may not counterbalance tree deaths caused by natural mortality or by disturbances. In the present study, we have gathered evidences that regeneration failure occurs at large geographical scale and for the latest regeneration stages, affecting sapling abundance and ingrowth rate of conifers and broadleaves in central (inland plateau), south-western and southern Peninsular Spain (Fig. 3.1A, 3.1B, 3.2A and 3.2B), consistent with recent studies at smaller spatial scales (Acácio *et al.* 2008; Adame *et al.* 2010; Plieninger *et al.*; 2010; Urbieta *et al.* 2011). The higher mean values of sapling abundance (Fig. 3.3A) and ingrowth rate (Fig. 3.4A) of broadleaves compared to those of conifers could be attributed to their resprouting ability and their higher shade-tolerance (Espelta *et al.* 1995; Gracia *et al.* 2001). Thus, broadleaves can maintain a high sapling population surviving for longer periods of time under their own canopy (Gracia *et al.* 2001), while conifers have low sapling populations (Fig. 3.3A) because they are more shade-intolerant and their ability to survive under their own canopy is reduced. However, this lower sapling abundance of conifers is partially compensated by their higher percentage of saplings reaching adulthood (2.5% of conifer saplings reach the adult stage each year versus 1.4% of broadleaves).

Determinants of sapling abundance and ingrowth

The variance explained by the models of current sapling abundance (Table 3.2) and ingrowth rate (Table 3.3) was high compared to previous studies (Bravo *et al.* 2008; Adame *et al.* 2010; Plieninger *et al.* 2010), probably because we included a wider geographical, climatic and stand structure gradient, and also because we considered factors that are not usually accounted for, such as disturbances (i.e., wildfires, grazing and forest management). The relatively high proportion of variance explained by the models also suggests that the responses of the different conifer and broadleaf species was reasonably homogeneous, supporting our approach of pooling the species belonging to each group (cf. Table 3.1).

Stand structure effects

As expected, the variable with highest effect on ingrowth rate was sapling abundance, with a clear positive effect in all cases (Tables 3.3A and 3.3B). The sapling bank of conifers was more effective than that of broadleaves (i.e., the slope of the relationship is steeper for conifers; Fig. 3.8). Thus, the higher values of ingrowth rate of broadleaves (Fig. 3.4A) can be explained because of their ability to maintain a greater sapling bank (Fig. 3.3A) than conifers (Gómez-Aparicio *et al.* 2008; Adame *et al.* 2010; Gazol & Ibàñez 2010). For any range of adult tree density (the primary source of seeds or sprouts), sapling abundance was higher for shade-tolerant broadleaves than for conifers (Fig. 3.5A), consistent with previous results (Pausas *et al.* 2004a, b, Gómez-Aparicio *et al.* 2006; Gazol & Ibàñez 2010; Urbieta *et al.* 2011). Similarly, the ingrowth rate for any stand basal area was always lower in conifers than in broadleaves (Fig. 3.6B), suggesting that even at very low competition intensity, conifers do not have any advantage over broadleaves. Thus, the expected advantage of conifers at low canopy cover, assumed by their low shade tolerance, does not seem to translate into a higher ingrowth. Moreover, basal area change, a measure of canopy closure rate, had a steeper positive effect on the ingrowth rate of broadleaves (Table 3.3A and 3.3B) for any stand basal area (Fig. 3.9 and 3.10). Overall, our results suggest that the studied conifers may not be able to maintain their sapling bank at high stand basal area (Fig. 3.6A, cf. Pausas *et al.* 2004a; Urbieta *et al.* 2011).

The positive effect of tree density of the dominant species on ingrowth showed a tendency to saturate (Fig. 3.5B), likely because high tree density is also an indication of high competition. This was consistent with the negative effect of total basal area observed here (Fig. 3.6) and elsewhere (Adame *et al.* 2010). The pattern of declining sapling abundance with total basal area was similar in the two groups of species, but the more shade-intolerant conifers always showed a stronger reduction, reaching very low values at high basal area (Fig. 3.6A). Only *P. nigra* showed a lower reduction according to its greater shade-tolerance (Table 3.1) (Rodrigo *et al.* 2004). All broadleaved species, including the relatively shade-intolerant *Q. suber*, showed a similar pattern of sapling abundance reduction with total basal area. Finally, the small but positive effect of understory canopy cover on ingrowth rate for broadleaves (Table 3.3B) suggests a facilitative effect (Gómez-Aparicio *et al.* 2004; Pulido & Díaz 2005; Gómez-Aparicio *et al.* 2008) that could be related to the better maintenance of soil moisture because understory reduces the impact of solar radiation especially in summer (Quero *et al.* 2006; Puerta-Piñero *et al.* 2007; Pausas *et al.* 2009; Plieninger *et al.* 2010).

Climate effects

Although climate has a determinant role in forest structure, the low direct influence of climatic variables in our models is consistent with other studies that show nil or weak effects (Gazol & Ibàñez 2010; Plieninger *et al.* 2010). Large-scale climatic effects can be masked by a broad variety of local factors (stand structure, local site characteristics…), so that their direct effect can be very small (Ribbens *et al.* 1994; Collins & Carson, 2004; Gomez-Aparicio *et al.* 2009). However, although the effect of climatic variables was low, the differences observed between conifers and broadleaves could have important consequences in the future scenarios of climate change. Although all species showed a decrease of sapling abundance as mean annual temperature increased (see also Plieninger *et al.* 2010), broadleaved species were more responsive than conifers (Fig. 3.7A). However, these differences disappeared at the ingrowth level and the negative effect of temperature was similar for the two groups of species (Fig. 3.7B). Surprisingly, broadleaves and conifers always never responded to the direct increment of water availability (WAI), both as sapling abundance and ingrowth rate (Tables 3.2A, 3.3A and 3.3B, only conifer sapling abundance responded positively to WAI, table 3.2A), probably because the direct effect of WAI is strongly modified by local conditions (either overstory and understory canopy closure and other local site characteristics). The lack of effect of recent warming on recruitment is consistent with the relatively low direct effect of climatic variables observed in this study.

Disturbance effects

The effect of disturbances (old and recent management, grazing and wildfire) on tree recruitment was similar in magnitude to that of climatic variables. The processes that take place after a disturbance can be complex and dependent on its type and intensity. It seems clear that a more accurate knowledge of the intensity of disturbances (and not only their occurrence) would allow a better characterization of their effects on recruitment and would also increase the variance explained by the models (Adame *et al.* 2010; Plieninger *et al.* 2010). However, we can provide some general indications about their influence on recruitment taking into account the different regeneration strategies of conifers and broadleaves (Table 3.1). Thus, the positive effect of old management (previous to the IFN2 survey) on ingrowth rate of all species could be a response to canopy opening, improving light conditions for the establishment and growth of new individuals. When thinning or logging intensity is low, gaps created on the canopy may not be large enough to allow the regeneration of shade-intolerant conifers, but enough for broadleaves (Espelta *et al.* 1995; Gracia *et al.* 2001). The surprisingly negative effect of recent forest management (the one carried out in the period between the two surveys) on sapling abundance of conifers and broadleaves (Table 3.2A and 3.2B) and on ingrowth rate of conifers (Table 3.3A) could be a direct consequence of some silvicultural practices, such as precommercial thinning, understory clearance or soil treatments that could damage or kill saplings (Urbieta *et al.* 2011).

The almost nil effect of grazing (either of livestock or wild animals) could be due to the low grazing pressure of Spanish forests (only 2% of conifer plots and 8.5% of broadleaved plots showed signs of grazing). Additionally, in the case of broadleaves their high sprouting capacity rapidly counteracts the effect of grazing (Pausas *et al.* 2009). Finally, wildfires had a negative effect on sapling abundance and ingrowth rate of conifers (Tables 3.2A and 3.3A) but did not have any effect on sapling abundance of broadleaves and even had a positive effect on ingrowth rate of this group. This is an expected result because, on the one hand, most conifers usually have problems for regenerating after fire (Rodrigo *et al.* 2004), with the exception of *P. halepensis* (Pausas *et al.* 2004b), because fire kills most saplings and seedlings, and many species do not have a seed bank to recover after fire (Arnan *et al.* 2006). On the other hand, in the case of broadleaves, the pattern observed is consistent with the fact that saplings can recover and grow after fire by resprouting either from the stump or the crown (Rodrigo *et al.* 2004).

Present and future regeneration dynamics of forests in Peninsular Spain

Understanding the main factors affecting the sapling-adult transition and, in particular, the main differences between conifers and broadleaves is essential for predicting future stand dynamics. In this paper we describe forest regeneration patterns, in particular concerning the key transition phase from saplings to adult trees, at large temporal (~10 years) and spatial scales (across Peninsular Spain) and over a wide range of environmental conditions and stand structures. We have shown that stand structure, as a complex balance of competitive and facilitative effects, and the abundance of individuals of the same species (as a source of seeds and sprouts) are currently the main determinants of regeneration in the studied forests. The effect of the future drier and warmer climate (EEA 2008) on regeneration dynamics remains uncertain, but it may be critical if increased drought stress results in widespread forest die-off (Allen *et al.* 2010), both because tree mortality would modify forest structure and because subsequent recruitment dynamics would determine, to an important extent, whether a given tree mortality episode results in a vegetation shift (cf. Lloret *et al.* 2012).

The comparison of the results obtained for conifers and broadleaves shows that their sapling abundance and ingrowth are associated to similar environmental factors, but that there is a consistent difference in overall regeneration success between the two groups. Thus, the highest values of ingrowth rate of broadleaves compared to conifers allow forecasting a likely increment of broadleaves to the detriment of conifers (i.e., transition of monospecific conifer forests to mixed forests with broadleaves and, at a larger temporal scale, their replacement by broadleaves) (Gomez-Aparicio *et al.* 2009; Urbieta *et al.* 2011). Nonetheless, further studies and monitoring of regeneration along wide environmental gradients, together with spatially explicit, mixed-species demographic models incorporating the ingrowth component will be needed for predicting the composition of future forests (Bravo *et al.* 2008) and designing adaptive management strategies to mitigate the impact of future environmental changes (Urbieta *et al.* 2011).

Acknowledgements

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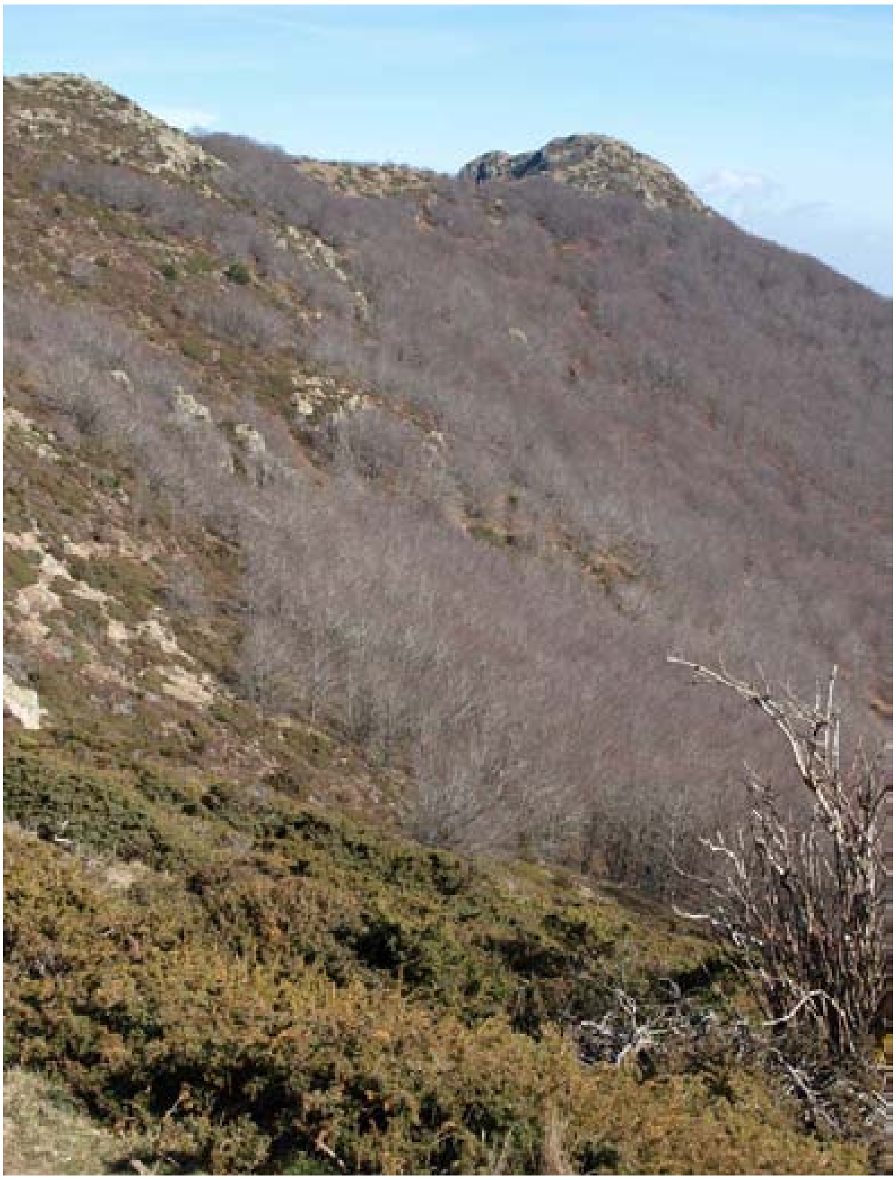

