Avaluació regional de la dinàmica recent de l'ecotò bosc subalpí-prats alpins als Pirineus

Memòria presentada per **Enric Batllori Presas** per optar al grau de Doctor per la Universitat de Barcelona.

El Doctorand

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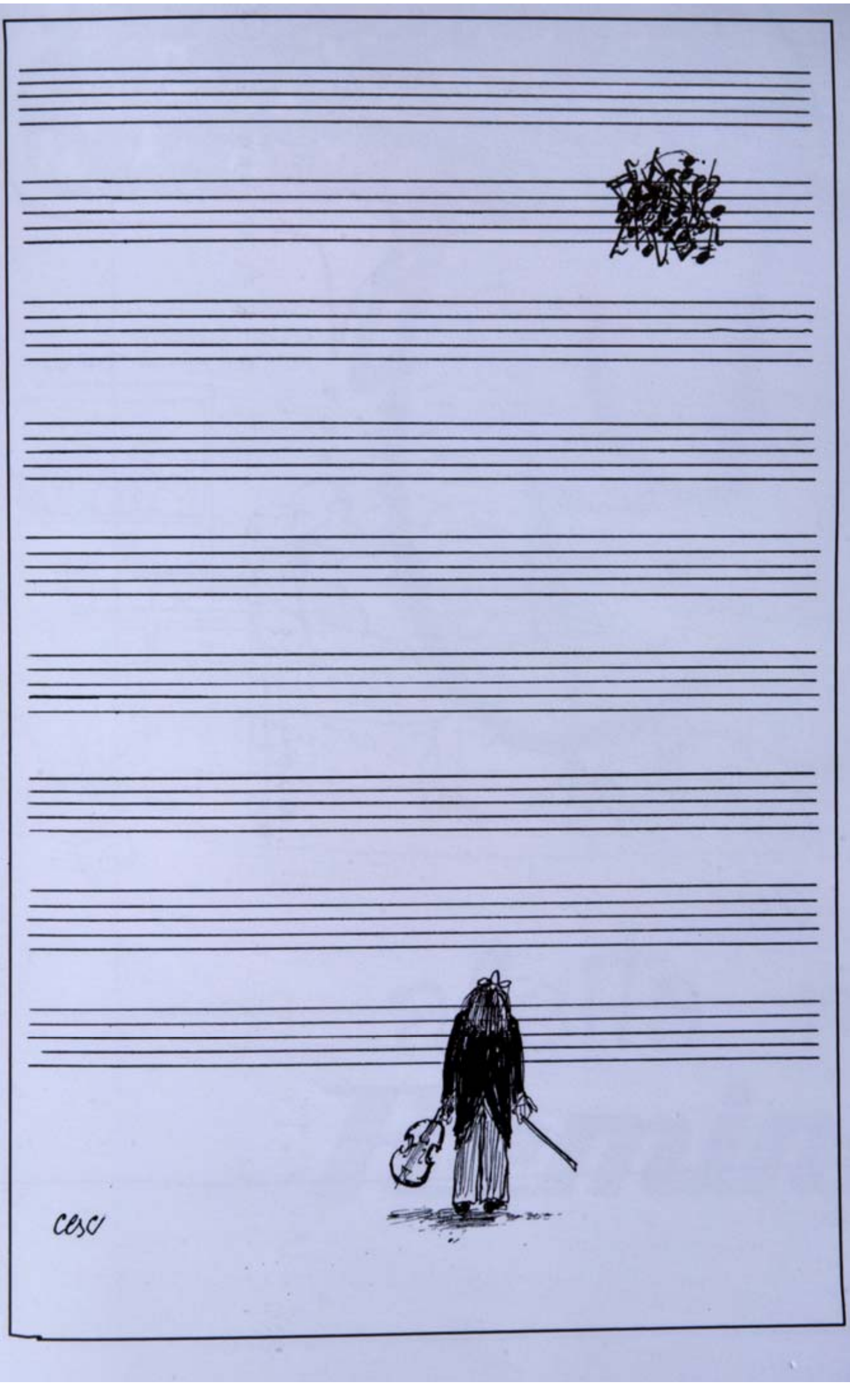
Barcelona, Maig de 2008

S'hauria de saber que les coses no tenen remei
i estar, en canvi, disposat a canviar-les
F. Scott Fitzgerald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Fa temps que rumio com han de ser els agraïments, o sent sincers, com vull que siguin. Finalment, m'he decantat per l'opció no clàssica, i per tant, no necessàriament políticament correcte. La primera cosa és no posar-hi títol perquè quedi clar que és un tema a part, que trobo que es fa difícil de definir amb una sola paraula. Hi ha moltes emocions barrejades que un pensa que vol posar, però al final, el que probablement més gent es llegeix de la tesi, i el primer que es llegeix, és el que es fa a última hora i ja sense temps per "brodar-ho" com un voldria. "meeeelon, que no tas acostao? Ai ènri..." total, que la tesi se'n va a la impremta d'aquí una hora i encara estem així, buscant les paraules entre les dues neurones que tinc, i no hi ha manera d'ordenar-les correctament. Per sort fa temps que tinc clar que volia posar una imatge per il·lustrar les meves sensacions, i quan vaig veure les notes amuntegades vaig saber que era aquesta. Primer perquè és fantàsticament gràfica per no haver de dir el que he sentit, i encara sento, en molts moments. Però a més a més, té la gràcia que inclou la música, que a mi m'és fonamental. I és justament amb la música quan les persones se'm fan més presents, perquè és un fil conductor amb moltes persones importants a la meva vida. De fet, si pogués hi posaria cançons entre les lletres, i segur que cadascú sabria quina és la seva.

Evidentment "la cosa", que és el nom que ha tingut la carpeta de la tesi durant tot el procés per una qüestió de pànic escènic, no hauria estat possible sense moltes persones. Ja sigui ajudant-me directament amb el tema que ens ocupa (aquesta és una llista que més val no començar perquè no em voldria deixar a ningú), o justament per fer-me'n oblidar (encara més important). Vull pensar que ja he estat capaç de donar-les individualment quan tocava, perquè ara i aquí no em sento còmode per donar-les perquè no podria evitar els sentimentalismes, però per si no ha quedat prou clar: gràcies!

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Introducció

Marc conceptual

El límit altitudinal del bosc, o ecotò superior bosc-prat alpí, constitueix per definició, la frontera entre l'estatge subalpí i l'estatge alpí separant, per tant, sistemes ecològics adjacents (Malanson et al. 2006). És una de les fronteres més aparents entre sistemes ecològics que s'origina degut a l'increment gradual de l'adversitat de les condicions climàtiques en altitud i que, finalment, comporta el límit biològic per al creixement dels vegetals en port arbori, el límit de l'arbre (Körner 1999). Per sota el límit de l'arbre hi ha el límit del bosc pròpiament dit, que genèricament correspondria al bosc dens situat a major altitud. La zona compresa entre aquestes dues froteres és l'ecotò pròpiament dit (figura 1), l'extensió del qual depèn, fonamentalment, de la brusquedat del gradient dels factors físico-químics en altitud (Smith et al. 2003). Hi ha una gran subjectivitat en la definició d'aquestes dues fronteres que delimiten l'ecotò, evidenciant com va dir Armand (1992), que "qualsevol frontera natural és en realitat una zona de transició [...] i per tant la seva localització és en principi inexacte i determinada per convenció".

En aquest estudi, el límit de l'arbre correspon a la posició de més altitud de l'últim individu de la població de com a mínim 2 m d'alçada (Hustich 1979, Kjällgren & Kullman 1998, Kullman 2000, 2002). Hi ha autors que han utilitzat definicions diferents, així per Sinclair i Payette (1995) el límit de l'arbre està determinat per una alçada mínima de 2.5 m, mentre que per Körner i Paulsen (2004) per individus amb una alçada superior a 3 m. Holmeier (2003) conclou que l'alçada dels individus que defineixen aquesta frontera s'ha de determinar tenint en compte el gruix de neu típic de la zona d'estudi. En el cas dels Pirineus, les condicions hivernals no solen implicar un gruix de neu superior a 1-1.5 m en les parts altes de vessants amb un pendent regular (Butlletins nivològics, Institut Geològic de Catalunya). Per tant, l'alçada mínima de 2 m utilitzada per definir el límit de l'arbre implicaria l'acoblament de bona part de la capçada d'aquests individus amb les condicions atmosfèriques durant tot l'any. La definició del límit del bosc està sotmesa, encara, a una major arbitrarietat ja que la delimitació d'una de frontera és més complicada com més gradual és aquesta (Choesin i Boerner 2002). El bosc experimenta una disminució progressiva de l'alçada dels individus i del recobriment de les capçades al llarg del gradient altitudinal, sempre que no hi hagi un factor extern que la condicioni (p.e., vents extrems, allaus o un canvi de substrat) (Körner 2007a). Per tant, la posició d'aquesta frontera depèn del que s'entengui per bosc, terme en el que hi pot haver moltes diferències entre autors (p.e., Lescop-Sinclair i Payette 2005, Lavoie i Payette 1996, Lloyd i Cristopher 2003, Gamache i Payette 2005) sobretot en estudis a escala detallada. La definició de bosc aquí utilitzada es basa en una cobertura de capçades mínima, d'entre el 30-40 % (Holtmeier 2003), d'indivus amb una alçada mínima de 5 m. A l'escala de paissatge, tenint en compte les definicions emprades en aquest estudi, el límit de l'arbre i el límit del bosc consisteixen la línia imaginària que uneix la posició dels individus superiors a 2 m d'alçada i el bosc dens a major altitud, respectivament.

La formació de boscos arreu del planeta, en absència de perturbacions naturals o antròpiques (p.e., tales, incendis, pastures), està limitada per condicions climàtiques excessivament seques, humides o fredes (Körner 2007a). En el cas de la transició natural bosc subalpí-prat alpí, que s'observa a tots els sistemes muntanyosos del planeta suficientment alts, les causes de la seva formació és un tema encara avui de debat on no hi ha un consens generalitzat. Aquesta transició, que pot estar formada per espècies molt diferents pertanyets a diversos gèneres i famílies (p.e., *Araucaria*, *Betula*, *Dracophyllum*, *Fagus*, *Larix*, *Libocedrus*, *Nothofagus*, *Picea*, *Pinus*, *Podocarpus*), està situada a alçades molt diferents en funció de la latitud; des de prop del nivell del mar a les latituds polars fins a més de 4000 m d'altitud a les muntanyes tropicals (Holtmeier 2003). Aquest fet és el que ha motivat la recerca d'una explicació general per a la formació dels boscos en altitud. Sembla que la formació de l'ecotò superior no es deu a la durada del període de creixement (que varia entre 95 i 365 dies en funció de la latitud), ni a limitacions reproductives que impedeixen el reclutament d'individus a altituds superiors (Körner 1999, Körner i Paulsen 2004). De fet, en la majoria d'ecotons és comú la presència d'individus molt per sobre del límit de l'arbre que, tot i que no assoleixen el port arbori, evidencien l'arribada de llavors fèrtils i la seva germinació a gran altitud. Limitacions en la fotosíntesi degut a les baixes temperatures també han estat descartades com a causants de la posició del límit superior del bosc (Tranquillini 1979, Körner 1998). En aquest sentit, Hoch i Körner (2003) descriuen l'increment de la quantitat de carbohidrats no-estructurals a favor del gradient altitudinal, fet que corroboraria que el creixement al límit superior del bosc estaria més limitat per la síntesi de carboni estructural que no pas per la fotosíntesi. A més a més, juntament amb els resultats experimenals de Li et al (2002) sobre *Pinus cembra*, sembla que l'adquisició de carboni atmosfèric, sigui quina sigui la durada del període de creixement, tampoc seria limitant per al creixement dels arbres al límit superior del bosc. Contràriament a aquests resultats, Hättenschwiler et al. (2002), en base a increments experimenals en la concentració de CO_2 sobre *Larix decidua* i *Pinus uncinata*, conclouen que l'increment que detecten en el creixement dels individus indicaria que l'adquisició fotosintètica de carboni pot ser un factor limitant a la zona de l'ecotò superior. Els mateixos autors però, constaten que no és gens clar si aquesta resposta inicial del creixement es mantindrà al llarg del temps. A més a més, altres factors com ara la concentració de nutrients del sòl o la disponibilitat hídrica podrien tenir un paper molt important pel que fa a la resposta del creixement dels arbres a elevades concentracions de CO_2 (Körner 2007b). Les respostes oposades que té l'augment de CO_2 sobre el creixement dels individus, emfatitza que les respostes de la vegetació a la concentració de CO_2 són específiques, i per tant que els resultats basats en una sola espècie tenen una extensió molt limitada per a la detecció de respostes globals (Körner et al. 2005, Keel et al. 2007).

La causa més factible que explicaria el límit superior del bosc, independentment de la latitud i de l'espècie dominant a l'ecotò, és la temperatura del sòl a la zona on es troben les arrels (Körner i Paulsen 2004, Körner 2007a). La temperatura mitja de la zona radical al límit superior del bosc arreu de tot el planeta és de 6.7 ºC (± 0.8 SD), suggerint la presència d'un llindar tèrmic que limitaria el creixement dels individus amb port arbori. Aquest llindar no sembla depenent de les espècies, de la latitud ni de limitacions fisiològiques, sinó de la pròpia arquitectura del port arbori que és la responsable que els individus estiguin més acoblats a les condicions atmosfèriques, tant a nivell de la capçada com a la zona radical. Així les baixes temperatures de la zona on es troben les arrels, que reben l'ombra de la capçada reduïnt les oscil·lacions tèrmiques i la temperatura mitjana per manca d'insolació directa, semblen ser el factor limitant per al creixement de tiges i fulles a la capçada, que està molt limitat per l'activitat meristemàtica de les arrels (Körner 1999). Per contra, les espècies alpines de mida petita, que es troben fins molt més amunt que el límit superior del bosc, poden crèixer degut a la gran insolació que reben durant el dia i a la presència de microclimes arran de terra que fan que s'arribi a temperatures que permeten l'activitat meristemàtica. Les plantes alpines s'han hagut d'adaptar evolutivament a les grans oscil·lacions tèrmiques entre el dia i la nit, i a soportar alts nivells de radiació ultraviolada.

Determinar quina és la causa de formació del límit superior del bosc ha estat un tema central d'estudi de molts ecòlegs, ja que per la modelització de la dinàmica d'aquesta frontera en el context del canvi climàtic i d'usos del sòl, és necessari conèixer quin és el factor que limita els processos de creixement i regeneració dels arbres a l'ecotò. Però a banda de les teories basades en el balanç anual de carboni o en les baixes temperatures com a factor limitant al límit superior del bosc, Smith et al. (2003) aporten una visió més mecanicista per tal explicar possibles dinàmiques de les poblacions situades al marge de la seva àrea de distribució. La seva perspectiva recau en la importància dels processos de facilitació, o interaccions positives, que tenen lloc quan la modificació de les condicions ambientals (físiques i/o biòtiques) per part dels individus té un efecte positiu sobre els individus veïns (Callaway 1995). Els processos de facilitació tenen més importància quan les condicions ambientals a les que estan sotmeses els individus són adverses, com és el cas de l'ecotò superior. Així Smith et al. (2003), emfatitzen la importància de la facilitació en la modificació dels factors que més limiten, en altitud, l'establiment dels plançons i el seu creixement successiu fins a individus de port arbori. Processos de facilitació que tindrien lloc a varis nivells: a nivell microambiental la facilitació, exercida per objectes inanimats o resultant d'interaccions intra- o inter-específiques, és molt important per la supervivència dels plançons durant els primers estadis del cicle vital (Ball et al. 1997, Germino i Smith 1999, 2002). A nivell atmosfèric, o de les condicions ambientals generals, les caracterítiques de l'estructura de la part aèria (orientació i agrupació de les branques i acícules) és molt important en processos de facilitació intra-individu (*structural self-facilitation*) que afavoreixen el creixement. Aquests processos de facilitació estan estretament relacionats amb la protecció de la neu, que entre altres coses, protegeix els individus de les baixes temperatures atmosfèriques durant l'hivern, evita els efectes de l'abrasió hivernal, redueix la fotoinhibició de la fotosíntesi per excessiu contrast tèrmic, protegeix de l'herbivoria hivernal i incrementa la disponibilitat hídrica a l'inici del període de creixement (Hadley i Smith 1986, Neuer et al. 1999, Germino i Smith 2002, Baumeister i Callaway 2006). Finalment, Smith et al. (2003) així com d'altres autors (e.g., Malanson 1997, Alftine i Malanson 2004, Bekker 2005), donen molta importància als processos de retroalimentació positiva per a l'establiment d'individus a l'ecotò, que derivarien d'increments en els processos de facilitació degut a l'agregació espacial de la regeneració que afavoreix la retenció de la coberta de neu. En resum, la visió mecanicista implica que la dinàmica espacial del límit superior del bosc depèn en últim terme de l'existència de processos de facilitació al llarg del cicle vital dels individus, que milloren les adverses condicions ambientals permetent el desenvolupament dels plançons fins a individus de port arbori.

Independentment del factor causant del límit altitudinal i latitudinal del bosc, on sembla que els factors abiòtics controlen en últim terme els processos ecològics que hi tenen lloc, els ecotons han estat motiu d'estudi des de fa molt temps (Hansen et al. 1988 *i referències allà citades*) ja que es consideren paradigmàtics per l'anàlisi de la resposta dels patrons de distribució de la vegetació a les fluctuacions climàtiques (Brubaker 1986, Hansen i di Castri 1992). La seva importància com a monitors de canvis climàtics recau en el fet que les respostes dels ecosistemes degut a la variació ambiental són detectats primerament a les zones de frontera, en aquest cas el límit del bosc pròpiament dit i el límit de l'arbre. Hi ha autors però, que qüestionen la idoneïtat dels ecotons com a monitors dels canvis ambientals degut a la inèrcia de les seves fronteres (p.e., com a resultat de plasticitat fenotípica de les espècies) que provocaria que els patrons de distribució no estiguessin en equilibri amb les condicions climàtiques (Noble 1993). D'aquesta manera, alguns límits de distribució podrien estar en posicions relictuals tenint en compte les condicions climàtiques actuals (Hofgaard 1999). Tot i aquesta controvèrsia en el paper dels ecotons com a monitors del canvi climàtic, el que sí que sembla evident és que el clima és un dels factors més limitants pels processos poblacionals als límits altitudinals de l'àrea de distribució de les espècies (Tranquillini 1979, Grace i Norton 1990, Theruillat i Guissan 2001). Justament per això, i degut a la gran diversitat d'espècies presents en els ambients d'alta muntanya, moltes d'elles relictuals o amenaçades, la vulnerabilitat de la biodiversitat de la vegetació alpina en front de possibles respostes del límit superior del bosc en el context del canvi climàtic, és d'interès internacional (Luckman i Kavanah 2000, Becker et al. 2007).

Avui en dia, hi ha un consens generalitzat en que les temperatures han incrementat a nivell global durant el segle XX (IPCC 2007), prenent valors que són significativament diferents de la mitjana a llarg termini (Mann et al. 1999). Paral·lelament, hi ha estudis que evidencien que els canvis climàtics del segle passat han afectat la biota en termes fisiològics, de productivitat i creixement, així com també han produït l'alteració del rang de distribució de moltes espècies (Parmesan i Yohe 2003, Root et al. 2003, Holzinger et al. 2008). Per tant, degut a la seva sensibilitat climàtica, és particularment interessant determinar i entendre els canvis de les poblacions al seu límit de distribució, tant altitudinal com latitudinal. Són molts els estudis que descriuen una resposta d'aquests ecotons al llarg del segle XX en paral·lel a l'increment de les temperatures (p.e., Payette & Filion 1985, Scott et al. 1987, Payette & Lavoie 1994, Sceicz & MacDonald 1995, Kullman 1997, MacDonald et al. 1998, Camarero 1999, Stöcklin & Körner 1999, Payette et al. 2001, Juntunen et al. 2002, Camarero & Gutiérrez 2004, Kullman 2005, Danby & Hik 2007). L'impacte del canvi climàtic s'ha traduït generalment en la consolidació de les poblacions existents al seu límit de distribució, processos de densificació de l'ecotò, més que en canvis en la seva distribució altitudinal o latitudinal. Quan s'han produït, els canvis observats en la posició del límit de l'arbre han estat generalment el resultat d'una resposta fisiognòmica dels individus (p.e., ràpid creixement vertical de formes prostrades) i no a l'establiment de nous individus a altituds o latituds superiors (Payette i Lavoie 1994, Holtmeier et al. 2003). Però quan els canvis en la vegetació són considerats a escala detallada i durant un període temporal curt (dècades o segles), altres factors a part del canvi climàtic són responsables de la variació ambiental als límits de distribució de les espècies. Les perturbacions naturals o antròpiques són molt importants en la dinàmica d'aquestes poblacions (Solberg 2002, Dirnböck et al. 2003, Holtmeier i Broll 2005). A les regions muntanyoses de tot Eurasia, alteracions antròpiques a la zona del límit superior del bosc (p.e., tales i focs per incrementar l'àrea de pastura) han estat molt comuns des de fa molt de temps (Walter 1976, Körner 1999). Però durant el darrer segle, el despoblament i la davallada de l'economia tradicional de l'alta muntanya ha suposat un important canvi en els usos del sòl, que en el cas dels Pirineus ha estat especialment acusat des de 1950s (García-Ruiz et al. 1996). Així s'ha de parlar d'un canvi global, on els canvis climàtics que han tingut lloc al llarg del segle XX han anat acompanyats de canvis molt importants en els usos del sòl. En aquest sentit, hi ha estudis que indiquen que la resposta observada als ecotons està en molts casos més influenciada per la disminució de la pressió antròpica que per la variació de les condicions climàtiques (Hofgaard 1997, Gehring-Fasel et al. 2007). Però independentment dels factors que han provocat la resposta observada dels límits de distribució de les espècies al llarg del segle XX, cada vegada són més els estudis que descriuen respostes diferencials d'aquesta frontera i que contemplen una aturada, i fins i tot una reversió, de les tendències poblacionals descrites fins al moment (Daniels i Veblen 2003, 2004, Dalen i Hofgaard 2005, Payette 2007). Per això són importants els estudis a escala regional, ja que permeten detectar la variabilitat espacial en la resposta dels ecotons, podent evidenciar tendències poblacionals diferencials sota una influència climàtica comú.

Àrea i espècie d'estudi

Aquesta tesi ha estat realitzada al límit superior del bosc del sector central i oriental dels Pirineus catalans i d'Andorra. El límit superior del bosc als Pirineus es situa entre els 2200-2450 m en funció de les caracterítiques locals de les condicions climàtiques, la topografia i el substrat (Carreras et al. 1996a). L'espècie dominant que constitueix el límit superior del bosc dels Pirineus, en qualsevol tipus de substrat i orientació, és gairebé sempre el pi negre, *Pinus uncinata* Ram. ex DC. (Cantegrel 1983, Ninot et al. 2007). Es tracta d'una conífera heliòfila, de creixement lent i elevada longevitat, que presenta una gran amplitud ecològica degut a la seva adaptabilitat a la disponibilitat hídrica i de nutrients (Blanco et al. 2001, Erschbamer i Wallnöfer 2007). La seva gran resistència a les baixes temperatures hivernals i a la sequera fisiològica degut a l'acció del vent i del gel, l'aconsegueix degut a trets anatòmics i fisiològics. Presenta acícules curtes, estretes i coriàcies, que es disposen quasi sempre de dos en dos sobre braquiblasts que s'agrupen densament als extrems de les branques. Aquesta darrera característica fa que es redueixi el contrast tèrmic entre el dia i la nit, degut a una menor exposició al sol i a les fredes temperatures nocturnes, minimitzant per exemple els efectes negatius de la fotoinhibició de la fotosíntesi (Smith et al. 2003). A més a més, l'elevada concentració de resina a les acícules fa molt difícil la destrucció dels teixits orgànics per congelació. Les seves branques són especialment flexibles i la capçada adopta una forma més o menys cònica, fent que aquesta espècie estigui molt ben adaptada per suportar l'acció mecànica del vent i la neu. Les pinyes són petites (2-6 cm de longitud), pèndules, asimètriques i es disposen pràcticament sobre les branques. Els pinyons són petits i alats, maduren al cap de 2 anys de formació de la pinya i són dispersats pel vent a finals d'hivern (Ceballos i Ruiz de la Torre 1979). El creixement radial s'inicia amb l'activació del cambium al més de maig, mentre que la formació de noves traqueides té lloc fonamentalment a finals de juny i principis de juliol (Camarero et al. 1998). El desenvolupament de la fusta tardana, engruiximent i coloració de la paret cel·lular, té lloc des de finals de juliol fins a finals d'octubre.

Objectius

Els Prineus, representen l'enclau meridional de distribució de moltes espècies alpines europees, algunes d'elles amenaçades (Bolòs i Vigo 1984, Ozenda 1985, Carreras et al. 1996b). En aquest sentit, són un cas paradigmàtic per l'anàlisi de la dinàmica del límit superior del bosc i la vulnerabilitat del paisatge supraforestal, és a dir de la possible pèrdua d'espècies alpines com a resultat de l'ascens altitudinal de les poblacions de l'ecotò (Luckman i Kavanah 2000). Tot i això, fins al moment només s'han realitzat estudis de caire local que descriuen la dinàmica de 3 ecotons dels Pirineus centrals (p.e., Camarero 1999, Camarero i Gutiérrez 2004, Camarero et al. 2006), i per tant manquen dades que permetin avaluar la variabilitat en la resposta dels ecotons a escala regional. Entrendre la resposta dels ecotons i dels processos que la condicionen és part indispensable per a disposar del coneixement necessari per a la gestió del paissatge pirinenc en el context del canvi global. Aquesta tesi, pretén descriure la dinàmica recent del límit superior del bosc als Pirineus, a escala regional, i identificar els factors més importants que la determinen. Són varis els estudis que emfatitzen la importància d'intensificar la recerca en els factors que controlen els patrons espacials i temporals de la regeneració al límit superior del bosc, ja que en últim terme, la permanència o expansió d'aquestes poblacions depèn dels processos de regeneració (Hättenschwiler i Smith 1999, Cuevas 2000, Holtmeier 2003, Holtmeier et al. 2003, Smith et al. 2003). A més a més, la dinàmica de la classe regeneradora ha estat considerada el millor indicador de la sensibilitat del límit superior del bosc als canvis ambientals (Holtmeier i Broll 2005). En aquest sentit, la disponibilitat de llocs segurs per al reclutament és un dels factors que més condiciona la dinàmica de la regeneració als ecotons (Hobbie i Chapin 1998, Camarero i Gutiérrez 1999, Dirnböck et al. 2003, Dullinger et al. 2004). En base a aquestes consideracions, els objectius concrets d'aquesta tesi, recollits en les 5 publicacions que es presenten, són:

I) la descripció general de l'estructura demogràfica de 12 ecotons bosc subalpí-prats alpins. Article: *Regional treeline dynamics in response to global change in the Pyrenees*

L'obtenció de l'estructura demogràfica de les poblacions al límit superior del bosc permetrà avaluar quina ha estat la resposta dels ecotons en front del canvi global, i determinar la variabilitat existent en la seva dinàmica a escala regional. Una de les limitacions més importants per a l'estudi demogràfic de les poblacions sense la utilització de mètodes destructius, és a dir tallant seccions a la base dels arbres que incloguin el coll de l'arrel, és la fiabilitat en la determinació de l'edat dels individus. En aquest sentit, es presenta una nova metodologia que permet determinar el grau de presició en l'estima de l'edat, que és molt important a l'hora de seleccionar la resolució a la que es poden presentar els resultats.

II) l'estudi del nínxol de regeneració de l'espècie i l'extensió dels processos de facilitació en la supervivència dels plançons. Article: *Recruitment, survival and seedlings facilitation at alpine treeline: implications on their dynamics and potential responses to climatic warming.*

No hi ha estudis detallats del nínxol de regeneració de *P. uncinata* que incloguin les característiques del substrat i considerin la importància dels processos de facilitació a nivell microambiental per a la supervivència dels plançons. L'anàlisi del microhabitat de la regeneració natural així com de la posició dels plançons respecte elements que podrien exercir efectes de facilitació (*Rhododendron ferrugineum*, estructures del microrelleu i roques) permetrà definir els llocs segurs per al reclutament de l'espècie. La realització i monitorització d'una plantació experimental en un dels ecotons, servirà per determinar quines són les condicions que més limiten la supervivència i el creixement dels plançons, i com aquesta està influenciada per processos de facilitació exercits per individus de la mateixa espècie. Tot i la importància de la facilitació en la dinàmica de regeneració al límit superior del bosc, no s'han trobat estudis experimentals per caracteritzar-ne la seva extensió.

III) determinar quin és el patró de distribució espacial de la regeneració a la zona de l'ecotò. Article: *Spatial patterns of recent regeneration indicate equal short-term sensitivity of alpine treelines to global change at a regional scale.*

La descripció dels patrons de densitat i d'edat de la regeneració, poc estudiats a petita escala, és indicador de quins processos modulen la resposta del límit superior del bosc a la variabilitat ambiental. Determinar on té lloc la regeneració, la descripció del patró espacial al llarg de diferents fases del cicle vital, i la interacció entre l'estructura espacial de la regeneració i els individus de mida més gran (pinetons, joves i adults) i els potencialment reproductors permetrà detectar quins processos poden condicionar la dinàmica del límit superior del bosc. A l'hora es podrà avaluar si els ecotons estudiats estan afectats pels mateixos processos, o si per contra, les condicions locals tenen un gran efecte en la dinàmica dels ecotons.

IV) avaluar la influència climàtica sobre el creixement i l'establiment del pi negre. Article: *Climatic influence on* Pinus uncinata *growth and recruitment dynamics at alpine treeline*

Les condicions ambientals són un dels factors que més condiciona la dinàmica de les poblacions al seu límit de distribució. Per tant, la descripció de les relacions entre el clima i el creixement radial dels individus i la regeneració és indispensable per entendre la resposta observada als ecotons. En base als resultats obtinguts, es podrà determinar si és esperable que es mantinguin les respostes observades als ecotons com a resultat dels increments continuats de la temperatura predits en el marc del canvi climàtic.

V) la descripció l'estructura de les comunitats vegetals i de la distribució de les espècies al llarg del gradient altitudinal. Article: *Vegetation patterns at alpine treeline: the role of tree cover on abrupt changes in alpine communities species compositon*

Hi ha una manca d'estudis detallats de la vegetació del límit superior del bosc a escala regional dels Pririneus. La descripció conjunta de la diversitat i de l'estructura de la comunitat al llarg del gradient altitudinal, és molt important per poder-ne interpretar la seva dinàmica. Determinar la influència del patró espacial de la cobertura del *P. uncinata* sobre la distribució de les espècies i els patrons de diversitat, permetrà avaluar quins factors són més condicionants per l'estructura i composició de les formacions vegetals al llarg de l'ecotò.

Resultats

Capítol I. Regional treeline dynamics in response to global change in the Pyrenees

Resum

Són molts els estudis realitzats a Europa, Nord i Sud Amèrica, que descriuen tendències regionals de densificació als límits altitudinals o latitudinals del bosc en paral·lel a l'augment de les temperatures del segle XX. Als Pirineus, però, hi ha una manca d'estudis a escala regional que permetin determinar quina ha estat la resposta general del límit superior del bosc.

L'objectiu d'aquest estudi és determinar si s'ha produït un augment en la regeneració a la zona de l'ecotò al llarg del Pirineus, si hi ha períodes de reclutament sincrònics a totes les poblacions, i si la posició del límit de l'arbre s'ha mantingut estàtica en les últimes dècades. L'estudi s'ha realitzat a 12 ecotons bosc subalpí-prats alpins dominats per *Pinus uncinata* als Pirineus centrals i orientals. A cada localitat es va delimitar un parcel·la rectangular d'entre 940 i 7600 m^2 incloent la transició des del bosc fins als prats alpins. En total es van marcar, mapar i caracteritzar més de 3600 individus. La presa de dades biomètriques i l'estimació de l'edat dels individus ha permès determinar per cada localitat quina és l'estructura d'edat i de mida de la població, i caracteritzar el patró de transició de l'edat i la mida al llarg de l'ecotò. La datació dels individus es va fer mitjançant tècniques dendrocronològiques i es va desenvolupar una nova metodologia que permetés determinar l'error en les estimes de l'edat dels arbres, ja que la resolució de l'estructura demogràfica de les poblacions depèn de la presició en les estimes de l'edat.

S'han detectat episodis sincrònics de reclutament, passats i presents (a la meitat del segle XIX i durant la segona meitat del segle XX), a escala regional dels Pirineus. Totes les poblacions estudiades han experimentat un augment en la densitat d'individus des de 1950s en paral·lel al canvi climàtic i a importants canvis en els usos del sòl. La transició de l'edat i la mida dels individus presenta disminucions graduals o amb canvis sobtats al llarg de l'ecotò.

L'increment del caràcter forestal de la zona de l'ecotò de les últimes dècades s'ha produït amb canvis bruscs en la densitat d'individus reclutats, fet que indica la importància dels processos de retroalimentació postius en la dinàmica de la regeneració al límit superior del bosc. En la meitat dels ecotons estudiats s'ha produït un ascens del límit de l'arbre en paral·lel a la densificació de la zona de l'ecotò, indicant la gran sensibilitat a les variacions ambientals que pot tenir aquesta frontera.

La presència d'episodis sincrònics de reclutament d'individus a escala regional posa de manifest la influència de factors externs, com el macroclima, en la dinàmica del límit superior del bosc. Però als Pirineus, l'ecotò superior ha estat molt afectat per perturbacions antròpiques (p.e., ramaderia). En absència de perturbacions naturals (vents extrems, allaus, etc.), la presència de patrons de transició de l'edat dels individus amb canvis sobtats al llarg de l'ecotò serien indicadors d'una recent afectació antròpica del límit superior del bosc.

Regional treeline dynamics in response to global change in the Pyrenees

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Article enviat a: *Journal of Ecology*

Summary

1. Many studies in northern Europe, North and South America, describe regional trends of population densification at altitudinal and polar treelines during the 20th century. The purpose of this study was (1) to ascertain if this regeneration enhancement is present across the alpine ecotones of the Pyrenees, (2) if synchronous recruitment trends are common among the studied populations and (3) to determine the treelimit stability during recent decades.

2. Twelve *Pinus uncinata* dominated populations at treeline were studied on the Iberian eastern range of the Pyrenees. Rectangular plots ranging from 940 to 7600 m^2 were set along the forest-alpine grassland transition, more than 3600 *P. uncinata* individuals were mapped. Tree size and age were used to establish the demographic structure at each stand, and to characterize abrupt or smooth transition patterns along the treeline ecotone. A new procedure for estimating missing rings in off-center cores was developed to ensure a correct interval for the age-classes distribution analysis.

3. Past and recent synchronous recruitment trends (mid 19th century, second half of the 20th century) were apparent at treeline over the studied area of the Pyrenean range. The observed ecotone densification since the 1950s occurred in the context of climatic warming and substantial land use abandonment. Both gradual and step-like transition patterns in tree age and size along the ecotone were observed.

4. Regeneration enhancement in the last ~30 years appears as an abrupt change in population age structures. This rapid shift in recruitment tendencies could indicate positive feedback mechanisms. In 50% of the surveyed treelines ecotone densification has been coupled to treelimit shifts in the recent past. This indicates both great treelimit sensitivity to short-term climatic changes and the presence of differential treeline dynamics at a regional scale.

5. *Synthesis.* The observed past and recent synchronous recruitment trends suggest the presence of regional climatic factors modulating treeline structure and dynamics. However, treeline dynamics in the Pyrenees have been widely affected by local anthropogenic activities. We suggest that the presence of step-like treeline transitions in tree age can be considered an evidence of the effects of recent human-induced disturbances when no other major natural disturbances affect the treeline dynamics.

Keywords: demographic structure, dendroecology, global change, *Pinus uncinata*, Pyrenees, recruitment, step-like transition, treeline

Introduction

Although the alpine (altitudinal) and arctic (latitudinal) treelines ecotones are likely to be sensitive to climate warming (Hansen & di Castri 1992; Kullman 1999; Payette *et al*. 2001), the degree to which treeline response may lag climate change and the extent to which sensitivity to the climate may vary among sites remains largely unknown (Lloyd & Fastie 2003). The greater sensitivity of populations at the species' range limit (as is the case of alpine or arctic ecotones) responds to the fact that the climate is expected to be among the main constraints on tree recruitment in these populations (Camarero & Gutiérrez 2007). However, climate change is only one factor of environmental change that may affect the location of treelines (Holtmeier & Broll 2005). As in Eurasian mountainous regions, where traditional human use near the treeline is common (Körner 1999), forest-grassland ecotones often appear to be affected by changes in natural or anthropogenic disturbance regimes (League & Veblen 2006). Thus, past and present land use (Hofgaard 1997, 1999; Stöcklin & Körner 1999) and non-linear responses to climatic change (Arseneault & Payette 1997; Lloyd 2005) are all possible factors confounding the effect of climate on treeline populations (Kullman 2000). The complexity of several interacting factors, whose individual degree of impact on treeline dynamics depends on particular local conditions, may explain the great regional and temporal variability in the importance of treeline driving parameters (Walther *et al*. 2005).