Capítol 4

Rapid and Directional Changes in Tree Distribution Lead to Increased Dominance of Broadleaf Species

This chapter is in *review;*

Jordi Vayreda, Marc Gracia, Jordi Martinez-Vilalta, and Javier Retana (in review)

Abstract

Tree species have been reported to shift their geographic distribution by tracking changes in temperature. However, forests are not only responding to climatic drivers but to a suit of changing and interacting factors. By using data from more than 20,000 plots over two consecutives forest inventories we show that the distribution of most tree species in peninsular Spain has moved upwards towards cooler environments. We also show that most of the observed patterns, including some unexpected geographic shifts, are explained by forest structure. Forest abandonment and changes in disturbances (e.g., fire regimes) during the last decades have led to the expansion of broadleaves over conifers, due to their greater ability to cope with biotic factors such as competition. It is unclear whether this trend will continue under the greater aridness projected by climate models given the greater ability of conifers species to cope with extreme drought events.

Introduction

Forests are valued globally for the ecological, economic, social, aesthetic and recreational services they provide to the well being of society (Bonan 2008). World's forests, for instance, are responsible for removing ~30% of all anthropogenic C emissions and, thus, have a key role in the global carbon cycle (Canadell *et al.* 2007; Pan *et al.* 2011). Since the distribution of forests is primarily determined by climate (Woodward 1987; Ellenberg 1988), there is a growing concern that anthropogenic climate change may alter the distribution, composition and function of forests and the services they provide (IPCC 2007; Bonan 2008). Some plant species have been already reported to shift their geographic distribution tracking changes in temperature. These shifts have been observed frequently in mountains, implying movements uphill in elevation (Lenoir *et al.* 2008, 2009; Chen *et al.* 2011), whereas documented poleward shifts in latitude remain scarce (Jump *et al.* 2009; Zhu *et al.* 2012). Vegetation shifts require that tree mortality and recruitment are not balanced through time (cf. Lloret *et al.* 2012), due to increased tree mortality in the trailing edge of the species' geographic distribution leading to local extinction, to colonization at the leading edge of the species' range, or both.

Table 4.1. Ecological characteristics related with tolerance to biotic and abiotic factors for the eleven species studied, grouped in conifers and broadleaves, and the typical climate domain of each species.

	Biotic-related			Abiotic-related			
	Resprouter	Shade-tolerance	seed-dispersal distance	Drough-tolerance	Tolerance to high temperature (heat)	Tolerance to low temperature (cold)	Climate-type
Conifers							
Pinus halepensis	No	Low	Small (wind)	Very high	Very high	Low	Mediterranean
Pinus nigra	No	Intermediate	Small (wind)	High	High	Medium	Mediterranean
Pinus pinaster	No	Low	Small (wind)	Medium	High	Medium	Mediterranean
Pinus pinea	No	Low	Medium (animal)	Very high	Very high	Medium	Mediterranean
Pinus sylvestris	No	Low	Small (wind)	Medium	Medium	High	Temperate
Pinus uncinata	No	Low	Small (wind)	Low	Low	High	Alpine
Broadleaves							
Fagus sylvatica	Yes	High	Large (animal)	Low	Low	High	Temperate
Quercus faginea	Yes	High	Large (animal)	Medium	High	Medium	Mediterranean
Quercus ilex	Yes	High	Large (animal)	High	High	Medium	Mediterranean
Quercus pyrenaica	Yes	High	Large (animal)	Medium	Medium	High	Mediterranean
Quercus suber	Yes	Intermediate	Large (animal)	Medium	High	Low	Mediterranean

Tree species can be particularly sensitive to climate change because they are sessile organisms with long life-span, two traits that do not allow rapid adaptation to environmental changes (Lenoir *et al.* 2008; Lindner *et al.* 2010). Most studies carried out until now do not consider other possible drivers and mostly focus on shifts induced by changes in climate, mainly temperature (Chen *et al.* 2011). However, distribution shifts do not always occur in the expected direction (Crimmins *et al.* 2011; Lenoir *et al.* 2008, 2010) and these apparently inconsistent responses have been related to changes in local conditions, such as changes in vegetation cover through time (e.g., Lenoir *et al.* 2010). Clearly, forests are not only responding to climatic drivers but to a suit of changing and interacting factors. As a consequence of this complexity of factors, there has been limited progress in understanding the main drivers of recent shifts in tree species' distributions (Lenoir *et al.* 2010). Integrative studies are needed to identify the underlying causes of colonization and extinction processes, taking into account all the possible abiotic and biotic drivers, especially those that are direct or indirect consequences of human activities.In this study we focus on the forests in peninsular Spain ($18.3 \cdot 10^6$ ha of forest), including alpine, temperate and Mediterranean species. These forests are an active carbon sink, accumulating C at a rate of ~1.4 Mg C ha^{-1} yr^{-1} (Vayreda *et al.* 2012). Our first aim is to document the recent and directional changes in the geographic distribution of the most abundant forest tree species in peninsular Spain, both at the species level and at the level of wide functional groups (conifers vs. broadleaves). Secondly, we aim at determining whether these changes can be attributed mainly to climate or also to other drivers such as land-use changes (i.e., recent disturbances such as wildfires or abandonment of forest management). In particular, we examine to what extent these drivers could explain the rapid geographic expansion of broadleaf over conifer species and the implications of this shift in the context of global change.

Material and methods

Large-scale forest inventory surveys provide an opportunity to evaluate shifts in geographic distribution of tree species over large territories. This study uses data from the two last national forest inventories in Spain, including 20,471 plots surveyed at the IFN2, conducted from 1985 to 1996, and resurveyed at the IFN3, from 1997 to 2008. The time lag between inventories ranged from 9 to 12 years (see supplementary information: study area). We focused on the 11 most abundant tree species that naturally occur in peninsular Spain, accounting for 81% of the total forest area and distributed over a wide range of geographic, topographic (Table 4.S1A) and climatic gradients (Table 4.S1B). Mean annual temperatures in peninsular Spain increased by more than 1ºC (Table 4.S1B) during the time period between inventories relative to the previous 30 years (see supplementary information: recent temperature trend calculation). Annual precipitation did not show an overall significant trend during the same period, partially due to its large interannual variability (see supplementary information: recent temperature trend calculation).

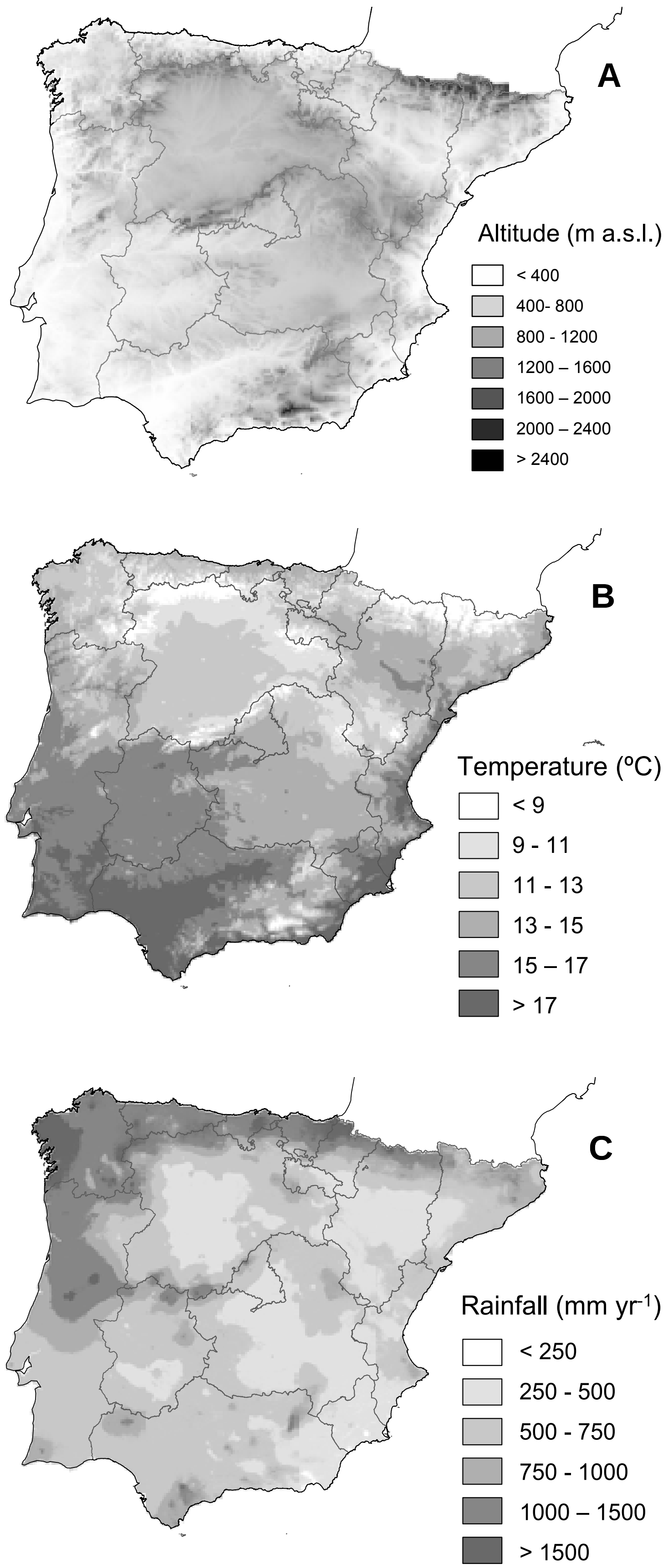

Figure 4.1. Maps of (A) Altitude (m a.s.l.), (B) mean annual temperature (ºC) and (C) annual rainfall (mm/yr) in the Iberian Peninsula.

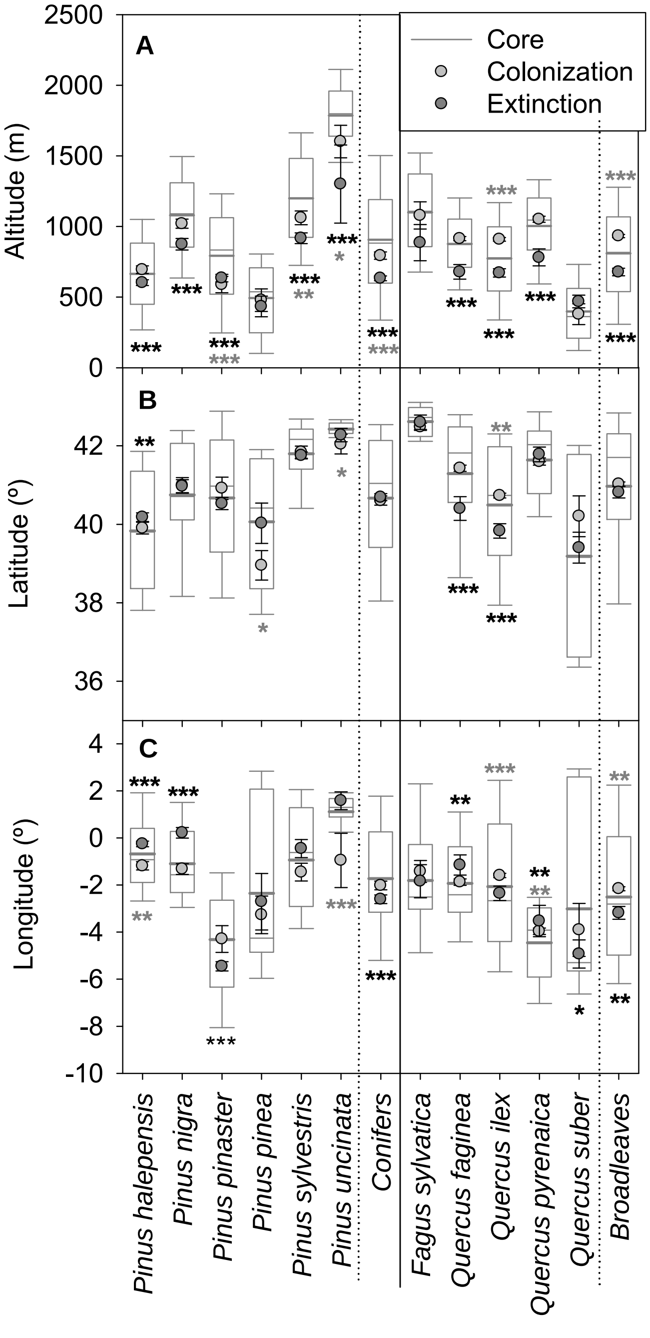

Figure 4.2. Mean ± standard error of geographic variables (A, Altitude (m); B, Latitude (º) and C, Longitude (º)) for plots with colonization occurrence (light grey circles) and those showing extinction occurrence (dark grey circles) for the eleven species studied and for the two groups of species (conifers and broadleaves). The boxplots (indicating the mean, median, quartiles, 5 th and 95th percentiles) characterize the core distribution range of each species or group of species at IFN2 (1985-1996). Each geographic variable was analyzed independently for each species and for conifers and broadleaves. The significance level for each response variable (grey for colonization and black for extinction) is indicated by: ***, p<0.001; **, p< 0.01 and *, p<0.05. Symbols appear above the boxplot when the value for extinction/colonization is higher that the one corresponding to the core distribution, and below when the opposite is true (see text for details).

Table 4.2. Z-values of the GLZ models (binomial error distribution and logit link function) comparing the geographic characteristics (Altitude, Latitude and Longitude) of plots showing: A) Colonization; B) Extinction and C) Demographic growth; and D) Demographic decline with those in the core distribution range (IFN2). Results are separated by species and by species type (conifers and broadleaves). All Z-values showed are significant (p<0.05); n.s., not significant. The number and distribution of plots by levels of the response variable are shown at the bottom of each table.

A) Colonization	*Pinus halepensis*	*Pinus nigra*	*Pinus pinaster*	*Pinus pinea*	*Pinus sylvestris*	*Pinus uncinata*	Conifers	*Fagus sylvatica*	*Quercus faginea*	*Quercus ilex*	*Querucs pyrenaica*	*Quercus suber*	Broadleaves
Altitude	n.s.	n.s.	-3.62	n.s.	-3.32	n.s.	-3.89	n.s.	1.89	10.36	n.s.	n.s.	8.98
Latitude	3.92	n.s.	n.s.	-2.34	n.s.	n.s.	n.s.	n.s.	n.s.	2.62	n.s.	2.98	n.s.
Longitude	-5.06	n.s.	n.s.	n.s.	-2.21	-4.15	n.s.	n.s.	n.s.	2.84	3.03	-2.59	2.48
% plots													
Colonization = 0	98.3	98.6	99.0	99.1	98.8	98.7	98.9	98.5	92.1	92.3	94.5	99.1	94.9
Colonization = 1	1.7	1.4	1.0	0.9	1.2	1.3	1.1	1.5	7.9	7.7	5.5	0.9	5.1
Number of plots	6161	4432	4213	1645	5223	625	18738	1377	2697	8199	2249	1780	15678

B) Extinction	*Pinus halepensis*	*Pinus nigra*	*Pinus pinaster*	*Pinus pinea*	*Pinus sylvestris*	*Pinus uncinata*	Conifers	*Fagus sylvatica*	*Quercus faginea*	*Quercus ilex*	*Querucs pyrenaica*	*Quercus suber*	Broadleaves
Altitude	n.s.	-2.38	-4.62	n.s.	-6.95	-3.55	-11.87	-1.78	-3.85	-3.20	-5.10	n.s.	-4.33
Latitude	n.s.	-3.45	-5.40	n.s.	-3.96	n.s.	n.s.	n.s.	-4.46	-3.91	n.s.	2.47	n.s.
Longitude	3.52	3.34	-4.05	n.s.	n.s.	n.s.	-5.08	n.s.	4.16	n.s.	4.13	-3.48	-2.27
% plots													
Extinction = 0	96.9	98.6	95.6	99.3	98.9	99.2	97.9	99.4	98.2	98.6	98.6	98.5	98.9
Extinction = 1	3.1	1.4	4.4	0.7	1.1	0.8	2.1	0.6	1.8	1.4	1.4	1.5	1.1
Number of plots	6251	4431	4363	1641	5222	622	18924	1364	2528	7677	2156	1790	15043

Table 4.2 (bis).

C) Growth	*Pinus halepensis*	*Pinus nigra*	*Pinus pinaster*	*Pinus pinea*	*Pinus sylvestris*	*Pinus uncinata*	Conifers	*Fagus sylvatica*	*Quercus faginea*	*Quercus ilex*	*Querucs pyrenaica*	*Quercus suber*	Broadleaves
Altitude	-3.30	n.s.	-3.14	2.91	3.56	3.33	4.68	4.38	2.61	10.16	4.64	-2.80	8.26
Latitude	n.s.	8.13	n.s.	n.s.	3.48	n.s.	6.04	-2.45	8.11	10.79	n.s.	2.10	12.72
Longitude	-2.76	-4.17	n.s.	-5.94	n.s.	-2.69	4.52	n.s.	-2.78	8.57	2.19	3.07	11.77
% plots													
Growth = 0	71.9	73.3	81.6	88.4	73.2	67.0	71.0	77.4	70.6	60.4	61.1	88.0	61.9
Growth = 1	28.1	26.7	18.4	11.6	26.8	33.0	29.0	22.6	29.4	39.6	38.9	12.0	38.1
Number of plots	5569	4227	3388	1519	4691	530	16624	1245	2410	7310	1936	1594	13915

D) Decline	*Pinus halepensis*	*Pinus nigra*	*Pinus pinaster*	*Pinus pinea*	*Pinus sylvestris*	*Pinus uncinata*	Conifers	*Fagus sylvatica*	*Quercus faginea*	*Quercus ilex*	*Querucs pyrenaica*	*Quercus suber*	Broadleaves
Altitude	-5.57	-9.91	-6.27	n.s.	n.s.	n.s.	-10.62	n.s.	-3.01	n.s.	-4.13	-2.06	-8.21
Latitude	n.s.	-6.05	n.s.	n.s.	4.97	n.s.	7.34	n.s.	-2.38	n.s.	-3.15	n.s.	7.52
Longitude	n.s.	-11.65	-2.55	3.38	n.s.	-3.55	-13.05	n.s.	n.s.	-4.76	2.88	n.s.	-8.24
% plots													
Decline = 0	85.4	93.8	73.9	91.7	86.6	79.4	83.7	89.0	93.5	92.3	84.3	87.7	88.4
Decline = 1	14.6	6.2	26.1	8.3	13.4	20.6	16.3	11.0	6.5	7.7	15.7	12.3	11.6
Number of plots	4686	3304	3740	1465	3965	447	14109	1083	1819	4783	1403	1598	9736

By comparing the same plots between the two inventories we defined two dichotomous response variables at the level of species and functional groups (conifers and broadleaves): Colonization (plots where the species or group of species were not present at the IFN2 and appeared at the IFN3), and Extinction (plots where a species or group of species disappeared between IFN2 and IFN3; i.e., all adult trees died and there was no regeneration) (see supplementary information: definition of response variables). Binomial generalized linear models were used to compare (separately) plots where colonization or extinction were observed with the remaining plots (the core range where the corresponding species or group of species was present at both the IFN2 and the IFN3) (see supplementary information: statistical analyses), in terms of geographic characteristics (altitude, latitude and longitude), climate (mean annual temperature and amplitude, annual precipitation), recent temperature trend, forest structure (total basal area) and disturbance effects (prior occurrence of wildfire and forest management). Models were fitted by species or functional groups (conifers and broadleaves). To gain a better understanding of the underlying processes we also analyzed demographic changes inside the core distribution range of each species or functional type, defining two additional dichotomous variables: Growth (plots with an increase of more than 10% of the number of trees per hectare between the two surveys) and Decline (plots with a decrease of more than 10%)) (see supplementary information: definition of response variables). We used the same approach as before to compare plots with positive or negative demographic trends (separately) with plots where there was no clear change in abundance (i.e., the number of trees of the corresponding species or functional group remained within 10% of the initial values observed at IFN2.

Results and discussion

Despite the relatively short period of time elapsed between inventories (9-12 years) we detected clear changes in the geographical distribution of tree species and also of functional groups (Fig. 4.2). The geographic patterns were more consistent with trailing range contraction (i.e., extinction) than with leading range expansion (i.e., colonization) (see, for similar patterns, Kelly & Goulden 2008; Breashears 2008; Lenoir *et al.* 2010; Zhu *et al.* 2012). As expected from overall climate change trends (Jump *et al.* 2009), the clearest directional changes were obtained with elevation: eight out of eleven species and the two functional groups exhibited extinction downhill of their distribution while only one species (*Quercus ilex*) and broadleaves in general showed also colonization uphill (Fig. 4.2A). Fewer changes were detected in relation to latitude (Fig. 4.2B). In general, there were no significant differences for temperate species and minor changes were detected for the main Mediterranean conifer species, while extinction occurred predominantly at the southern edge of the range of the two most abundant Mediterranean broadleaf species (*Q. ilex* and *Q. faginea*). No latitudinal changes were detected at the functional group level. Geographic shifts in longitude showed an idiosyncratic pattern for both colonization and extinction, with movement to the west or to the east depending on the species or functional group (Fig. 4.2C). Similar and even more significant geographic patterns were detected when we analyzed demographic changes in tree abundance within the range of each species or functional group (Fig. 4.4) indicating, in the majority of cases, that colonization and extinction were consistent with demographic changes. Most species showed a significant and directional increase of the number of trees uphill and a decrease downhill (Fig 4.4A), while an increase northward was only observed for broadleaves (Fig 4.4B).