In this paper the term treeline ecotone (or merely treeline) is used in a general sense, and refers to the transition from the uppermost closed forests, or timberline, to the treeless alpine vegetation (Körner 1998, 1999): the forest-alpine grassland ecotone. Hence, the altitudinal limit of upright tree growth, the treelimit, is included. Most authors would agree with this general definition, however many terms and conventions are used to define timberline and treeline boundaries (Holtmeier 2003). In this study, the timberline position is defined by a coverage threshold of 30-40 % (Holtmeier 2003) given by arboreal (at least 5 m height) pines (Smith et al. 2003). The treelimit is defined, based on the mean snow cover depth of the study region (Holtmeier 2003), as the uppermost upright tree with a minimum height of 2 m (Kullman 2001, 2003).

Many studies show that the impact of recent warming in forest-grassland ecotones has been rather on the consolidation of preexisting tree populations than on the position of the treeline (Payette & Filion 1985; Scott *et al.* 1987; Payette & Lavoie 1994; Sceicz & MacDonald 1995; Kullman 1997; MacDonald *et al.* 1998; Camarero 1999; Stöcklin & Körner 1999; Payette *et al.* 2001; Juntunen *et al.* 2002; Camarero & Gutiérrez 2004; Kullman 2005; Danby & Hik 2007). Such treeline population response has occurred in the context of warmer conditions in arctic and subarctic regions since the beginning of 20th century (Payette & Lavoie 1994) and since the 1970s in most European ranges (Diaz & Bradley 1997).

The future position of treelines is of concern due to the possible loss of alpine species due to upward encroachment of subalpine forests (Luckman & Kavanah 2000). The Pyrenees mountains may be a paradigmatic example in this sense since they encompass the southermost distribution range of many European alpine species, including endemic and endangered species (Bolòs & Vigo 1984; Ozenda 1985; Carreras et al. 1996a). However, temporal dynamics of tree recruitment at alpine treeline have not been extensively investigated in the Pyrenees. More demographic studies at a regional scale are required to ascertain how current treeline dynamics can affect the alpine flora. Thus, we decided to conduct a dendroecological study to find out if any regional pattern is detectable in the size and age structures of mountain pine populations over the Spanish Pyrenees. The major problem for the analysis of tree population age structures is the difficulty of accurately determining the ages of all the trees in a stand (Norton *et al.* 1987; Villalba & Veblen 1997a). When describing age frequency distributions the error in establishment dates can significantly change the shape of age-class distributions if the resolution of analysis is too fine in comparison to the extent of the dating error (Wong & Lertzman 2001). Thus we developed a new procedure to date off-center cores which permits us to quantify the error in age determination.

In this study, we focused on changes in tree recruitment at several alpine treeline ecotones in the Spanish Pyrenees to assess the treeline dynamics at a regional spatial scale. We developed static age structures of living Pinus uncinata individuals to: (1) ascertain if densification processes occurred during the 20th century, (2) detect if synchronous recruitment trends are common among the treelines studied and (3) assess the stability of treelimit position during recent decades. Limitations of static age distributions are well acknowledged (Johnson *et al*. 1994). Hence, our interpretation of the results only intend to find out if in the global change context general recruitment trends exist over the alpine ecotones in the Pyrenees without making detailed inferences on population dynamics. Due to the lack of local land use changes data, the transition pattern in tree ages and sizes (total height and basal diameter) was analysed to ascertain which may be the most plausible driving factor (climate or land use changes) of recent treeline dynamics.

Materials and methods

Study area

We conducted this study on the Iberian eastern half range of the Spanish Pyrenees (Catalan Pyrenees) and Andorra (Fig. 1). We combined field visits with aerial photograph interpretation to place 12 rectangular plots at the upper treeline (or alpine ecotone) including the transition from subalpine forests to the alpine grasslands (Fig. 1, Table 1). We sampled 10 small plots (980 m^2 to 1650 m^2; 10 m width × variable length) and 2 big plots (6000 m^2 and 7600 m^2; 40 m width × variable length) for inter- and intra-site comparisons of treeline structure. Plot length varied depending on each site's transition characteristics. This study was mainly restricted to the north-facing treeline ecotones, and the sites selected for sampling covered a wide range of slope steepness, bedrock and plant communities. The studied stands were located on homogeneous slopes, out of avalanche paths and major rocky outcrops. None of the sampled trees inside the plots presented fire induced scars, which suggests the absence of recent fires in the study sites. Thus, past disturbance regimes of the studied ecotones were mainly human induced. Field sampling was conducted between 2003 and 2006 during the end of spring and the summer.

The studied ecotones are dominated by *Pinus uncinata* Ramond ex DC., which reaches its southern and western distribution limit in the Iberian peninsula. *P. uncinata* is a shade intolerant conifer which forms most of the alpine ecotones of the Spanish Pyrenees, constituing dense forests between ~ 1700 m and ~ 2200 m asl. Potential treeline elevation has been fixed at ~ 2200-2450 m asl in the Pyrenees (Carreras *et al*. 1996b; Bolòs *et al*. 2005).

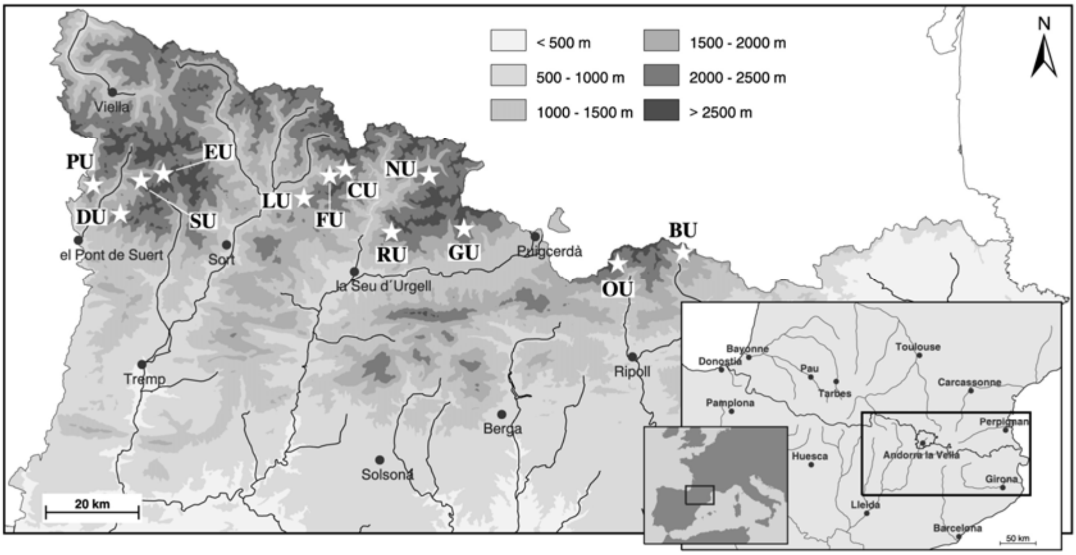

Figure 1. Map showing the location of study sites in the Catalan Pyrenees (Spain) and Andorra. (see table 1 for codes).

Table 1. Characteristics of the stands of *Pinus uncinata* sampled at the alpine treeline in the Catalan Pyrenees (Spain) and Andorra.

Code	Latitude	Longitude	Plot size (m^2)	Altitude (m a.s.l.)*	Slope (º)	Aspect	Bedrock
PU	42º 31’	0º 45’	6000	2199 - 2268	28	N	lime
DU	42º 28’	0º 49’	1200	2010 - 2069	30	N	lime
SU	42º 32’	0º 53’	1500	2270 - 2338	27	NW	lime
EU	42º 33’	0º 56’	940	2299 - 2339	24	W	granodiorite
LU	42º 31’	1º 21’	1180	2363 - 2405	21	N	slate
FU	42º 33’	1º 23’	7600	2352 - 2435	24	NW	slate
CU	42º 33’	1º 25’	1160	2250 - 2297	26	NW	lime
RU	42º 26’	1º 32’	1650	2236 - 2271	24	W	slate
NU	42º 34’	1º 37’	980	2266 - 2314	29	N	lime
GU	42º 27’	1º 44’	1500	2312 - 2365	16	NE	slate
OU	42º 23’	2º 08’	1500	2241 - 2308	27	N	slate
BU	42º 24’	2º 19’	1500	2184 - 2241	22	N	slate

* metres above sea level

Sampling and dendrochronological procedures

Each *P. uncinata* tree inside the plot was tagged and mapped. Basic biometric measurements were registered (total height, basal and breast height diameters) and the current treelimit position was determined for each site. All individuals big enough (more than 10-12 cm basal diameter) were cored at the base to determine tree age. Each tree was cored repeatedly using an increment borer until a core through the pith (or as near as possible) was obtained. Furthermore, as mineral soil level is not a good indicator of root collar level (Gutsell & Johnson 2002), cores were obtained by excavating a "coring hole" at the tree base and/or angling the increment borer to approach the root collar as much as possible (Villalba & Veblen 1997a). The mean core height extraction was 0.09 ± 0.04 m. The age determination for seedlings size class (< 0.5 m height) and small saplings size class (> 0.5 m height and < 7.5 breast height diameter) was done through bud scar counting along the main stem. More than 3600 *P. uncinata* individuals were measured and aged for this study.

Cores were air dried, mounted and sanded following standard procedures (Stokes & Smiley 1968). We used a stereomicroscope to detect light rings, frost-damaged rings and narrow rings of each core as cross-dating features (Filion *et al.* 1986; Yamaguchi 1991). During the cross-dating process missing rings were rarely encountered, representing 0.1% of the analysed rings. Moreover, 60% of the samples that presented absent rings were missing only one. As ageing was the only objective of the cores taken at the base, we tried to get as many cores through the pith as possible (53.3% of extracted cores) to minimise age determination uncertainties. However, trees at the alpine ecotone, growing on steep slopes, commonly present trunk deformities at the base. Hence, off-center cores were commonly collected.

The only accurate ageing method is by cutting trees at the base and then locating the root collar through consecutive cross-section analysis (Gutsell & Johnson 2002). Obviously, this is a destructive method that was inconvenient in the studied area for many reasons (e.g., some plots are located within protected areas). Cores missing the chronological center of the tree (or pith) pose a major problem because information about the earliest years of the tree is not known. Different methods for calculating missing rings as a function of growth rate of the missing radius of cores have been proposed (Norton *et al.* 1987; Villalba & Veblen 1997a; Wong & Lertzman 2001; Rozas 2003; Clark & Hallgren 2004). We developed a new procedure to date off-center cores based on the length of the missing radius and the core height extraction.

Age of off-center increment cores

We used a pith locator (concentric circles matched to the curvature of the inner rings) to calculate the missing radius length (MSR) (Norton *et al*. 1987; Fulé *et al*. 1997; Bosch & Gutiérrez 1999). Conversion of MSR into a number of missing rings was done with the mean of the annual growth rate (MGR) of the 5 outer contiguous rings of the year used as reference to calculate the MSR of each core (Fig. 2).

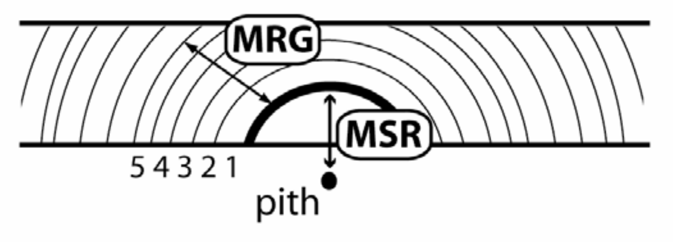

Figure 2. The bold ring is the one used to calculate the length of the missing radius (MSR) with the pith locator. Left arrow shows the 5 contiguous rings used to calculate the mean growth rate (MGR).

The accurancy of this method was previously tested with the results of 720 simulated MSR. At each study site 60 simulations were done, 15 simulations at each of the 4 following MSR categories: 0.25 cm, 0.5 cm, 0.75 cm and 1 cm. For each category and sampling site, simulations were done with randomly choosen cores of the set of total samples containing pith. Thus, each core could be used for more than one MSR category. Dating errors of each MSR simulation were calculated as the difference between the true ages of the cores and the ages estimated using MGR to convert the simulated MSR into a number of missing rings. Mean dating errors and standard deviation for all MSR categories (0.25 cm, 0.5 cm, 0.75 cm and 1 cm) are presented in Table 2 for each study site. To account for dating error of each off-center core depending on its MSR, we used the difference between the mean error ± 1 standard deviation at each MSR category.

We restricted the dating process to cores which had a maximum MSR of 1 cm since greater distances were considered too imprecise. Cores which had not reached the center (mainly due to tree rot) were also rejected. Thus, a small proportion of trees (< 4%) were discarded from the analysis because of rotten piths or excessive ageing uncertainty.

Table 2. Mean dating error ± standard deviation of the simulations for different missing radius lengths (MSR) from the pith (0.25 cm, 0.5 cm, 0.75 cm and 1 cm).

Site	0.25 cm		0.5 cm		0.75 cm		1 cm	
	N rings	sd	N rings	sd	N rings	sd	N rings	sd
PU	3	2.7	6	3.9	6	4.3	9	5.0
DU	3	3.3	4	2.7	5	2.7	8	4.6
SU	3	2.4	5	3.5	8	3.1	9	5.9
EU	3	3.9	6	5.4	6	4.9	9	6.5
LU	3	1.9	5	3.6	8	4.0	8	4.7
FU	3	2.7	4	3.6	7	4.6	9	5.8
CU	3	2.9	6	2.8	7	4.1	8	4.4
RU	4	2.4	6	3.1	7*	4.2*	8*	5.1*
NU	4	1.8	7	3.3	10	6.1	8*	5.1*
GU	5	2.3	7	2.6	9	4.0	10	3.5
BU	2	1.8	5	2.9	6	4.3	8	5.5
OU	3	2.5	5	2.8	7	2.6	7	4.4
Mean Dating error	6 years		8 years		8 years		9 years	

* mean values of the other plots due to unrepresentative sample size

Age corrections for coring height

The procedure above gave the age of the tree at coring height. We used annual height growth rate of 270 seedlings and small saplings (individuals < 1.5 m) to account for age-height corrections.We collected the 270 small pines from 6 representative stands of the 12 study sites. Although it would be preferable to sample each stand because of inter-site differences in initial growth rates (Villalba & Veblen 1997a), we could not do this due to technical problems. Thus, we used initial growth rates of the nearest of the 6 sampled stands for the age corrections for coring height of the 6 non-sampled sites. Seedlings and saplings were collected between timberline and treeline zones near the study plots. It must be assumed that initial growth rates of the old cored trees of the forests are probably similar to that of seedlings now located at open areas above timberline (Villalba & Veblen 1997a).

The 270 small pines were removed, along with their roots, and a cross-section was cut at the base containing root and stem tissue. Cross-sections were progressively sanded, obtaining thinner disks of 1,5 cm to 2 cm. The root collar was detected noting the shift in the central pith, from a vascular cylinder in the root to an undifferentiated parenchyma cells in the stem (Gutsell & Johnson 2002; Telewski 1993). Cross-sections were dated by ring counting and height growth rate of each individual obtained. Mean height growth rate was then used to estimate the number of missings rings due to coring height.

We used the height growth rate variabililty among the collected pines at each site to ascertain the dating error due to coring height. Based on the mean height growth rate ± 1 standard deviation, we calculated the age variability in 0.01 cm height intervals between slow (mean height growth rate – 1 standard deviation) and fast (mean height growth rate + 1 standard deviation) growing individuals. We considered these age differences as the dating error per each coring height.

As the age estimation of the small and poorly lignified individuals based on bud scar counting underestimates true age (age at root collar) (Camarero 1999), cross-sections of the collected 270 pines were also used to develop age correction functions to minimise this error. Age correction functions were developed for each of the 6 stands by means of a linear regression on age at root collar compared to age obtained by internode counting (Fig. 3). The age correction function of the nearest of the 6 sampled stands was used for age correction of the seedlings and small saplings of the 6 non-sampled sites.

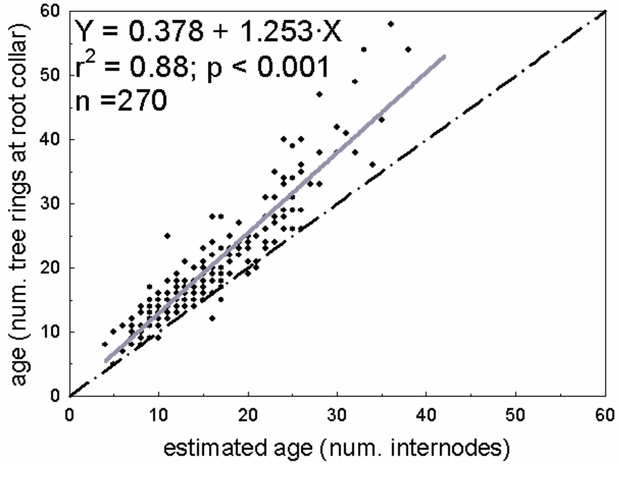

Figure 3. Mean age correction function (gray bold line) for the collected 270 small pines (up to 1.5 m high). Dashed line corresponds to the 1:1 relation “age at root collar” = “estimated age by internodes counting”.

In sumary, total tree age, or the best estimation of the germination date of each individual, was: (1) the number of rings in the core when pith was present plus (2) rings lost due to coring height. While in the off-center cores, age was the sum of: (1) rings in the core, plus (2) rings missing from the pith, plus (3) rings lost due to coring height. Tree age estimation error depends on MSR and coring height, and with the method used it can be quantifyed for each core. Therefore, we determined that the demographic structure of each plot could be presented in 15 years width classes as the majority of the individuals dated with cores (87%) presented lower dating errors. Given the resolution of the analysis (15 years) and the low frequency of absent rings detected, we considered that missing rings do not add uncertainty to the age estimates in this study. Uncertain tree age estimations, due to more than 15 years dating error, are presented for each plot separately. Age structures must be interpreted as reasonable estimates for the assessment of recruitment patterns, a trade-off between regeneration and mortality events.

Data treatment

The temporal patterns of recruitment (age frequency distributions) were compared between the 12 study sites using Kolmogorov-Smirnov tests with Bonferroni adjustment of the significance level ($\alpha = 0.05$/number of comparisons) (Cuevas 2002; Gamache & Payette 2005; Chauchard *et al.* 2007). The same procedure was used to analyse the pattern of recruitment in 4 subplots (10 m width) of the 2 bigger sampled plots (PU and FU) to account for intra-site differences in the age structure. Furthermore, we compared the apparent number and position of pulses of tree recruitment for each stand. We identified pulses as abrupt recruitment increases where the number of trees was at least 50% greater than the preceding age classes (modified from Wells *et al.* 1998; and Wong & Lertzman 2001).

The presence of population depletion trends in the age structures was verified by applying both negative exponential and power function models (Hett & Loucks 1976; Ågren & Zackrisson 1990; Szeics & MacDonald 1995; Gamache & Payette 2005), two models which reliably describe the age structure of tree populations. The major difference between the two models is that the negative exponential assumes a constant mortality rate whereas the power function describes a situtation where mortality changes with age. Following Hett & Loucks (1976), age data of each stand were analysed using the appropriate linear regression of log-transformed data. This analysis was confined to the range that excluded the oldest 1% of individuals in each of the populations to avoid the influence of outliers on age models, and a value of 1 was added before log-transformation to permit inclusion of empty age classes (Ågren & Zackrisson 1990; Szeics & MacDonald 1995).

To characterize abrupt or smooth transition patterns along the ecotone, tree age, total height and basal diameter through the altitudinal gradient were evaluated in all the study plots by fitting linear or smooth spline functions. We used the standardised values of these variables to allow for comparisons among both variables and study sites. Standardisation was done by dividing all the values of each variable by the greatest value in each site. Linear and smooth spline functions were adjusted to the 95th quantile of the variables in order to describe the general pattern of the transitions since low values were very abundant.

Results

A densification process during the second half of the 20th century was detected at all the treeline ecotones studied. Size demographic structures (Fig. 4) are plotted individually for each stand as frequency distribution of 5 cm dbh classes (diameter at breast height). The first category (0-5 dbh class) in each plot represents the abundance of individuals which do not reach 1.30 m of total height, which includes seedlings, small saplings and some stunted individuals. All stands, except BU and CU, have the J-shaped distribution of pine stems expected of uneven-aged forests stands (Hett and Hemlock 1976). Although BU is characterized by a bimodal size structure distribution, the abundance of 0-5 dbh class is clearly greater than the rest. In contrast, the CU population size structure follows a rather bell-shaped distribution, with the 5-10 cm dbh class being the most abundant. Despite the J-shaped distribution was the most common pattern, 67% of Kolmogorov-Smirnov paired test (Bonferroni adjusted $p < 0.001$) denotes significant differences between the size structure of the populations studied. The major difference among the studied sites is the range of tree size classes, encompassing maximum dbh values between 35 cm and 70 cm for all stands.

The tree age structure of the 12 stands studied were plotted as frequency distributions in time intervals of 15 years (Fig. 4). The ~ 3600 aged mountain pines surviving today range from 1 to nearly 400 years old. Although we intensively examined the area inside each plot, due to the difficulty of detecting very small seedlings (1 to 3 years) we think that the sampling probably underestimated the frequency of recently established seedlings. Thus, the presented age structures are confined to pines established prior to year 2000. Mountain pines older than 200 years are scarce in the stands studied. This finding explains why 8 of the 12 presented age frequency distributions have the older age classes empty. In fact, only 4.5% ± 4% (mean ± 1SD) of the individuals of all plots were established before 1895. The majority of the sampled pines (79%) were < 50 years old and thus established recently, from the mid 1950s to the late 1990s. Individuals < 15 years old (establishment period 1986-2000) represent around 50% (ranging from 40% to 67%) of total population in 7 of the 12 studied plots. Only in 1 plot fewer than 5% of individuals established in the 1986-2000 period, while in the remaining 4 plots this age class represents ~20% of total population.

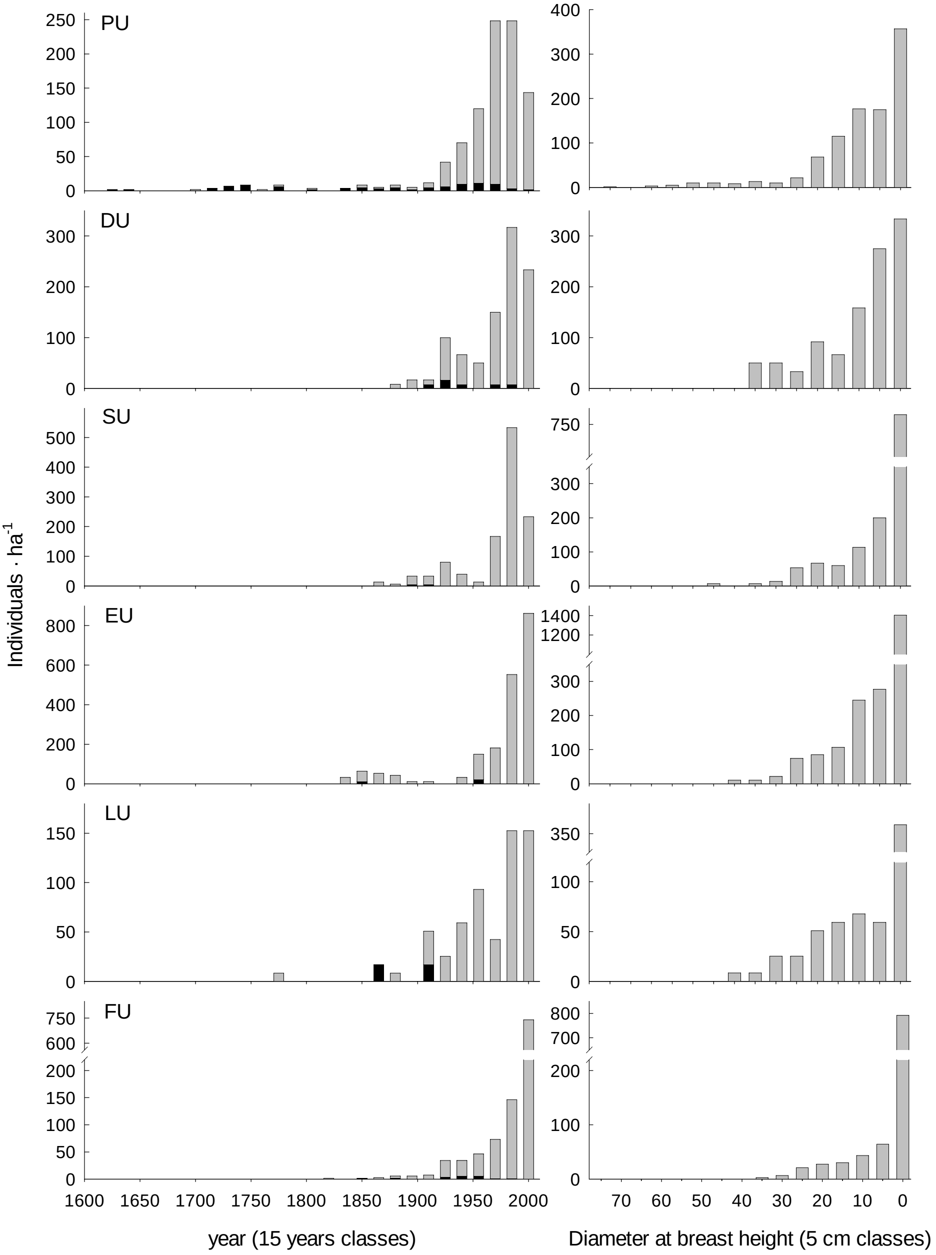

Figure 4. Age frequency distributions (left) and diameter at breast height (dbh) frequency distributions (right) for all living *Pinus uncinata* individuals at the 12 treelines studied across the Catalan Pyrenees (Spain) and Andorra. Sites are arranged following the west-east gradient. In the age frequency distributions, light grey bars indicate individuals with dating error < 15 years, black bars indicate individuals with a greater dating error. Note that vertical scale varies between populations.

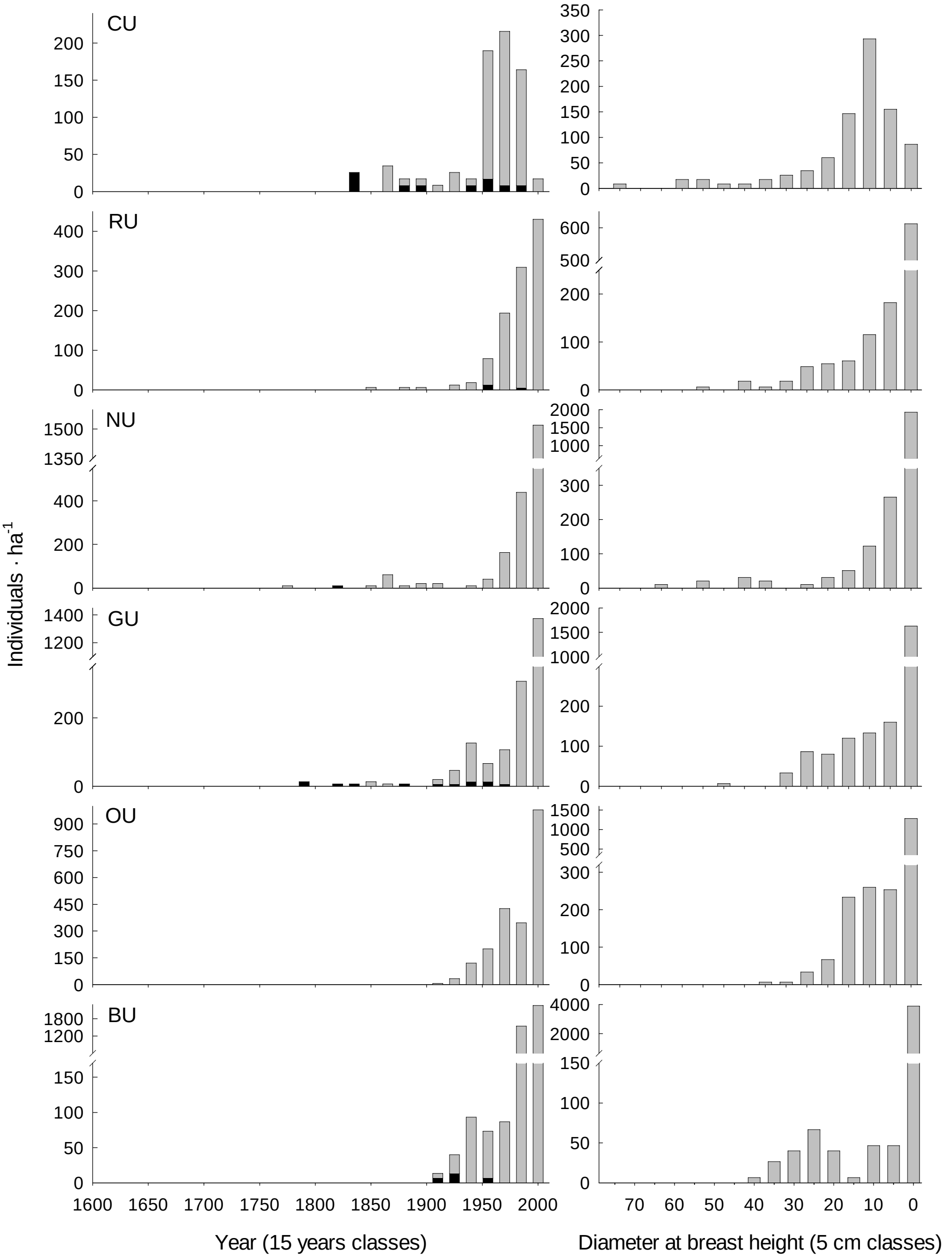

Figure 4. *Continued*

The described densification process during the second half of the 20th century has mainly occurred inside the ecotone, thus below the current treelimit. A total of 88.3% ± 14.3% (mean ± 1SD) of the individuals recruited since 1950s have established above the timberline and below the treelimit (Fig. 5). However, the treelimit position in 50% of the treeline ecotones studied has risen during this period. This was evidenced by the age < 50 years of the trees forming the current treelimit of such treeline ecotones (Fig. 5). The youngest individual which marks the treelimit position established in 1988 in the PU plot, while the oldest established in the 19th century (1890) in the NU plot.

The results of negative exponential and power models adjusted to age frequency distributions are presented in Table 3. Negative exponential modelling provided the best fit for 5 populations, whereas the power function provided the best fit for 6 populations. Both models explained a high degree of variance in all cases. Annual rates of mortality ranged between 0.09%-0.35% and 0.91%-2.13% for negative exponential and power function models, respectively. Mortality rates obtained in mature subalpine *P. uncinata* forests range between 0.56%-0.6% (Bosch & Gutiérrez 1999), while other subalpine conifer mortality rates range between 0.6%-2.15% (Hett & Loucks 1976; Harcombe 1986; Brang 1988). Only one of the studied plots, CU, presented an age structure that could not be significantly described with either of the adjusted models. This population clearly presents a different age structure from the rest of the stands, with scarce regeneration since the 1970s. There are 3 other plots (PU, DU, SU) that do not present the youngest age class (1986-2000) as the most abundant, but still large numbers of recruits recently established in these populations.

Whereas two of the stands (FU and RU) present unimodal distributions where the youngest class is the mode, the age structure of the 10 remaining populations presents a multimodal age frequency distribution. Six of the stands studied present a more or less bimodal distribution (BU, DU, EU, NU, OU, SU), and the other four a multimodal distribution (CU, GU, LU, PU). When comparing the temporal pattern of recruitment between plots, significant differences are present between most of the study sites (54 out of 66 paired Kolmogorov-Smirnov test, Bonferroni-adjusted $p < 0.001$). Intra-site comparisons of the age frequency distributions in PU and FU showed that, in contrast to the differing age structures between plots, 92% of paired Kolmogorov-Smirnov test (Bonferroni-adjusted $p<0.01$) show no significant differences between subplots of the same population.

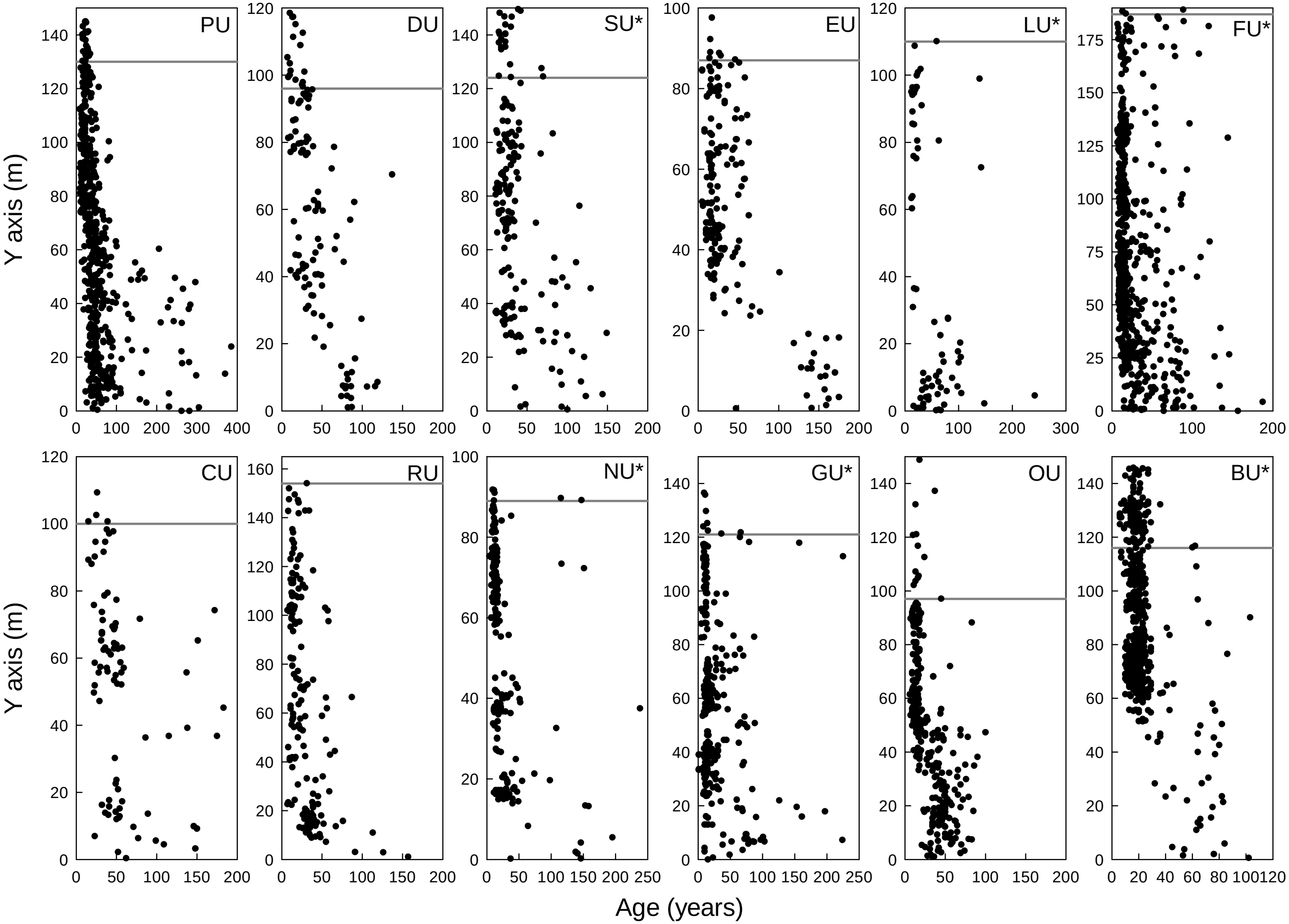

Figure 5. Age and position (Y axis) of all living *Pinus uncinata* individuals of each population. Horizontal line at each plot represents the current treelimit position at each site, and the * symbol denotes populations where treelimit is a tree established before year 1950.

Table 3. Mortality rate coefficients for the fitted linearized negative exponential and power function models to the age structure data of the 12 treelines studied. Annual mortality rates derive from the mortality rate coefficients.