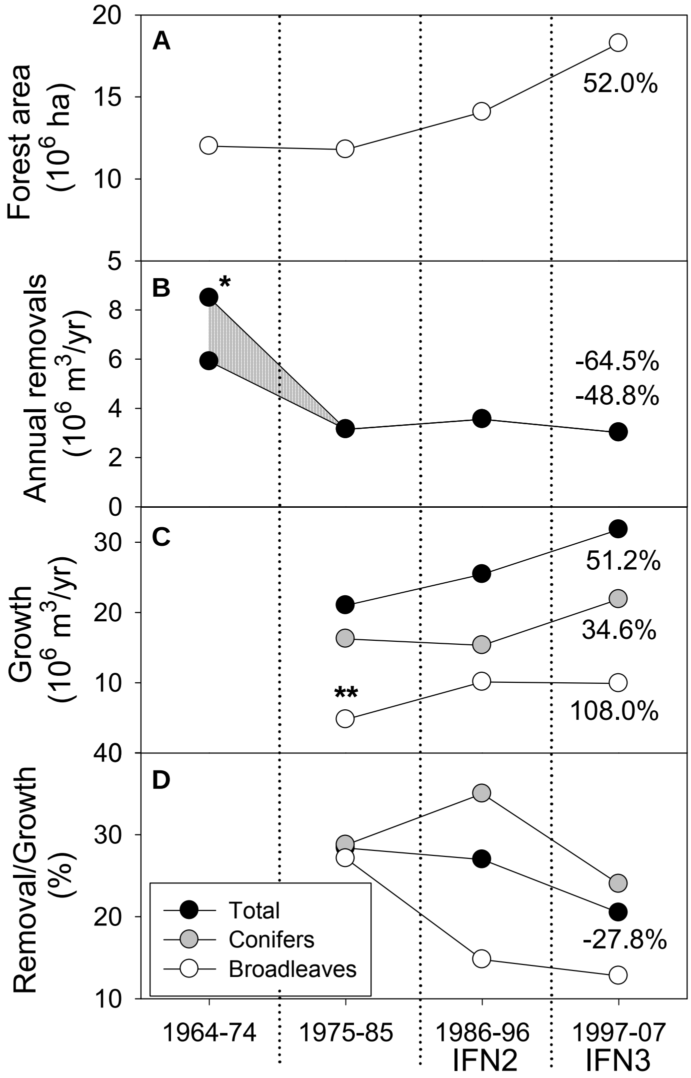

Figure 4.3. Recent changes in key forest characteristics in peninsular Spain, separated by time intervals of approximately 10 years. The panels indicate: A) Forest area (millions of hectares) (sources: INE (2010); Grupo de Estudios de Historia Rural (1999); Ximénez de Embún y Ceballos (1939); Tafunell y Carreras); B) Mean of annual removals of autochthonous species (wood and firewood) (millions m^3/year) (source: Anuarios Estadísticos del Instituto Nacional de Estadística: http://www.ine.es/inebaseweb/libros.do?tntp=25687); C) Mean annual growth of autochthonous species (millions m^3/year) (sources: Ministerio de Agricultura– ICONA. (1975-1985), Ministerio de Agricultura– ICONA. IFN2 (1986-1996) and MARM. IFN3 (1997-2007)); and D) Mean Removal/Growth ratio (%). The values close to each symbol indicate the percent change in relation to the first period. "*", historical series before 1972 were less detailed and several assumptions were required to estimate annual removals for the 1964-1974 period; for this reason, a range is plotted that represents uncertainty between the two extreme values estimated using alternative assumptions. "**", growth of evergreen broadleaves was not available.

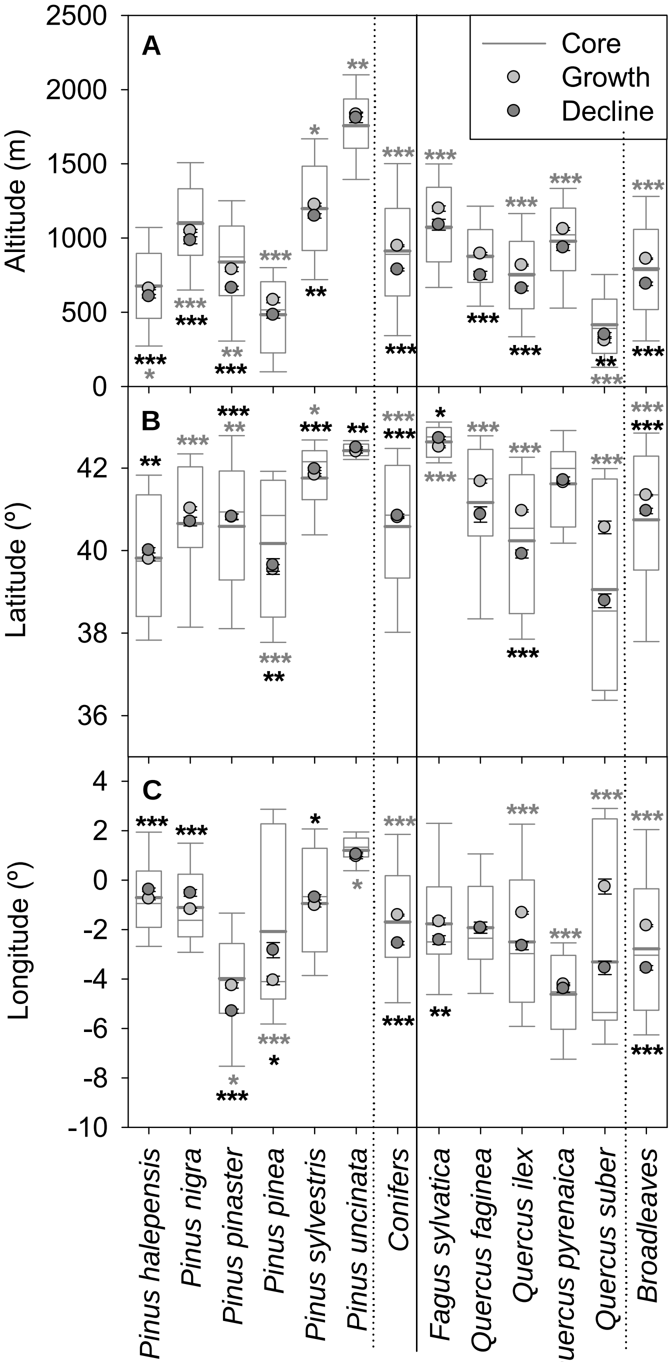

Figure 4.4. Mean ± standard error of geographic variables (A, Altitude (m); B, Latitude (º) and C, Longitude (º)) for plots showing demographic growth (light grey circles) and those showing demographic decline (dark grey circles), for the eleven species studied and for the two groups of species (conifers and broadleaves). The boxplots (indicating the mean, median, quartiles, 5th and 95th percentile) characterize the core distribution range of each species or group of species at IFN2 (1985-1996). Each geographic variable was analyzed independently for each species and for conifers and broadleaves. The significance level for each response variable (grey for colonization and black for extinction) is indicated by: ***, p<0.001; **, p< 0.01 and *, p<0.05. Symbols appear above the boxplot when the value for Growth/Decline is higher that the one corresponding to the core distribution, and below when the opposite is true (see text for details).

Table 4.3. Z-values of the GLZ models (binomial error distribution and logit link function) comparing variables characterizing the climate, competition and disturbance regime of plots showing: A) Colonization; B) Extinction and C) Demographic growth; and D) Demographic decline with those in the core distribution range (IFN2). Results are separated by species and by species type (conifers and broadleaves). All Z-values showed are significant ($p<0.05$); n.s., not significant. The number and distribution of plots by levels of the response variable are shown at the bottom of each table TMP, Mean annual temperature (ºC); PREC, Annual precipitation (mm/yr); TR, Annual temperature range (difference between maximum and minimum annual temperature); TREND_MT, Recent temperature trend (ºC); BA_TOTAL (IFN2), Total basal area at IFN2 (m^2/ha); FIRE (IFN2), wildfire occurrence previous to IFN2 and; MANAG. (IFN2), Occurrence of management practices previous to IFN2.

A) Colonization	*P. halepensis*	*Pinus nigra*	*Pinus pinaster*	*Pinus pinea*	*Pinus sylvestris*	*Pinus uncinata*	Conifers	*F.sylvatica*	*Q. faginea*	*Quercus ilex*	*Q. pyrenaica*	*Quercus suber*	Broadleaves
TMP	n.s.	n.s.	n.s.	n.s.	n.s.	2.17	n.s.	n.s.	-2.49	-10.5	n.s.	n.s.	-10.7
PREC	4.98	n.s.	n.s.	n.s.	n.s.	n.s.	2.36	n.s.	-3.5	-4.33	-3.31	n.s.	-7.5
TR	2.94	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	-2.95	n.s.	n.s.	n.s.
TREND_MT	n.s.	n.s.	-2.48	n.s.	-3.56	n.s.	n.s.	n.s.	n.s.	-2.75	2.497	n.s.	n.s.
BA_TOTAL (IFN2)	-10.3	-7.15	-5.97	-3.79	-7.82	-2.98	-14.2	-2.15	-5.92	-11.3	-4.37	n.s.	-14.3
FIRE (IFN2)	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
MANAG. (IFN2)	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	3.216	4.00
% plots													
Colonization = 0	98.3	98.6	99.0	99.1	98.8	98.7	98.9	98.5	92.1	92.3	94.5	99.1	94.9
Colonization = 1	1.7	1.4	1.0	0.9	1.2	1.3	1.1	1.5	7.9	7.7	5.5	0.9	5.1
Number of plots	6161	4432	4213	1645	5223	625	18738	1377	2697	8199	2249	1780	15678
B) Extinction													
TMP	-3.03	n.s.	5.48	n.s.	6.35	3.48	3.63	2.26	5.54	4.64	n.s.	n.s.	2.52
PREC	n.s.	-2.56	3.89	3.20	n.s.	n.s.	6.07	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
TR	n.s.	n.s.	n.s.	n.s.	2.51	n.s.	n.s.	n.s.	n.s.	3.23	n.s.	n.s.	n.s.
TREND_MT	-3.91	-2.52	n.s.	n.s.	n.s.	n.s.	-4.76	n.s.	-2.06	-4.82	-3.06	n.s.	-2.43
BA_TOTAL (IFN2)	-4.06	-3.44	-4.24	-2.79	n.s.	n.s.	-7.9	n.s.	n.s.	n.s.	n.s.	-2.85	-5.03
FIRE (IFN2)	24.08	13.34	14.24	4.44	11.30	n.s.	32.16	3.94	9.76	17.76	5.36	n.s.	19.1
MANAG. (IFN2)	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	3.48
% plots													
Extinction = 0	96.9	98.6	95.6	99.3	98.9	99.2	97.9	99.4	98.2	98.6	98.6	98.5	98.9
Extinction = 1	3.1	1.4	4.4	0.7	1.1	0.8	2.1	0.6	1.8	1.4	1.4	1.5	1.1
Number of plots	6251	4431	4363	1641	5222	622	18924	1364	2528	7677	2156	1790	15043

Table 4.3 (bis).

C) Growth	*Pinus halepensis*	*Pinus nigra*	*Pinus pinaster*	*Pinus pinea*	*Pinus sylvestris*	*Pinus uncinata*	Conifers	*Fagus sylvatica*	*Quercus faginea*	*Quercus ilex*	*Querucs pyrenaica*	*Quercus suber*	Broadleaves
TMP	n.s.	n.s.	n.s.	n.s.	-6.39	-2.52	-13.41	-3.25	-7.55	-18.45	-4.27	-2.53	-23.89
PREC	-4.82	n.s.	2.56	n.s.	n.s.	n.s.	-3.31	n.s.	-3.79	-2.85	-6.24	-2.88	-14.37
TR	-2.93	-2.08	n.s.	4.92	n.s.	n.s.	-3.65	2.57	-2.21	-7.32	n.s.	n.s.	-6.76
TREND_MT	2.11	4.63	-2.04	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	-2.93	n.s.	-6.13	-7.14
BA_TOTAL (IFN2)	-3.85	-5.83	-5.43	-4.36	-11.82	-4.19	-15.64	-4.87	-5.65	-4.06	-6.05	n.s.	-13.19
FIRE (IFN2)	-2.76	-2.41	n.s.	n.s.	n.s.	n.s.	-3.26	n.s.	n.s.	n.s.	n.s.	3.14	-2.73
MANAG. (IFN2)	2.98	n.s.	n.s.	-3.37	n.s.	n.s.	n.s.	n.s.	n.s.	-3.13	n.s.	n.s.	-2.35
% plots													
Growth = 0	71.9	73.3	81.6	88.4	73.2	67.0	71.0	77.4	70.6	60.4	61.1	88.0	61.9
Growth = 1	28.1	26.7	18.4	11.6	26.8	33.0	29.0	22.6	29.4	39.6	38.9	12.0	38.1
Number of plots	5569	4227	3388	1519	4691	530	16624	1245	2410	7310	1936	1594	13915
D) Decline													
TMP	3.23	12.02	4.78	n.s.	n.s.	n.s.	9.64	n.s.	4.02	3.86	3.55	n.s.	6.04
PREC	n.s.	8.04	n.s.	n.s.	n.s.	n.s.	10.48	n.s.	n.s.	4.79	2.67	n.s.	9.25
TR	n.s.	-4.04	-7.02	n.s.	n.s.	3.72	-5.60	n.s.	n.s.	n.s.	n.s.	n.s.	-3.14
TREND_MT	n.s.	2.31	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	2.28	n.s.	n.s.	2.02
BA_TOTAL (IFN2)	11.88	10.74	7.49	4.04	12.67	2.37	18.79	3.95	2.93	4.63	2.25	2.27	7.17
FIRE (IFN2)	23.86	15.82	9.49	12.72	8.39	n.s.	30.83	2.30	10.30	10.14	9.67	n.s.	18.03
MANAG. (IFN2)	n.s.	n.s.	n.s.	n.s.	-2.80	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	-2.13
% plots													
Decline = 0	85.4	93.8	73.9	91.7	86.6	79.4	83.7	89.0	93.5	92.3	84.3	87.7	88.4
Decline = 1	14.6	6.2	26.1	8.3	13.4	20.6	16.3	11.0	6.5	7.7	15.7	12.3	11.6
Number of plots	4686	3304	3740	1465	3965	447	14109	1083	1819	4783	1403	1598	9736