Site	Negative exponential (r^2)	Mortality Rate Coefficient	Annual Mortality rate	Power function (r^2)	Mortality rate coefficient	Annual Mortality rate
PU	0.63**	-0.014	0.09	0.71**	-1.502	1.48
DU	0.86**	-0.028	0.19	0.69*	-1.149	2.11
SU	0.64*	-0.024	0.16	0.61*	-1.177	2.05
EU	0.28	-0.016	0.11	0.43*	-1.314	1.79
LU	0.53*	-0.024	0.16	0.46*	-1.139	2.13
FU	0.93**	-0.035	0.23	0.94**	-1.754	1.15
CU	0.23	-0.012	0.08	0.1	-0.395	4.49
RU	0.80*	-0.045	0.30	0.74*	-1.969	0.93
NU	0.46*	-0.024	0.16	0.63*	-1.817	1.08
GU	0.67**	-0.027	0.18	0.78**	-1.851	1.05
OU	0.91**	-0.049	0.33	0.71*	-1.589	1.36
BU	0.85*	-0.053	0.35	0.86*	-1.987	0.91

goodness of fit given by r^2; * $p < 0.05$, ** $p < 0.001$

Although the age frequency distributions of the 12 plots studied show differing age structures, two apparent trends are shared by the vast majority of them. The most evident and striking, is that the age distributions of all treeline ecotones, except CU, present at least one abrupt increase in tree recruitment after 1955. Moreover, in five populations two abrupt increases in their age frequency distributions were detected during this period. However, the recruitment increases were not synchronous between all the stands studied. Three periods of enhanced recruitment were detected: 1956-1970, 1971-1985 and 1986-2000. The most ubiquitous was the recruitment increase in the 1971-1985 period, observed in eight treeline ecotones, while the other periods of enhanced recruitment were detected in four stands. Dead seedlings were scarce in the studied populations, only 2.63% of the total sampled seedlings (ranging from 0% to 14% among plots). Finally, the other successful recruitment period, which occurred in the mid of the 19th century (period 1836-1865), was observed in six of the nine populations which include old enough individuals.

Standardised age, total height and basal diameter along the altitudinal gradient evidenced gradual and step-like patterns. Three of the treeline ecotones, representative of all the stands studied, are presented in Figure 6. In the PU plot, a differential pattern of altitudinal decrease in tree age, total height and basal diameter can be observed. Whereas tree age showed a step-like distribution, total tree height and basal diameter presented a gradual decrease along the altitudinal gradient. This pattern was also observed in the EU and CU plots. In the FU plot, a gradual decrease of tree age, total height and basal diameter occured. This was the most common situation, also detected in the DU, SU, LU, RU, NU and GU plots. Finally, in the OU and BU stands, all the analysed variables showed a step-like distribution along the altitudinal gradient.

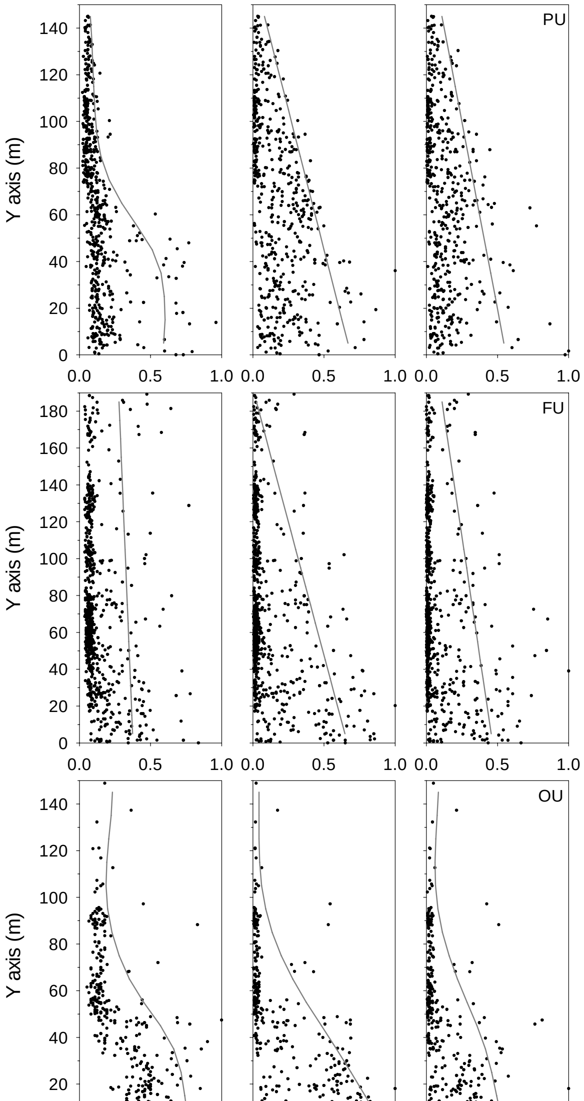

Figure 6. Standardised tree age, total height and basal diameter through the altitudinal gradient (*Y* axis) in three of the treeline ecotones representative of all the stands studied. Grey lines represent linear or smooth spline fitting to the 95th quantile of the presented variables to highlight gradual decrease and step-like patterns, respectively.

Discussion

Size structure distribution highlights that all the studied populations, except one, are dominated by small individuals (seedlings and saplings). This would suggest that tree establishment was abundant in these stands in recent decades (Stöcklin & Körner 1999). Suppressed growth of some trees due to extreme site conditions and/or competition processes may explain why some stands present wider age discontinuities than might be expected from their diameter distribution (Lusk & Ogden 1992). In turn, this would explain that size distributions are more similar among plots than age distributions are. Although the assumptions of stable population size and constant recruitment and mortality rates may seldom be met in natural populations (Johnson *et al*. 1994), fitting negative exponential and power functions to empirical data may still be useful as a means of detecting deviations from these simple models (Hett & Loucks 1976; Ågren & Zackrisson 1990). Deviations of the actual age structure from the modelled or predicted age structures may reflect changing patterns of regeneration and/or survival over time. Such deviations can be identified by an inspection of the residuals. In our study, the analysis of the residuals (results not shown) provided no clear patterns among all the populations since recruitment presented fluctuations of periods above and below the values predicted at each site. These departures from the theoretical models may indicate that seedlings establishment and survival at treeline varied through time among and between sites (Daniels & Veblen 2004).

In general, the power function, which includes a changing mortality rate, provides a better description of population depletion in stands with older age classes. In two of the stands studied (FU, RU), the marked J-shaped distribution would indicate sustained inputs of individuals. In these two populations, the number of pines in the classes since the 1986-2000 class drop rapidly. Although the fitted models also present noticeable deviations between the predicted and observed values, the age structure of these stands are compatible with an assumption of constant recruitment and mortality rates that could be indicative of stable populations in the long term (Payette 2007). However, the age distributions of these two treelines could only represent a transient state of an ever-changing population structure (Ågren & Zackrisson 1990).

Keeping in mind the limitations of static age structure interpretation, it seems that some observed trends among the 12 studied populations could not be merely a methodological artifact. The plots studied show differing age structures, but several features are shared among them. The dominance of multimodal age distributions (83% of studied populations), also observed in other alpine or forest-tundra ecotones (Sceicz & MacDonald 1995; Camarero 1999; Cuevas 2002), indicate that recruitment in treeline forest ecosystems is episodic rather than gradual (Cullen *et al.* 2001; Walther *et al.* 2005). Based on the differing structure of the age frequency distributions it may seem that the periods of enhanced recruitment are more or less randomly distributed over time, but there are no periods of abundant recruitment that are not periods of abundant recruitment in at least several other plots. This is the case of the increased recruitment in the mid 19th century (mid 1830s to mid 1860s). Nearly 70% of the populations that are sufficiently old, present this change in the age frequency distribution. It is important to note that due to cumulative effects of mortality, past periods of enhanced recruitment become increasingly difficult to detect as the cohort ages (Villalba & Veblen 1997b). Thus, we think that the detected presence of enhanced pine recruitment from the mid 1830s to the mid 1860s in several plots distributed over the Pyrenees is a real trend. Furthermore, this enhanced regeneration, also present in other treeline populations studied in the Pyrenees (Camarero 1999), coincides with positive growth trends since 1830 reported in the Pyrenees (Bourquin-Mignot & Girardclos 2001) and Central Italy (Piovesan *et al.* 2003) attributed to the end of the Little Ice Age.

Substantial densification in treeline populations during the 20th century seems to be a common phenomenon in northern and high-elevation environments, and is more frequently occurring than actual treeline advance (Payette & Filion 1985; Scott *et al.* 1987 Payette & Lavoie 1994; Sceicz & MacDonald 1995; Kullman 1997; MacDonald *et al.* 1998; Camarero 1999; Stöcklin & Körner 1999; Payette *et al.* 2001; Juntunen *et al.* 2002; Shiyatov 2003; Camarero & Gutiérrez 2004; Kullman 2005; Danby & Hik 2007). This densification trend is also apparent in all the 12 studied populations over the Pyrenees, but is particularly pronounced during the past 50 years in 92% of the stands studied. Despite the high mortality rates expected at treeline, the overall annual mortality rates derived from the adjusted negative exponential and power function models are similar to those reported in lower subalpine forests (Hett & Loucks 1976; Harcombe 1986; Brang 1988; Bosch & Gutiérrez 1999). Our results indicate that past and present environmental conditions are not causing severe tree mortality at the stands studied. In addition, there was a low presence of dead seedlings in the populations studied (2.63% of total sampled seedlings). Thus, it is reasonable to believe that under current climate conditions a large part of the regeneration pool should survive and that the high seedling density observed in recent decades most likely represents real increases in stand density (Lloyd & Fastie 2003; Gamache & Payette 2005). The latter trend contrasts with the results of other studies in the Pyrenees and isolated

Spanish *Pinus uncinata* populations (Camarero & Gutiérrez 2004; Camarero & Gutiérrez 2007), and other alpine areas (Cuevas 2002; Villalba & Veblen 1997b), that reported most evident tree recruitment increase in the first half and the mid of the 20th century and a deficit in seedling establishment after the 1970s-1980s.

The observed trend in the age frequency distributions during the second half of the 20th century does not appear as a gradual increase in tree frequency up to a peak over time. Instead, all the populations studied (except CU) show at least one sharp increase in recruitment after 1950, and 83% of them show an abrupt recruitment increase after the 1970s. Recent studies in west-central Sweden (Kullman 2005), reported a clearly discernible process of conspicuous infilling (scattered young trees and saplings are spreading out into previously treeless mires) since the mid 1980s. Gamache & Payette (2005), also describe an important increase in seedling establishment since the late 1970s in the treelines of the southernmost tundra of Northen Québec. Finally, massive stone pine (*Pinus cembra* L.) regeneration has also been detected in the Western Italian Alps since the 1960s (Motta *et al.* 2006). To some extent, the rapid shifts in recruitment tendencies since the 1950s could be indicative of positive feedback processes. Increasing stand density can modify the distribution pattern of individuals which can play a role in positive feedback wherein trees are able to modify environmental conditions (Alftine & Malanson 2004). Such modifications (e.g., snow distribution and wind conditions) promote further seedling establishment, growth and survival (MacDonald 1998; Smith *et al.* 2003; Bekker 2005; Kullman 2005). The importance of mechanisms of this kind is suggested to increase with stress conditions (Callaway *et al.* 2002) and to maintain patterning of alpine treelines (Sveinbjörnsson *et al.* 2002; Alftine & Malanson 2004).

The presence of significant differences in inter-site but not in intra-site comparisons of the demographic age structure at treeline emphasizes the importance of local factors (i.e., climate, natural or anthropogenic disturbance regimes) uniformly affecting entire populations. The observed differential treeline responses may result from changes occuring and interacting at different scales (Resler 2006). However, the coincidence of periods of enhanced recruitment in alpine ecotone populations of mountain pine over a large area of the Pyrenees (i.e., mid 19th century, second half of 20th century), suggests that a common external factor, like the climate, has an important role in synchronizing these patterns (League & Veblen 2006; Camarero & Gutiérrez 2007). Other authors relate variation in treeline populations age structure to climatic variation (Kullman 1987; Payette *et al.* 1989; Gamache & Payette 2005; Kullman 2005). In contrast, several studies conclude that recent establishment of trees in the treeline ecotone results from declined human land-use (Hofgaard 1997, 1999; Holtmeier 2003; Cairns & Moen 2004; Motta *et al*. 2006; Gehring-Fasel *et al*. 2007). In the Pyrenees, as in many parts of the world, seasonal farming in high mountain areas has a long tradition, as well as logging and/or burning to lesser extent. However, important land-use abandonment during the 20th century (more pronounced since 1950s) is a general phenomenon across all the Pyrenees (García-Ruiz *et al*. 1996). This occurred in parallel to climatic warming (Diaz & Bradley 1997). Given that local conditions greatly determine treeline responses, it is not feasible to determine the driving factor (climate or land use changes) of the treeline ecotones studied based on the general trends mentioned above. However, we suggest that treeline transition characteristics, gradual decline or step-like transitions along the altitudinal gradient, may serve to illustrate different stages concerning time since land use abandonment and its implications for treeline dynamics. Both natural (e.g. topography-induced extreme winds, snow avalanches, rockfall) and anthropogenic disturbances (e.g. fires, grazing pressure) are very important factors in determining local treeline pattern and position (e.g. Mast *et al*. 1998; Holtmeier & Broll 2005; Korner 2007). In absence of such disturbances, a gradual transition from the subalpine forest to the treeless alpine area, resulting from the increased unfavourable environmental conditions with altitude, is expected. Since the study sites are located in homogeneous slopes avoiding major natural disturbances, we propose that step-like distribution patterns might derive from human-induced perturbations.

The most common pattern in the treelines studied is a progressive decline in tree age and in tree size (total height and basal diameter) through the altitudinal gradient. Populations' dynamics in these ecotones may be mainly influenced by climate and therefore such treelines may present high sensitivity to climatic change, just as formerly the natural climatic treeline had been in the past, although its position could be lower than the potential treeline altitude (Holtmeier & Broll 2005). In contrast, the observed treeline dynamics in step-like ecotones may result from recent land-use changes. Hence, the cessation of anthropogenic activity at alpine treeline, in the context of warmer temperatures, might have triggered the described treeline responses in some of the stands studied. The most clear example of this situation may be the two study sites where both tree age and size present step-like transitions. Furthermore, the lack of old trees in these stands (oldest individual < 120 years) and the dominance of recently established pines (1986-2000 period) reinforce the idea that the recent land use changes may have triggered the observed densification trends. Similarly, the three stands studied that present step-like patterns in tree age coupled to a progressive reduction in tree size along the altitudinal gradient may have been affected by human-induced perturbations more recently than we initially though in the field based on the tree size smooth transitions. But the demographic structure of these populations may indicate that land use changes are not as recent as in the two plots mentioned above. The scarcity of dead individuals and tree remnants in the populations where step-like patterns are only present in tree age evidence the great responsiveness of tree growth to short term environmental variation under the current climatic conditions (Payette & Lavoie 1994; Kullman 2002). This is reinforced by the age of the tree forming the current treelimit (<50 years) in these three treeline ecotones. Overall, our results suggest that gradual transitions in tree size (total height and basal diameter) could mask in some cases the effect of recent perturbations, which may be evident by the tree age transition pattern.

Our results show that treelimit stability since 1950, as reported by previous treeline studies in the Pyrenees (Camarero 1999; Camarero & Gutiérrez 2004), is not ubiquitous at a regional scale and emphasizes once again the presence of differential treeline responses (Dalen & Hofgaard 2005). Treelimit upward shifts have been evidenced in this study by the age of the tree forming the current treelimit, which is less than 50 years in 50% of studied treelines. Given the absence of dead tree remnants, these young trees forming the current treelimit have established and vertically grown up to 2 m height during the second half of the 20th century rising the treelimit in the recent past. The rate and magnitude of the detected upward shifts in the Pyrenees cannot be assessed accurately with the current data. Detailed studies on treelimit position (e.g., extensive age determination of trees at 2 m height) are needed. But the detected upward shift in some of the populations studied suggests that important changes in alpine vegetation could occur. For example, treeline upward shifts and densification processes may lead to a loss and fragmentation of the habitat of alpine species (Dirnböck *et al*. 2003), which in turn may increase their extinction risk. However, it is not obvious how treeline ecotones will respond to the increased temperatures and decreased precipitation predicted for sourthern Europe (IPCC 2007), which could lead to drought stress limitations for tree growth and drought-induced tree mortality (Camarero & Gutiérrez 2004; Wilmking *et al*. 2004; Suarez *et al*. 2004; Wilmking & Juday 2005). Long-term monitoring at alpine treeline and interdisciplinary projects (e.g. including ecological and historic documentation research) are required to improve our understanding of treeline responses to global change.

Main conclusions

Despite the differing age structure of populations at alpine treeline, a regional densification trend in the ecotone has occurred over a large area of the Pyrenees during the 20th century as reported in many other altitudinal and latitudinal treelines. This occurred in the context of climatic warming and important land use abandonment during the second half of the 20th century. In fact, the observed afforestation process has been particularly important during the past 50 years, and more apparent in the vast majority of populations since the beginning of the 1970s. Furthermore, the observed recent densification trend has occurred as rapid shifts in recruitment tendencies, which may be indicative of the importance of positive feedback mechanisms in the treeline dynamics. In contrast with previous reports for the Pyrenees, current treeline densification has been coupled to treelimit rise in half of the studied ecotones. This highlights both the presence of differential treeline responses and, to some extent, indicates the great responsiveness of the treelimit to short-term climatic changes. Moreover, the detected upward shifts at treeline could trigger important changes in alpine vegetation if future climatic conditions do not become limiting for tree growth and recruitment (e.g. drought stress). The presence of recent and past synchronous recruitment trends suggests the important role of a common external factor like climate modulating recruitment trends at a regional scale. But the differing intensity of anthropogenic disturbances over time and space may have strongly modulated the treeline population trends at local scale. We suggest that in absence of major natural perturbations (e.g. snow avalanches, extreme winds), step-like patterns in tree age along the altitudinal gradient are feasible records of human-induced perturbations.

Acknowledgements

We are grateful to all the people who helped us with the field work. This study was supported by the project REN2002-04268-C02 (Spanish Ministry of Research). Enric Batllori thanks the support of a MEC-FPU grant. The authors thank Pete Fulé and the reviewers for their constructive comments on the initial manuscript.

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Capítol II. Seedling recruitment, survival and facilitation in alpine *Pinus uncinata* treelines. Implications and potential responses to climate warming

Resum

La temperatura és el factor que més limita el creixement i la regeneració al límit superior del bosc. Tot i això, l'esperada expansió altitudinal de l'ecotò superior en resposta a al canvi climàtic no ha estat generalitzada. La manca d'una sincronització precisa entre la dinàmica del límit superior del bosc i la variabilitat climàtica ha de respondre a altres factors, a part del règim climàtic, que determinen l'establiment dels plançons i el seu creixement. Entre els factors més limitants per a la dinàmica de regeneració al límit superior del bosc hi ha la disponibilitat d'hàbitat favorable per a la germinació, i els efectes de faciltació que afavoririen la posterior supervivència i el creixement del plançons.

En aquest estudi s'analitza la rellevància d'aquests dos factors al límit superior del bosc de *Pinus uncinata* dels Pirineus. Per determinar el nínxol de regeneració de l'espècie s'ha analitzat el microhàbitat dels plançons establerts naturalment en parcel·les rectangulars situades al llarg de la transició bosc-prats alpins. De cada plançó s'anotava la vegetació i el substrat on es trobaven, i la distància a elements que potencialment podrien exercir efectes de facilitació, i per tant, millorar la seva supervivència. També es presenten els resultats d'una plantació experimental que pretén determinar si existeixen interaccions positives entre els plançons i individus adults de la mateixa espècie que afavoreixin la supervivència i el creixement vertical dels plançons. Es van transplantar 820 plançons a diferents distàncies i orientacions d'individus conspecífics, i se'n va determinar la seva supervivència i creixement durant 2 anys.

La caracterització del microhàbitat dels plançons indica que els plançons de *Pinus uncinata* s'estableixen sobre terra fina, graves i matèria orgànica, en llocs on hi ha un recobriment lax de vegetació. La proximitat de la gran majoria dels plançons mostrejats a roques, estructures del microrelleu i arbustos com el *Rhododendron ferrugineum* sembla indicar que els processos de facilitació a petita escala determinen els llocs segur de reclutament de l'espècie. Els resultats de la plantació experimental evidencien que els individus conspecífics exerceixen importants efectes de facilitació (relacionats amb l'acumulació diferencial del mantell nival) sobre el plançons, modulant-ne fortament el el seu patró espacial de supervivència. Els resultats presentats, semblen indicar que la disponibilitat de llocs segur per al reclutament i la facilitació exercida per individus conspecífics modulen fortament la dinàmica de regeneració al límit superior del bosc.

Seedling recruitment, survival and facilitation in alpine *Pinus uncinata* treelines. Implications and potential responses to climate warming

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Article enviat a: *Global Ecology and Biogeography*

Abstract

Aims. Alpine treeline ecotones are harsh environments where low temperatures constrain tree regeneration and growth. However, the expected upward shift of treelines in response to climate warming has not been ubiquitous. The lack of coupling between treeline dynamics and climate change might be explained by factors other than climate variation that determine seedling establishment and growth in alpine treeline ecotones. Two of the main constraints on tree recruitment at the treeline are the availability of suitable habitat for establishment and the potential effects of facilitation on seedling survival and growth.

Location. We assess the relevance of these factors for *Pinus uncinata* forest-alpine grassland ecotones in the Spanish Pyrenees.

Methods. We analysed the microhabitat of naturally established seedlings in rectangular plots set along the treeline ecotone, assessing the habitat type and the proximity to potentially protective elements that may improve microsite conditions. We tested whether positive interactions exerted by conspecific individuals influence regeneration at the treeline by performing a transplantation field experiment to evaluate the extent of microsite improvement on seedling survival and longitudinal growth. A total of 820 seedlings were transplanted at different distances and orientations (resulting in 12 positions) and monitored over two climatically contrasting years.

Results. Safe sites for *P. uncinata* recruits consisted of sparse vegetation covering bare soil, gravel or litter, and close to structural elements such as stones, microtopographical shelters and shrubs which may ameliorate microsite conditions. The field experiment showed that positive interactions enhance seedling survival and growth, altering the spatial patterns of recruit survivorship, especially during winters when the snowpack is shallow and irregular.

Main conclusions. Our results suggest that scarce safe-site availability and uneven facilitation by conspecific individuals may distort or counter the response of treelines to climate warming.

Key words: ecotone, facilitation, generalized linear models, *Pinus uncinata*, Pyrenees, treeline, recruitment, regeneration niche.

Introduction

Alpine treeline ecotones across most of the world's mountains are being studied because of their potential for monitoring the effects of climate warming on forest ecosystems (Slatyer & Noble 1992; Körner & Paulsen 2004; Holtmeier & Broll 2005). The basic assumption behind this potential is the expected upslope shifts of forests worldwide in response to climate warming during the 20th century (Brubaker 1986; Parmesan & Yohe 2003). However, despite global climate warming, upward advance of alpine treelines is not ubiquitous (Meshinev *et al.* 2000; Cullen *et al.* 2001; Shiyatov 2003; Camarero & Gutiérrez 2004; Millar *et al.* 2004; Dalen & Hofhaard 2005). Indeed, different responses to recent climate warming have been detected, which suggests that treeline dynamics depends on species-specific traits and environmental constraints operating at local and regional scales as well as on temperature (Noble 1993; Hofgaard 1997; Lloyd & Graumlich 1997; Dullinger *et al.* 2004; Danby & Hik 2007). Moreover, climate is only one aspect of environmental variation at the treeline, and other factors also have to be considered. Land use may be one of the most important of such factors (Dirnböck *et al.* 2003). We therefore need a deeper understanding of the mechanisms involved in such varied responses in order to be able to use alpine treelines as monitors of the effects of climate warming and land use changes.

Assessment of treeline response to environmental variability at regional and local scales is much more complex than at the global scale (Holtmeier & Broll 2005). First, treeline ecotones may vary with local conditions such as topography (Resler 2006), the disturbance regime (Cullen *et al*. 2001; Daniels & Veblen 2004), ecotone composition (Danby & Hik 2007) and climate variability (Camarero & Gutiérrez 2004). Second, species-specific traits such as seed production and dispersal (Dullinger *et al*. 2004), lifespan, and persistence through slow vegetative growth (e.g., krummholz individuals) may cause non-linear responses to climate trends ranging from rapid threshold-type responses (Kullman 2002; Danby & Hik 2007) to lagged responses or even treeline inertia (Kullman 1989; Payette 2007).

To wholly understand the seemingly paradoxical responses of treeline ecotones to climate warming, we need a deeper knowledge of the mechanisms involved in tree establishment above the upper forest limit, i.e. within the treeline ecotone (Wiegand *et al*. 2006). Seedling establishment is a key component in plant distribution patterns (Harper 1977) and seedling life stage is especially crucial at climatically stressing sites such as alpine treelines. The success or otherwise of regeneration determines whether the treeline shifts or remains static in response to environmental changes (Hättenschwiler & Smith 1999; Cuevas 2000; Holtmeier 2003). In addition to seed production and dispersal constraints, the availability of safe sites above the forest limit, i.e. "forest invasiveness", has been regarded as the most limiting factor for tree regeneration and treeline advance (Hobbie & Chapin 1998; Camarero & Gutiérrez 1999; Dullinger *et al*. 2004). Preferential recruitment at safe sites is linked to the regeneration niche concept (Grubb 1977), which reflects the fine-scale environment where a tree species germinates and establishes. In spite of the relevance of the regeneration niche in population processes, few studies describe in detail the microhabitat where most seedlings establish at alpine treelines.

In harsh environments such as treelines, establishment depends not only on safe site availability but also on facilitation or the positive interactions of neighbours buffering one another from stressful conditions (Callaway 1995). In treeline ecotones, microsite facilitation – intraspecific, interespecific or by sheltering of surface features – may be critical for seed germination to subsequent seedling performance (Ball *et al.* 1997; Germino & Smith 1999; Germino *et al.* 2002; Resler 2006). Some authors have described the positive influence of conspecific mature trees on seedling abundance in alpine treeline ecotones (Holtmeier & Broll 1992; Callaway 1998; Hättenschwiler & Smith 1999). However, to our knowledge, no study has experimentally tested in the field the extent of conspecific facilitation on seedling survival and growth at alpine treeline. Furthermore, positive interactions become more important when climatic stress increases, such as during suboptimal climatic years (Kitzberger *et al.* 2000); windy and dry (little snow cover) winter conditions in the case of alpine treelines. Thus, the role of conspecific individuals in facilitating seedling survival and growth should be tested in climatically contrasting years.

In this study, we describe the regeneration niche of *Pinus uncinata* and test the effects of conspecific individuals on seedling survival and growth at the Pyrenean alpine treeline. To address these issues we: (1) analysed the substrate and vegetation cover of naturally established seedlings, (2) quantified the seedlings' distance to elements which potentially provide microsite facilitation (stones, microtopogric shelters and shrubs) and (3) transplanted seedlings in the field to study positive interactions by potential "nurse" krummholz. We hypothesize that seedling survival and growth will be most affected by the pattern of wind-driven snowpack accumulation near krummholz mats during climatically unfavourable years.

Materials and methods

Study sites and species

The study was conducted at 11 sites located in the eastern half of the Spanish Pyrenees (Catalan Pyrenees) and Andorra (Fig. 1; Table 1). At each site we place a rectangular plot that contained the alpine treeline ecotone, each thus including the forest limit (closed forest at high altitude) and the treelimit (uppermost elevation of trees with a minimum height of 2 m). The area of the plots varied from 960 to 7600 m^2 depending on the transition characteristics. This study was mainly restricted to north-facing treelines and together they covered a wide range of landforms and plant communities. Field sampling was conducted between 2003 and 2007; in late spring and summer.

The ecotones studied are dominated by *Pinus uncinata* Ram. ex DC., which reaches its southern and western distribution limits in the Iberian Peninsula. This species is a shade-intolerant conifer which dominates most of the subalpine forests and treeline ecotones in the Spanish Pyrenees, on any substrate and at any exposure (Ninot *et al.* 2007). This pine forms dense forests between ~ 1700 m and ~ 2200 m a.s.l. whose canopy density and tree height diminish near the timberline, due to the strongly limiting environmental conditions there (Erschbamer & Wallnöfer 2007). The potential treeline elevation may reach between 2200-2450 m in the Pyrenees, depending on continentality, exposure and landform (Carreras *et al.* 1996; Bolòs *et al.* 2005). Above the forest limit, the alpine zone is typically covered by contrasting vegetation mosaics which include short meso-xerophilous pastures of *Festuca airoides* Lam. or *Kobresia myosuroides* (Vill.) Fiori, ericaceous dwarf shrubs (of *Rhododendron ferrugineum* L., *Arctostaphylos uva-ursi* (L.) Spreng. and *Vaccinium uliginosum* L.), together with sparse scree and rocky substrata vegetation (Braun-Blanquet 1948; Carrillo & Ninot 1992; Illa *et al*. 2006). Other shrubs (*Juniperus communis* subsp. *alpina* L.) and dwarf shrubs (*Loiseleuria procumbens* (L.) Desv., *Calluna vulgaris* (L.) Hull and *Dryas octopetala* L.) are also common at the treeline.

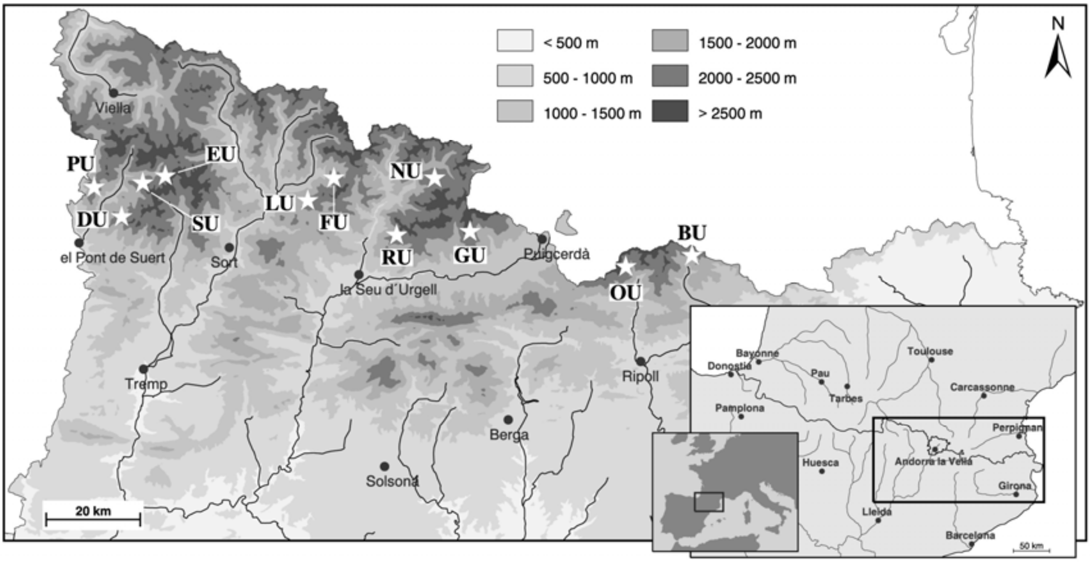

Figure 1. Location of the study sites in Catalan Pyrenees, NE Spain, and Andorra.

Field data

Natural regeneration was carefully examined in each plot. The ages of all seedlings (individuals < 0.5 m high) were determined in the field by counting the terminal bud scars (internodes) along the main stem. As seedling age estimates based on the number of internodes tend to underestimate the true, root-collar age (Camarero 1999), we collected 270 small pines (up to 1.5 m) from six representative plots to calculate age correction functions. We considered this sampling to be sufficiently representative of the 11 sites studied, and for the sites not sampled we used the function calculated for the nearest of the six sampled stands. The seedlings together with their roots were collected from within the treeline ecotones studied, near the study plots. A cross-section of about 2 to 4 cm thickness was cut at the base of each pine containing root and stem tissue. The root collar for each disc was detected in the laboratory through progressive sanding and noting the shift in the central pith, from a vascular cylinder in the root to undifferentiated parenchyma cells in the stem (Gutsell & Johnson 2002). Cross-sections were dated by ring counting and age at the root collar was then compared with the age obtained from counting the internodes at the field. A linear fit was obtained to improve seedling age estimates (Fig. 2).

Table 1. Characteristics of the stands of *Pinus uncinata* sampled at the alpine treeline in the Catalan Pyrenees (Spain) and Andorra.

Code	Latitude	Longitude	Plot size (m^2)	Elevation (m)	Slope (º)	Aspect	Bedrock
PU	42º 31’	0º 45’	6000	2199 - 2268	28	N	lime
DU	42º 28’	0º 49’	1200	2010 - 2069	30	N	lime
SU	42º 32’	0º 53’	1500	2270 - 2338	27	NW	lime
EU	42º 33’	0º 56’	940	2299 - 2339	24	W	granodiorite
LU	42º 31’	1º 21’	1180	2363 - 2405	21	N	slate
FU	42º 33’	1º 23’	7600	2352 - 2435	24	NW	slate
CU	42º 33’	1º 25’	1160	2250 - 2297	26	NW	lime
RU	42º 26’	1º 32’	1650	2236 - 2271	24	W	slate
NU	42º 34’	1º 37’	980	2266 - 2314	29	N	lime
GU	42º 27’	1º 44’	1500	2312 - 2365	16	NE	slate
OU	42º 23’	2º 08’	1500	2241 - 2308	27	N	slate
BU	42º 24’	2º 19’	1500	2184 - 2241	22	N	slate

For all seedlings under 10 years (n = 913) the vegetation and substrate cover with which they were associated (surrounding substrate in a radius of 5 cm) were recorded. This included the main soil and vegetation types as follows: bare soil, gravel, medium-size stones (diameter 5-10 cm), organic matter, dense low shrubs, dwarf shrubs and pastures. Seedling age was limited to 10 years in order to obtain a more accurate estimation of the prevailing microsite composition during the first years. Furthermore, we compared the vegetation and substrate cover of seedlings with age ≤ 5 years (n = 96) and seedlings with 10 ≥ age > 5 years (n = 817) to ascertain whether habitat type changed, which, if found to be the case, could lead to misinterpretation of the results in terms of the description of typical recruit microhabitat. The presence of and distance to the nearest elements that modify and potentially improve microsite conditions (stones, microtopographic shelters and the low shrub *Rhododendron ferrugineum*) were determined for 1667 seedlings at 8 sites. These elements are appropriate for microsite facilitation at alpine treeline ecotones, and they are regarded as potential protective elements (Germino *et al.* 2002; Akhalkatsi *et al.* 2006; Resler 2006).

To compare the microsite availability at each site with the seedling regeneration niche, the major types of vegetation and substrate cover were estimated in each plot by means of phytosociological relevés of 0.5 m^2 set every 2 m along the altitudinal axis of each plot. This quantification provided a good estimate of microhabitat availability at the study sites.

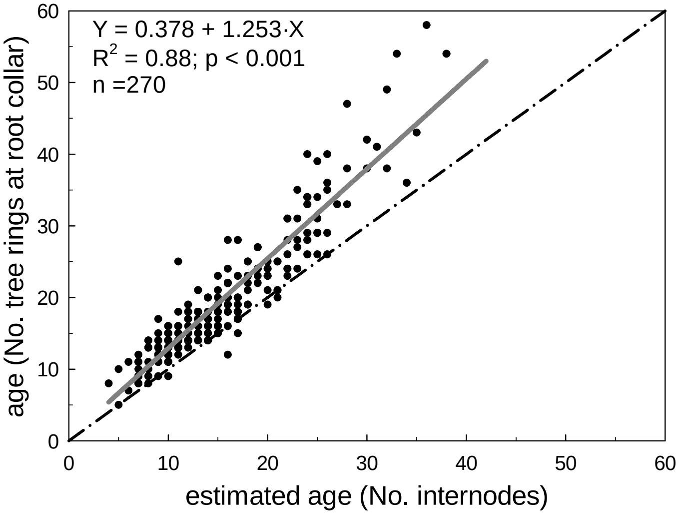

Figure 2. Age-correction function (gray bold line) for the collected 270 seedlings. The dashed line corresponds to the *x* = *y* function.

Field experiment

We performed a field experiment to test the influence of potential “nurse” krummholz on seedling survival and height increase at the Serrat de Capifonts site (Fig. 1, Table 1); a N-facing and relatively undisturbed treeline. The field experiment consisted of transplanting seedlings (grown for 3-4 years in a nursery and mostly 20-30 cm high) at various positions with respect to 60 krummholz “nurse” individuals. Around each krummholz, we planted one seedling at each of the 12 points resulting from the combination of three distances (0.25, 0.5 and 1 m) and four orientations (leeward, windward, westward –hereafter right– and eastward –hereafter left) from the krummholz crown. To assess how positive interactions changed over time as a function of climatic stress, the field experiment was performed during the winters 2004-2005 and 2005-2006. These had contrasting climatic conditions with snow depth much lower in the first than in the second winter (Fig. 3). Thus, we planted 360 seedlings in October 2004 and 360 more in October 2005, and we treated these two groups of seedlings as two distinct cohorts (2004, 2005). Furthermore, two groups of 50 seedlings were planted in 2004 within the treeline ecotone: one, within the ecotone but without the protection of krummholz individuals or low shrubs, and the other above the treelimit far away from any krummholz or low shrub.

Each cohort was monitored over a two years period; seedling survival was assessed at the beginning and at the end of each growing season and height was measured at the end of each growing season. Most of the *P. uncinata* seedlings surveyed were not affected by herbivory during the years studied; only 0.2% presented signs of browsing, probably produced by the wild ungulate *Rupicapra pyrenaica* B. Current livestock grazing pressure in the area is very low.

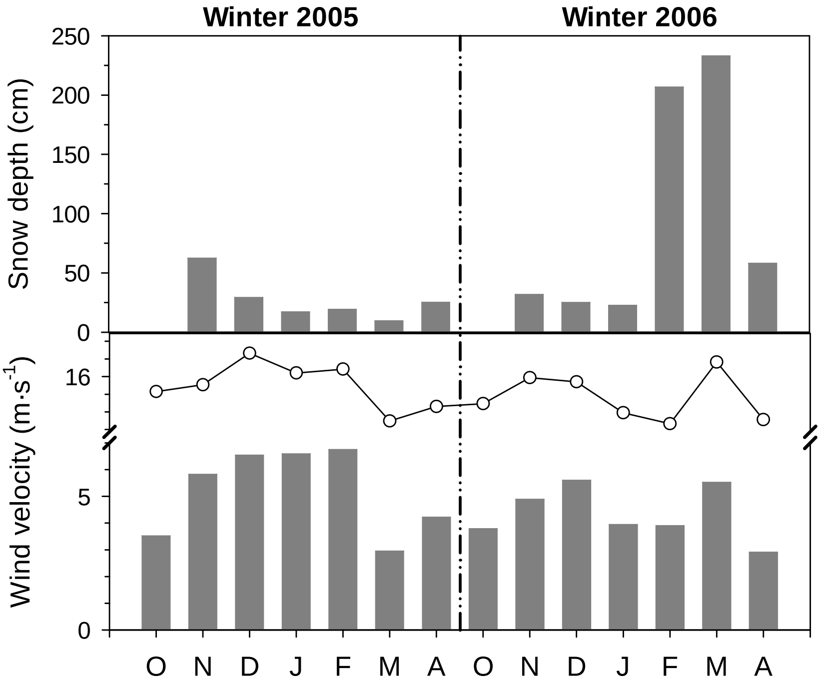

Figure 3. Snow depth (top) and wind velocity (bottom) for the two climatically contrasting winters studied (winter 2005, 2004-2005; winter 2006, 2005-2006) in the study plot where the field experiment was performed. Mean wind velocity is represented by vertical grey bars and the empty circles show mean values of the maximum wind speeds. Data provided by the Catalan Meteorological Service (SMC).

Statistical analysis

To evaluate seedling habitat up-take, we performed chi-squared tests comparing the occupied microhabitat with the available microhabitat (Callaway 1992). The Yates' correction was applied when at least one expected frequency was lower than five, to prevent overestimation of statistical significance for small data sets. To compare the distributions of distances from seedlings to protective elements among plots, we used paired Kolmogorov-Smirnov tests with the Bonferroni adjustment of the significance level.

To evaluate the effects of nurse krummholz individuals on seedling survival and growth as a function of the seedling position with respect to the krummholz, we used generalized linear models (GLMs). GLMs were performed for the first and second year after plantation using winter and seedling position (distance and orientation) as predictors. For survival analysis, we performed logistic regression models (GLMs with logit link function) since survival data presented a binomial error distribution (Wilson & Hardy 2002). Orientation and winter were defined as predictor factors with 4 and 2 levels respectively, and distance as a predictor ordinate factor with 3 levels (0.25 m, 0.5 m, 1 m). Furthermore, the initial seedling height was introduced as a covariate. When performing the growth models, we sorted the data as a multinomial ordination (2 cm growth classes) since this variable did not follow a normal distribution, and was heterocedastic. This allowed us to perform GLMs with a Poisson distribution, which yields results equivalent to those of the multinomial distribution (Burnham & Anderson 2000). Predictors for the growth GLMs were the same as in the survival analysis.

Finally, for the 2004 cohort we developed a more precise model to test whether nurse krummholz size had a significant effect on the pattern of seedling survival. For this purpose, we performed GLMs with the predictors mentioned above plus a new covariate; the ratio krummholz height:crown width. This is a potential indicator of the size of snowdrift accumulation near krummholz individuals (Daly 1984).

For all the fitted GLMs, chi-square tests were conducted to evaluate whether GLM predictors explained a significant fraction of the total variance or not (Guisan *et al.* 2002). Tukey's honest-significant-differences test was used to compare the means for the levels of each factor, since this procedure allows the problem of 'false positives' to be resolved when doing multiple comparisons (i.e., it rejects a null hypothesis more often than the significance level) (Crawley 2005). Covariate effects were examined graphically. GLMs were computed using the 'glm' routine in R v 2.6.1 (R Foundation 2007).

Results

Seedlings showed clear habitat preferences at all the study sites, as expressed by chi-squared tests (Fig. 4; Table 2). Seedlings were found more frequently than expected in substrates dominated by bare soil, gravel and litter. In contrast, dense and low shrubs (*R. ferrugineum*, *J. communis* subsp. *alpina*) appeared to be unsuitable for successful seedling establishment. Domination by grassland species and dwarf shrubs had only a moderate or no effect on seedling abundance. The microsite characteristics of the seedlings did not significantly differ between the age classes (1-5 yrs. *vs*. 6-10 yrs.; Student's t-test, $p = 0.98$).

Most seedlings (86%, $n = 1427$) were located close to at least one of the protective elements considered (stones, microtopograpic shelters and *R. ferrugineum*). The percentage of the different protective elements at the plots varied greatly (Fig. 4), ranging between 4% and 67% for stones, 7% and 89% for microtopographic shelters, and 3% and 50% for *R. ferrugineum*. Despite these differences between plots, seedling distance from the different protective elements was very similar at all sites (Table 2). For instance, the mean distances (± 1 SD) from seedlings to stones, microtopographic shelters and *R. ferrugineum* were 0.27 ± 0.19 m, 0.28 ± 0.2 m and 0.27 ± 0.22 m respectively. Furthermore, most paired Kolmogorov-Smirnov comparisons revealed no significant differences between the distribution distances of seedlings to the protective elements either among or within the plots (97% and 95% respectively). Preferential recruitment at specific microsites or near protective elements did not correspond to greater growth at those sites: no significant height differences were found between microsites within or among plots (*results not presented*).

Table 2. Comparison of the seedlings microsites and their availability in each plot based on chi-squared tests, and mean distance (± 1 SD, in m) to the noted protective elements (right part of the table). Abbreviations: N1, number of seedlings with age < 10 years; N2, number of surveyed seedlings in each plot.

	N_1	N_2	χ^2	df	*P*	*Rhododendron ferrugineun*	Medium-size stones	Microtopographical shelters
PU	33	124	35,77	6	0.001	-	0.21 ± 0.16	0.24 ± 0.17
DU	15	26	128,68	6	0.001	0.39 ± 0.19	0.32 ± 0.17	-
SU	15	61	976,69	6	0.001	0.27 ± 0.28	0.24 ± 0.17	0.27 ± 0.24
EU	30	108	233,28	6	0.001	0.26 ± 0.25	0.26 ± 0.27	0.33 ± 0.28
LU	9	28	20,98	6	0.002	0.30 ± 0.24	0.36 ± 0.17	0.35 ± 0.13
FU	290	488	4906,98	6	0.001	0.20 ± 0.21	0.22 ± 0.16	0.25 ± 0.17
RU	41		49,78	4	0.001			
NU	79	157	518,63	6	0.001	0.20 ± 0.15	0.28 ± 0.18	0.26 ± 0.18
GU	86		31,59	4	0.001			
OU	115		219,21	6	0.001			
BU	200	513	112,88	6	0.001	0.27 ± 0.18	0.28 ± 0.23	0.27 ± 0.23
All plots	913	1505	1511,05	6	0.001	0.27 ± 0.22	0.27 ± 0.19	0.28 ± 0.20

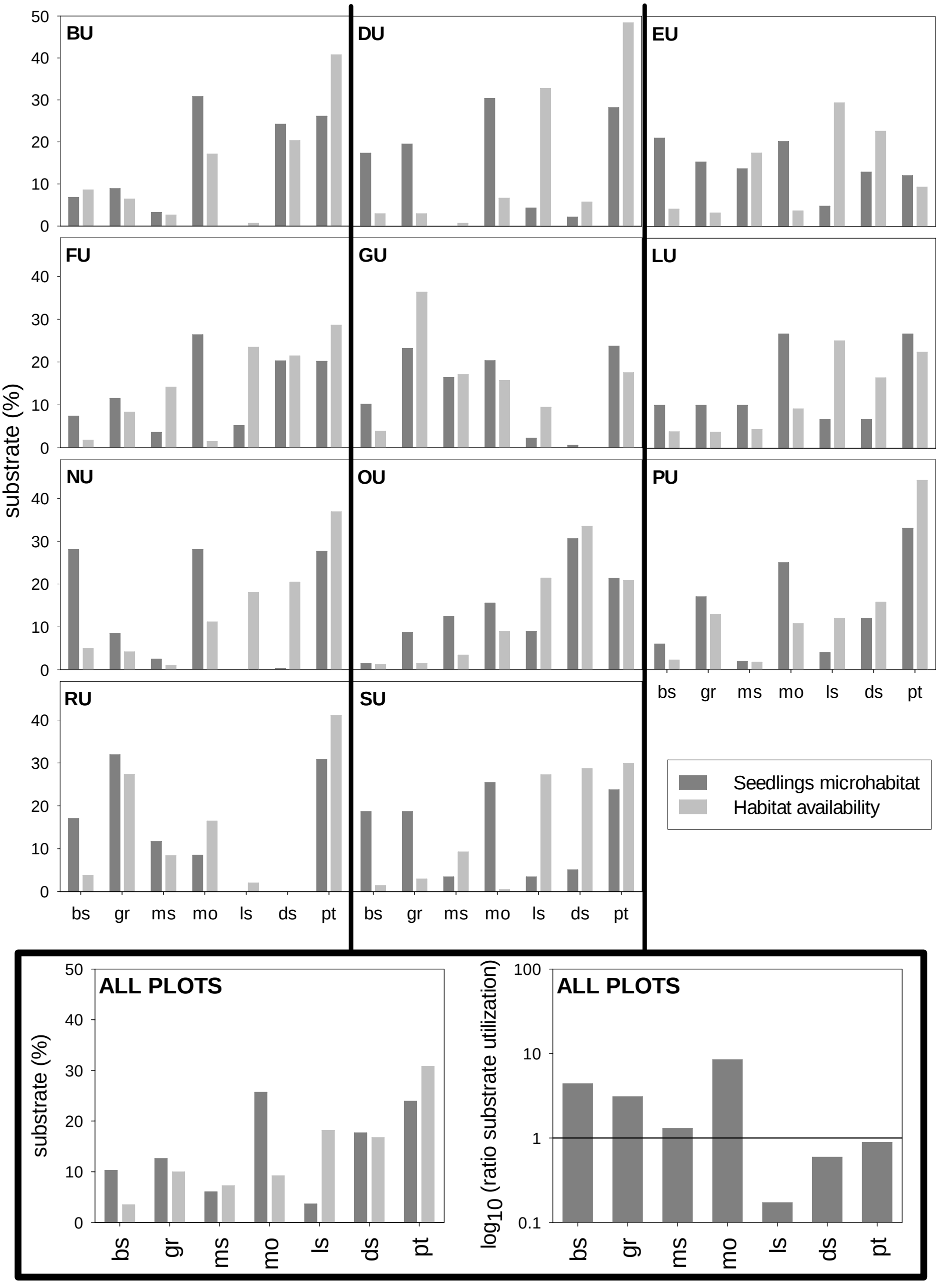

Figure 4. Comparsions between the availability (%) of substrate and vegetation types (grey bars) and seedlings microhabitat (dark-grey bars) in all the study sites. The bottom graphs show the mean values for all study plots (left), and the ratio seedlings habitat : habitat availability (substrate utilization, right). Codes of substrate and vegetation types are: bs, bare soil; gr, gravels; ms, medium-size stones; mo, litter; ls, low-density shrubs; ds, dwarf shrubs; and pt, pastures. See Table 1 for sites codes.

The survival patterns of transplanted seedlings revealed that those in the first cohort (2004) suffered considerable winter effects, since more than 60% died after this harsh winter when the snow cover was very shallow (Figs. 3, 5). In contrast, only about 30% of the second cohort (planted in 2005) died after the first year in the field. However, there was no difference in second-year survival between the 2004 and 2005 cohorts; mortality values were 26% and 25% respectively. Summer mortality was very low for both cohorts; null the first year after the plantation, and up to 2.7 % the second year. The mortality of the two groups of seedlings planted without the protection of any krummholz or low shrub was very high during the first year, both within the ecotone and above the treelimit (90%), and clearly higher than in any other location. The second-year mortality for the remaining individuals was 33%, a value similar to that observed for seedlings planted near krummholz individuals.

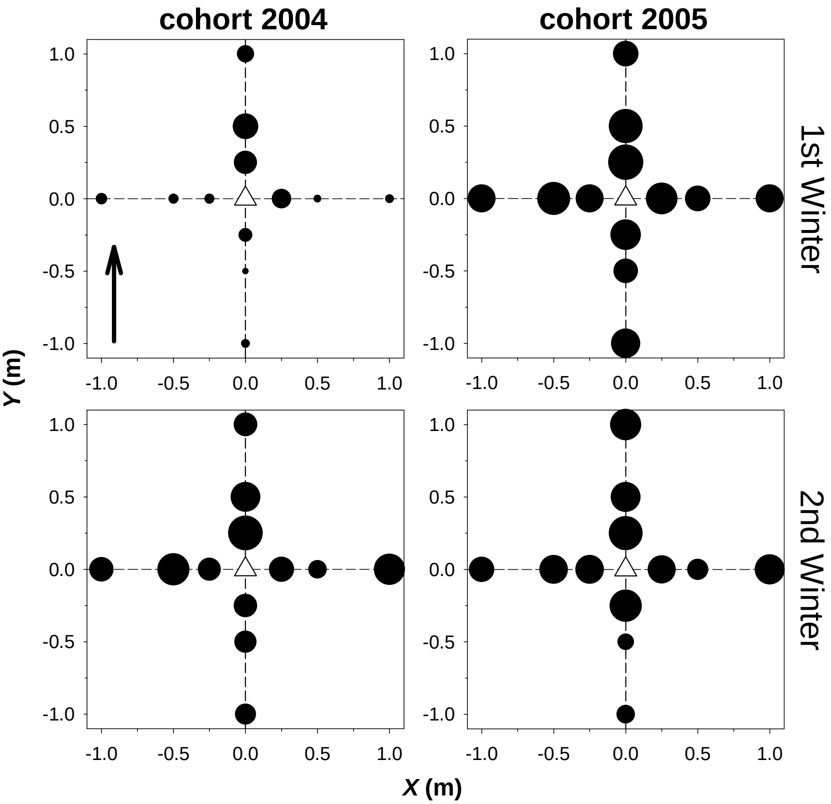

Figure 5. Illustration of the survival of transplanted seedlings after two winters according to position around the nurse krummholz and considering the two cohorts planted in autumn 2004 (left) and autumn 2005 (right). Circle area is proportional to survival (%) at each position, as recorded at the end of the growing season. The arrow indicates the predominant winter wind direction (from the north and uphill).

Results of GLMs based on the patterns of seedling survival after the first year of plantation revealed significant effects for position around nurse krummholz (including the interaction of distance and orientation), winter conditions and initial seedling height (Table 3). In contrast, GLM results for the second year after plantation showed significant influences only for orientation and initial seedling height (Table 3). Seedling survival was significantly ($p < 0.01$) higher close (0.25 m) to nurse krummholz cover, compared to farther away (0.5-1 m), only during the harsh 2004-2005 winter (first year of the 2004 cohort) (Figs. 6, 7). However, seedling orientation from nurse krummholz significantly increased the survival differences among groups during both years. Leeward seedlings showed significantly higher survival ($p < 0.001$) after the first winter than those situated in any other location (Fig. 6). First-year survival differences were more marked for the 2004 cohort after the harsh 2004-2005 winter (56.7% in leeward positions *vs*. 18.1% in the other positions) than for the 2005 cohort after the mild 2005-2006 winter (83.3% in leeward positions *vs*. 66.3% in other positions). The interaction between distance and orientation with respect to nurse krummholz revealed that 0.25 m and 0.5 m leeward positions promoted significantly ($p < 0.001$) higher seedling first-year survival than any other location. Furthermore, at leeward positions, first-year survival was significantly lower ($p < 0.05$) at 1 m distance from a nurse krummholz than in the closer positions. Second-year survival was significantly different ($p < 0.001$) between leeward and windward positions, and although greater, leeward survival was not significantly different to that at the left and right positions.

Seedling survival was significantly affected by the nurse krummholz mat size and shape, as measured by the ratio height:crown width (Fig. 7), only during the harsh winter. Whereas seedling survival was greater near bigger krummholz mats after the harsh 2004-2005 winter, krummholz size did not affect survival after the mild 2005-2006 winter. Leeward seedlings always had higher survival rates than windward recruits irrespective of krummholz size and initial seedling height.

Initial seedling height negatively influenced seedling survival and growth during the first year, whereas it had a positive effect on survival during the second year (Figs. 6 and 7). During the first winter, initial seedling height had a smaller effect on survival for seedlings in a leeward position than for those in other positions.

GLM analysis for seedling height growth during the first year after plantation (Table 3) showed significant effects for position around nurse krummholz, winter conditions (plus the interaction between orientation and winter) and initial seedling height. Second-year growth appeared not to be significantly affected by any of the parameters considered (Table 3). The seedling height growth was significantly greater (p < 0.001) after the milder winter conditions (growth of 2005 cohort > growth of 2004 cohort). Furthermore, the orientation-winter interaction factor showed that, except for the leeward position, growth was greater irrespective of orientation when the winter was less severe. Proximity to a krummholz mat appeared to affect seedling growth positively, but this effect was only significant (p < 0.05) when comparing the 0.25 m and 1 m positions. For orientation, significant differences (p < 0.05) only occurred between leeward and strictly windward positions. Finally, as for survival, seedling height had a negative influence on first-year growth. However, this negative influence was lighter on growth than on survival (Fig. 6).

Table 3. Summary of the GLMs of seedling survival and height increase during the two winters studied. Chi-squared values illustrate which predictors explained a significant fraction of the total variance. Predictor codes are: dis, seedling distance from krummholz mat; ori, orientation of planted seedling; win, winter; ihe, initial seedling height. Numbers in bold indicate significant predictors (*P* < 0.05).

First- / second-winter	Df	Deviance	*P*
Survival			
dis	2	19.20 / 2.50	0.001 / 0.29
ori	3	44.36 / 16.91	0.001 / 0.001
win	1	150.98 / 1.39	0.001 / 0.24
ihe	1	25.25 / 64.63	0.001 / 0.001
dis × ori	6	17.74 / 7.00	0.01 / 0.32
dis × win	2	0.44 / 1.19	0.80 / 0.55
ori × win	3	2.40 / 1.94	0.49 / 0.59
dis × ori × win	6	9.15 / 4.63	0.17 / 0.59
Growth			
dis	2	7.30 / 0.87	0.03 / 0.65
ori	3	13.12 / 1.55	0.004 / 0.67
win	1	78.12 / 0.35	0.001 / 0.56
ihe	1	4.06 / 0.03	0.04 / 0.86
dis × ori	6	5.08 / 1.08	0.53 / 0.98
dis × win	2	2.73 / 0.51	0.25 / 0.77
ori × win	3	22.65 / 0.52	0.001 / 0.92
dis × ori × win	6	4.43 / 1.85	0.62 / 0.93

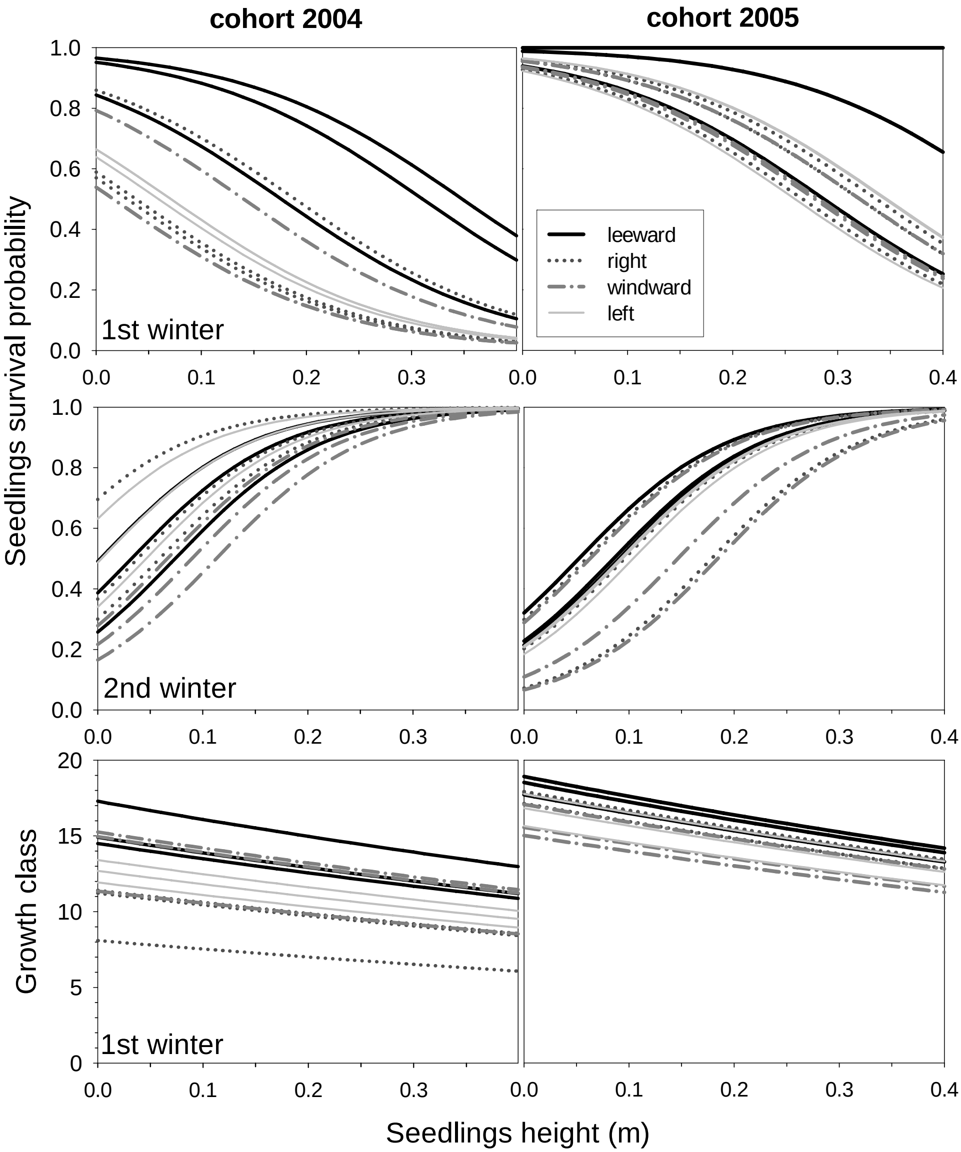

Figure 6. Effects of initial seedling height on survival during the first and second winters after plantation (top and middle graphs respectively), and on growth (bottom) based on GLMs. Left panels correspond to the 2004 cohort, and right panels to the 2005 cohort. Each line type represents the four orientations with respect to nurse krummholz mats, and the three replicates of each line type correspond to the three distances to the nurse krummholz (0.25, 0.5 and 1 m).

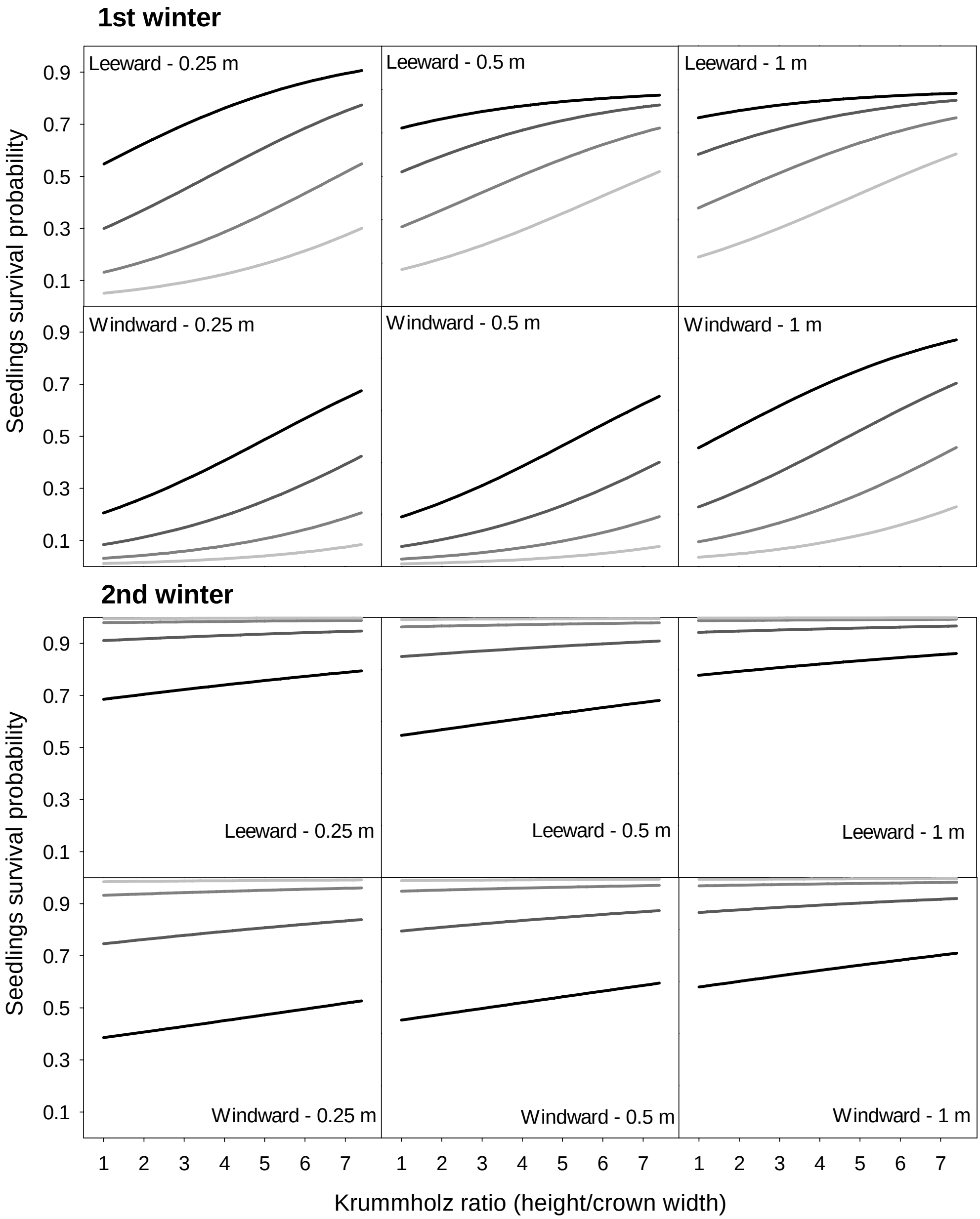

Figure 7. Comparison between leeward and windward GLM-predicted effects of krummholz size (ratio, height:crown width) on seedling survival of the 2004 cohort during the two winters studied. In each subplot, the grey intensity pattern represents seedling height equal to 0.1, 0.2, 0.3 and 0.4 m, ranging from black to the lightest grey. As noted, each subplot represents a distinct orientation and distance from the nurse krummholz

Discussion

Our results show that *P. uncinata* regenerates at specific microsites, and subsequent growth and survival is facilitated by conspecific krummholz individuals. The positive interactions we detected were stronger for leeward locations and during harsh winter conditions (i.e., strong winds and shallow, irregular snowpack). Overall, we quantified the role of two potential bottlenecks for successful recruitment within the treeline ecotone which can modulate treeline dynamics and responses to climate warming.

We found that *P. uncinata* seedlings were clearly more abundant in microgaps with moderate plant cover and over substrates such as bare soil, gravel and litter. Alpine pastures include many small gaps (Illa *et al.* 2006) suitable for seedling establishment without severe competition for water or light. Seedlings growing surrounded by moderate plant cover (e.g. grass cover) may benefit from a reduction in sky exposure and low-temperature photoinhibition, resulting in enhanced survival (Germino & Smith 1999; Germino *et al.* 2002). In contrast, dense, low shrubs (e.g., *R. ferrugineum* and *J. communis* subsp. *nana*) seem to constrain the recruitment of *P. uncinata*, which is a shade-intolerant species (Cantegrel 1983; Pornon & Doche 1995). However, the vast majority of seedlings (87%) occurred near potentially protective elements (0.27 ± 0.2 m), including *R. ferrugineum*, stones and microtopograpic shelters. *P. uncinata* seedlings were associated with the different protective elements according to their relative abundances at each site, as has been found in other harsh environments (Kitzberger *et al.* 2000). Furthermore, we found no significant differences in the distribution distances of seedlings with respect to the different protective elements.

Overall, our findings support the idea that microsite facilitation plays a key role in tree recruitment at alpine treelines (Smith *et al.* 2003). Facilitation may include: greater shade during the daytime, avoidance of extreme cold during clear nights, higher night temperatures, wind protection, increased suitability of soil and snow accumulation (Holtmeier & Broll 1992; Akhalkatsi *et al.* 2006). We believe that stones, microtopographic shelters and *R. ferrugineum* mats contribute to microsite facilitation for nearby *P. uncinata* recruits, and may thus constitute key elements for the regeneration niche of this pine. In turn, the spatial distribution of these elements would strongly affect the spatial patterns of tree recruitment, thus determining the invasiveness of alpine pastures and the extent of ecotone encroachment and treeline shifts.

Our results clearly indicate that winter conditions at alpine treelines may be the most limiting factor for *P. uncinata* seedling survival. Extreme winter temperatures have already been identified as determining factors for tree survival and growth in alpine treelines, since they cause frequent freeze–thaw events which induce xylem embolism and frost drought (Tranquillini 1979; Mayr 2007). Severe winter conditions such as those linked to strong winds and a reduced snowpack (as observed during the first winter studied) may result in high juvenile tree mortality and sudden treeline retrogression (Kullman 1989; Noble 1993). Other treelines that are more affected by summer water stress have also shown mortality peaks in response to summer drought (Lloyd & Graumlich 1997; Kitzberger *et al.* 2000; Cuevas 2000). We can not rule out a similar response at our study sites, since two years is a short experimental period. Medium-term monitoring of the transplanted seedlings is necessary to ascertain the role of summer drought on seedling survival in Pyrenean *P. uncinata* treelines. Nevertheless, the contrasting winter conditions experienced by the two transplanted cohorts emphasize the relevance of our findings regarding the important effect of winter conditions on seedling survival. Long-term monitoring of transplanted seedlings in alpine treelines is therefore critical to assess treeline dynamics under expected warmer conditions and a declining snow cover in southern Europe mountain regions (IPCC 2007).

Part of the observed first-year mortality might also be due to a lack of ability of the transplanted seedlings to acclimatize to adverse environmental conditions. However, the difference in first-year survival rates between the two cohorts (30%) cannot be attributed solely to acclimatization. The seedlings in both cohorts came from the same nursery, and were all planted in the first half of October. Thus, the difference between first-year performance of the cohorts seems to be mainly related to the contrasting winter conditions of the two years studied. In February of 2005, strong north winds swept away most of the snow cover at the study sites and left the seedlings exposed to abrasion by wind-blown ice particles and to extremely low temperatures. This is known to cause frost drought (Tranquillini 1979; Hadley & Smith 1986; Holtmeier *et al.* 2003; Mayr 2007). The harsh 2004-2005 winter also caused desiccation of needles (*personal observation*) on the vertical leaders of naturally established seedlings and saplings and on the evergreen shrub *R. ferrugineum*, which may be evidence of photoinhibition damage caused by the reduced snow cover (Neuer *et al.* 1999).

Krummholz mats tend to accumulate thicker snowdrifts to their leeward side, which may lead to more seedlings due to the increased snowpack protection (Hättenschwiler & Smith 1999). An increase in conifer seedling survival rates in the leeward shelter of krummholz mats has been reported for alpine treelines in the Rocky Mountains (Germino & Smith 2001) and in prairie-forest ecotones in

Montana (Baumeister & Callaway 2006). In accordance with this, our results show significant enhanced seedling survival at the leeward side of nurse krummholz mats. This effect is not so great after mild winters but it is observed irrespective of winter severity. Differences in snowdrift accumulation around krummholz mats are more accentuated after extremely windy conditions, such as those experienced during the winter of 2004-2005 at the study site. This could explain the strikingly enhanced survival of 2004 cohort seedlings to the leeward side of nurse krummholz mats, compared to those to the windward side (> 3 times greater). Furthermore, as proximity to nurse krummholz mats on the leeward side appeared to have a significant positive effect on seedling survival, the enhanced survival at 0.25 and 0.5 m compared to 1 m is linked to increased snow retention in the vicinity of the krummholz mats. In contrast, the proximity of krummholz mats had no influence on survival for seedlings in windward locations under windy conditions. This is due to the shallow snowpack on the windward side of the mats (Daly 1984).

At the treeline studied, increased krummholz size has a greater effect on facilitation after harsh winters than after mild ones. Furthermore, seedling height modulates the extent of such facilitation processes, which leads to differing effects depending on winter conditions. Thus, in accordance with Kitzberger *et al.* (2000), the degree of facilitation is highly sensitive to climate variability. The negative influence of low initial seedling height on later survival after mild winters with heavy snowfall may be related to a restricted growing season due to the increased duration of the snowpack (Hättenschwiler & Smith 1999). Conversely, during harsh winters, seedlings short enough to remain covered by the snowpack may be protected from scouring for most of the winter. Thus seedling height, which is not related to the regeneration niche, alters the degree of facilitation resulting from snow-wind interactions emphasizing the variation in facilitation caused by subtle factors (Callaway 1998).

Facilitation at the treeline has been closely related to snow cover, which reduces winter abrasion, provides insulation from low temperatures and increases the availability of meltwater (Tranquillini 1979). Snow cover accumulation and distribution is mainly dependent on wind regime and on the location of adult individuals which modify the snowpack patterns (Daly 1984). This tree-snow interaction might generate a positive-feedback switch (Wilson and Agnew 1992) and determine the spatial pattern of seedling establishment; for instance, in the form of wind-directed fringes (Malanson 1997; Camarero *et al.* 2000, 2005; Bekker 2005). Our results support the idea that directional positive feedback processes in which snow-wind interactions play an essential role may determine the spatial pattern of recruitment in alpine treeline ecotones (Alftine & Malanson 2004). For instance, the observed clustered and wave-like spatial patterns of seedlings at the treeline have been explained by spatially autocorrelated feedbacks produced by the spatial dependence of microsite quality (Malanson 1997). However, spatially autocorrelated patterns of regeneration may also be linked to environmental gradients or to subtle growth and demographic changes over the ecotone (Wiegand *et al*. 2006). In this study we present empirical evidence of facilitation of leeward seedling survival produced by conspecific individuals through wind-related snow accumulation. We suggest that similar positive interactions may be part of the mechanism behind the formation of clustered or directional spatial patterns of tree recruitment at the treeline. Furthermore, seedling features, such as height, may affect facilitation and the intensity of these feedback processes (Bekker 2005).