The results of the statistical analyses carried out for the different drivers considered (Table 4.3A-D) indicate that, independently of the other factors, extinction (eight out of the eleven species, Fig. 4.5A) and demographic decline (seven out of eleven species, Fig. 4.6A) occurred preferentially in warmer areas, while demographic growth occurred mainly in colder areas (seven out of eleven species, Fig 4.6A). This agrees with many evidences that suggest that tree species respond mainly to temperature shifting uphill to escape rising temperatures (Hickling *et al.* 2009; Parmesan 2006; Lenoir *et al.* 2008). However, the patterns with regards to climate were not always consistent. Thus, the fact that for seven out of eleven species extinction occurred preferentially in plots where recent warming has been less acute (Fig. 4.5D) suggests that shifts in altitude may be driving the observed responses to temperature, and not the opposite. Moreover, the three most abundant Mediterranean broadleaf species (*Q. faginea*, *Q. ilex* and *Q. pyrenaica)*, which occupy areas that are supposed to be strongly limited by water availability, appear to be moving to drier areas (Fig 4.5B, 4.6B). Similarly, five out of eleven species are shifting to areas where the temperature range is wider (Fig. 4.5C, 4.6C) and, consequently, the evaporative demand is higher (see the opposite pattern in Crimmins *et al.* 2011).

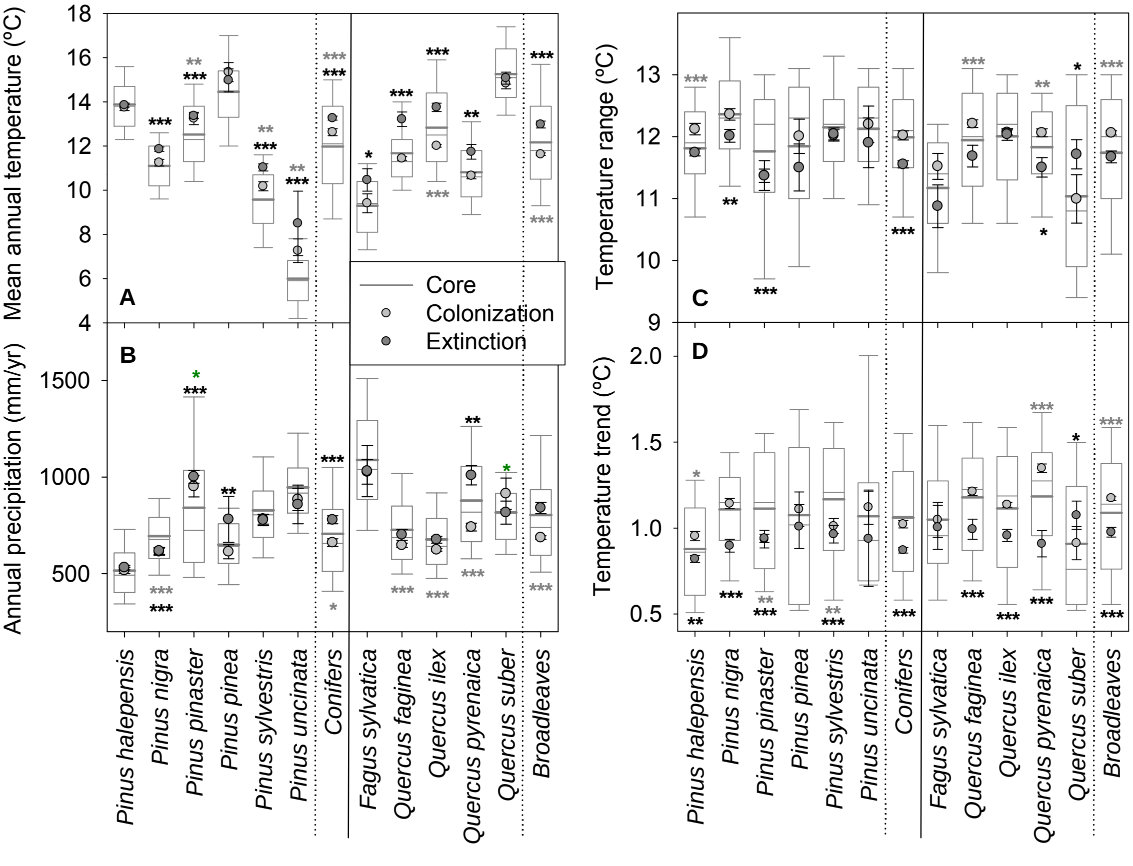

Figure 4.5. Mean ± standard error of geographic variables climatic variables (A, Mean annual temperature (ºC); B, Cumulated annual precipitation (mm/yr); C, Annual temperature range and D, Recent temperature trend (ºC)) for plots showing colonization occurrence (light grey circles) and those showing extinction occurrence (dark grey circles), for the eleven species studied and for the two groups of species (conifers and broadleaves). The boxplots (indicating the mean, median, quartiles, 5th and 95th percentile) characterize the core distribution range of each species or group of species at IFN2 (1985-1996). Each climatic variable was analyzed independently for each species and for conifers and broadleaves. The significance level for each response variable (grey for colonization and black for extinction) is indicated by: ***, p<0.001; **, p< 0.01 and *, p<0.05. Symbols appear above the boxplot when the value for colonization/extinction is higher that the one corresponding to the core distribution, and below when the opposite is true (see text for details).

Our results show that colonization and extinction of species responded much more clearly to drivers related to forest structure (considering total basal area in the plot at the IFN2 as a proxy of competitive interaction), including disturbances, rather than to climate. Indeed, ten out of the eleven species showed a strong negative effect of total basal area on colonization (Table 4.3A), indicating that low competition for resources was almost always the primary driver of colonization. On the other hand, wildfire occurrence showed the strongest (and positive) effect on extinction in ten out of the eleven species (Table 4.3B), confirming that wildfires are almost always the main cause of local extinction of tree species in Mediterranean areas, affecting specially conifer species (Retana *et al.* 2002; Rodrigo *et al.* 2004, 2007). In short, some of counterintuitive geographic shifts observed could be better explained as a consequence of changes in management practices in the past (at least three decades ago), so that the majority of species undergoing recent range shifts may not be at demographic equilibrium with climatic conditions (Channel & Lomolino 2000; Angert *et al.* 2011).

Strong land and habitat changes have occurred in Spain in the last four decades (Fig. 4.3), similar to those occurred in the majority of European countries (Nabuurs *et al.* 2003; Ciais *et al.* 2008) and in general in the northern hemisphere (Pan *et al.* 2011). In Spain there has been a strong increment of forest area (ca. 6.5 million has, with an increment of 52% since the 1964-1974 decade) (Fig. 4.3A). This is mainly related to the massive rural exodus and the intensification of agricultural exploitations, with the consequent abandonment of marginal croplands and the increment of tree regeneration due to natural forest dynamics but also due to large-scale reforestation programs (polítiques de Aforestació de Terres Agraries, Afforestation of Agricultural Land Policy–PAC) (SEFC 2010). In addition, annual removals of wood and firewood from forests decreased strongly between 1964-1974 and 1975-1985 (49%-65% decrease depending on the assumptions considered [cita a material i mètodes]), mainly due to a generalized substitution of firewood by fossil fuels, and has remained almost constant from 1975-1985 onwards (Figure 4.3B). This relatively low and constant level of forest management over the last decades explains why recent forest management (previous to IFN2) showed almost no significant effect on colonization, extinction or demographic trends in the studied species (Tables 4.3A–4.3D).

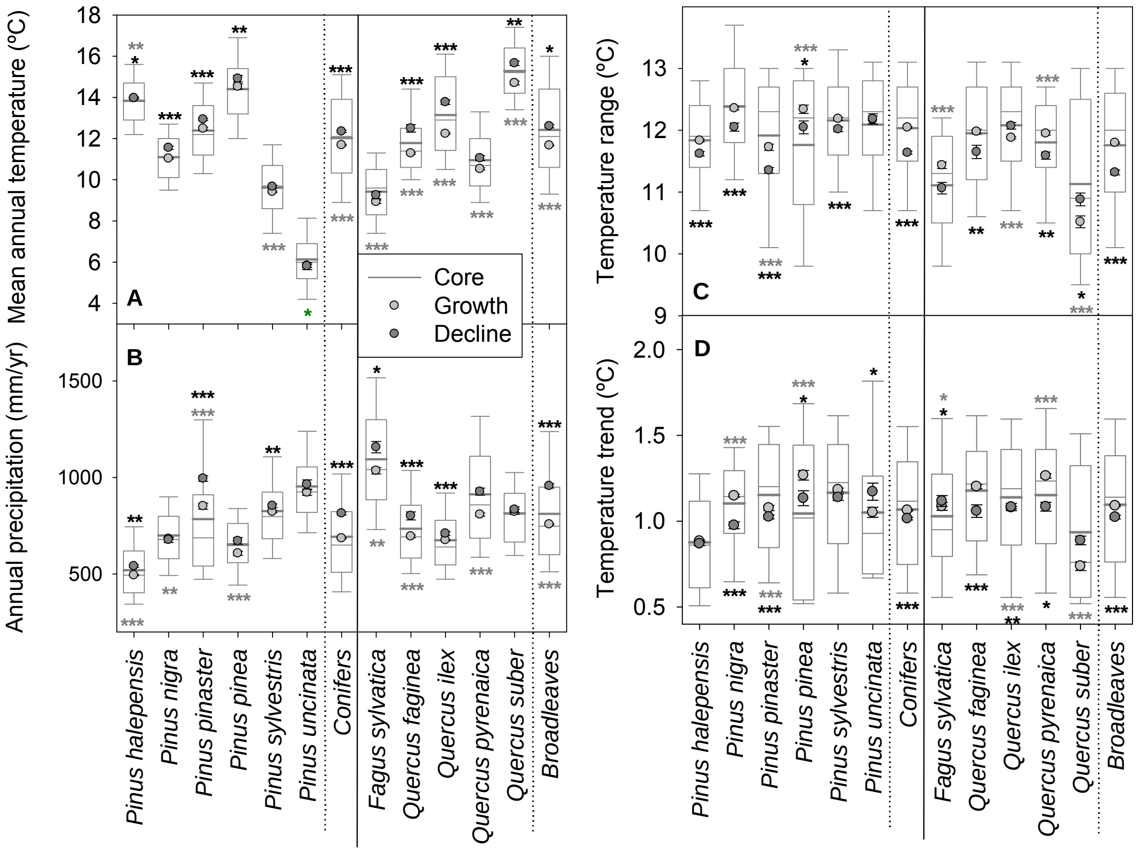

Figure 4.6. Mean ± standard error of geographic variables climatic variables (A, Mean annual temperature (ºC); B, Cumulated annual precipitation (mm/yr); C, Annual temperature range and D, Recent temperature trend (ºC)) for plots showing demographic growth (light grey circles) and those showing demographic decline (dark grey circles), for the eleven species studied and for the two groups of species (conifers and broadleaves). The boxplots (indicating the mean, median, quartiles, 5^{th} and 95^{th} percentile) characterize the core distribution range of each species or group of species at IFN2 (1985-1996). Each climatic variable was analyzed independently for each species and for conifers and broadleaves. The significance level for each response variable (grey for colonization and black for extinction) is indicated by: ***, p<0.001; **, p< 0.01 and *, p<0.05. Symbols appear above the boxplot when the value for growth/decline is higher that the one corresponding to the core distribution, and below when the opposite is true (see text for details).

The recent changes occurred in forests of peninsular Spain do not only imply geographical shifts of species but also significant changes in forest tree composition, with a large and generalized increase of broadleaves, particularly at intermediate and high altitudes, and a significant decrease of conifers at low to intermediate altitudes (Fig. 4.7A). Overall, for every two plots showing extinction of conifers, only one plot experimented colonization by a conifer species. On the other hand, for every plot experimenting extinction of broadleaves, five plots showed colonization by a broadleaf species (Table 4.2). For conifers no clear patterns were obtained with latitude and longitude, while broadleaves showed higher values of colonization than of extinction in the whole range of these geographic gradients (Fig. 4.7B and 4.7C and Fig. 4.8A-C). Interestingly, in many parts of these ranges (Fig. 4.8), the net increase in tree density of broadleaves was considerably higher than the net decline in conifer density, indicating that broadleaves were also colonizing areas without trees. Overall, and consistently with the observed patterns with altitude (Fig. 4.7), conifers showed a reduction in their distribution in warmer areas, whereas there was no net change at cooler sites (Fig. 4.5A and 4.9), leading to a general decline with a slight lean (a mixture of lean and crash distributional changes according to Breashears et al. 2008). On the other hand, the pattern for broadleaves was a generalized increase, particularly towards uphill, colder areas (Fig. 4.5A and 4.9) (a march distributional change in the sense of Breashears *et al.* 2008).

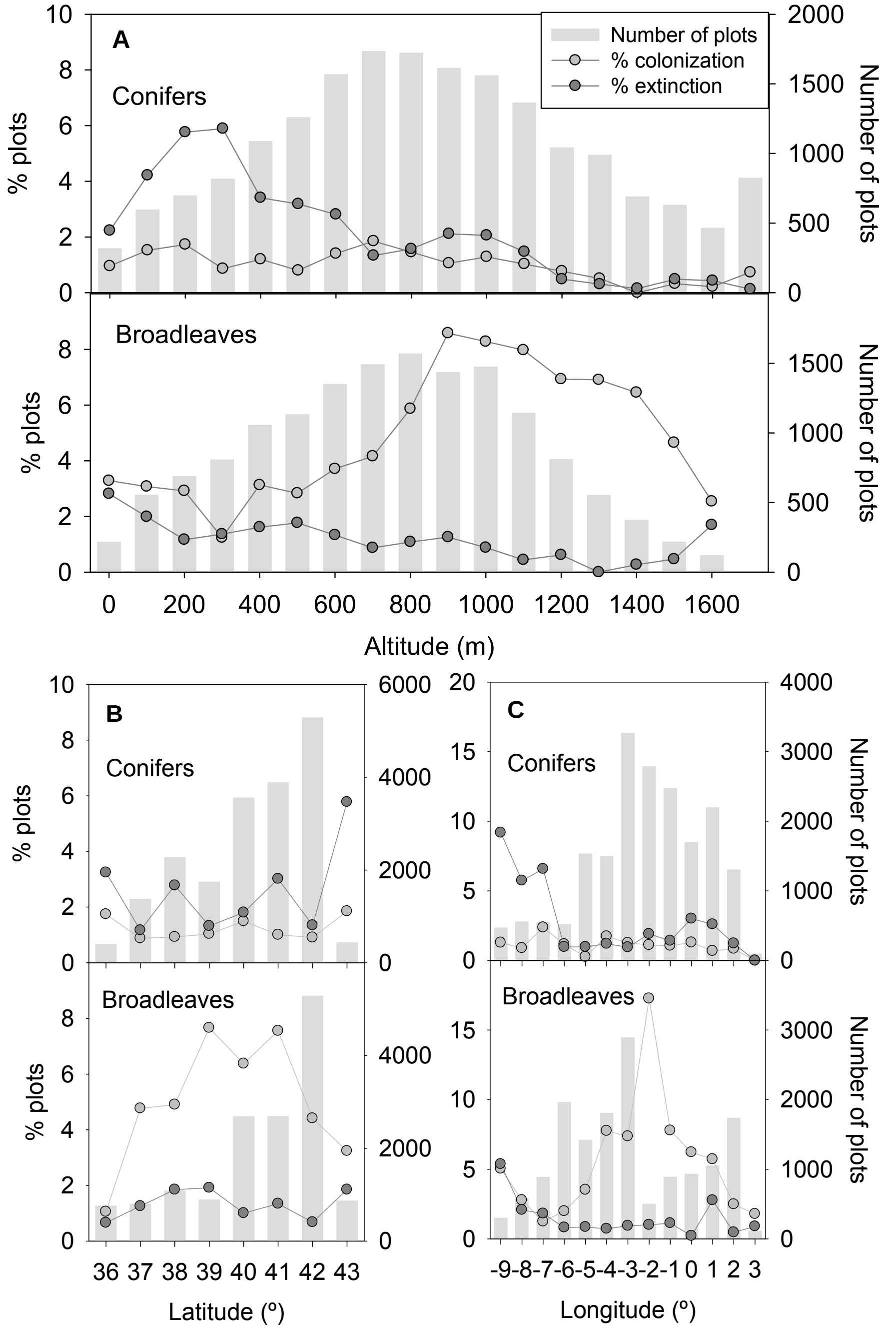

Figure 4.7. Percent plots, lines (left axis), showing colonization (light grey circles) and extinction (dark grey circles) in relation to the number of plots of the corresponding forest type (conifers or broadleaves), grey bars (right axis), in each range of: A) Altitude (m); B) Latitude (°) and C) Longitude.

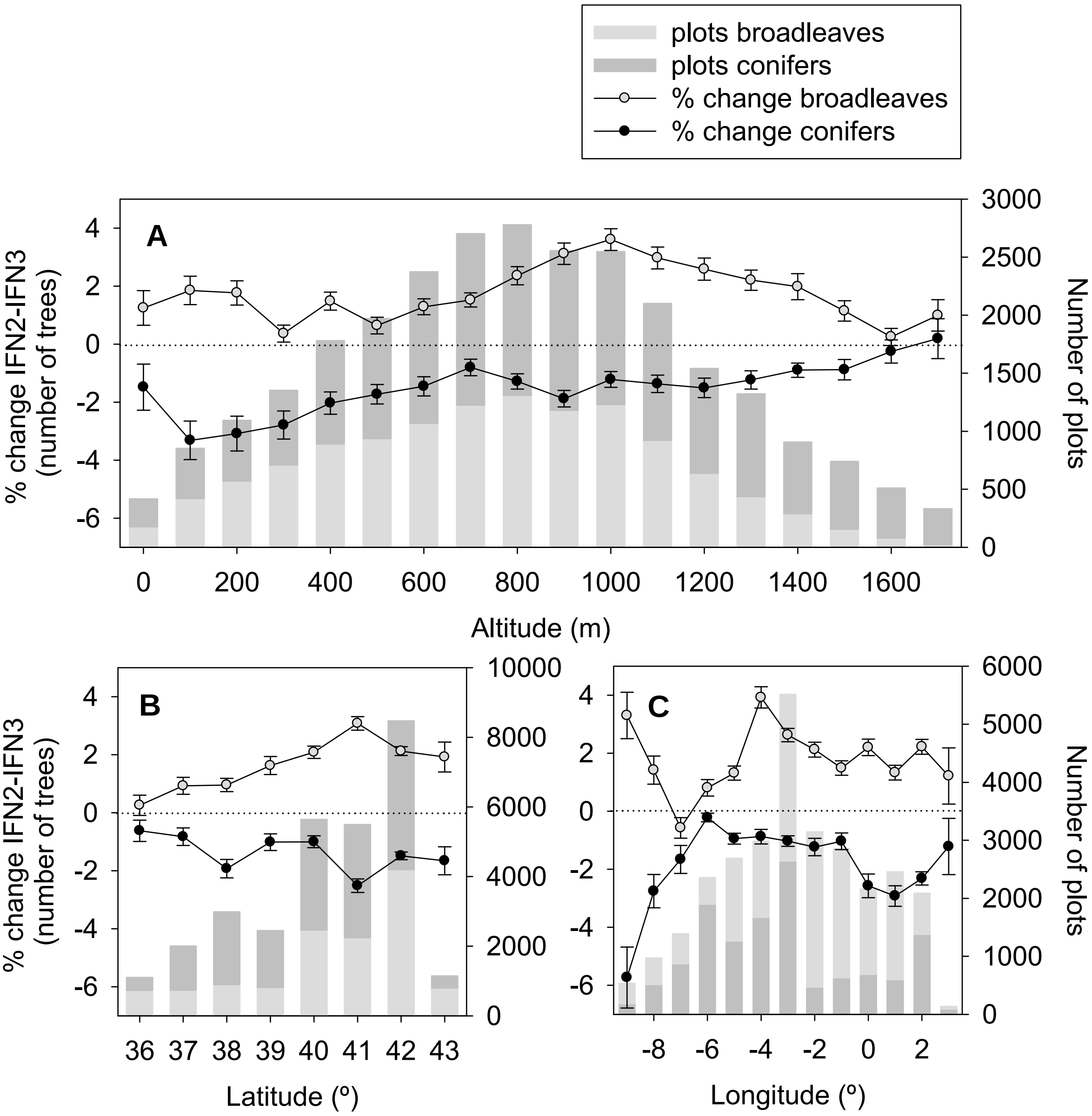

Figure 4.8. Average ± standard error of the relative difference (%) in the number of trees per hectare between IFN3 (1997-2008) and IFN2 (1985-1996) in relation to geographic variables (A, Altitude (m); B, Latitude (º) and C, Longitude (º)), grouping by functional type: autochthonous broadleaves (light grey circles) and conifers (black circles). Each mean value was calculated using all plots that belong to the corresponding geographic range (left axis). Stacked bars show the number of plots in each geographic range (right axis); bars are dark grey for conifers and light grey for broadleaves.

Three main reasons could explain the increase of broadleaves over conifers. The first would be determined by the significant socioeconomic change occurred in the 70's in the region, when the annual removal of autochthonous species decreased drastically (Fig 4.3B). Moreover, this significant reduction of firewood affected much more intensely broadleaf than conifer species (Fig. 4.3D). The second reason relates to several ecological traits that favor colonization by broadleaves (Table 4.1). Thus in broadleaves, long-distance, seed dispersal mediated by animals facilitates the colonization of distant areas (Montoya *et al.* 2008). Moreover, the exclusive capacity of broadleaf species to resprout after disturbances (e.g., after wildfire or thinning) gives them higher capacity for a rapid recovery after disturbance. The third reason relates to the changes occurred in these forests due to the progressive densification and the consequent increase of competition for resources (Fig. 4.3B–4.3D). This has leaded to an increase of forest canopy cover with the consequent stronger competitive interactions among coexisting species that favor a progressive replacement of shade-intolerant conifers by shade-tolerant broadleaves (Table 4.1).