Finally, seedlings growth is also affected by wind-related snow cover; 31% of transplanted seedlings lost more than 30% of their initial height after the first winter due to the exposure and death of the apical shoot (Smith *et al.* 2003). Apical death was related to a reduced snowpack, which also affected seedlings survival. However, the second-year growth results may evidence that a wide set of factors influence seedling growth at the treeline, such as water use efficiency (Cui & Smith 1991), nitrogen availability (Lloyd 1998), litter accumulation and fungal pathogens (Facelli 1999), competition (Germino *et al*. 2002) as well as fertility and nutrient regimes (Körner 2003, Handa *et al*. 2006).

Conclusions

Pinus uncinata seedlings mainly establish in sparse vegetation patches, on bare soil, gravel or litter. Furthermore, the regular proximity of seedlings to protective elements (stones, surface microtopography, low shrubs) indicates that microhabitat enhancement may determine the safe sites for *P. uncinata* recruitment at alpine treelines. Since alpine landscapes in the Pyrenees are characterized by a complex mosaic of pastures, ericaceus dwarf shrubs, stones and rocky outcrops, they seem to be highly invasible habitats for *P. uncinata*. Whether the species will be able to expand successfully upwards into current treeless zones in response to global change will depend, among other factors, on its biological traits (seed production, viability and dispersal) and whether climatic conditions favour seedling survival and growth. Harsh winter conditions such as severe winds and reduced snow cover are important factors in determining seedling mortality. However, the positive effects of conspecific individuals on recruits may reduce this mortality. Seedling survival was higher on leeward than on windward sides of krummholz mats, which may be related to wind-directed snowdrift accumulation patterns. Such directional facilitation may generate spatially autocorrelated tree-snow positive feedbacks causing the clustered, elongated or wave-like spatial patterns of tree recruitment observed at many alpine treelines. However, the intensity and variation of such facilitation change according to annual climate conditions and seedling size.

Acknowledgements

We are grateful to various colleagues who helped us with the field work, and especially to A. Ferré who, besides working hard on the transplant experiments, produced Figure 1. This study was supported by the project REN2002-04268-C02 (Spanish Ministry of Research). EB and JJC thank the support provided by a MEC-FPU grant and by the Fundación Aragón I+D, respectively.

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Biosketches

Enric Batllori is currently a PhD student in the Department of Ecology and Department of Vegetal Biololgy, University of Barcelona. His PhD research is focused on the recent regeneration dynamics at alpine *Pinus uncinata* treeline ecotones in the context of global change.

Dr J. Julio Camarero is currently a researcher in the Pyrenean Institut of Ecology (CSIC). He received his PhD at the University of Barcelona on the structure and dynamics of alpine *Pinus uncinata* treeline ecotones. His research is focused on dendroecology, spatial statistics, ecotones and forest ecology.

Dr Emilia Gutiérrez is a professor in ecology and forest ecology at the Department of Ecology, University of Barcelona. Her current research interests include dendroecology, forest dynamics and phenology.

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Capítol III. Spatial patterns of recent regeneration indicate equal short-term sensitivity of alpine treelines to global change at a regional scale.

Resum

Determinar els factors que condicionen la dinàmica de reclutament al límit superior del bosc és indispensable per avaluar la possible expansió altitudinal d'aquestes poblacions en front del canvi global. Tot i això, els efectes del canvi climàtic i dels canvis en els usos del sòl han estat rarament estudiats a petita escala. En aquest estudi s'han analitzat els patrons espacials de l'establiment recent d'individus a 12 ecotons bosc subalpí-prats alpins, dominats per *Pinus uncinata*, als Pirineus. S'han estudiat 5 ecotons recentment afectats per perturbacions antròpiques i 7 ecotons que fa temps que no són alterats per l'home. A cada localitat s'hi va delimitar una parcel·la rectangular al llarg de la transició bosc-prats alpins, incloent el límit del bosc pròpiament dit i el límit de l'arbre, d'entre 940 i 7600 m^2 depenent de les característiques de cada ecotò. Tots els individus van ser mapats i se'n van anotar les principals caracterítiques biomètriques (alçada, diàmetre basal i a l'alçada del pit), se'n va determinar l'edat i es va anotar si eren individus potencialment productors de llavors (presència de pinyes).

Es van analitzar els patrons de distribució espacials dels individus en diferents estadis del cicle vital, així com els patrons espacials de densitat i d'edat de la classe regeneradora. Els patrons de distribució espacial van ser descrits mitjançant tècniques d'anàlisi univariants i bivariants (patró de distribució dels diferents tipus d'individus i la interacció entre ells) així com tècniques d'anàlisi d'autocorrelació del patró de superfícies (patrons d'edat i densitat).

Independentment del grau d'afectació antròpica recent, la regeneració al límit superior del bosc té lloc principalment a la zona de l'ecotò (entre el límit del bosc pròpiament dit i el límit de l'arbre), i la distribució espacial dels plançons mostra una agregació significativa a petita escala (de 0.5 a 3 m). La densitat de plançons presenta una autocorrelació espacial més forta que l'edat, i les relacions d'atracció o repulsió espacial entre els plançons i els individus més grans (pinetons, joves i adults) són febles en la gran majoria dels ecotons estudiats. Finalment, la regeneració durant els períodes 1950-1974 i 1975-1999 no s'ha produit segregada en l'espai al llarg de la transició bosc-prats alpins.

Aquests resultats indiquen que la producció i dispersió de les llavors no són un factor limitant per la dinàmica de regeneració del *P. uncinata* a l'ecotò, i que el patró de distribució espacial dels plançons respondria a la distribució dels llocs segurs de reclutament. L'absència d'una forta atracció espacial entre els plançons i els individus més grans fa pensar que els processos de facilitació que aquests

exerceixen sobre la classe regeneradora no han modulat el patró espacial del reclutament recent. Un major o menor grau d'afectació antròpica recent no implica diferències en els patrons espacials del reclutament, i per tant, la resposta de la regeneració recent en front del canvi global ha estat equivalent entre aquestes poblacions a escala regional. Tot i això, són esperables respostes diferencials entre ecotons a mitjà termini degut a les condicions climàtiques locals resultants de l'heterogeneitat topogràfica de l'alta muntanya.

Spatial patterns of recent regeneration indicate equal short-term sensitivity of alpine treelines to global change at a regional scale

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Article enviat a: *Ecology*

Abstract

The understanding of recruitment dynamics in alpine treeline ecotones is essential to ascertain the potential shifts in the distribution of tree species in response to global change. However, the interacting effects of global change components such as climate warming and land use modifications on treeline dynamics have been rarely assessed at small spatial scales. To evaluate the relative role of both effects on tree regeneration at treeline we assessed the spatiotemporal patterns of recruitment at twelve *Pinus uncinata* treelines in the Catalan Pyrenees and Andorra, recently affected by human-induced disturbances (five treelines) or undisturbed for a long time (seven treelines). A total of 3639 *P. uncinata* individuals were mapped and tagged in twelve treeline ecotones. Rectangular plots ranging from 940 to 7600 m^2 were set along the forest-alpine grassland transition, and tree size, age and potential reproductive status were assessed at each stand. The spatiotemporal patterns of seedlings, large trees and reproductive individuals were described using univariate and bivariate point-pattern (pair-correlation functions) and surface-pattern analyses (Moran spatial correlograms, spatially-corrected correlation). Regeneration at treeline occurred within the ecotone where seedlings appeared strongly aggregated at short distances (0.5-3 m), irrespective of treeline type. Seedling density showed a stronger spatial autocorrelation (i.e., patchiness and wave-like patterns) than seedling age, and recruits presented weak spatial interactions with larger and reproductive trees. Furthermore, recruits of two different periods (1950-1974 and 1975-1999) were not spatially segregated at the plot scale. Our results suggest that seed dispersal and production are rather unlikely limiting factors for tree establishment in alpine *P. uncinata* treelines and that recruitment patterns may result of the spatial distribution of suitable microsites for regeneration irrespective of treeline type. The absence of spatial attraction between seedlings and conspecific tree-like individuals suggests that facilitation does not influence recent recruitment spatial patterns. Alpine treeline types presented equivalent short-term spatial responses of regeneration at a regional scale in response to current global change. However, contrasting spatiotemporal patterns of older trees and treeline dynamics may be expected in the long term if local topographical conditions and tree-to-tree interactions modulate the response of these ecotones to climate.

Keywords: ecotone, forest limit, Moran correlogram, pair-correlation function, *Pinus uncinata*, Pyrenees, recruitment.

Introduction

The alpine treeline ecotone is a prominent boundary which represents the upper elevational limit for tree growth in mountains, being therefore an important ecological threshold (Holtmeier and Broll 2005, Körner 2007). In this paper the term treeline ecotone (hereafter treeline) refers to the transition from the uppermost closed forest (timberline or forest limit) to the treeless alpine vegetation (Körner 1999, Holtmeier 2003). The altitudinal limit of tree growth, the treelimit, is defined as the uppermost upright tree with a minimum height of 2 m (sensu Kullman 2003) and forms the upper border of the ecotone, which encompasses the area between the timberline and the treelimit. The alpine treeline is considered to be a thermally limited ecotone (Körner and Paulsen 2004), and thus climate has been proposed to be one of the main factors governing the geographical distribution and dynamics of such tree populations (Daniels and Veblen 2004). Consequently, treelines are assumed to be sensitive to past changes in climate (Hansen and di Castri 1992) and thus have been regarded as useful indicators of climate warming effects on forest ecosystems (Grace *et al.* 2002). However, climate change is only one aspect of environmental change that may affect the location of treelines (Holtmeier and Broll 2005). Dirnböck *et al.* (2003) concluded that tree recruitment rates in alpine grasslands strongly depend on the density and canopy height of the community to be invaded. In addition, Dullinger *et al.* (2004) illustrated that seed dispersal and the invasibility of the tundra matrix rivalled temperature change in controlling treeline shifts. Furthermore, in Eurasian mountain regions, treelines were often affected by human-induced disturbances (Körner 1999).

Recruitment dynamics is a key component in populations located at the distribution limits of the species (e.g., treeline) since tree recruitment has been shown to be more sensitive to climate than adult mortality (Brubaker 1986, Lloyd 1997). Furthermore, treeline shift, either as an upward advance or a downward retreat, is directly related to natural tree regeneration (Smith *et al.* 2003) which is greatly influenced by local surface microtopography (Resler 2006). Thus, the spontaneous advance of forest-forming tree species into present treeless area within the treeline and beyond the treelimit may be the best indicator of treeline sensitivity to environmental changes (Holtmeier and Broll 2005). Many studies in northern Europe, North and South America, describe regional densification trends rather than treeline shifts at altitudinal and polar treelines during the 20th century in the context of global warming (e.g., MacDonald *et al.* 1998, Stöcklin and Körner 1999, Payette *et al.* 2001, Juntunen *et al.* 2002, Camarero and Gutiérrez 2004, Kullman 2005, Danby and Hik 2007). Recent dendrochronological reconstructions also revealed a regional densification trend at *P. uncinata* treeline in the Pyrenees since the mid 20th century (Batllori and Gutiérrez 2008, *submitted*). Understanding current treeline dynamics is essential to reallistically forecast the effects of the ongoing climate and land use variations on marginal tree populations (Camarero and Gutiérrez 2007).

In the Pyrenees, as in many parts of the world, seasonal farming in high mountain areas has a long tradition, as well as logging and burning to a lesser extent (mainly to enlarge pastures). However, a drastic land use abandonment occurred during the 20th century, specially accused since 1950s, across all the Spanish Pyrenees (García-Ruiz *et al.* 1996). Nevertheless, few studies have investigated if recruitment patterns and dynamics in human-disturbed treelines after the cessation of anthropogenic activity differ from those in relatively undisturbed treelines. The spatial structure of an ecosystem, the way its individuals are organized in space, plays an important role in its functioning and dynamics (Kuuluvainen *et al.* 1996, 1998; Strand *et al.* 2007; Wiegand *et al.* 2007). Thus, the analysis of recent recruitment spatial patterns could contribute to a deeper understanding of the mode and tempo of the recent treeline densification processes reported in the Pyrenees as it has done elsewhere (Lingua *et al.* 2008). Few data exist on how global change effects affect treeline dynamics at small spatial scales, which are the most relevant for understanting recruitment processes (Grubb 1977, Veblen 1992). To increase the understanding of treeline recruitment responses to current global change a thorough analysis of fine-scale tree spatial patterns in such populations is required. Furthermore, in the case of Pyrenees, both recently human-disturbed and treelines that have not been affected by local human activities for a longer period, which are sensitive to climate just as the natural climatic treeline (Holtmeier and Broll 2005), must be considered. A main concern in studies involving fine-scale spatial patterns is that limited resources can preclude the collection of sufficient data to adequately represent large areas (Fulé and Covington 1998). In this respect, we studied 12 treeline populations placing 2 big plots and 10 smaller plots to solve the trade-off between huge sampling effort and a relevant sample size. This allowed us to obtain detailed and well-replicated data of recent treeline dynamics encompassing the regional variability of the Pyrenean treelines. The aim of this study was to ascertain if different treeline types are characterized by distinct recruitment patterns in the context of current global change over the NE Spanish Pyrenees and Andorra. Our specific objectives were: (1) to describe the fine-scale spatial pattern of recent tree regeneration within the treeline ecotone, (2) to detect if there is any spatial interaction between seedlings and larger conspecific individuals, including potential reproductive trees (bearing cones), which could explain the observed patterns of regeneration and (3) to determine possible age-related patterns of regeneration and their implications on recent treeline dynamics. These analyses will serve to resolve if spatial patterns of tree recruitment at treeline could be related to any features of the sites studied.

Methods

Study area

The studied treelines are located in the eastern half range of the Spanish Pyrenees (Catalan Pyrenees) and Andorra (Fig. 1, Table 1). A combination of field visits and aerial photographs interpretation was used to select 12 sites where a rectangular plot, with its longer side parallel to the altitudinal gradient, was placed from the closed forest to the treeless alpine pastures. We placed 2 big plots including and area of 6000 m^2 and 7600 m^2 (40 m wide × variable length) and 10 small plots ranging between 960 to 1650m^2 (10 m wide × variable length). Plot area varied depending on each treeline transition characteristics. The study sites presented uniform topography and no avalanche paths or evidences of recent fires were present, and they are not intensively grazed nowadays. Field sampling was conducted between 2003 and 2006, in late spring and summer.

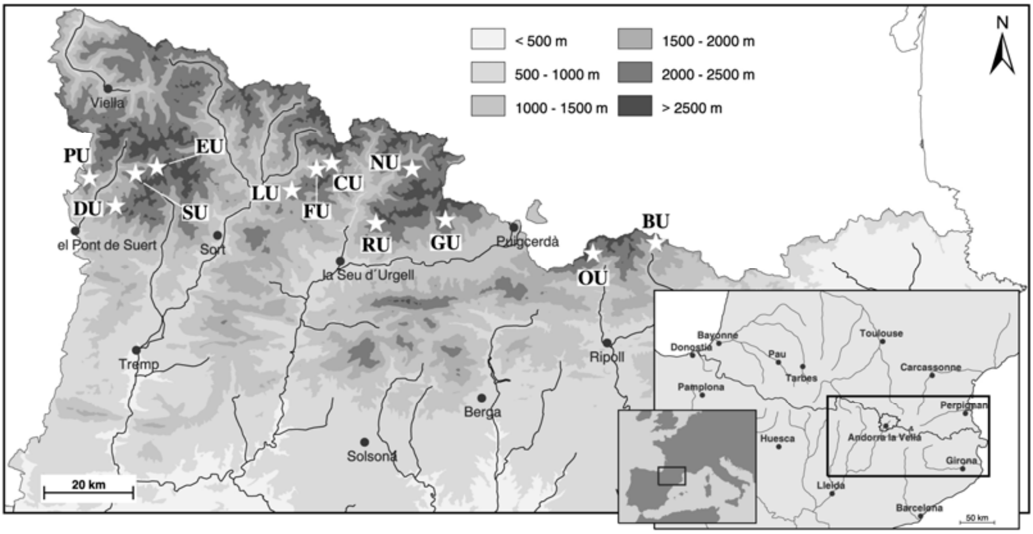

Figure 1. Map showing the location of study sites in the Catalan Pyrenees, NE Spain, and Andorra.

The treelines studied are dominated by *Pinus uncinata* Ramond ex DC. and comprise a wide range of slope steepness, bedrock and plant communities thus being a good representation of the *P. uncinata* treeline ecotones on north-facing slopes in the Pyrenees. This pine is a shade-intolerant conifer which dominates most of the forests in the upper subalpine zone, on any substrate and at any exposure (Ninot *et al.* 2007). According to climatological, soil and vegetation data, potential treeline elevation in the Pyrenees is located between 2200-2450 m a.s.l. depending on continentality, exposure and landform (Carreras *et al.* 1996). Above the timberline, the alpine zone is typically covered by contrasting vegetation mosaics, which include short meso-xerophilous pastures of *Festuca airoides* Lam. (on acidic substrata) or *Kobresia myosuroides* (Vill.) Fiori (in carbonated soils), ericaceous dwarf-scrubs (e.g., *Rhododendron ferrugineum* L., *Vaccinium uliginosum subs. mycrophillum* L.), and sparse vegetation of rocky substrata and scree (Braun-Blanquet 1948; Carrillo and Ninot 1992).

The 12 treelines studied can be classified in two groups concerning their recent disturbance regime as inferred from tree age and size transition patterns along the ecotone (Batllori and Gutiérrez, 2008 *submitted*) (Table 1). Since the treelines studied are not affected by major natural disturbances (e.g., topography-induced extreme winds, snow avalanches, rockfall) step-like transition patterns in tree size and/or age along the ecotone may be indicative of recent human-induced perturbations. The presence of step-like patterns in both tree age and size would reflect the most recent occurrence of anthropogenic disturbances. Five of the treelines studied presented step-like patterns of transition in tree size and/or age and thus recent land use changes may have triggered their recent dynamics (Table 1). In contrast, the other seven study sites would not be recently affected by human-induced disturbances and their recent dynamics were regarded as climatically driven.

Table 1. Characteristics of the twelve alpine *Pinus uncinata* treelines sampled in the Catalan Pyrenees, NE Spain, and Andorra.

Site Code	Latitude / Longitude	Plot size (m^2)	Altitude (m a.s.l.)	Slope (º)	Aspect	Bedrock	Transition Pattern[†]	
							Tree age	Tree size
PU	42º 31' / 0º 45'	6000	2199 - 2268	28	N	lime	step-like	gradual
DU	42º 28' / 0º 49'	1200	2010-2069	30	N	lime	gradual	gradual
SU	42º 32' / 0º 53'	1500	2270 - 2338	27	NW	Lime	gradual	gradual
EU	42º 33' / 0º 56'	940	2299 - 2339	24	W	granodiorite	step-like	gradual
LU	42º 31' / 1º 21'	1180	2363 - 2405	21	N	slate	gradual	gradual
FU	42º 33' / 1º 23'	7600	2352 - 2435	24	NW	slate	gradual	gradual
CU	42º 33' / 1º 25'	1160	2250 - 2297	26	NW	lime	step-like	gradual
RU	42º 26' / 1º 32'	1650	2236 - 2271	24	W	slate	gradual	gradual
NU	42º 34' / 1º 37'	980	2266 - 2314	29	N	lime	gradual	gradual
GU	42º 27' / 1º 44'	1500	2312 - 2365	16	NE	slate	gradual	gradual
OU	42º 23' / 2º 08'	1500	2241 - 2308	27	N	slate	step-like	step-like
BU	42º 24' / 2º 19'	1500	2184 - 2241	22	N	slate	step-like	step-like

[†] The transition pattern was detemrined by means of linear and smooth-spline regressions between the relative altitude and tree age and size (Batllori and Guriérrez 2008, *submitted*)

Field sampling

The location of all tree stems in each plot, using rectangular coordinate axes (x, y), was noted for analysis of the tree spatial pattern. Basic biometric measurements (diameter at breast height: DBH; total tree height: Ht) and the presence of cones were registered for 3639 *P. uncinata* individuals. Following Bosch *et al.* (1992), individuals were classified concerning its size as follows: adults (DBH > 17.5 cm), poles (7.5 cm < DBH < 17.5 cm), saplings (DBH < 7.5 cm and Ht > 0.5 m) and seedlings (Ht < 0.5 m). In most analyses, we grouped adults, poles and saplings forming the class "large trees" given the small sample size of some of these size types in some plots. Potentially reproductive individuals were defined as those bearing cones (Lloyd and Fastie 2003).

All individuals big enough (basal diameter > 10 cm) were cored at the base to determine tree age while seedlings and small saplings were dated on the field by counting the terminal bud scars (internodes) along the main stem. As the age estimation based on the number of internodes underestimates the true age (age at root collar) (Camarero 1999), we collected 270 seedlings and small saplings (up to

1.5 m high) in 6 of the study plots to obtain age-correction functions. We used the age-correction function of the nearest of the 6 sampled stands for the correction of seedlings age of the 6 non sampled sites. The 270 seedlings and saplings were collected, along with their roots, between the timberline and the treeline nearby the study plots. Following Gutsell and Johnson (2002) the age at the root collar was determined for each collected individual through progressive sanding of basal cross-sections. The age at root collar (a_r) was then compared with the age obtained from internodes counting at the field (a_i) and a linear function was fitted to obtain the age-correction functions (e.g., $a_r = 0.38 + 1.25\ a_i$; $r^2 = 0.88$, $p < 0.001$). Age was estimated using this procedure for a total of 1932 mapped seedlings.

Spatial analysis methods

Tree distribution pattern within the treeline was characterised by means of point-pattern analysis using second-order statistics. The Ripley's $K(t)$ function is based on the expected number of points within a circle of radius t around a randomly chosen point divided by the point density, and is expressed as a function of the radius t (Ripley 1981, Diggle 2003, Møller and Waagepetersen 2003). This second-order statistic has been widely used in most previous studies on mapped tree patterns within treeline ecotones (e.g., Camarero *et al.* 2000; Lingua *et al.* 2008). A square root transformation of $K(t)$, the $L(t)$, is usually represented as a function of distance to remove the scale dependence and stabilize the variance; $L(t) = (K(t)/\pi)^{0.5} - t$ (Besag 1977). This approach has been extended to the bivariate case, where individuals of one group (e.g., adults) are taken as centre points and neighbours of the other group are counted (e.g., seedlings), yielding two different estimates which are combined in a weighted average $L_{12}(t)$ (Lotwick and Silverman 1982; Goreaud and Pélissier 2003). Values of $L_{12}(t) > 0$ indicate positive interactions between the two analysed patterns (attraction), and values of $L_{12}(t) < 0$ indicate repulsion.

However, the Ripley's $K(t)$ function is cumulative since, at each scale, all point pairs included in the distance class t are used to estimate the $K(t)$ value. Thus, larger scales contain information from smaller scales, and positive and negative deviations from complete spatial randomness (CSR) acting at different spatial scales may cancel out each other. Moreover, since $K(t)$ integrates over all point pairs with distance up to t, this function will usually peak at larger scales than other locally-focused functions (Appendix 1). Therefore a local approach independently characterising a pattern at different scales might be more appropriate in the case of tree regeneration (Schurr *et al.* 2004; Wiegand *et al.* 2007).

A locally-oriented second-order statistic suitable to characterize a point pattern at fine spatial scale is the pair-correlation function $g(t)$, which is not cumulative and allows for a precise assessment of the scales where significant point-point interactions occur (Stoyan and Stoyan 1994; Stoyan and Penttinen 2000). In the case of CSR (i.e., a homogeneous Poisson process), $g(t) \equiv 1$. Values of $g(t)$ greater or lower than 1 indicate that inter-point distances of t are more (clustering) or less (inhibition) frequent than expected under CSR, respectively. In the bivariate case, values of $g_{12}(t)$ greater or lower than 1 and located outside the confidence intervals indicate significant positive (attraction) or negative (repulsion) spatial interactions. The maximum of $g(t)$ indicates typical inter-tree distance, and if $g(t)$ has only one peak, clump size can be inferred from the scale at which $g(t)$ falls to 1 (Stoyan and Stoyan 1994). The estimation of $g(t)$ cannot be based on point pairs of exactly the distance t because such pairs are rare. We therefore used the estimator $\hat{g}(t)$ which includes an edge-effect correction term and a weight function (Epanečnikov kernel) that maximizes those point pairs with a distance exactly equal to t, and allows the inclusion of point pairs roughly at distance t but with a lower weight (Stoyan and Stoyan 1994). In bivariate analyses, the mark correlation function is estimated by $\hat{g}_{12}(t)$, which has a similar interpretation that $\hat{g}(t)$.

Since first-order effects due to environmnental local heterogeneity may confound or obscure second-order effects related to direct tree-to-tree spatial interactions, whose detection is one of the objectives of this study, the selection of a null model was highly relevant for detecting these second-order effects (Stoyan and Stoyan 1994; Wiegand *et al.* 2007). An appropiate bivariate null model must consider whether the two types of points analysed correspond to trees which were coetaneous or not (Goreaud and Pélissier 2003). Thus we assumed that pattern II (e.g., seedlings) did not influence the development of pattern I (e.g., large trees), but pattern I might have influenced the development of pattern II. For example, for investigating the relationship between large trees and seedlings and to test for repulsion or attraction between seedlings and larger trees, the locations of the seedlings must be randomized while keeping the locations of large trees fixed. We used heterogeneous Poisson processes as null models because they retain the large-scale structure of the pattern but remove its local heterogeneity (Stoyan and Stoyan 1994; Wiegand and Moloney 2004). Following Wiegand *et al.* (2007) small- and large-scale effects may be attributed to second-order tree-to-tree interactions and environmental heterogeneity, respectively. The statistical modelling of tree location as a function of environmental variability followed by the application of an inhomogeneous $g(t)$ function would allow for a more excat separation of first- and second-order effects, but this is a hard task when the number of investigated point-pattern types is high (Baddeley *et al.* 2000; Diggle *et al.* 2007).

The simultaneous testing of several spatial scales may increase the Type-I error leading to the rejection of the null model even if it is true (e.g., in cases when the value of *g(t)* is close to a simulation envelope). Hence, in addition to the scale-dependent information quantified by the pair-correlation function, we used a goodness-of-fit test (GOF) to summarize the total squared deviation between the observed pattern and the theoretical result across the analysed distances in the univariate analyses (Diggle 2003; Loosmore and Ford 2006; Wiegand *et al.* 2007).

The spatial pattern of seedling density and age was described using Moran correlograms where the Moran's *I* coefficients are plotted against distance (Legendre and Fortin 1989 and references therein). Moran's *I* spatial autocorrelation coefficient usually ranges from -1 (negative spatial autocorrelation) to +1 (positive spatial autocorrelation), with zero being the expected value for no spatial autocorrelation. Significance of each calculated Moran's *I* coefficient was done by comparing it with those coefficients obtained with 999 Monte Carlo simulations. Furthermore, the significance of each entire correlogram was also tested at the 5% level using a Bonferroni correction to take into account the dependence among the autocorrelation coefficients calculated for each distance class (Fortin and Dale 2005). Different shapes of all-directional spatial correlograms correspond to different spatial structures (Legendre and Fortin 1989). For instance, a spatial gradient produces a correlogram that starts with positive values at short distances, crosses the abscissa axis at the expected value of null significant autocorrelation (mean patch size), and ends with negative values for larger distance classes (negative autocorrelation).

To study the spatial relationships, at the plot scale, between the density of different size and reproductive tree classe or between regeneration age classes we used spatially-corrected correlation (SCC). Due to the presence of spatial autocorrelation in spatially-derived data such as density, a correction must be made when the significance of the correlation coefficient is tested based on the estimation of the effective sample size according to the amount of spatial autocorrelation (Clifford *et al.*, 1989).

Spatial analyses

Univariate and bivariate point-pattern analyses were performed to characterise the small-scale spatial distributions of the different classes of individuals (seedlings, large trees and respoductive individuals) and the relationships between them, respectively. Bivariate point-pattern analyses were only performed between large trees or reproductive individuals and seedlings. Since tree patterns may be analysed up to a maximum distance equal to half the length of the shortest rectangular plot side, univariate point patterns analyses were performed, with a spatial resolution of 0.5 m, up to 5 m in the smaller plots and up to 20 m in the bigger plots. The same was applied in the bivariate analyses but at 1 m resolution. We only analysed those continuous areas within each plot where density was greater than 200 and 100 individuals ha^{-1} in the case of seedlings and large or reproductive trees, respectively. For all these analyses, we performed 99 Monte Carlo simulations of the null model and used the 5-lowest and 95-highest simulated $g(t)$ or $g_{12}(t)$ values for each analysed distance as simulation envelopes. All point-pattern analyses were performed using the software Programita (Wiegand and Moloney 2004).

In order to describe the surface pattern of seedlings density and age along the treeline, we quantified its spatial autocorrelation using Moran correlograms. We converted the original x-y point data into gridded data using a 5 m × 5 m grid. In all analyses, we used 5-m distance classes and discarded those classes with less than 20 point pairs. In addition, areas with very low recruits density, which are common at treeline, were not considered in the correlogram analyses (Camarero *et al.* 2000). The plot area considered in this analysis for each site was: PU, y = 70-150; DU, y = 75-120; SU, y = 60-150; EU, y = 30-95; LU, y = 60-110; FU, y = 90-190; RU, y = 40-160; NU, y =60-90; GU, y = 20-140; OU, y =30-110; and BU, y = 60-140. The CU plot did not present seedlings and therefore the spatial analyses involving this class were not performed. All the autocorrelation analysis were performed using the program PASSAGE ver. 1.1 (Rosenberg 2002).

We used spatially-corrected correlation (SCC) to study the spatial relationships, at the plot scale, between the density of size and reproductive tree classes (seedlings; reproductive individuals; large trees including adults, poles and saplings; trees with Ht > 2 m). Finally, spatiotemporal analyses involved the comparison by means of SCC of the spatial pattern of two regeneration age classes (1950-1974, 1975-1999), which broadly corresponded to saplings and seedlings, respectively. To perform these analyses we converted the point data to gridded data as for the surface pattern analysis, and we used the Spearman rank correlation coefficient. SCC analyses were performed using the software SAM (Rangel *et al.* 2006).

Results

The establishment of *Pinus uncinata* seedlings at treeline mainly occurred within the ecotone, above the timberline and below the treelimit, in all the plots studied (Figs. 2, 3). When focusing on the spatial pattern of regeneration within the ecotone, the univariate pair-correlation function *g(t)* revealed a strongly clustered pattern at small scales in all the plots studied although it was only significant in seven of them (Table 2; Appendix 2). Despite not significant in five treelines, the spatial pattern of recruits tended towards aggregation in such treelines as indicated by the positive deviations from the heterogeneous Poisson null model evidenced by the GOF tests in all the study sites (e.g., site SU; Appendix 2).

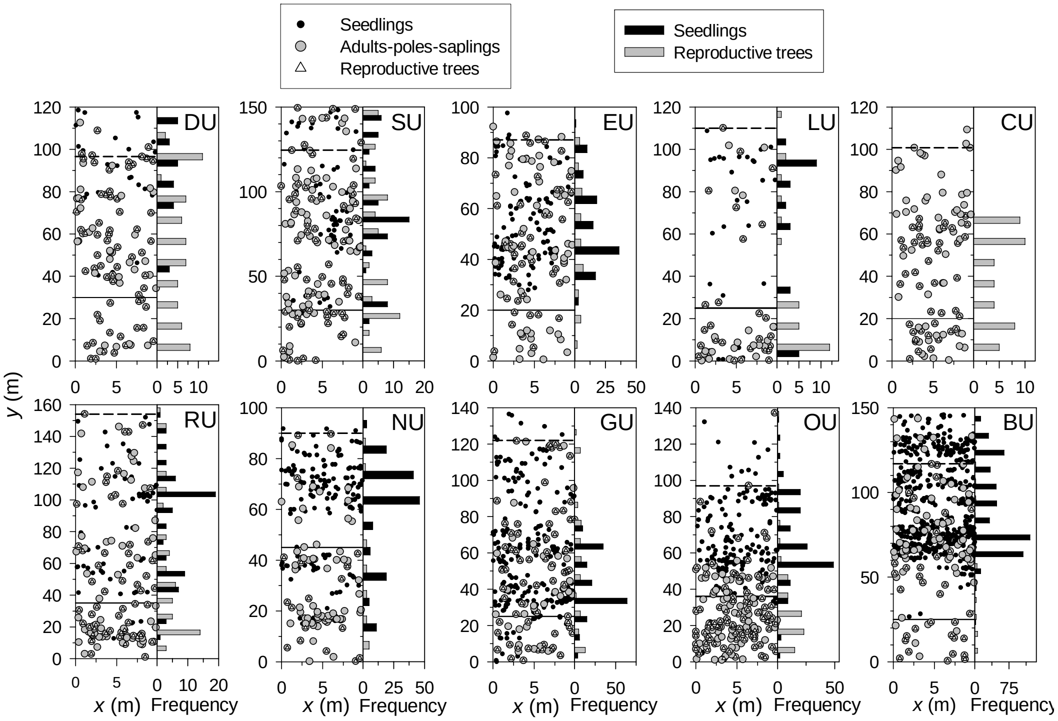

Figure 2. Mapped point patterns of *P. uncinata* individuals in the ten treeline ecotones studied using small plots. The bar graphs show the frequency of seedlings and potentially reproductive individuals (bearing cones) every 10 m along the altitudinal *y* axis (note the different scales). The horizontal solid and dashed lines indicate the the timberline and the treelimit position, respectively.

Irrespective of the treeline type, the substrate and the alpine vegetation composition, seedlings presented an aggregated pattern at 0.5 m-1.5 m. Furthermore, seedlings aggregation was also significant at greater distances (up to 3 m) in the FU site. In contrast, the spatial pattern of large individuals, including adults, poles and saplings, revealed that their distribution was not significantly different from the CSR in most analysed distances (Figs. 2, 3; Table 2; Appendix 2). However, some local clustering at ca. 1 m was observed at sites PU and NU. The spatial patterns of potentially reproductive individuals were similar to those detected for large trees (results not presented).

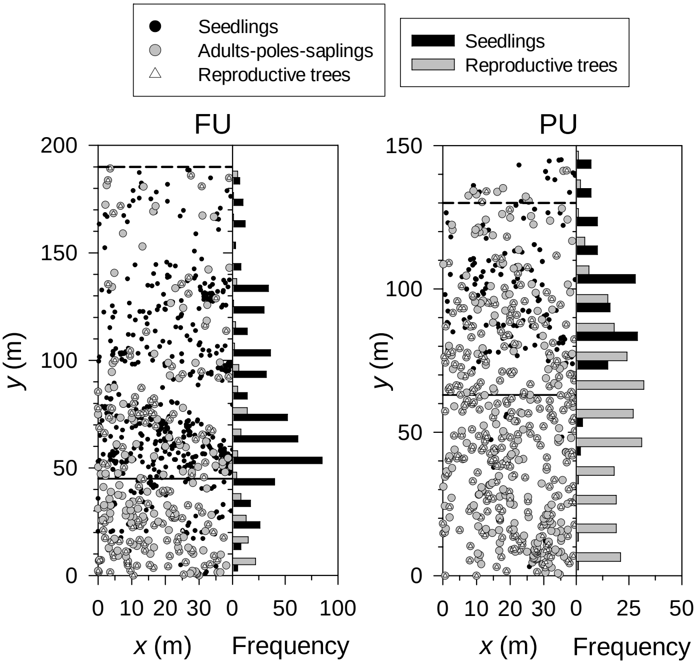

Figure 3. Mapped point patterns of *P. uncinata* individuals in the two treeline ecotones studied using big plots. The bar graphs show the frequency of seedlings and potentially reproductive individuals (bearing cones) every 10 m along the altitudinal *y* axis (note the different scales). The horizontal solid and dashed lines indicate the timberline and the treeline position, respectively.

The results of the bivariate spatial analyses between seedlings and larger trees (adults, poles and saplings) based on the pair-correlation function $g_{12}(t)$ did not suggest contrasted patterns depending on site characteristics (Figs. 4, 5). It is important to mention that when considering the whole treeline ecotone, an apparent repulsion was observed between seedlings and large trees in all the treelines studied (Figs. 2, 3; Table 3). However, when analysing the area where regeneration occurs, above the timberline, seedlings and large trees interactions corresponded to spatial independence in three sites (DU, SU, GU), presented attraction in three sites (PU, EU, FU) and repulsion in the five remaining sites. The negative spatial interactions between seedlings and larger trees at short (0-5 m) spatial scales (Fig. 4, 5) reinforce the segregation between recruitment and larger trees. This pattern occurred both in recently disturbed (OU and BU) and relatively undisturbed treelines (LU, RU and NU). Whereas an absence of interaction between recruits and larger trees was observed in DU, SU and GU sites, significant aggregation at short (1-4 m) and intermediate (10-13 m and 17 m) distances appeared in the two big plots and in the EU plot (only at 1-4 m) (Figs. 4, 5).