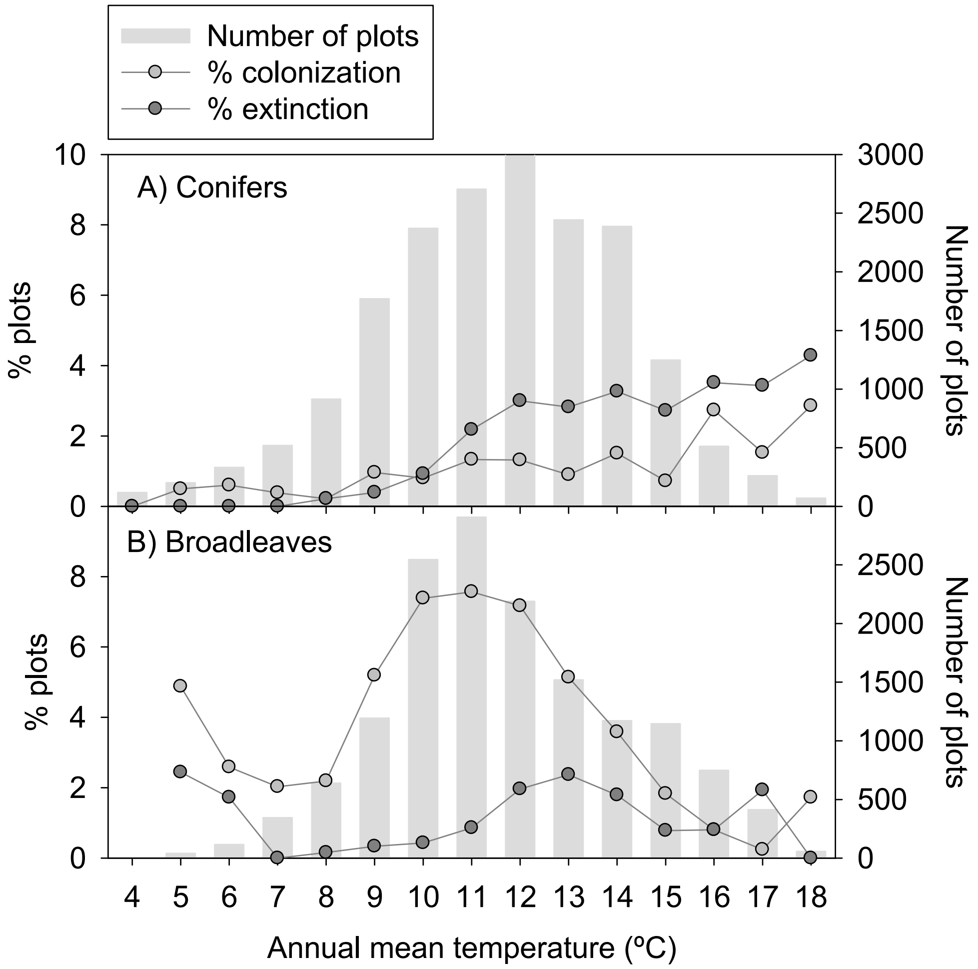

Figure 4.9. Percent plots, lines (left axis), showing colonization (light grey circles) and extinction (dark grey circles) in relation to the number of plots of the corresponding forest type, grey bars (right axis), in each annual mean temperature range: A) Conifers and B) Broadleaves.

Conclusions

The recent shift from conifers to broadleaves may have important consequences on ecosystem functioning and the services provided by forests. For instance, extensive plot-level data from the Spanish national forest inventory (Vayreda *et al.* 2012, in press) shows that broadleaves store 38% more carbon per hectare than conifers, although the overall carbon fixing capacity (per ha) of the two forest types is similar. Functional differences between conifers and broadleaves, including higher hydraulic efficiency and photosynthetic capacity in the latter (Reich *et al.* 2003) likely explain the greater competitive ability of broadleaves in fertile sites (Lusk *et al.* 2003) and may allow them to increase their dominance wherever abiotic stress factors remain within acceptable limits. At the same time, however, conifers tend to have a higher ability to withstand extreme abiotic stress (Table 4.1), which explains why they tend to dominate more extreme habitats (alpine, nutrient-poor soils…) (Ellenberg 1988; Richardson *et al.* 1998; Coomes *et al.* 2005). Given that conifers are also generally considered to be more resistant to drought stress and to operate with wider hydraulic safety margins (Hacke *et al.* 2001; Maherali *et al.* 2004), these factors are likely to become increasingly relevant in the context of climate change, as drought stress and the frequency and intensity of extreme climatic events are projected to increase worldwide (IPCC 2007). In the particular case of Mediterranean forests, with the large decline in water availability projected in virtually all climate scenarios (EEA 2008), it remains to be seen whether the new climatic conditions will oppose to the current trend of broadleaves' expansion resulting from recent changes in forest management. In that context, the current trend towards increased dominance of shade-tolerant, relatively drought sensitive broadleaves may result in a long-term reduction of ecosystem resilience in the region.

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Supplementary information

Study area

The studied area comprises the forested areas of Spain excluding the Canary and Balearic Islands (ca. 18.4 million ha or 37.3% of the total land area of peninsular Spain; MARM 2007a), located between 9º 2’W and 3º 2’E and 36º 0’N and 43º 5’N). 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 N of the area, and is characterized to be relatively wet and cold (wet Spain, with mean temperature of 12.7ºC and annual precipitation of 1500 mm). The rest of Spain falls within the Mediterranean climate, which is characterized by mild winters and hot and dry summers (dry Spain, with mean temperature of 15.3 ºC and annual precipitation of 650 mm). Mean annual temperature and annual precipitation in forest areas in Spain are highly variable in space, ranging from 4 to 18ºC (Fig. 4.1B) and from 200 to 2500 mm (Fig. 4.1C), respectively, due to topographic gradients of orography and continentality.

We excluded from the analyses forest plantations (e.g., *Eucalytus globulus*, *Quercus rubra*, *Pinus radiata*, *Picea abies*, *Pseudotsuga menziesii*…), open woodlands (i.e., dehesas) and plots that had experienced disturbances (wildfire or management practices) during the time period between surveys. Overall the total number of resurveyed plots used in this study was 32,926. The set of species considered was distributed in a wide range of geographic, topographic (Fig 4.1A) and climatic gradients (Fig. 4.1B ans 4.1C), and also showed a wide range of ecological requirements (Table 4.S1).

Definition of response variables

By comparing the same plots between the two inventories we defined two dichotomous response variables at the species and groups of species (conifers and broadleaves) levels. Firstly, we compared plots were colonization had occurred (colonization=1) with plots where adult individuals (diameter at breast height, DBH, ≥ 7.5 cm) of the corresponding species or group of species were already present at IFN2 (colonization=0). According to the definition used here, colonization occurred whenever a new species or group of species appeared in a plot; that is, no adult tree was observed at the IFN2 and at least one was reported at the IFN3 sampling. Secondly, we compared plots were a species or group of species had gone extinct (extinction=1) with plots where there were no changes (extinction=0 and colonization=0). Analogous to colonization, extinction occurred when a species or group of species disappeared from a given plot (i.e., all adult trees died between IFN2 and IFN3). To a better understanding of the underlying processes we also analyze changes in demographic patterns at shorter time scales inside their current range distribution defining two additional dichotomous variables: Growth, when there was an increase of more than 10% in the number of trees per hectare between the two surveys (Growth= 1) and Decline, where there was a decrease of more than 10% (Decline=1). Both were compared with plots where tree density remained approximately unchanged (within 10% of the initial value). In both cases plots with colonization and extinction were excluded.

Recent temperature trend calculation

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 recent climatic trends occurred during the time interval between the two inventories. The first data set was obtained from the Digital Climatic Atlas of the Iberian Peninsula (Ninyerola *et al*. 2005), a collection of digital maps at 200x200 m resolution with average annual and monthly data for total rainfall and maximum, mean and minimum temperatures (period 1950–1999). Based on the geographic coordinates of the IFN3 plots we determined the values of temperature and rainfall at each plot.

The second data source consisted of monthly temperature and precipitation per year with a spatial resolution of 0.5x0.5 degree of latitude/longitude grid (201 cells in Peninsular Spain). This information was downloaded from http://climate.geog.udel.edu/~climate (Center for Climatic Research, Department of Geography, University of Delaware; Matsuura & Willmott 2009). This data source allowed us to obtain the climatic trends in temperature and precipitation. Yearly averages were computed using monthly values from March to August each year; that is, with a month ahead in relation to the mean growing season of the vegetation in the Iberian Peninsula (Orshan 1989). An absolute temperature trend was defined as the difference between the mean value of temperature for the study period and the mean value for a reference period. The study period comprised the years between the two surveys plus two extra years before the IFN2 sampling to include lagged climatic effects on growth and mortality. The reference period corresponded to the 30 years before the IFN2 sampling. Absolute (March-August) temperature trends across the Iberian Peninsula ranged from -0.15 ºC to 2ºC (Table 4.S1B), with an average increment of +1 ºC. Recent precipitation trends were not included in the final models because the number of grid cells showing significant trends was < 5%.

Statistical analyses

We used generalized linear models (GLZ) with a binomial distribution and a logit link function to model the four dichotomous variables as a function of altitude, latitude and longitude (geographic distribution shifts), mean annual temperature (ºC), annual precipitation (mm/year), temperature range (difference between maximum and minimum annual temperature), recent temperature trend (i.e., warming), total basal area at the IFN2 (as a measure of competitive interaction), wildfire and management occurrence previous to the IFN2, the two last variables as measures of the effect of previous disturbances on forest dynamics. Models were separated by species or groups of species. The statistical analyses were performed individually for each explanatory variable (Fig. 4.2, 4.4 and 4.5) and in two multi-variable analyses (tables 4.2 and 4.3), one including the three geographic variables and the other one including all variables associated with drivers of change (climate, warming, competition and disturbance).

Table S4.1. Mean, range (5th - 95th percentile) and sample size (number of plots) for each species and group of species for all the continuous explanatory variables considered in the study. A) Geographic variables; B) Climate variables, recent temperature trend and total basal area.

A)	Altitude (m)		Latitude (°)		Longitude (°)		Size
	Mean	(p5%–p95%)	Mean	(p5%–p95%)	Mean	(p5%–p95%)	
Pinus halepensis	665	(180–1160)	39.8	(37.4–42.1)	-0.7	(-3.3–2.2)	6251
Pinus nigra	1080	(530–1602)	40.8	(37.9–42.6)	-1.1	(-4.1–1.9)	4431
Pinus pinaster	793	(152–1335)	40.7	(37.2–43.2)	-4.3	(-8.5–0.0)	4363
Pinus pinea	494	(54–873)	40.1	(37.1–42.0)	-2.4	(-6.7–3.0)	1641
Pinus sylvestris	1200	(617–1762)	41.8	(40.2–42.8)	-0.9	(-5.3–2.2)	5222
Pinus uncinata	1786	(1292–2165)	42.4	(42.2–42.7)	1.1	(-0.5–2.1)	622
Conifers	**907**	**(206–1664)**	**40.7**	**(37.5–42.8)**	**-1.7**	**(-7.2–2.2)**	**18924**
Fagus sylvatica	1100	(512–1601)	42.6	(42.0–43.1)	-1.8	(-5.0–2.4)	1364
Quercus faginea	876	(402–1358)	41.3	(38.2–42.9)	-1.9	(-5.0–2.1)	2528
Quercus ilex	774	(254–1349)	40.5	(37.6–42.6)	-2.1	(-6.1–2.6)	7677
Quercus pyrenaica	1003	(226–1420)	41.6	(40.1–42.9)	-4.5	(-7.5–2.7)	2156
Quercus suber	397	(84–824)	39.2	(36.3–42.4)	-3.0	(-7.1–3.0)	1790
Broadleaves	**809**	**(213–1443)**	**41.0**	**(37.3–43.0)**	**-2.5**	**(-7.2–2.5)**	**15043**

B)	Temperature (ºC)		Precipitation (mm)		TR (ºC)		Temperature trend (ºC)		Basal area (m^2/ha)		Size
	Mean	(p5%–p95%)	Mean	(p5%–p95%)	Mean	(p5%–p95%)	Mean	(p5%–p95%)	Mean	(p5%–p95%)	
Pinus halepensis	13.9	(11.9–16.2)	516	(310–809)	11.8	(10.2–13.1)	0.88	(0.48–1.41)	8.1	(0.8–21.7)	6251
Pinus nigra	11.1	(9.2–13.0)	695	(449–968)	12.4	(10.8–14.1)	1.11	(0.61–1.60)	12.9	(1.2–32.5)	4431
Pinus pinaster	12.5	(9.9–15.4)	841	(441–1581)	11.8	(9.1–13.2)	1.11	(0.52–1.65)	15.5	(1.3–39.2)	4363
Pinus pinea	14.5	(11.7–17.8)	650	(419–886)	11.8	(9.5–13.3)	1.08	(0.48–1.80)	12.1	(1.4–27.9)	1641
Pinus sylvestris	9.6	(6.8–12.2)	828	(525–1258)	12.1	(10.8–13.7)	1.17	(0.55–1.69)	18.0	(2.1–41.7)	5222
Pinus uncinata	6.0	(4.0–08.5)	946	(656–1346)	12.1	(10.3–13.3)	1.07	(0.58–2.00)	22.7	(3.1–45.3)	622
Conifers	12.0	(7.6–15.8)	706	(366–1280)	12.0	(10.0–13.5)	1.06	(0.51–1.65)	12.9	(1.1–35.2)	18924
Fagus sylvatica	9.3	(6.9–11.9)	1088	(633–1600)	11.2	(9.6–12.5)	1.05	(0.47–1.69)	21.7	(3.2–44.2)	1364
Quercus faginea	11.7	(9.2–14.9)	727	(472–1099)	11.9	(10.4–13.6)	1.18	(0.61–1.68)	10.2	(1.0–32.1)	2528
Quercus ilex	12.8	(9.9–16.1)	677	(422–997)	12.0	(10.2–13.4)	1.11	(0.51–1.67)	8.4	(0.8–28.1)	7677
Quercus pyrenaica	10.8	(8.4–14.5)	878	(540–1351)	11.8	(10.0–13.0)	1.18	(0.46–1.69)	13.0	(1.0–37.4)	2156
Quercus suber	15.3	(12.8–17.8)	817	(554–1146)	11.0	(8.9–13.1)	0.91	(0.52–1.65)	12.3	(1.3–28.2)	1790
Broadleaves	12.2	(8.4–16.1)	804	(449–1385)	11.7	(9.7–13.3)	1.09	(0.48–1.69)	10.9	(0.9–32.7)	15043

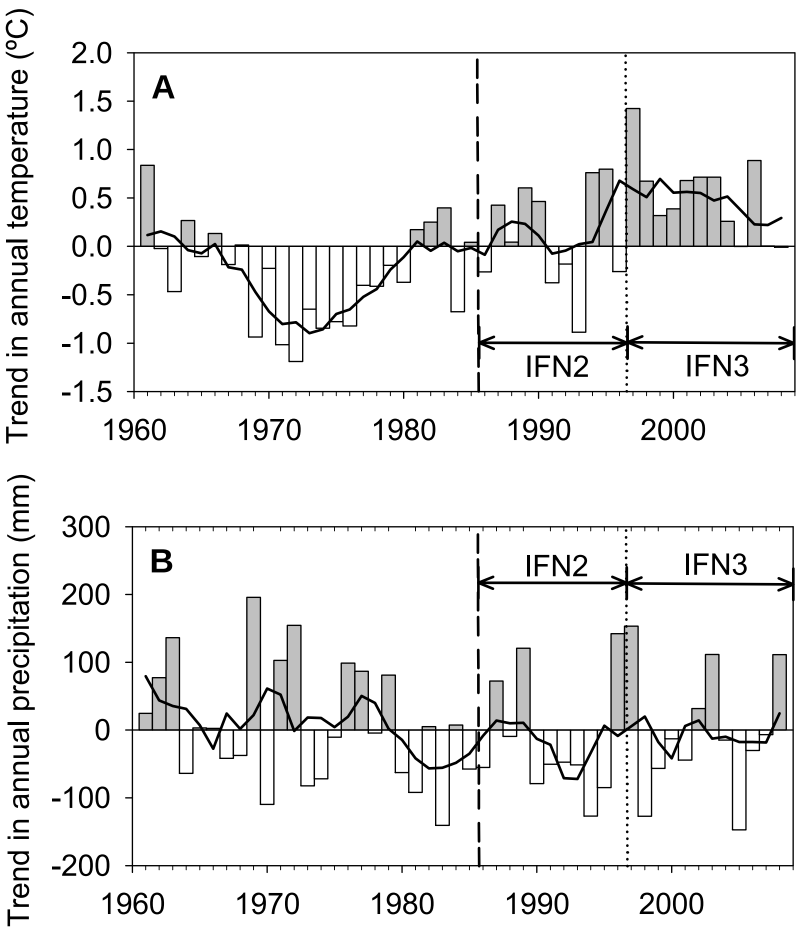

Figure 4.S1. Climatic trend, averaged for all peninsular Spain, from 1961 to 2008 using the overall mean for the whole period as baseline for (A) mean annual temperature (ºC) and (B) annual precipitation (mm/yr). Grey bars indicate positive anomalies, whereas white bars correspond to negative ones. The solid curve is the smoothed average using a 5-year window. The vertical lines split between the time interval previous to forest inventory surveys (1961-1984), the IFN2 period (1985-1996) and the IFN3 period (1997-2008). Climatic series were obtained from the Spanish meteorological agency (AEMET, Agencia Española de Meteorología), and are the mean of 190 meteorological stations for temperature and mean of 612 stations for annual precipitation.

Conclusions generals

Conclusions generals

En aquesta tesi s'ha analitzat l'impacte recent del canvi global sobre els boscos de l'Espanya peninsular per mitjà del segon i tercer inventaris forestals nacionals en dos aspectes particularment rellevants per les enormes implicacions que poden tenir en quant a l'alteració de les funcions i els serveis ecosistèmics dels boscos. D'una banda s'han analitzat els efectes sobre els estocs i els canvis en els estocs de C i per tant en la capacitat d'embornal de C dels boscos i, de l'altra, s'han abordat des del punt de vista dels canvis demogràfics en relació a les diferents estratègies de regeneració i de supervivència de les diferents espècies o grups funcionals, per determinar canvis en la composició dels boscos i en la distribució geogràfica a escala regional.

Capítol 1: Estocs de C

1.1. Els boscos de l'Espanya peninsular tenen un estoc mitjà de carboni (C) en la biomassa viva (arbres + sotabosc, part aèria + subterrània) de 45.1 Mg C/ha i un estoc de C absolut de 621 Tg C (el 7.8% del C acumulat als boscos Europeus). El patró espacial de l'estoc mitjà segueix un gradient nord-sud de major a menor acumulació de C. El sotabosc representa un gens negligible 11.9% del C total, essent encara més elevat als boscos Mediterranis.

1.2. L'efecte de les variables climàtiques sobre l'estoc de C arbori és principalment indirecte a través de la riquesa estructural (nombre de classes diamètriques). Quan es consideren totes les variables predictores a la vegada la seva capacitat predictiva directa es redueix fins a no tenir pràcticament cap efecte en les coníferes. Per contra, els factors locals (característiques del lloc i les pertorbacions) tenen un major efecte en aquest grup.

1.3. La riquesa estructural és el principal predictor de l'estoc de C arbori, amb els valors més alts en els boscos amb més riquesa estructural. Aquest resultat indica que quan els arbres ocupen diferents estrats verticals i horitzontals, poden maximitzar l'ús dels recursos, mentre que una estructura homogènia redueix significativament els efectes de complementarietat. Aquests resultats suggereixen que una gestió forestal que porti el bosc a una estructura de bosc irregular (*uneven-aged*) i madur (conservant els arbres més grossos) és preferible per aconseguir una major acumulació de C.

Capìtol 2: Canvis en els estocs de C

2.1. Els boscos de l'Espanya peninsular no explotats recentment (període entre inventaris) han estat acumulant carboni entre el 1990 i el 2000 a una taxa d'aproximadament 1.4 Mg C ha^{-1} any^{-1}, valor semblant al dels boscos Europeus. No és clar si aquesta taxa podrà persistir durant molt de temps tenint en compte que ja hem començat a observar canvis en la capacitat d'embornal com a conseqüència de l'escalfament i la gestió forestal recents.

2.2. L'estoc de C i la densitat de peus (variables estructurals) són les principals variables determinants del creixement i de la capacitat d'embornal de C dels boscos. La interacció positiva entre totes dues variables indica que, donat que els boscos encara són joves i estan lluny de la seva màxima capacitat d'estoc, tenen un elevat potencial d'acumulació de C que, probablement, podria mantenir-se almenys a curt i mitjà termini. Ara bé, l'escalfament recent ha reduït la taxa de creixement i d'acumulació de C, especialment de les zones del nord més humides dominades per espècies eurosiberianes situades al límit sud de la seva àrea de distribució. Per contra, a les zones seques del sud –amb espècies mediterrànies presumiblement més adaptades a suportar llargs períodes de sequera– l'escalfament a penes ha tingut cap efecte.

2.3. L'efecte negatiu de l'escalfament sobre el creixement i la capacitat d'embornal de C desapareix quan es consideren només els boscos gestionats. Aquest resultat destaca el possible paper de la gestió per ajudar mitigar l'efecte del canvi climàtic. No obstant, donat que l'efecte de la gestió en alguns casos ha estat molt dèbil i, en alguns casos fins i tot no significatiu, ens assenyala que cal més recerca per aprofundir en els seus efectes.

Capítol 3: Reclutament

3.1. L'abundància mitjana de plançons (peus de 2.5 a 7.5 cm de DN) de planifolis és quatre vegades superior a la de les coníferes mentre que el reclutament (*ingrowth*) d'arbres adults (DN ≥ 7.5 cm) és el doble. Aquests valors més alts de reclutament de planifolis es pot atribuir a la seva major habilitat per mantenir un banc de plançons al sotabosc durant més temps degut a la seva major tolerància a l'ombra.

3.2. L'estructura del bosc (densitat de peus de l'espècie i àrea basal total) és el factor que més determina l'abundància de plançons i del reclutament, tant en coníferes com en planifolis, mentre que les pertorbacions (foc, gestió forestal i herbivoria), el clima (temperatura i disponibilitat hídrica) tenen un efecte directe menor, i no s'han trobat efectes detectables de l'escalfament recent.

3.3. L'avantatge que suposadament s'ha atribuït a les coníferes d'una millor resposta en condicions de baixa competència, assumida per la seva baixa tolerància a l'ombra i major capacitat de colonització, queda en entredit ja que la seva taxa de reclutament sempre es manté per sota de la dels planifolis. Aquesta resposta diferencial al tancament de les capçades suggereix que en el futur hi haurà un augment dels planifolis en detriment de les coníferes. Aquesta transició podria produir-se més ràpidament en els llocs amb major productivitat perquè el tancament de capçades es produiria més ràpidament. En el futur serà molt útil combinar informació d'inventaris forestals amb models demogràfics en boscos mixtos que incorporin el reclutament i que siguin espacialment explícits per fer prediccions de les tendències futures dels boscos.

Capítol 4: Canvis en la distribució de les espècies

4.1. Moltes espècies arbòries de la Península Ibèrica s'han mogut muntanya amunt cap a ambients més frescos. Els canvis més rellevants s'han produït sobretot com a conseqüència de l'extinció a baixa altitud més que no per colonització muntanya amunt. No obstant, els boscos no només estan responent a factors climàtics sinó a un tot un conjunt de factors de canvi i d’interaccions. De fet la majoria de patrons observats, inclosos alguns canvis geogràfics contraintuitius, es poden explicar per factors de canvi que tenen a veure sobretot amb canvis en l’estructura del bosc i com a conseqüència de pertorbacions (p.e., focs) .

4.2. S’ha observat una ràpida expansió dels planifolis en detriment de les coníferes, que es pot atribuir majoritàriament als canvis en la gestió forestal (i.e., l’abandonament de les pràctiques forestals) i a les pertorbacions, que durant les darreres dècades han estat molt significatius. És probable que la major habilitat dels planifolis per fer front a factors biòtics de canvi com ara la major capacitat de competència pels recursos sigui un factor molt determinant per explicar aquest canvi. Tenint en compte que com projecten els models climàtics les condicions d’aridesa augmentaran en el futur, no és gens clar que aquesta tendència pugui continuar durant molt més temps. Les coníferes, atesa la seva major capacitat per fer front a condicions climàtiques més extremes, podrien jugar un paper molt rellevant en el futur.