Table 2. Summary of the spatial distribution of *P. uncinata* seedlings and large trees (A-P-S, adults, poles and saplings) in all the plots studied based on the univariate point-pattern analyses using the pair-correlation function *g*(*t*). The goodness-of-fit test (GOF) and its associated probability (*p*) summarize the deviation between the observed and the simulated patterns, with higher values of GOF indicating a stronger spatial pattern. Statistical significant values at the 95 % level are indicated by (+) for aggregated (clumped) and (-) for regular (dispersed) point patterns, and (•) indicates a random pattern. N is the number of trees analysed.

Site	Size class	GOF	*p*	N	Distance (m)									
					0.5	1	1.5	2	2.5	3	3.5	4	4.5	5
PU	Seedlings	31	0.70	122	•	•	•	•	•	•	•	•	•	•
	A-P-S	81	0.19	466	•	+	•	•	•	•	•	•	•	•
DU	Seedlings	30	0.71	24	•	•	•	•	•	•	•	•	•	•
	A-P-S	9	0.92	101	•	•	•	•	•	•	•	•	•	•
SU	Seedlings	71	0.29	61	•	•	•	•	•	•	•	•	•	•
	A-P-S	87	0.13	134	•	•	•	•	•	•	•	•	•	•
EU	Seedlings	99	0.01	107	+	+	+	•	•	•	•	•	•	•
	A-P-S	25	0.76	61	•	•	•	•	•	-	•	•	•	•
LU	Seedlings	81	0.19	27	•	•	•	•	•	•	•	•	•	•
	A-P-S	25	0.76	52	•	•	•	•	•	•	•	•	•	•
FU	Seedlings	99	0.01	495	+	+	+	•	•	•	•	•	•	•
	A-P-S	15	0.86	254	•	•	•	•	•	•	•	•	•	•
CU	Seedlings	-	-	0	--	--	--	--	--	--	--	--	--	--
	A-P-S	48	0.52	72	•	•	•	•	•	•	•	•	•	•
RU	Seedlings	96	0.04	68	•	+	+	•	•	•	•	•	•	•
	A-P-S	57	0.43	116	•	•	•	•	•	•	•	•	•	•
NU	Seedlings	99	0.01	158	+	+	•	•	•	•	•	•	•	•
	A-P-S	18	0.15	87	•	+	+	•	•	•	•	•	•	•
GU	Seedlings	99	0.01	231	+	+	+	•	•	•	•	•	-	-
	A-P-S	85	0.15	102	•	•	•	•	•	•	•	•	•	•
OU	Seedlings	94	0.05	146	•	+	•	•	•	•	•	•	•	•
	A-P-S	54	0.46	152	•	•	•	•	•	•	•	•	•	•
BU	Seedlings	97	0.03	485	+	+	+	•	•	•	•	•	•	•
	A-P-S	76	0.23	110	•	•	•	•	•	•	•	•	•	•

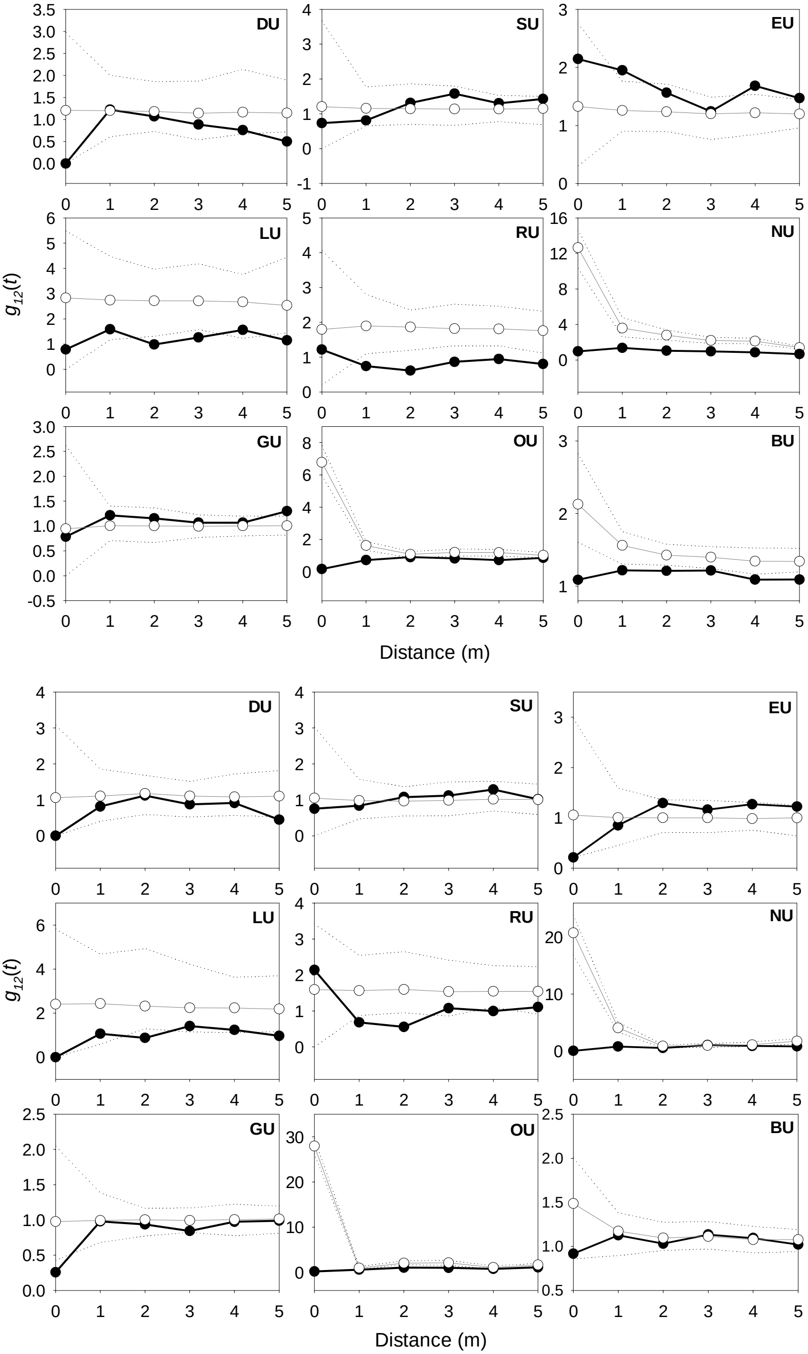

Figure 4. Summary of spatial interactions between types of individuals based on the bivariate point-pattern analyses in the small plots using the pari-correlation function $g_{12}(t)$. Two interactions were analysed: large *P. uncinatata* trees (A-P-S : adults, poles and saplings) *vs*. seedlings (top) and reproductive individuals *vs*. seedlings (bottom). The different lines correspond to the calculated g_{12} (*t*) function (thick line, filled symbols) and the expected g_{12} function under the heterogeneous Poison null model (gray line, empty symbols), and the simulation envelopes (dotted lines) corresponding to the 5% and 95% confidence intervals.

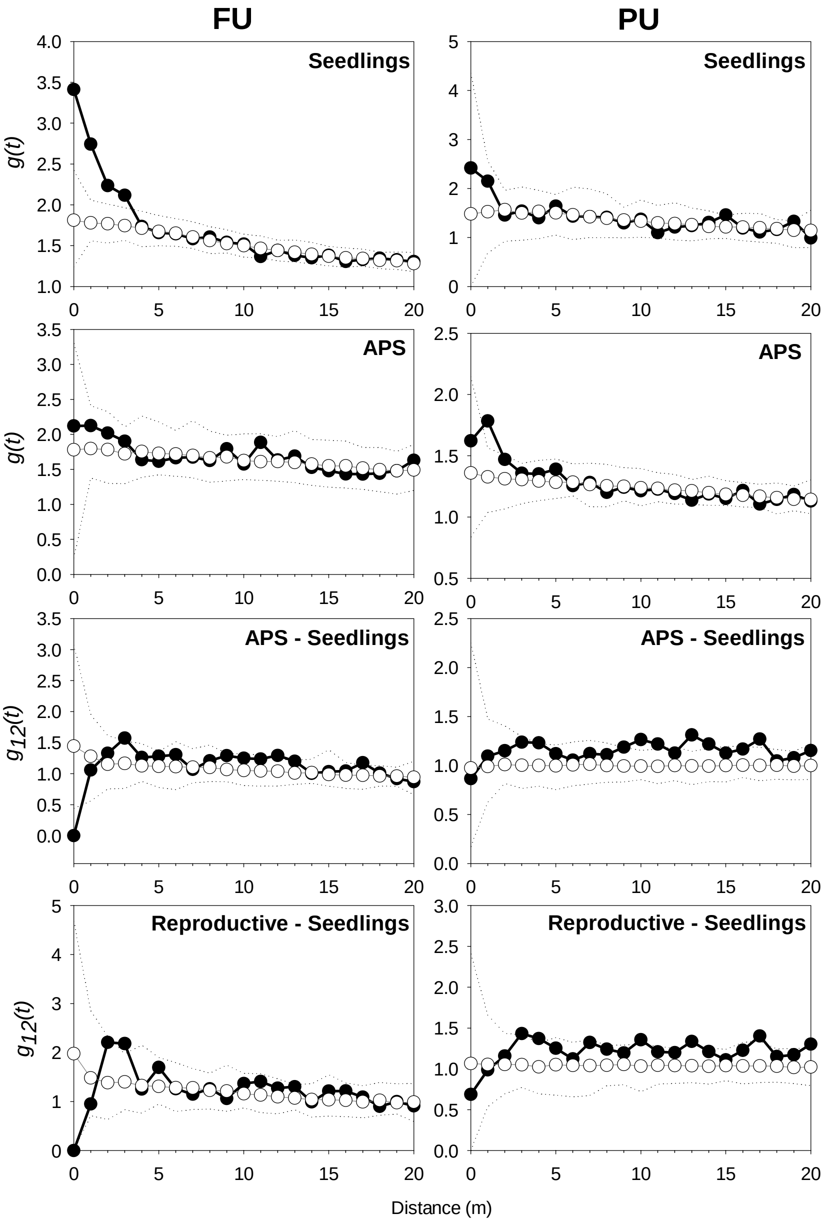

Figure 5. Univariate and bivariate point pattern analyses in the two treeline ecotones studied using big plots based on the pair-correlation functions ($g(t)$, $g_{12}(t)$). *P. uncinata* classes are: seedlings, large trees (APS, adults, poles and saplings), and reproductive individuals. The different lines correspond to the calculated $g(t)$ / $g_{12}(t)$ (thick line, filled symbols) and the expected $g(t)$ / $g_{12}(t)$ functions under the heterogeneous Poison null model (gray line; empty symbols), and the simulation envelopes (dotted lines) corresponding to the 5% and 95% confidence intervals.

Table 3. Spatially-corrected relationships among the density of different type of *P. uncinata* individuals according to its size or reproductive status based on the Spearman correlation coefficient. The sample size (number of 5 × 5 meters grids) compared for each plot is noted in brackets in the first cell of each subtable. Comparisons are made between: All – all pine individuals; A-P-S, large trees including adults, poles and saplings; > 2 m – pines with height > 2 m; Reprod. – potentially reproductive individuals (bearing cones); seedlings –individuals with height < 0.5 m. The symbol * indicates the significant coefficients at $p < 0.05$ level.

PU (n = 240)	A-P-S	> 2 m	Reprod.	Seedlings
All	0.82*	0.67*	0.58*	0.31*
A-P-S		0.80*	0.71*	-0.07
> 2 m			0.89*	-0.11
Reprod.				-0.11

CU (n = 48)	A-P-S	> 2 m	Reprod.	Seedlings
All	1.00*	0.93*	0.54*	--
A-P-S		0.91*	0.67*	--
> 2 m			0.58*	--
Reprod.				--

DU (n = 48)	A-P-S	> 2 m	Reprod.	Seedlings
All	0.86*	0.66*	0.71*	0.30*
A-P-S		0.81*	0.81*	-0.11
> 2 m			0.78*	-0.18
Reprod.				0.04

RU (n = 66)	A-P-S	> 2 m	Reprod.	Seedlings
All	0.73*	0.57*	0.57*	0.36*
A-P-S		0.67*	0.76*	-0.08
> 2 m			0.84*	-0.28
Reprod.				-0.09

SU (n = 60)	A-P-S	> 2 m	Reprod.	Seedlings
All	0.85*	0.46*	0.51*	0.57*
A-P-S		0.57*	0.69*	0.20
> 2 m			0.62*	-0.14
Reprod.				-0.03

NU (n = 40)	A-P-S	> 2 m	Reprod.	Seedlings
All	0.47*	0.12*	0.15	0.88*
A-P-S		0.73*	0.66*	0.14
> 2 m			0.62*	0.01
Reprod.				-0.28

EU (n = 38)	A-P-S	> 2 m	Reprod.	Seedlings
All	0.67*	0.25	0.34*	0.84*
A-P-S		0.64*	0.51*	0.18*
> 2 m			0.69*	-0.02
Reprod.				-0.03

GU (n = 60)	A-P-S	> 2 m	Reprod.	Seedlings
All	0.68*	0.42	0.47	0.84*
A-P-S		0.82*	0.84*	0.27
> 2 m			0.84*	0.08
Reprod.				0.08

LU (n = 48)	A-P-S	> 2 m	Reprod.	Seedlings
All	0.73*	0.58*	0.70*	0.39*
A-P-S		0.71*	0.69*	0.11
> 2 m			0.70*	-0.07
Reprod.				0.07

OU (n = 60)	A-P-S	> 2 m	Reprod.	Seedlings
All	0.57	0.51	0.61	0.51*
A-P-S		0.74*	0.86*	-0.10
> 2 m			0.83*	-0.05
Reprod.				-0.13

FU (n = 304)	A-P-S	> 2 m	Reprod.	Seedlings
All	0.53*	0.29*	0.36*	0.79*
A-P-S		0.58*	0.67*	0.09
> 2 m			0.47*	0.03
Reprod.				0.07

BU (n = 60)	A-P-S	> 2 m	Reprod.	Seedlings
All	0.52*	-0.28	-0.28	0.99*
A-P-S		0.34	0.37	0.26
> 2 m			0.77*	-0.47
Reprod.				-0.42*

However, when considering the relationship between seedlings and only the potential reproductive individuals slightly different patterns of interaction appeared. While an absence of significant interactions, irrespective of site conditions, was observed in the vast majority of the smaller plots studied (Fig. 4), significant attraction effects appeared at short (3 m) and intermediate-distances (10-17 m) at the big plots (Fig. 5).

The analysis of spatial autocorrelation for seedlings age revealed that in most sites there was no evident spatial pattern of seedling age along the treeline (Fig. 6). However, 2 plots (GU, OU) presented age pacthes ca. 30-40 m wide, whereas in other sites (FU, NU) a gradient of decreasing seedling age upwards was observed (Fig. 6). Furthermore, the spatial patchiness of seedling age appeared rather independent of the degree of spatial autocorrelation for seedlings density in all the plots studied. In several plots (GU, OU and BU) the pattern of recruits density corresponded to several patches which can be interpreted as ascending "waves" of regeneration (Figs. 2, 6), while in 2 plots (PU, NU) one big patch of recruits density was detected. The pattern of seedlings density corresponded to a gradient with sharp steps in the FU plot (Figs. 3, 6), and an absence of spatial pattern was observed in the remaining treelines studied. Five of the treelines studied (DU, SU, EU, LU and RU) presented an absence of significant spatial pattern both for seedlings age and density. Only in the OU plot the patch size was roughly coincident for both variables, since seedlings showed irregular patchiness for age and density forming patches ca. 20-30 m wide. In contrast, in the two other sites where irregular patchiness of recruits density was detected (GU and BU plots with patch sizes ca. 20 m wide) seedlings age presented no spatial pattern (BU) or the patch size was not coincident betwee seedlings age and density (GU). The two plots that presented a big patch of seedlings density (PU and NU with patch sizes of 50 m and 20 m, respectively), revealed no spatial autocorrelation (PU) or a gradient (NU) in seedlings age. Finally, in the FU plot both seedlings age and density autocorrelation patterns corresponded to a gradient with sharp steps along the treeline ecotone (Figs. 3, 6).

Spearman's correlation coefficients corrected for the presence of spatial autocorrelation (SCC) between the density of seedlings and large trees, tree-like (height > 2 m) and reproductive pines were weak and non significant at the 5-m scale of the gridded data in all the stands studied (except in the EU site) (Table 3). The positive and significant relationship between all sampled individuals and the seedlings class in each plot evidences the importance of the recent regeneration class within the ecotone at the study sites. In fact, recruits represent a mean of 54% of all sampled individuals in the plots studied, reaching values up to 82%.

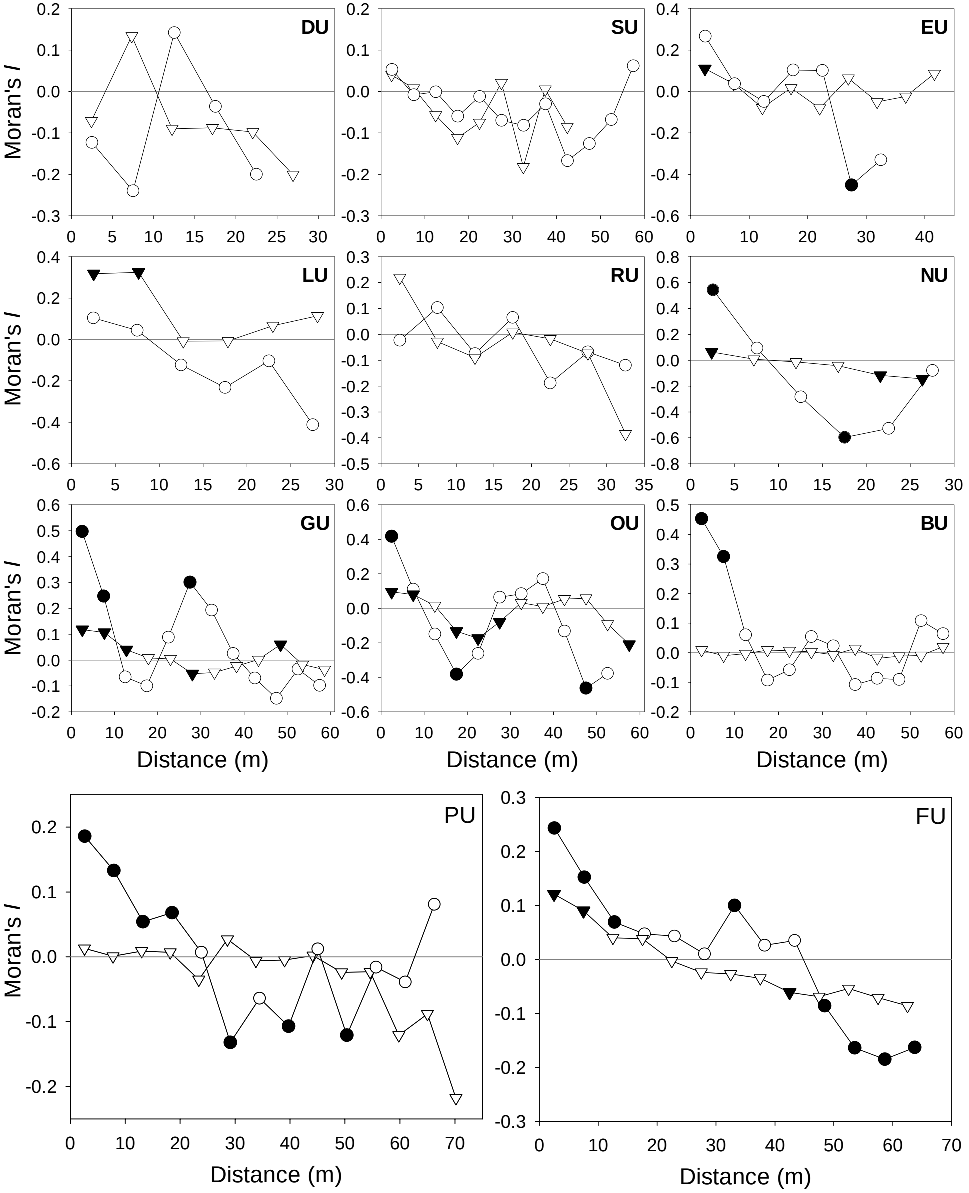

Figure 6. Spatial correlograms based on Moran's *I* index for density (circles) and age (triangles) of seedlings in all the treeline ecotones studied. Solid symbols indicate significant values at $p < 0.05$, and open symbols indicate non-significant values. The correlograms of seedling density in sites NU, GU, OU, BU, and PU were globally significant ($p < 0.05$). The correlograms of seedling age in sites LU, NU, GU, OU, and FU were globally significant ($p < 0.05$).

Conversely, for tree-like and potentially reproductive individuals (trees bearing cones) non-significant SCCs were obtained with all sampled individuals in 5 of the study sites. However, significant and positive SCCs were obtained between tree-like and reproductive individuals in all the plots. In contrast, in several of the study sites seedlings density was negatively correlated with the density of reproductive individuals although this relation was only significant at the BU site.

No spatial aggregation or segregation between the two recruitment classes (1950-1974 and 1975-1999) at the plot scale in most the treelines studied was evidenced by the SCC analysis (Table 4, Apendix 3). In seven of the study sites recruits established in the two different periods were positively correlated, although this relationship was only significant in DU and EU sites. In the other hand, we detected negative SCCs between recruitment periods in the other five treelines studied, but none of them was significant.

Site	N	r_s	p	p_c
PU	240	0.16	0.38	0.71
DU	48	0.40	0.01	0.01
SU	60	0.18	0.73	0.73
EU	38	0.55	0.01	0.04
LU	48	-0.01	0.06	0.09
FU	304	0.03	0.05	0.35
CU	48	-0.15	0.59	0.66
RU	66	-0.10	0.49	0.52
NU	40	0.12	0.02	0.17
GU	60	0.27	0.08	0.22
OU	60	-0.05	0.33	0.66
BU	60	-0.10	0.64	0.65

Table 4. Spatially-correcten relationships among the density of *P. uncinata* recruits established in two periods (1950-1974 and 1975-1999) based on the Spearman correaltion coefficient (r_s). N refers to the sample size (number of 5 × 5 m grids) at each plot. The p and p_c columns refer to the uncorrected and spatially-corrected probability levels. Bold r_s values correspond to $p_c < 0.05$.

Discussion

Recruitment of *Pinus uncinata* at the treelines studied, irrespective of local site attributes, is characterised by strong clustering of seedlings at small distances (0-3 m). Contrastingly, larger trees (adults, poles and saplings) do not present a clustered distribution. Differential aggregation patterns concerning life cycle stage has been previously described at alpine treelines (Mast and Veblen 1999, Camarero *et al.* 2000, Srutek *et al.* 2002, Bunn 2004). Furthermore, Bunn (2004) speculated that the high inter-annual mortality of seedlings would be responsible of the no propagation of the seedlings spatial pattern to the adults spatial pattern. Despite the lack of precise mortality rates in the plots studied, a crude estimate of seedlings instantaneous mortality rates (obtained as the proportion of dead seedlings at the time of sampling; Lloyd and Fastie 2003) do not indicate high mortality rates under current climate conditions (Batllori and Gutiérrez 2008, *submitted*). The initial aggregated patterns of establishment may be followed by density-dependent mortality that reduces the degree of association over time (Humpries *et al.* 2007). Thus, medium-term monitoring of the treeline populations may be necessary to ascertain when the constraints responsible of the no propagation of the seedlings aggregated spatial pattern to the larger tree classes appear.

The spatial segregation between seedlings and larger trees at the plot scale was evidenced in all the treelines studied both by the bivariate point-pattern and the spatial autocorrelation analyses. Such spatial segregation may be attributable to the shade intolerance of *P. uncinata*, as is shown by its dependence on disturbances for regeneration (Bosch *et al.* 1992), leading to a lack of establishment under closed canopies. Thus, our results indicate that *P. uncinata* recruits predominantly establish above the timberline, within the ecotone, where favourable microsites for regeneration occurs (Batllori *et al.* 2008, *submitted*). Furthermore, the spatial clustering of seedlings in the ecotone may be indicative of positive feedback processes that modulate treeline populations response to the environmental changes and thus determine the spatial pattern of tree recruitment at treeline (Sveinbjörnsson *et al.* 2002, Alftine *et al.* 2003, Alftine and Malanson 2004, Bekker 2005). As trees become established, their presence modify the local environment and enhance additional seedlings' growth (Resler 2006). Hence, the observed seedlings aggregation at small spatial scales in the treeline ecotone may derive in increased facilitation, leading to greater recruitment, and thereby resulting in a positive feedback cycle (Smith *et al.* 2003). Our results indicate that in the study sites such feedback mechanisms may be important for treeline recruitment dynamics irrespective of treeline type, substrate and vegetation cover.

Tree clumping at treeline is related to the creation of more favourable microenvironments than those for isolated trees (Tranquillini, 1979). Moreover, seedling establishment at the proximity of stunted tree forms has been reported at alpine treelines and attributed to facilitation processes (Hättenschwiler and Smith 1999, Camarero *et al.* 2000, Germino *et al.* 2002). This facilitation has been related to the positive effects of wind-related snow accumulation at the leeward side of krummholz individuals (Batllori *et al.* 2008, *submitted*). However in the plots studied, the lack of positive relationships between seedlings and larger trees in the ecotone suggests that facilitation processes are not widespread amog the treelines studied in the Pyrenees. In fact, we mainly detected an absence of relationship or a repulsion between seedlings and larger trees. The weak spatial support for positive interactions such as facilitation may be attributable to the tree-like growth form of the larger individuals analysed in this study since tree-like and stunted individuals have different effects on wind-related snow cover accumulation (Scott *et al.* 1993; Smith *et al.* 2003). Thus, we suggest that the aggregation pattern at short distances between seedlings and larger trees detected in three of the treelines studied may result in part from frequent seed short-dispersal events. This would be evidenced by the similarity of the short and intermediate attraction effects between seedlings and larger trees (3-4 m, 12-13 m and 17 m) and to the ones found between seedlings and reproductive individuals (3 m, 10-13 m and 17 m). Despite high variation patterns in seed-dispersal rates away from adult trees are common in wind-dispersed pines (Nathan *et al.* 2000), our results showed strikingly equal intermediate-distance aggregation among the 2 big plots studied. Furthermore, the estimated most frequent dispersal distance for *P. uncinata* seeds, based on seedlings patterns in a relict population in central Spain and release experiments, was between 4 and 30 m (Camarero *et al.* 2005). Dispersal distances up to 39 m and higher have been reported for a similar pine species such as *Pinus* sylvestris (Hughes *et al.* 1994). Seed dispersal by wind is influenced by plant attributes including the aerodynamic properities of diaspores (wings or other dispersal appendages) and the height from which they are released (Dorp *et al.* 1996). *P. uncinata* produce small winged seeds, with large crops occurring every 2-4 years, that are primarily dispersed by wind in late winter (Ceballos and Ruiz de la Torre 1979). Moreover, our results revealed that reproductive individuals presented significant attraction with tree-like individuals, thus indicating that seed release may occur commonly above certain height. The mode of seed dispersal affects directly the spatial pattern of tree regeneration and spatial interactions with conspecific individuals (Seidler and Plotkin 2006). In view of these considerations, and having in mind that high wind speeds are characteristics of mountain environments (Barry 1992), we suggest that in the alpine *P. uncinata* treelines dispersal at medium-distances might be more effective than in lower populations. Thus, we hypothesize that the intermediate-distance aggregation pattern detected at the studied treelines may be reflecting frequent dispersal events at this ditances, and that rare long-distance events might include much greater distances not detected in our analyses.

The spatially-corrected correlation (SCC) analyses revealed that seedlings dominated the studied ecotones at the spatiotemporal scale of this study. The spatial pattern of tree ages can be useful as it can provide evidence for the presence or absence of regeneration patches of trees (Wallenius *et al.* 2002). Our results evidence an absence of regeneration patches for seedlings age in the majority of sites (seven out of eleven) and no significant spatial segregation between recruits of the two periods analysed (1950-1974 and 1975-1999). Furthermore, seedlings and reproductive individuals did not present positive significant SCCs in none of the study sites. These results may indicate, as described by Dalen and Hofgaard (2005) at the birch treeline in the Scandes Mountains, that seed production and dispersal are rather unlikely limiting factors for tree establishment at the treelines studied. In contrast to the absence of pattern in seedlings age, seedlings density-related patterns were detected in six of the study sites. As is the case of the treelines studied, steep slopes, high relief, and associated physical disturbances, has been pointed to contribute to fragmented and patchy tree distributions (Humphries *et al.* 2007). The patchy nature of vegetation at the alpine treeline has been related to establishment and subsequent survival in topographically-controlled microsites (Holtmeier and Broll 1992). Furthermore, microsite facilitation (generated structurally, intraspecifically or interspecifically) seems critical for seed germination and successful seedling establishment (Ball *et al.* 1997, Germino and Smith 1999, Germino *et al.* 2002) and thus the distribution of suitable microsites for regeneration may exert a strong influence on the spatial pattern of tree regeneration at treeline (Bunn 2004). In this study we described the presence of patchiness and wave-like patterns of recruits density along the treeline, which reinforces the idea that the local distribution of suitable microsites for regeneration may modify the response of these treeline populations to environmental changes. The spatial distribution of suitable microsites for recruits establishment is determined by complex interactions among substrate, vegetation cover, microtopography and the extent of microsite facilitative interactions. Thus, the observed seedlings spatial clustering without age-related patterns and irrespective of treeline type, substrate and alpine vegetation cover, strongly suggests that all studied ecotones may be functionally equivalent concerning availability and distribution of suitable microsites for regeneration.

Spatial analysis permits to describe the spatial pattern of tree populations and to infer its underlying processes (Loosmore and Ford 2006, Wiegand *et al.* 2007). However, it is important to acknowledge that the spatial pattern at any point in time is only indicative of recent dynamics (Malanson *et al.* 2006; Wiegand *et al.* 2006), and that spatial distribution can potentially be afected by several factors (Kuuluvainen and Rouvinen 2000). Our results suggest that the studied treelines, irrespective of its characteristics, reflect equivalent ecotone invasibility in the present global change conditions. This contrasts with the statement of Kjällgren and Kullman (1998) which remarked that even nearby sites may not be functionally equivalent. They attributed this to the fact that the subalpine landscape is topographically complex and thus that the environmental conditions decisive for tree growth change substantially over short distances. However, it must be taken into account that in this paper we hypothesized equivalent treeline functioning based on recruitment patterns at microsite scale whereas Kjällgren and Kullman (1998) referred to differences in growth conditions. Growth and regeneration may not equally reflect the environmental conditions since microclimates at the ground level create temperature gradients resulting in aerodynamic decoupling between atmospheric and microsite conditions (Körner 2007). Seedlings may be then limited by severe local climatic influences operating at small spatial scales when they reach a certain height and begin to project above the winter snow cover (Holtmeier *et al.* 2003, Smith *et al.* 2003). We suggest, in agreement with Resler (2006), that our results may indicate the similarity of the microtopographical conditions between the treelines studied. Thus, differences in local site conditions dependent on the macrotopography may result in medium-term treeline dynamics variability among sites resulting of the local interactions among micro- and macrotopography, which may cause geographically different patterns of treeline response to changing climate due to differential processes of mortality. A temporal perspective of treeline dynamics will be critical as biophysical constraints that can prevent tree development may change cyclically with intradecadal and decadal fluxes or directionally with progressive climate changes (Young and Leon 2007). Furthermore, fine-scale spatial heterogeneity, local site conditions, community structure and individual adaptability may modulate treeline responses to environmental change.

Conclusions

Pinus uncinata recruitment at treeline occurs above the timberline with a strong clustering at small spatial scales irrespective of treeline type and local characteristics. The null coincidence of seedlings density- and age-related patterns and the lack of spatial interactions between seedlings and reproductive individuals indicate that seed production and seed dispersal are rather unlikely limiting factors for current treeline dynamics. Furthermore, our results suggest that facilitation exerted by conspecific tree-like individuals does not have a strong influence on the spatial pattern of recruits. Thus, the spatial aggregation of recruits may respond to the distribution of suitable sites for recruitment that is determined by complex interactions among substrate, vegetation cover, microtopography and the extent of microsite facilitation. Our results indicate that feedback processes may modulate the regeneration dynamics at treeline due to its importance on facilitation processes at small spatial scales. The initial aggregated patterns of recruits establishment is not propagated at larger tree classes, which suggests that differential mortality processes may reduce the degree of association over time. Given that the spatial pattern of recruits is equivalent at all the studied treelines, we suggest that under the current climatic conditions a rather equal invasibility of the ecotone occurs over the north-facing slopes in the Pyrenees. This may be indicative, at a regional scale, that recently human-disturbed and undisturbed treelines for a longer period present equivalent short-term response and sensitivity in the current global change context. However, it may be expected that a temporal perspective would reveal differential treeline responses resulting from the interaction of micro- and macro-scale landscape features.

Acknowledgments

We are greateful to all the people who helped us with the field work. This study was supported by the project REN2002-04268-C02 (Spanish Ministry of Research). EB and JJC thank the support of a MEC-FPU grant and the Fundación Aragón I+D, respectively.

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Appendix 1. Comparison of point-pattern analyses based on Ripley's *L*(*t*) and the pair – correlation function *g*(*t*).

Considering all the studied plot in site FU, seedlings were significantly aggregated up to 5 m according to Ripley's *L*(*t*) but up to 3 m based on the pair-correlation function *g*(*t*) (Fig. A1.1.).

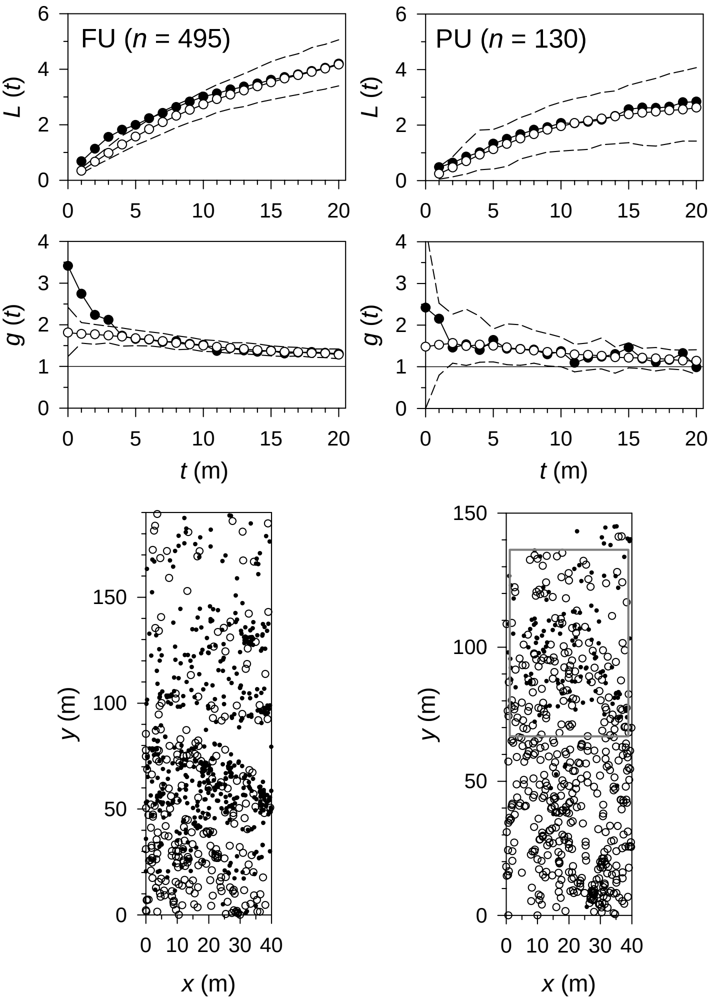

Figure A1. 1. Comparison of the mapped point patterns of *P. uncinata* seedlings (small closed circles) and large trees (bigger circles; adults, poles and saplings) in treeline ecotones studied using big plots (sites FU and PU) and the analyses based on the univariate Ripley's *L*(*t*) and the pair-correlation functions (*g*(*t*)). The different lines correspond to the calculated *L*(*t*) or *g*(*t*) functions (filled symbols) and the expected *L*(*t*) or *g*(*t*) functions under the heterogeneous Poison null model (open symbols), and the simulation envelopes (dashed lines) corresponding to the 5% and 95% confidence intervals based on the 99 simulations of the null model. Values of *L*(*t*) or *g*(*t*) located outside the confidence intervals indicate aggregated patterns in this case. In the case of PU site the analysed sub-area where seedlings were present is indicated with a rectangle.

Appendix 2. Graphical results of the univariate and bivariate point-pattern analyses based on the pair-correlation functions *g*(*t*) and $g_{12}(t)$.

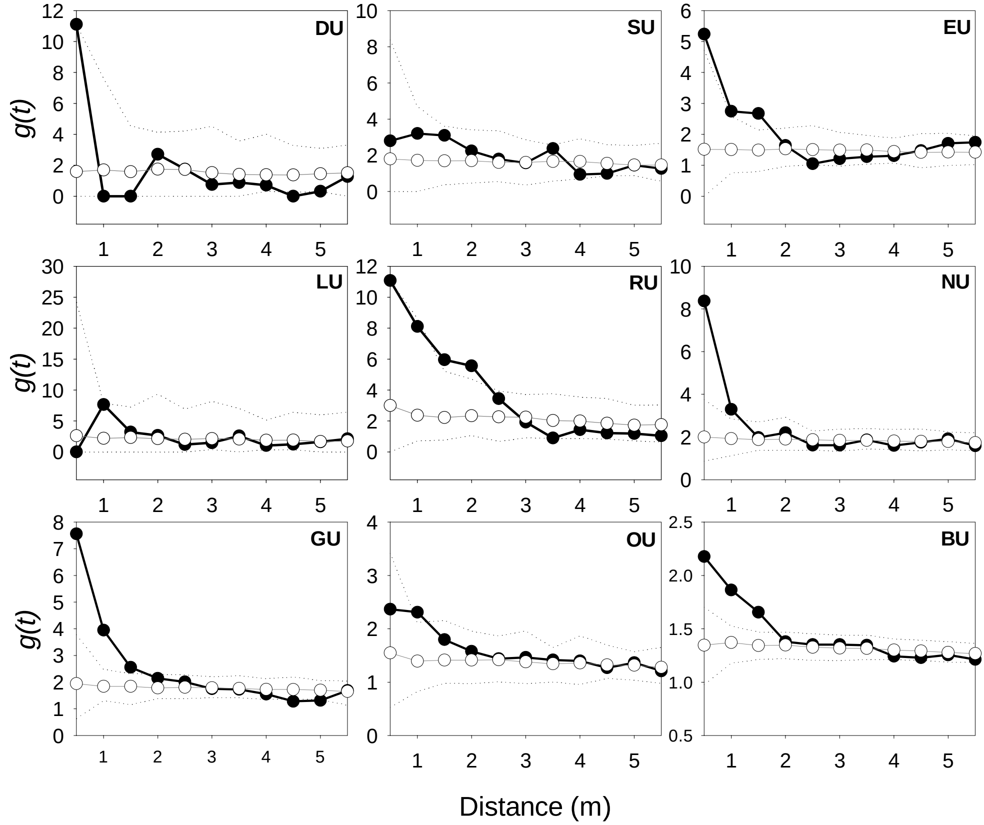

Figure A2.1. Point patterns of *P. uncinata* seedlings in the treelines studied using small plots based on the univariate pair-correlation function (*g*(*t*)). The different lines correspond to the calculated *g*(*t*) function (thick line, filled symbols) and the expected *g*(*t*) functions under the heterogeneous Poison null model (gray line, empty symbols), and the simulation envelopes (dotted lines) corresponding to the 5% and 95% confidence intervals based on the 99 simulations of the null model. Values of *g*(*t*) greater or lower than 1 and located outside the confidence intervals indicate aggregated or dispersed point patterns, respectively. Note that *g*(*t*) = 1 for random patterns. See also Table 2.

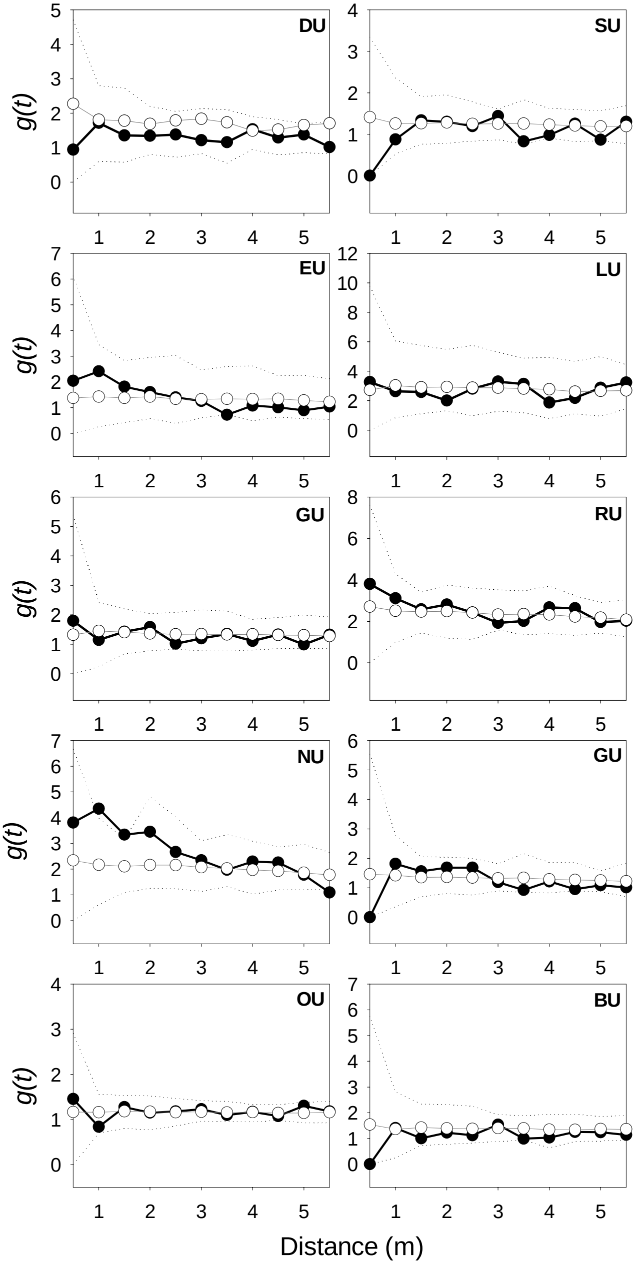

Figure A2.2. Point patterns of *P. uncinata* large trees (adults, poles and saplings) in the treelines studied using small plots based on the univariate pair-correlation function (*g*(*t*)). The different lines correspond to the calculated *g*(*t*) function (thick line, filled symbols) and the expected *g*(*t*) function under the heterogeneous Poison null model (gray line, empty symbols), and the simulation envelopes (dotted lines) corresponding to the 5% and 95% confidence intervals based on the 99 simulations of the null model. Values of *g*(*t*) greater or lower than 1 and located outside the confidence intervals indicate aggregated or dispersed point patterns, respectively. Note that *g*(*t*) = 1 for random patterns. See also Table 2.

Appendix 3. Graphical results of the spatial distribution of the two analysed recruitment periods (1950-1974 and 1975-1999)

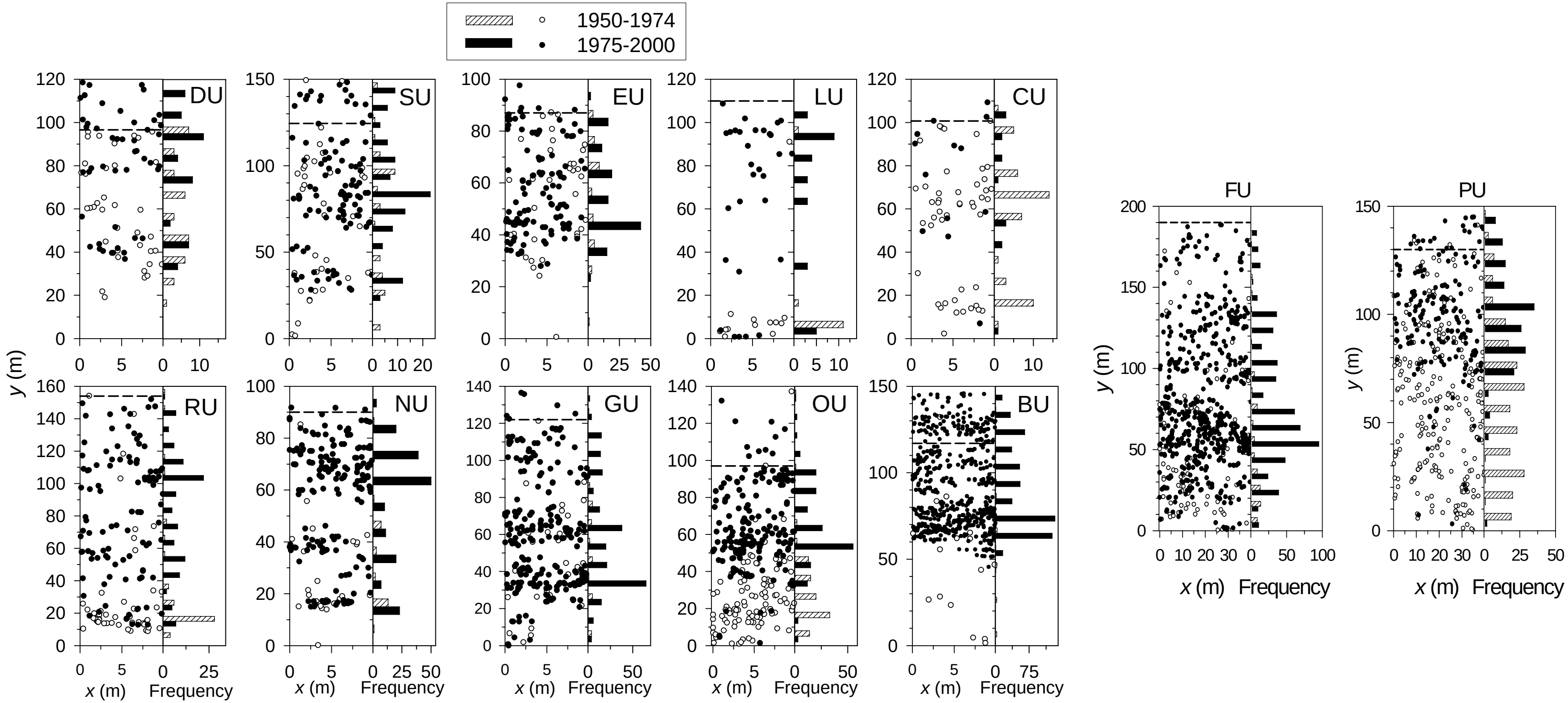

Figure A3.1. Mapped point patterns of *Pinus uncinata* recruits in the 10 small plots (left) and the 2 big plots (right) sampled based on their germination date considering two age classes (1950-1974, 1975-1999). The bar graphs show the frequency of both types of individuals every 10 m along the altitudinal *y* axis (note the different scales). The horizontal dashed lines indicate the treelimit position.

Capítol IV. Climatic influence on *Pinus uncinata* growth and recruitment dynamics at alpine treeline

Resum

En base al paradigma tradicional del límit superior del bosc, un augment de les temperatures afavoriria el creixement i la regeneració dels ecotons, i per tant, podria comportar l’expansió altitudinal d’aquestes poblacions. Però tot i que l’augment de les temperatures ha estat generalitzat arreu del planeta, s’han descrit respostes diferencials del límit superior del bosc indicant que els canvis que s’estan produïnt a l’ecotò no són homogenis a escala regional. Aquest fet, evidencia que les prediccions basades en respostes lineals dels ecotsistemes en front del canvi climàtic no són realistes. Per a entendre la resposta del creixement i dels processos de regeneració en front de les prediccions climàtiques futures, i per tant, poder predir en últim terme la dinàmica del límit superior del bosc, són necessaris estudis detallats de la relació d’aquests dos processos amb el clima.

Aquest estudi avalua la relació entre les variables climàtiques i el creixement radial i la regeneració al límit del bosc, a escala regional dels Pirineus, per determinar els factors climàtics que més limiten aquests processos. També es pretén determinar la variabilitat entre ecotons de les relacions entre el creixement i la regeneració amb el clima. S’han estudiat 12 ecotons dominats per *Pinus uncinata* i a cada localitat s’ha desenvolupat una cronologia local i s’ha determinat l’estructura demogràfica recent (període 1971-2000). Els ecotons estudiats estan situats a 4 regions climàtiques, per cada una de les quals s’ha construït una cronologia de referència de poblacions situades per sota el límit del bosc. S’han utilitzat anàlisis de correlacions i funcions resposta per descriure la relació entre les sèries de creixement locals (cronologies) i les variables climàtiques mensuals (temperatura i precipitació). La similitud en les variacions anuals del creixement radial entre localiats, i amb les cronologies de referència, s’ha determinat per mitjà d’un anàlisi de coordenades principals (PCoA) i per mitjà de coeficients de correlació de Pearson. Per determinar les variables climàtiques més relacionades amb les variacions en la densitat del reclutament, s’han utilitzat models lineals generalitzats (GLMs). El grau de sincronització dels episodis de reclutament entre ecotons ha estat analitzat mitjançant el test de Kolmogorov-Smirnov. Finalment, el grau de correlació entre el creixement i la regeneració també ha estat determinat.

El creixement de *Pinus uncinata* al límit superior del bosc està fortament influenciat per factors macroclimàtics comuns entre localitats, metre que els processos de regeneració estan molt més influenciats per les condicions locals. Aquest fet explica que les variacions anuals del creixement d’individus siguin sincròniques entre totes les localitats estudiades, per contra, l’estructura demogràfica de la regeneració presenta molta variabilitat entre localitats. Les característiques fisiològiques de l’espècie i la seva resposta en front de les condicions climàtiques generals de l’alta muntanya limiten el creixement i la regeneració de *P. uncinata*. Però les condicions climàtiques locals modulen fortament la resposta de les poblacions del límit superior del bosc. Aquest seria el cas de l’estrés hídric que

limita el creixement radial i la regeneració en alguns dels ecotons estudiats. Per tant, els nostres resultats emfatitzen la importància de respostes diferencials com a conseqüència de les característiques locals, invalidant les prediccions generals d'augment del creixement i els processos de regeneració en front de l'ascens predit de les temperatures. L'ascens continuat de les temperatures podria provocar l'aturada i fins i tot la reversió dels processos de densificació observats al llarg del segle XX al límit superior del bosc.

Climatic influence on *Pinus uncinata* growth and recruitment dynamics at alpine treeline

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Article enviat a: *Global Change Biology*

Abstract

Based on the traditional treeline paradigm, warmer temperatures would be favourable both for tree growth and recruitment at alpine treeline, and are thus regarded to promote upward shifts. However, in spite of the general warming trends around the globe, differential treeline dynamics highlights that treeline changes are not ubiquitous. This serves as evidence against general projections of climate change assuming linear ecological responses. To assess how tree growth and recruitment will respond to future climate scenarios, climate-treeline relationships are critical for accurate forescasts of potential landscape changes. We analysed relationships between tree radial growth and recruitment with climate at a regional scale in the Pyrenees. To achieve this, we developed local chronologies from 12 *Pinus uncinata* treeline ecotones, located in 4 climatic sub-regions, and evaluated the recent recruitment patterns at each treeline. We also developed a external reference chronology for each climatic sub-region. We aimed to ascertain the most limiting climatic factors for growth and recruitment at treeline, and to detect the spatial variability in climate-treeline relationships. We used correlation and response function analysis to evaluate the relationship between indexed radial growth and monthly climatic variables. Similarity among chronologies was analysed by PCoA analysis and by means of Pearson product-moment correlation coefficients. Generalized linear models (GLM) were developed to identify the climatic factors most closely related with variations in recruits frequency. The similarity of recent demographic processes between treeline ecotones was evaluated by means of paired Kolmogorov-Smirnov tests. Finally, correlation coefficients were used to asses the relationship between ring width and recruitment fluctuations. *P. uncinata* growth sensitivity was affected by macroclimatic conditions at the treelines studied whereas recruitment appeared much more influenced by local and microclimate conditions. This may explain that radial growth year to year variations are held in common by all sites while recruitment demographic structures presented high variability between sites. Species specific traits and the characteristics of the alpine climate may be the cause of general climatic constraints affecting tree growth and regeneration at a regional scale. However, local conditions significantly affected climate-treeline relationships, for instance, the variability in the extent of drought stress between ecotones. Based on the evidences of drought stress found at several treelines, the predicted warmer temperatures and reduced precipitation can distort the 20th century afforestation process at treeline.

Keywords: Climate change, Drought stress, Ecotone, *Pinus uncinata*, Pyrenees, Radial growth, Regeneration, Temperature, Treeline

Introduction

In high elevation forests, climate has been regarded to be the main limiting factor for tree growth, reproduction and establishment (Tranquillini 1979; Grace & Norton 1990; Körner 1998). The upper elevational limit of tree growth on mountain slopes, the alpine timberline or treeline ecotone, represents an abrupt transition in life form dominance and is one of the most prominent vegetation boundaries (Resler 2006). A common thermal threshold for forest growth at high elevation remains the most likely explanation of global alpine treeline elevations (Körner & Paulsen 2004). Hence, based on the traditional treeline paradigm, warm temperature is favourable to both tree radial growth and reproductive success and thus treeline ecotones are exceptional for the potential they offer for the assessment of the impact of climate change (Brubaker 1986; Stayler & Noble 1992). Consequently, one of the more consistent predictions is that the treeline ecotone will undergo a significant change in structure and position due to the current temperature rise (Grace *et al.* 2002). In fact, many studies reported important population responses at treeline during the 20th century in response to climate change (e.g. Payette *et al.* 2001; Juntunen *et al.* 2002; Gamache & Payette 2005; Kullman 2005; Danby & Hik 2007). However, despite broad-scale constraints on treelines imposed by global-scale thermal trends, factors other than temperature influence treeline elevation and structure at fine spatial scales (Daniels & Veblen 2004). For example, inverse relationships between growth and climate warming has been related to moisture stress at treeline in Alaska (Lloyd & Fastie 2002; Wilmking *et al.* 2004), and Lloyd & Graumlich (1997) reported that precipitation appears to be the most important factor determining the upper treeline in Sierra Nevada. Moreover, treeline stability (Cullen *et al.* 2001; Camarero & Gutiérrez 2004) and differential treeline dynamics (Dalen & Hofgaard 2005; Payette 2007) has also been described in the global warming context evidencing that treeline changes (e.g, treeline shifts) are not ubiquitous. Thus, regional to local scale factors can be responsible of abrupt changes and reversible responses in treeline dynamics, which may serve as evidences against general projections of global change assuming simple, linear ecological responses (Daniels & Veblen 2003; Millar *et al.* 2004; Lloyd 2005). Overall, in spite of multiple studies at treeline ecotone, the degree to which treeline response may lag climate change and the extent to which sensitivity to the climate may vary among sites remains largely unknown (Lloyd & Fastie 2003). It is not obvious how treelines will respond to future climate change predictions (IPCC 2007) and additional studies are therefore required to improve our understanding of climate-treeline relationships, and are critical for accurate forescasts of landscape change (Danby & Hik 2007).

One question particularly relevant nowadays is the possible loss of alpine species as a result of upward encroachment of subalpine forest under global warming regime (Luckman & Kavanah 2000). Pyrenees mountains may be a paradigmatic example in this sense since they encompass the southernmost distribution range of many European alpine species, including endemic and endangered species (Bolòs & Vigo 1984; Ozenda 1985; Carreras *et al.* 1996a). However, only local studies has been conducted in the central Pyrenees (Camarero & Gutiérrez 1999, 2004) and a deeper knowledge of treeline responses and its constraints at a regional scale is fundamental to forecast how current treeline dynamics can affect alpine flora in the global change context. But climate change is only one aspect of environmental change that may effect the location of treelines (Holtmeier & Broll 2005). Other factors also have to be considered of which land-use may be the most important (Dirböck *et al.* 2003). This is the case in the Pyrenean range where, as in many other Eurasian mountain systems, human activities (e.g. seasonal farming) were common at treeline (Körner 1999) but they have decreased drastically during the 20th century, specially since 1950s (García-Ruiz *et al.* 1996). In spite that responses due to land use abandonment can initially mask or even override climatic controls (Hofgaard 1997), anthropogenic treelines become sensitive to climate under sustained climate warming (Holtmeier & Broll 2005). The abundant tree seedlings which invade former pastures after pastoral use are more impeded by unfavorauble site conditions than might be expected in low level forest due to the low invasibility of subalpine grasslands (Dullinger *et al.* 2004). If these limiting conditions for tree establishment improve due to changing climate, the subsequent treeline dynamics (e.g., seedlings survival and growth) could be considered as climate-driven even though it actually occurs below the climatic treeline (Gehring-Fasel *et al.* 2007).

We focus our study in 12 semi-natural examples of treeline ecotones (not intensively exploited since ca. 1950s) close to the potential treeline altitude in the Pyrenees. In all of them important densification trends are observed during the second half of the 20th century, but specially after 1970s (Batllori & Gutiérrez 2008, *submitted*) coinciding with a sharp temperature rise (Diaz & Bradley 1997). Since no concrete data on domestic livestock management at the time are available, whether the observed densification trends are triggered by climate or land use changes remain uncertain. However, without a reactivation of pastoral use and under future climate warming predictions (IPCC 2007), changing environment may become the most important factor in determining such treelines dynamic (Holtmeier & Broll 2005). In this paper, we describe recent recruitment age structures and examine the influence of climate factors (temperature and precipitation) on radial growth and recruitment at alpine *Pinus uncinata* treeline ecotones at a regional scale in the Pyrenees. We specifically address the following questions: (1) if synchronous responses in tree growth and recruitment pulses are present over the studied range, (2) which are the main climatic factors related to tree growth and seedling establishment, (3) if these factors are regionally influencing radial growth and recruitment and (4) to ascertain if tree growth and establishment are influenced by the same factors. We expect great regional variability of the importance of climatic influences on treeline due to the climatic diversity resulting from topographic variation which modify coarse-scale climate trends.

Methods

Study area

The present study was conducted on 12 alpine *Pinus uncinata* treeline ecotones of the central and oriental range of the Iberian Pyrenees, Catalan Pyrenees and Andorra, located in 4 sub-regional climatic areas (Fig. 1). *P. uncinata* is a shade intolerant conifer which shows several attributes typical of good invaders (e.g. light-winged seeds, short pre-reproductive period) (Ceballos & Ruiz de la Torre 1979) and is one of the most widespread alpine timberline species (Erschbamer & Wallnöfer 2007). In the Pyrenees, this species forms most of the subalpine forests in the upper mountain regions, on any substrate and at any exposure (Ninot *et al.* 2007). Detailed studies of vegetation mapping and field surveys lead Carreras *et al.* (1996b) to draw the potential timberline elevation for the Catalan Pyrenees mostly between 2.200-2.450 m depending on exposure, continentality and landform. At treeline ecotone, *P. uncinata* forests show low canopy cover and the trees grow to smaller height due to the harsh environmental conditions. In this paper the term treeline ecotone (or merely treeline) is used in a general sense, and refers to the transition from the uppermost closed forest, or timberline, to the treeless alpine vegetation (Körner 1998). Hence, the altitudinal limit of upright tree growth, the treelimit, is included. We defined the timberline position by a coverage threshold of 30-40% (Holtmeier 2003) given by arboreal (≥ 5 m height) trees (Smith *et al.* 2003), and the treelimit position was determined by the uppermost elevation of upright trees with a minimum height of 2 m (Kullman 2000, 2002).

Since great differences occur between north- and south-facing ecotones in terms of vegetation structure (Braun-Blanquet 1948; Vigo 1979), we restricted this study to north facing slopes. *P. uncinata* forests are there characterized by a dense understorey of the shrubs *Rhododendron ferrugineum* and *Vaccicnium myrtillus* (association *Rhododendro–pinetum uncinatae* Rivas-Mart. 1968). Above timberline, vegetation comprises small spots of dwarf-shrubs, pastures, tree islands and isolated individuals (e.g., stunted individuals). Hence, such vegetation includes small-scale mosaics of structurally and floristically different plant communities (Illa *et al.* 2006; Vonlanthen *et al.* 2006) which in the study range are dominated by short meso-xerophilous pastures of *Festuca airoides* (on acidic substrata) or *Kobresia myosuroides* (in carbonated soils), ericaceous dwarf-scrubs (formed by *Rhododendron ferrugineum, Arctostaphylos uva-ursi, Vaccinium uliginosum* subsp. *microphyllum,* etc.), and sparse vegetation of rocky substrata and scree (Braun-Blanquet 1948; Carrillo & Ninot 1992).

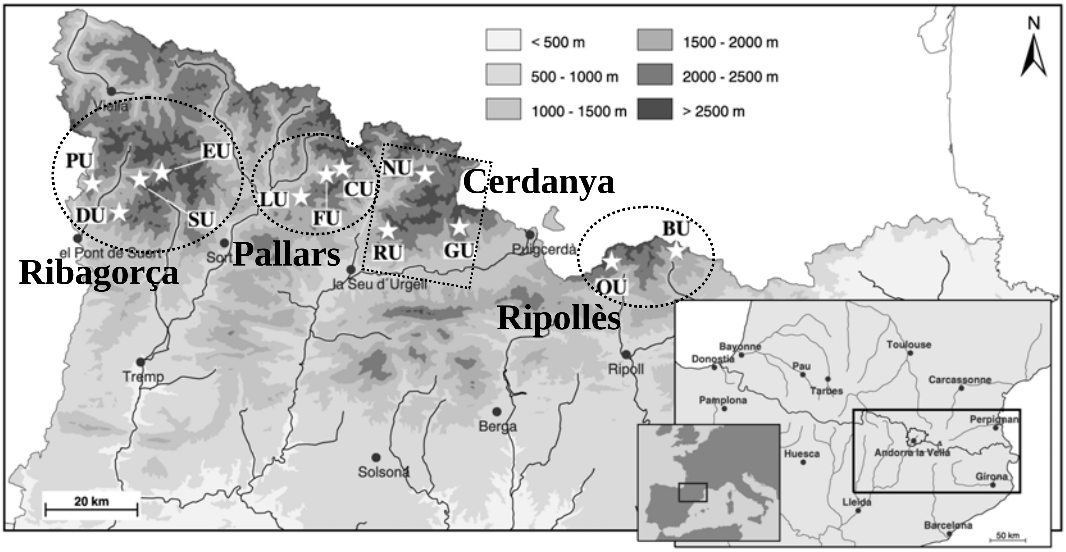

Figure 1. Location of the study sites in Catalan Pyrenees, NE Spain, and Andorra (see Table 1 for sites and codes). Dotted lines show the 4 climatic sub-regional areas used in the growth and recruitment climate relationships.

Field sampling

We combined aerial photograph interpretation (1956 and 2000 flights) with terrain inspection to select 12 sites (Fig. 1) including semi-natural examples of alpine treeline ecotones. The studied stands are located on homogeneous north-facing slopes out of avalanche paths, major rocky outcrops. No evidences of recent fires were found in none of the study sites. In fact, 5 of the treelines studied are inside protected areas. At each site we set a rectangular plot expanding upslope from the subalpine forest until the alpine grasslands, including both timberline and treeline. Plot area varied from 960 to 7600 m^2 depending on each site's transition characteristics (Table 1). Field sampling was conducted between 2003 and 2006 during the end of spring and the summer.

Each *P. uncinata* tree inside the plot was tagged and its location mapped using rectangular coordinate axes (x, y). For each tree, basic biometric measurements were registered (total height, basal and breast height diameters) and the presence of cones and its abundance was noted. All individuals big enough (diameter ≥ 10 cm at breast height) were cored at 1.30 m. Each tree was cored repeatedly using and increment borer until a core through the pith (or as near as possible) was obtained. Natural regeneration was carefully examined in each plot and the ages of all seedlings (individuals < 0.5 m height) and small saplings (height ≥ 0.5 m and breast height diameter < 7.5 cm) were determined in the field by counting the terminal bud scars (internodes) along the main stem. However, estimations of seedling age based on the number of internodes underestimate the true age (age at root collar) (Camarero 1999). In order to minimize such dating errors, we collected 270 seedlings and small saplings (individuals < 1.5 m high) from 6 representative of the 12 plots studied (45 small pines at each site) to obtain age-correction functions. The 270 small pines were collected, along with their roots, between timberline and treeline zone nearby the study plots. Progressive sanding of the basal cross-section of each collected individual allowed to determine the root collar where rings were counted to ascertain tree age (Gutsell & Johnson 2002). Age-correction functions were developed for each of the 6 stands by means of a linear regression on age at root collar compared to age obtained by internode counting. The age-correction function of the nearest of the 6 sampled stands was used for age correction of the seedlings and small saplings of the 6 non-sampled sites.

Table 1. Characteristics of the sampled *Pinus uncinata* treeline ecotones in the Catalan Pyrenees and Andorra.

Climate sub-region	Code	Latitude (North)	Longitude (East)	Plot size (m^2)	Altitude (m a.s.l.)	Slope (º)	Aspect	Bedrock
Ribagorça	PU	42º 31’	0º 45’	6000	2199 - 2268	28	N	lime
	DU	42º 28’	0º 49’	1200	2010 - 2069	30	N	lime
	SU	42º 32’	0º 53’	1500	2270 - 2338	27	NW	lime
	EU	42º 33’	0º 56’	940	2299 - 2339	24	W	granodiorite
Pallars	LU	42º 31’	1º 21’	1180	2363 - 2405	21	N	slate
	FU	42º 33’	1º 23’	7600	2352 - 2435	24	NW	slate
	CU	42º 33’	1º 25’	1160	2250-2297	26	NW	lime
Cerdanya	RU	42º 26’	1º 32’	1650	2236 - 2271	24	W	slate
	NU	42º 34’	1º 37’	980	2266 - 2314	29	N	lime
	GU	42º 27’	1º 44’	1500	2312 - 2365	16	NE	slate
Ripollès	OU	42º 23’	2º 08’	1500	2241 - 2308	27	N	slate
	BU	42º 24’	2º 19’	1500	2184 - 2241	22	N	slate

The comparison of the age at the root collar with the age obtained by internodes counting of the collected small pines < 30 years (n = 172), gave a mean error of 2.8 ± 0.12 years (mean ± 1SE). Hence, for the demographic analysis of recent recruitment we grouped the seedlings and small saplings into 3-year age-class frequency distributions, an age-class interval including the dating error (Wong & Lertzman 2001). Although we examined intensively all the area inside each plot, the sampling probably underestimated the frequency of newly established recruits due to the difficulty of detecting very small seedlings (1 to 3 years). Thus, recruitment age structures are confined to 1971-2000 period.

Finally, 4 *P. uncinata* subalpine forest stands in each of the sub-regional climatic areas were sampled in order to obtain a reference chronology for each sub-region. Sampling was focused on old dominant trees (Fritts 1976; Schweingruber *et al*. 1990) in open stands in the area lacking evidence of disturbances such as logging, large-scale blowdowns or insect outbreaks. At each site, a minimum of 15 trees were cored with an increment borer at ca. 1.30 m high and 1 to 3 cores were taken from each sampled tree.

Data analysis

For each site, cores were prepared following the standard dendrochronological techniques (Stokes and Smiley 1968). All samples were dated under a stereomicroscope and light rings, frost-damaged rings and narrow rings of each core were used as cross-dating features (Filion *et al*. 1986; Yamaguchi 1991). In accordance with Tardif *et al.* (2003), false or incomplete rings were rarely encountered. Afterwards, ring widths were measured to a presicion of 0.01 mm using the linear table Lintab (Frank Rinn S.A., Heidelberg, Germany) and the program TSAP-Win (Rinn 2003). Finally, cross-dating quality and measurement errors were further validated using the program COFECHA (Holmes 1983).

For each site, we selected cores from potentially reproductive individuals (bearing cones) and discarding old individuals (> 100 yr) to develop a chronology for each treeline. We selected only relatively young individuals since age-controlled climate responses have been described (Carrer & Urbinati 2004). We used the program ARSTAN (Cook 1985) to standardize all tree ring series. Standardization involved applying a spline function with a 50 % frequency response of 15 years (Cook & Peters 1981) and transforming ring-width values into a dimensionless index dividing the observed by the expected values given by the spline function (Fritts 1976). Finally, autoregressive modelling was performed on each chronology to remove temporal autocorrelation. We are aware that the used spline fit of 15 years may remove much long- and mid-term variation from the series (Macias *et al*. 2006), but our results are only referred to the short-term variation patterns of tree growth (1955-2000 period). The same standardization process, but applying a spline function with a 50 % frequency response of 32 years, was used to obtain the external reference chronology covering the 1900-2000 period for each sub-region. Eventually, 12 treeline and 4 reference chronologies were obtained (Table 2).

Meteorological data

We used 4 sub-regional climatic datasets (Fig. 1) to analyse growth and regeneration relationships with climate. These sub-regional climatic series were developed by Macias *et al.* (2006) based on 18 meteorological stations in the area. First, meteorological stations were grouped according to their homogeneity using the HOM routine from the Dendrochronology Program Library (DPL; Holmes 1996), then the MET routine from the same software was used to obtain the 4 sub-regional climatic series. Monthly average temperature and cumulated precipitation cover the period 1951-1999 in all sub-regional climatic series.

Statistical analyses

To asses the degree of similarity among chronologies the intercorrelation among residual chronologies was analyzed by Principal coordinate analysis (PCoA) and by means of Pearson product-moment correlation coefficients (Villalba *et al.* 1997; Lloyd & Fastie 2002). Residual instead of standard chronologies were used to avoid inflating the correlation coefficients due to serial autocorrelation present in the tree-ring series. The similarity between growth fluctuations was also analysed between the twelve treeline and the four external chronologies by means of Pearson product-moment correlation coefficients. The temporal patterns of recent recruitment (age frequency distributions) were compared between sites using paired Kolmogorov-Smirnov tests with Bonferroni adjustment of the significance level (α = 0.05/number of comparisons) (Cuevas 2002; Gamache & Payette 2005; Chauchard *et al.* 2007).

Relationships between indexed radial growth and climatic variables were assessed via Pearson's correlation and response function linear models (Fritts 1976; Fritts & Guiot 1990). For this analysis mean monthly temperatures and total monthly precipitation from October prior to growth (t-1) to October of the year of growth (t) (26 variables) were used. We extended the analysed period often used for studies of alpine species (Carrer *et al.* 1998; Carrer & urbinati 2001, 2004), from October prior to growth (t-1) to September of the year of growth (t), since late wood development and the formation of metabolic reserves in *P. uncinata* also occur during fall (Rolland & Scheller 1994; Camarero *et al.* 1998). Pearson's correlation and response functions were computed using the DENDROCLIM2002 program (Biondi & Waikul 2004) with 1000 bootstrap iterations both for correlation and response functions models. The statistical relationship between ring width and each monthly climatic variable was examined over the period common to the chronology and the instrumental climatic record (1955-1999 period).

Table 2. Chronology characteristics of the 12 treelines studied and the 4 reference chronologies (Ref-).

Climate Sub-region	Site	Time Span	Mean Years	Nº Trees	Nº Radii	m_{sx} (1)	R (2)	EPS (3)
Ribagorça	PU	1955-2000	86.5	17	24	0.132	0.470	0.865
	DU	1955-2000	54.2	12	18	0.141	0.612	0.872
	SU	1955-2000	56.5	16	28	0.152	0.542	0.852
	EU	1955-2000	61.3	15	23	0.125	0.616	0.902
Pallars	LU	1955-2000	57.0	10	18	0.149	0.687	0.896
	FU	1955-2000	54.0	24	39	0.180	0.554	0.910
	CU	1960-2000*	50.0	13	16	0.154	0.547	0.850
Cerdanya	RU	1955-2000	38.1	6	8	0.166	0.685	0.853
	NU	1955-2000	83.4	9	20	0.176	0.682	0.872
	GU	1955-2000	48.2	18	21	0.267	0.552	0.889
Ripollès	OU	1960-2000*	34.7	7	8	0.217	0.730	0.868
	BU	1955-2000	49.6	20	25	0.191	0.746	0.961
	Ref- Ribagorça	1900-2000	252.2	14	28	0.131	0.587	0.862
	Ref- Pallars	1900-2000	294.1	18	33	0.142	0.600	0.901
	Ref- Cerdanya	1900-2000	175.5	15	27	0.149	0.596	0.879
	Ref- Ripollès	1900-2000	170.0	13	25	0.122	0.604	0.873

(1) mean sensitivity index

(2) mean correlation of all series with the master chronology

(3) expressed population signal

* chronologies which present significant EPS for the period 1960-2000.

We used generalised linear models (GLM) to identify the climatic factors most closely related with variations in recruits frequency. Similarly to Daniels & Veblen (2004), we created a number of seasonalized variables for averaged temperature and total precipitation: summer (June–August), fall (September–October), winter (November–March) and spring (April-May). In GLMs, pine recruitment density in 3yr classes was used as dependent variable and seasonalized temperature and precipitation, averaged for the same 3yr intervals, were used as predictor variables. We did not use recruitment residuals since neither negative exponential nor power function models presented significant adjustments in many of the presented demograhic structures. Since temperature and precipitation conditions can also influence post-establishment survival and growth of recruits (Gamache & Payette 2005; Wang *et al*. 2006), we also performed GLMs between recruitment and 3 years forwarded climate data. We detected signs of overdispersion when performing GLMs, and following Crawley (2005), we tackled this problem by using a quasi-poisson approach, thereby directly estimating the dispersion parameters from the data set. The significance of the predictors was assessed by means of log-likelihood ratio tests. GLMs were computed using the glm routine in R 2.6.1 (R Foundation 2007).

To assess the degree of similarity between ring width and recruitment fluctuations we used Pearson product-moment correlation coefficients. Seedlings density variations in 3yr classes were correlated with the averaged indexed ring width for the same 3yr intervals. We also performed GLMs to see if recruitment-radial growth relationship could be better predicted using this procedure. As these GLMs failed to increase the determination coefficient and the significance relative to simple Pearson's correlations, they are not presented here.

Results

Pinus uncinata growth sensitivity was affected in a similar way by sub-regional conditions at the treelines studied. The vr-1 and vr-2 (first and second PCoA coordinates) were significant explaining 40.92% of the total variance (21.63 % and 19.29 % respectively). The scatter plot of the PCoA loading coefficients did not displayed clear groups of chronologies with similar growth patterns (Fig. 2), only OU and BU chronologies, the easternmost treelines studied, appeared separated form the rest of the study sites. Similarly, significant and positive correlations ($p < 0.05$) were observed among all the treeline chronologies (Table 3) without higher correlation coefficients between the sites in the same climate sub-region. These results indicate that year to year growth variations for the period 1955-2000 are held in common by all sites. Furthermore, the 4 reference chronologies presented significant and positive correlations ($p < 0.05$) among them and with the 12 treeline chronologies (Table 3).

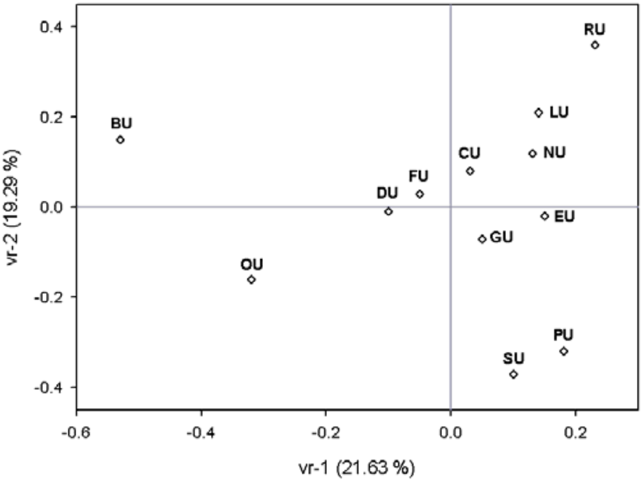

Figure 2. Scatter plot of the two first PCoA loadings for the growth indexes of all the treelines studied (see Table 1 for codes).

In contrast to chronologies similarity, 65% (43 out of 66) of the paired Kolmogorov-Smirnov tests revealed significant differences in the recruitment age structures of the 12 treelines studied. The demographic age structures for the 1971-2000 period, in 3-year classes, are presented in figure 3. The more ubiquitous maximum recruitment peaks occurred during the first half of the 1990s being present in 7 of the 12 treelines studied. Maximum recruitment in the 1980s were detected at 4 treelines, and the remaining treeline presented the highest level of recruitment in the 1970s. It is also apparent the null or low presence of recently recruited individuals (1998-2000 period) in all the study sites.

The 12 treeline chronologies as well as the 4 reference chronologies showed significant responses to the climate conditions of the current year, mainly spring and summer months, and to the late fall (November) prior the growing year (Fig. 4). More significant relationships between growth and monthly mean temperature were observed than between growth and total precipitation. Although significant temperature or precipitation effects were not strikingly coincident between sites, the general shape of response and correlation function analysis was very similar among the treelines studied. Furthermore, Pearson product-moment correlation coefficients indicated highly synchronous climate conditions between sub-regions (results not shown), except for Ripollès precipitation which was not correlated with the three other sub-regions. In general, temperature correlation and response functions coefficients indicated that high spring, summer and early fall temperatures of the growing season favoured tree growth. All the treelines studied showed a positive relation with May temperature of the current growth season, but this relation was only significant in 3 of the study sites.

Table 3. Pearson product-moment correlation coefficients between the 12 treeline and the 4 reference crhonologies (period 1955-2000). All correlation coefficients are significant at $p < 0.05$ level.

	DU	SU	EU	LU	FU	CU	RU	NU	GU	OU	BU	Ref. Ribagorça	Ref. Pallars	Ref. Cerdanya	Ref. Ripollès
PU	0.494	0.662	0.665	0.453	0.580	0.623	0.428	0.546	0.639	0.392	0.388	0.682	0.718	0.676	0.689
DU		0.521	0.600	0.558	0.525	0.622	0.568	0.559	0.615	0.586	0.570	0.488	0.559	0.543	0.707
SU			0.624	0.440	0.613	0.529	0.394	0.462	0.708	0.562	0.314	0.564	0.502	0.493	0.490
EU				0.662	0.655	0.725	0.705	0.747	0.832	0.488	0.514	0.744	0.713	0.683	0.646
LU					0.789	0.697	0.685	0.663	0.675	0.467	0.463	0.601	0.782	0.567	0.525
FU						0.721	0.531	0.613	0.698	0.540	0.635	0.718	0.726	0.628	0.546
CU							0.688	0.672	0.726	0.527	0.634	0.647	0.780	0.669	0.652
RU								0.633	0.658	0.413	0.448	0.471	0.640	0.497	0.471
NU									0.724	0.439	0.527	0.711	0.743	0.836	0.592
GU										0.645	0.578	0.710	0.729	0.637	0.643
OU											0.632	0.442	0.398	0.407	0.428
BU												0.497	0.499	0.547	0.543
Ref. Ribagorça													0.707	0.684	0.629
Ref. Pallars														0.791	0.752
Ref. Cerdanya															0.636

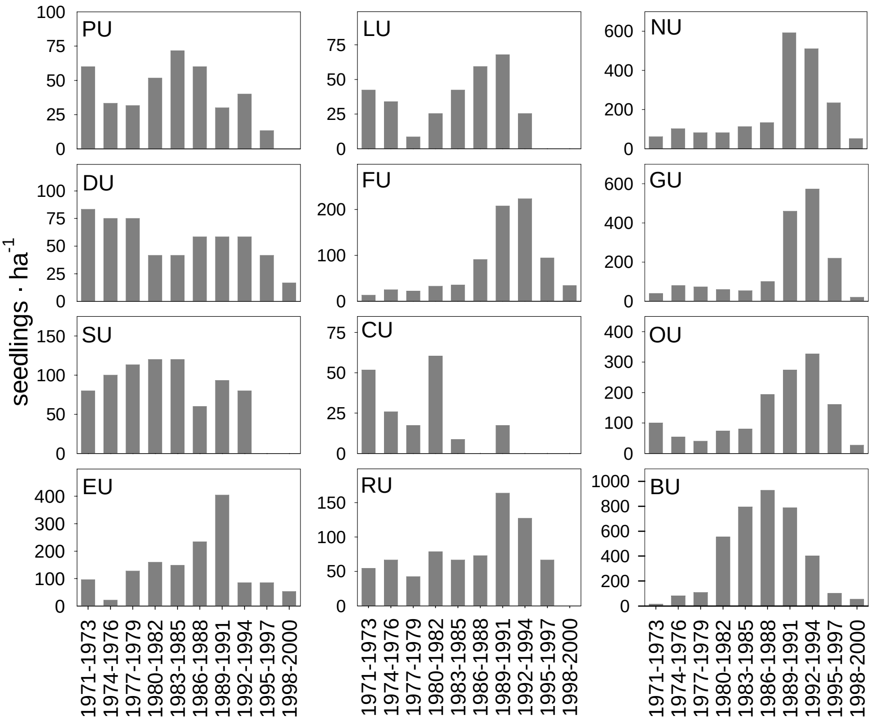

Figure 3. Recent age frequency distributions (1971-2000 period) in 3 year classes at the 12 treelines studied across the Pyrenees. Sites are arranged following the west-east gradient, from the top to the bottom and from the left to the right. Vertical scale varies between populations.

Temperatures during the summer months (june-august) also enhanced tree growth as evidenced by the positive although not significant correlation and response funcion coefficients.However, high July temperature had a negative effect on radial growth in several treelines (7 out of 12), but this relationship was only significant in one of the study sites. November temperature of the year prior to growth had positive effects in all the sutdy sites being significant in half of the treelines studied. Finally, winter temperatures appeared negatively related to tree growth except for February which had clear positive effects on tree growth. Contrastingly, March temperature presented a negative relationship with radial growth in all the study sites. In the other hand, few significant relationships were found between precipitation and radial growth. The correlation of late spring (May) and July precipitation with radial growth was generally positive in the treelines studied, although only significant in 2 of them. However, June, August and April precipitation appeared negatively related to radial growth in several sites, more frequently in the Ribagorça and Pallars sub-regions. Fall precipitation presented contrasted relationships with tree growth between the study sites. Whereas it showed a positive relationship in the easternmost treelines (OU and BU), this relationship was very weak or negative for the rest of the study sites. Finally, winter precipitation appeared both positively and negatively related to tree ring witdh.

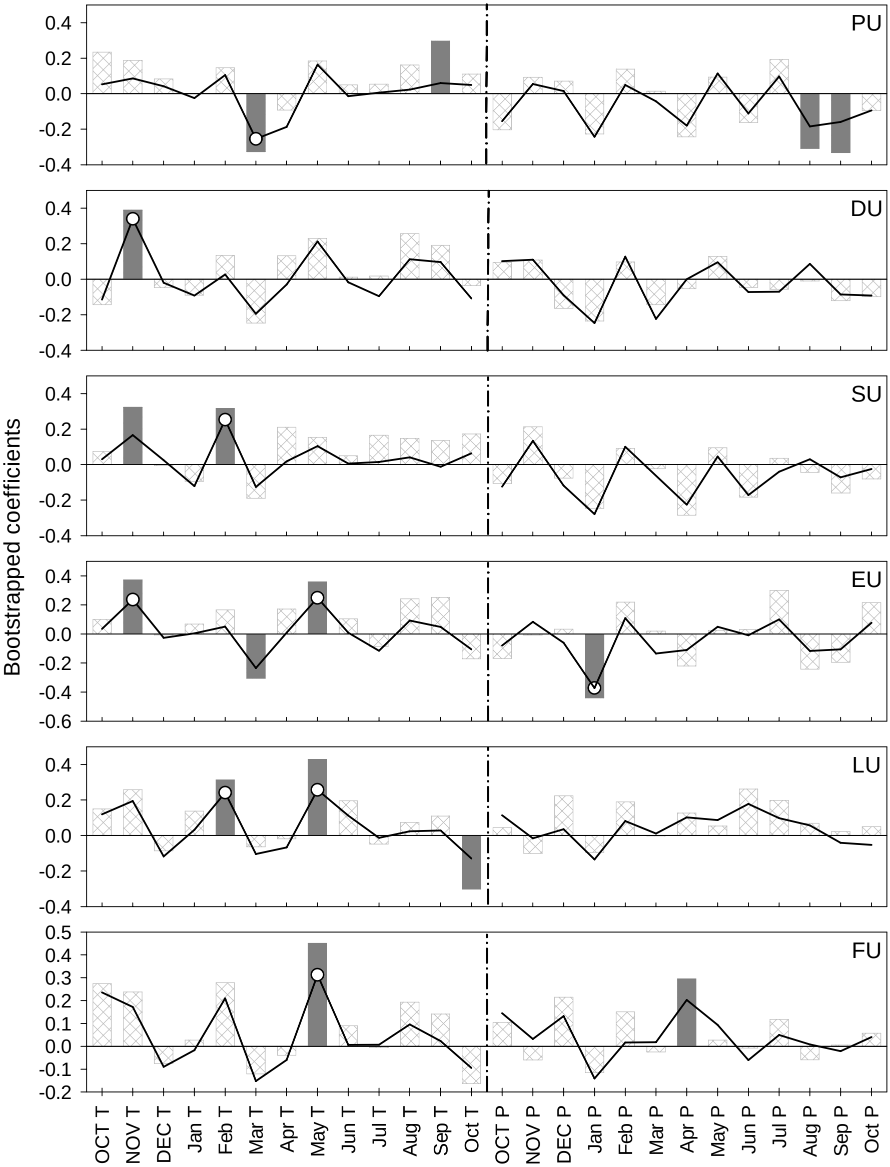

Figure 4. Bootstrapped correlations (bars) and response functions (lines) performed between the indexed radial growth of each treeline chronology with monthly climate data (averaged temperature and cumulated precipitation) from prior October to October of the growing season. Capitals: prior year months; lowercase: current year months. Significant correlation and response function coefficients ($p<0.05$) are indicated with gray bars and white circles, respectively.

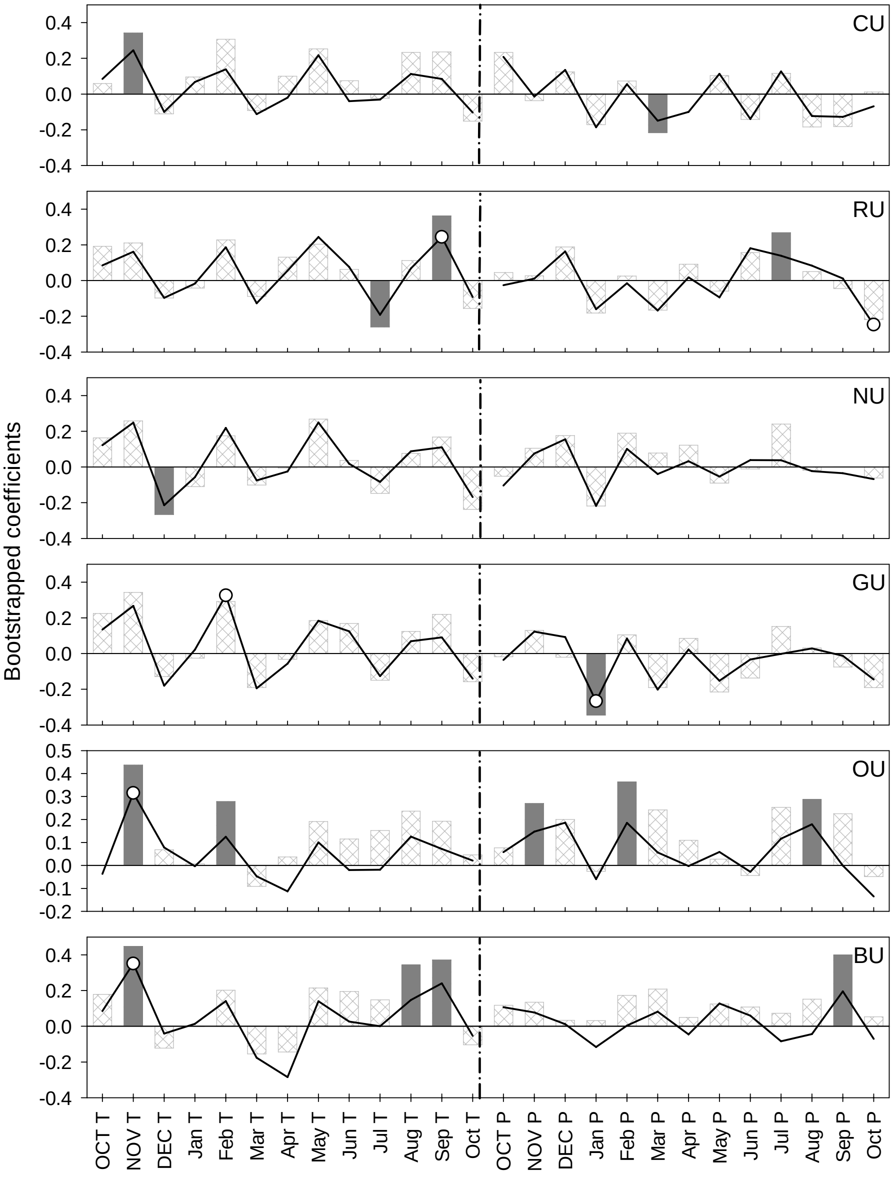

Figure 4. Continued

No major differences between growth and climate relationship appeared between the 12 treeline and the 4 external reference chronologies (Figs. 4, 5). High temperatures in spring and summer of the growing season and fall temperature of the preceding year also favoured tree growth in the reference chrologies. Significant relations were found for February and May temperatures in 2 and 3 of the reference chronologies respectively, whereas the positive effects of November temperature of the year prior to growth was significant in 2 of such chronologies. Precipitation also presented few significant relationships with tree growth.

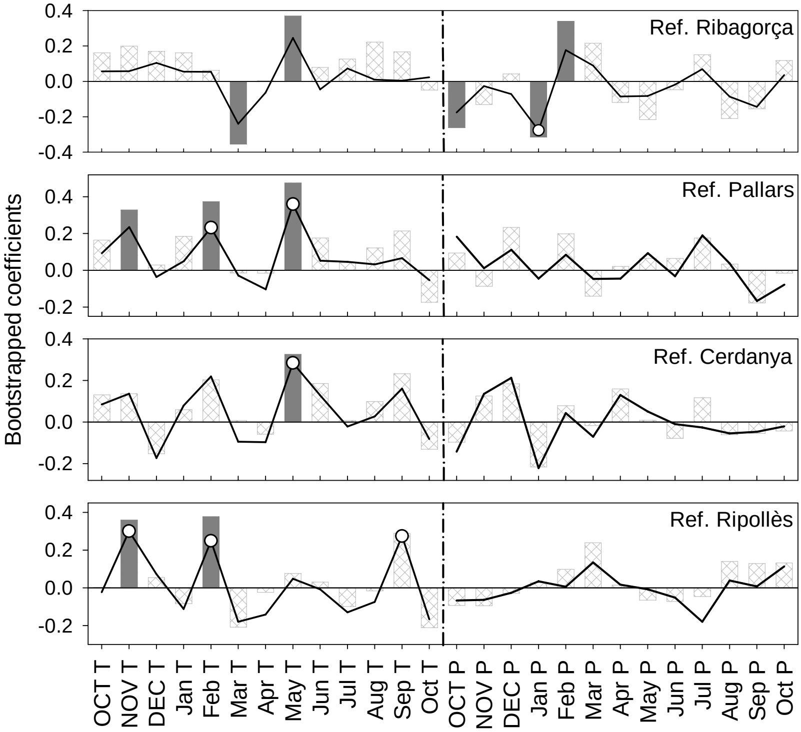

Figure 5. Bootstrapped correlations (bars) and response functions (lines) performed between the indexed radial growth of the 4 reference chronologies with monthly climate data (averaged temperature and cumulated precipitation) from prior October to October of the growing season. Capitals: prior year months; lowercase: current year months. Significant correlation and response function coefficients ($p<0.05$) are indicated with gray bars and white circles, respectively.

Recruitment relationship with seasonalized climate data showed high variability between sites but some regional and sub-regional trends were detected (Fig. 6). Winter and spring temperature presented negative effects on recruitment in Ribagorça sub-region treelines and postive effects in Cerdanya sub-region. In Pallars and Ripollès sub-regions a high variability and less influence of winter and sping temperature on recruitment was detected. Summer temperature presented a positive relationship with recruits density significant in 5 of the 12 treelines studied. But in one of the study sites (BU) this relationship was negative and significant. Finally, fall temperature presented negative influence on recruitment in Cerdanya sub-region whereas it had positive effects at the rest of treeline ecotones studied. Precipitation effects on recruitment were highly variable both between seasons and treelines studied, and no sub-regional trends could be described. However, summer precipitation showed a positive relationship with recruits density in 8 of the study sites. In the other hand, forwarded climate analysis presented less significant relationships with recruitment but regional and sub-regional trends could be also detected (Fig. 7). Forwarded winter and spring temperature presented contrasted results between western and eastern treelines. Whereas they were significant and positively related to recruits density in Cerdanya and Ripollès sub-regions (east), in Ribagorça and Pallars sub-regions these relationships were more variable and even presenting negative effects. Forwarded summer temperature showed again a positive relationship with recruits density in all the study range. In contrast, forwarded fall temperature was negatively related to recruitment in 10 of the 12 treelines studied.

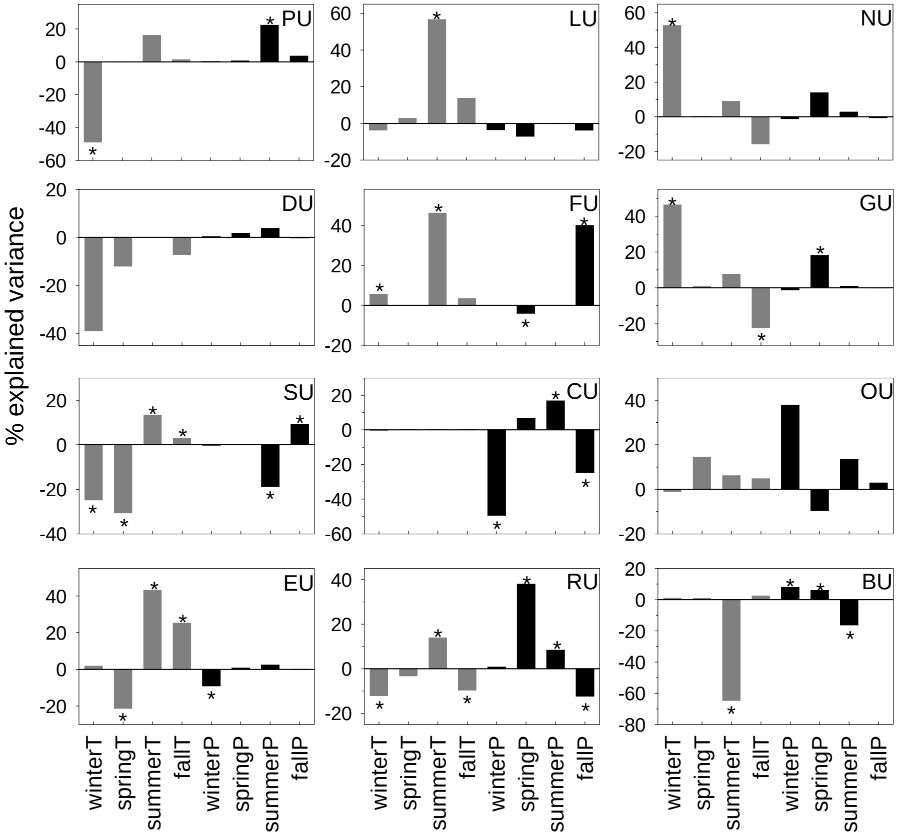

Figure 6. GLMs results for recruitment-climate relationship in 3 year classes (see text for details). The % of explained variance of each of the seasonalized variable on recruitment fluctuations is represented. * symbols indicate significant associations at $p < 0.05$.

Forwarded precipitation-recruitment analysis showed regional effects for winter and fall, whereas spring and summer precipitation presented contrasted sub-regional patterns. Very low or positive effects for forwarded winter precipitation on recruits density were detected. Similarly, forwarded fall precipitation-recruitment relationship was generally low, except for Pallars sub-region were contrasted effects appeared between sites. Eastern treeline ecotones, Cerdanya and Ripollès sub-regions, presented positive and very low relationships between recruitment and forwarded spring and summer precipitation, respectively. Contrastingly, forwarded spring and summer precipitation in western treeline ecotones, Ribagorça and Pallars sub-regions, showed negative (or very low) and generally positive relationships with recruits density respectively.

Finally, tree growth-recruitment relationship appeared to be non significant in none of the treelines studied (Table 4). Positive Pearson product-moment correlation coefficients were observed in 8 of the 12 study sites, whereas 2 presented negative correlation coefficients and the remaining 2 revealed an almost null relationship between tree growth and recruitment.

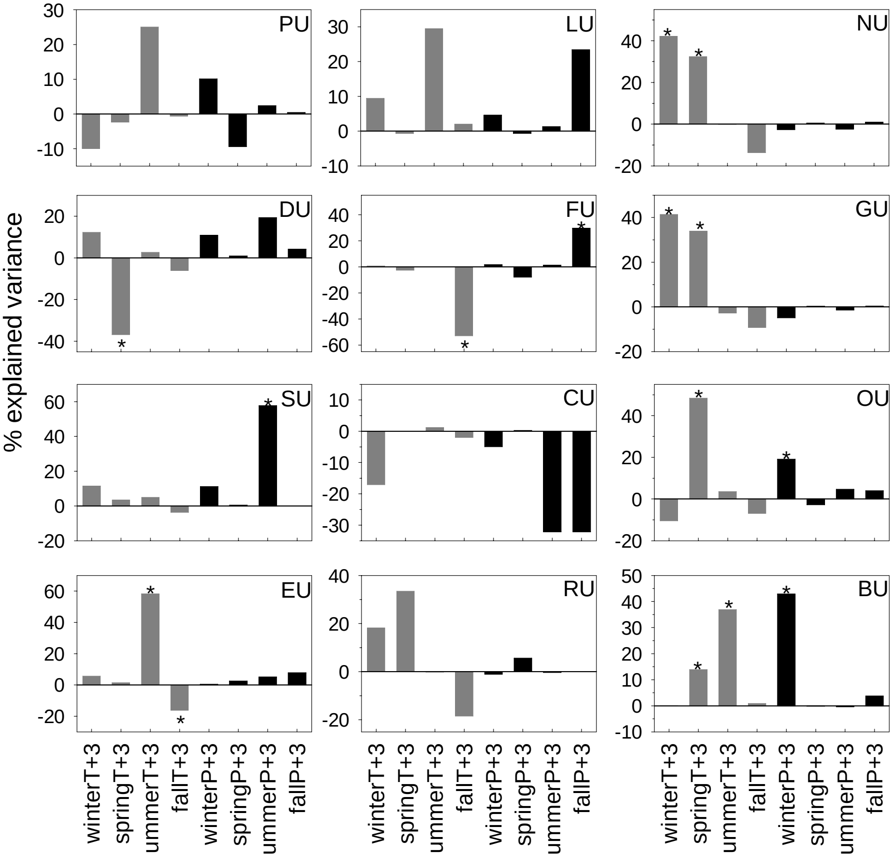

Figure 7. GLMs results for recruitment-forwarded climate relationship in 3 year classes (see text for details). The % of explained variance of each of the seasonalized variable on recruitment fluctuations is represented. * symbols indicate significant associations at $p < 0.05$.

Site Code	*r*	p
PU	0.125	0.731
DU	0.214	0.553
SU	-0.380	0.279
EU	0.186	0.607
LU	-0.121	0.738
FU	0.448	0.195
CU	0.136	0.708
RU	0.019	0.958
NU	0.012	0.973
GU	0.110	0.763
OU	0.625	0.054
BU	0.355	0.314

Table 4. Pearson product-moment correlation coefficients (*r*) and its significance level (p) between tree radial growth and recruitment at the 12 treelines studied.

Discussion

Climate-growth relationship

Although we expected great radial growth variation between sites due to the influence of topography on local climate regimes (Beniston 2003), growth year to year variations for the period 1955-2000 are held in common by all the treelines studied. Moreover, in accordance with Pfeifer et al. (2005), synchronous climate-growth relationships at a regional scale are evidenced by the general shape of correlation and response function analysis between sites. Furthermore, the reference chronologies of the 4 evaluated climate sub-regions presented very similar climate-growth relationships with the 12 treelnine ecotones indicating that radial growth is more strongly correlated with climate variation than with treeline elevation (Paulsen et al. 2000). Our results also confirm that tree radial growth at treeline, where open forests occur, is mainly controlled by climate and thus that stand dynamics processes (e.g. competition) have little effects on it. Overall, our results are in accordance with Tardif et al. (2003) which reported the influence of macroclimatic environmenal conditions on tree ring growth of *P. uncinata* stands from the Central Pyrenees. However, local effects in the described relationship between tree growth and environmental conditions can also be observed between the 12 treeline ecotones studied (e.g., July temperature, fall precipitation).

Temperature has been regarded as the main factor related to radial growth for *P. uncinata* (Gutiérrez 1991, Tardif et al. 2003). That may explain the low number of significant correlation coefficients between precipitation and tree growth at the study sites. Furthermore, our results are in accordance with other studies from cold environments. For example, Lloyd & Fastie (2002) describe that tree growth at treeline ecotones in Alaska are responding to temperature and not to precipitation. However, it must be taken into account that while a centrally located climate station can be highly representative of year-to-year variability in temperature, precipitation is much more local (Wilmking & Juday 2005).

Warm Novembers in the year before ring formation and warm Mays during the year of ring formation dominated the growth-climate association at *P. uncinata* treelines. As reported by Rolland & Schueller (1994), the general positive climate-growth relationship during fall may indicate the negative influence of cold temperatures in this season in the formation of metabolic reserves for following year radial growth. The described positive response to May temperatures is consistent with the tree-ring phenology and structure of *P. uncinata* in the Pyrenees (Camarero et al. 1998), which may begin radial growth by the end of May. Other authors reported the positive influence of late spring-early summer temperature on trees growing near the upper treeline (Villalba et al. 1997, Tardif et al. 2003). This is consistent with the fact that the cambial reactivation of evergreen conifers is triggered by temperature rise (Tranquillini 1979). Furthemore, the positive response to May temperature, and its greater influence during the second half of the 20th century (Tardif et al. 2003), is also found in many studies suggesting that trees begin to growth earlier due to an enlargement of the growing period (Walther et al. 2002, Wieser 2004, Menzel et al. 2006). In general, tree growth during the growing period (May-Sept) seems to be limited by low temperatures since most of the correlation and response functions coefficients showed a positive relationship between temperature and ring width. However, in contrast to Oberhuber (2004), Pfeifer et al. (2005) and Pelfini et al. (2006), we find inverse correlations of radial growth with July temperature (coupled to positive effects of July precipitation) in several of the treelines studied, which may indicate a negative effect of water stress. Other authors reported lower radial growth in treeline populations in Alaska associated with periods of warm Julys (Lloyd & Fastie 2002, Wilmking & Juday 2005). Lara et al. (2001) attributed the inverse correlation of radial growth with temperature to increased evapotranspiration and decreased water availability. In accordance with Barber et al. (2004) and Wilmking et al. (2004), the observed negative correlations of radial growth with July temperatures are indicative of drought stress. Hence, our results reinforce the idea that growth at treeline can be negatively affected if warming continues without significant gains in precipitation (D'Arrigo et al. 2004). However, not all the treeline studied populations presented such inverse correlation in the July climate-growth relationship, reinforcing the idea that drought stress on a regional scale is modified by local site factors (Wilmking & Juday 2005). Recently, Oberhuber et al. (2008) report that the strongest log-term stable climatic signal on tree growth at treeline during the last 200 years is a direct response to July temperature. However, they also detect a divergence of radial growth and July temperature since the mid 1980s, and suggest that this might be due to the impact of temporary drought stress during the growing season on radial tree growth. Our analyses of growth-climate relationship via correlation and response function coefficients apport evidence of drought stress during July of the growing year on tree radial growth at treeline. To our knowledge, this was not previously evidenced, nor in the Pyrenees neither in other European treeline populations.

The negative correlation coefficients between radial growth and temperature in March in all the study sites was previously reported in other alpine treeline studies (Oberhuber 2004, Pfeifer et al. 2005). This negative relationship in late winter, when in spite of low water demand due to low air temperatures plants cannot compensate even small loses from frozen soil, may be reflecting the detrimental effects of xylem embolism (Mayr 2007). In the same way, winter precipitation positive effects on tree growth may be attributable to the diminished effects of winter desiccation due to a persistent snow cover which prevents deep soil freezing (Pfeifer et al. 2005 and references therein). However, heavy snow accumulation may affect negatively tree growth due to delayed snow melting that would translate in lower root-zone temperatures at the beginning of the growing season which may lead to reduced growth (Körner & Paulsen 2004). This may explain the negative relationships also observed between tree growth and winter precipitation.

Climate-recruitment relationship

We find some evidences of differential effects of sub-regional climates on treeline recruitment through the west-east gradient of the Pyrenees revealing the influence of more continental or maritime climatic conditions respectively. The general positive relation of winter precipitation with seedling frequency may be attributable to the benefits of winter snow cover protection on recruits survival. Snow cover reduces winter abrasion and rates of desiccation (Smith et al. 2003), prevents low-temperature photoinhibition of photosynthesis (Neuer et al. 1999), increases availability of meltwater (Hofgaard 1997), offers protection against winter grazing and increases availability of nutrients from leaching (Baumeister & Callaway 2006 and references therein). However, negative effects of winter precipitation, observed in some of the treelines studied, may be related to the restricted growing season as a consequence of too much durability of the snow cover (Hättenschwiler & Smith 1999).

The positive relationship of warmer springs with seedlings establishment described by Camarero & Gutiérrez (2004) is not generally observed in the treelines studied. Recruitment at eastern treelines, Cerdanya and Ripollès sub-regions, may benefit of warm springs, whereas at western treelines, Ribagorça and Pallars sub-regions, recruitment relationship with spring temperatures is much more variable being negative in some cases. Winter temperature effects on seedling recruitment were also contrasted between western and eastern treeline ecotones. Such differences may be attributable to distinct local climatic characteristics (Resler 2006) due to the topographic complexity in alpine regions and to site factors as slope or exposure to wind (Barry 1992).

Recruits density appeared in general positively related with summer temperature both for current or forwarded climatic data. Moreover, summer precipitation also presented moderate positive relationships with recruits density, more pronnounced at western treeline ecotones. Accordingly to Daniels & Veblen (2004), the positive effects of summer precipitation may indicate the influence of moisture availability in seedling establishment. Previous studies at Pyrenean treeline ecotones (Camarero & Gutiérrez 2004) attributed low levels of recruitment at treeline due to summer droughts. Cuevas (2000) also determined that the major cause of lenga (*Nothofagus pumilio*) seedling mortality at alpine treelines in Chile was probably summer desiccation. However, our results seem to indicate stronger drought stress due to warm fall temperatures. This is evidenced by the positive relationship of recruitment with fall precipitation and the negative effect of fall temperature on recruits frequency in the forwarded climate-recruitment analysis.

Recruitment-growth relationship

Recruitment and tree growth do not present a significant relationship in none of the study sites. However, the sign of Pearson product-moment correlation coefficients indicate that in the vast majority of the populations studied, the climatic conditions that facilitate seedling establishment are similar to those favouring radial growth of trees (Camarero & Gutiérrez 1999). However, really weak and negative growth-recruitment relationships are also observed. This is in accordance with other studies that reported distinct and sometimes opposite climatic conditions favouring tree establishment and radial growth (Daniels & Veblen 2004). Since the spontaneous establishment of forest-forming tree species at treeline is considered to be the best indicator of treeline sensitivity to environmental changes (Holtmeier & Broll 2005), the lack of a precise synchronous relationship between radial growth and tree abundance fluctuations may reflect lags in the response of tree growth to climatic variations (Villalba et al. 1997).

We compared tree growth of potentially reproductive individuals with recruitment age structures to detect if any trade-off between growth and reproductive effort exists. Our results are not strong in this sense, but it seems that favoured growth conditions may generally enhance seed production as well. Thus, under future warmer conditions (IPCC 2007), we propose that growth reductions due to increased drought stress may lead to lower seed productivity, which coupled to reduced performance of already established recruits can distort or reverse the observed afforestation process described in many treeline studies (e.g. Payette et al. 2001, Juntunen et al. 2002, Gamache & Payette 2005, Kullman 2005, Danby & Hik 2007, Gehring-Fasel et al. 2007, Batllori & Gutiérrez 2008 *submitted*).

Recent recruitment at treeline

Variability in the age distributions may be due to interannual variation in seedling establishment, recruitment to the sapling class, survival, or mortality, which make difficult the interpretation of demographic processes from static age distributions (Johnson et al. 1994). However, the presented demographic structures confirm that recruitment at treeline ecotones follows a rather episodic than gradual pattern (Cullen et al. 2001, Walther et al. 2005). Climatic data are significantly related with variations in recruits frequency at most study sites, thus indicating important influences of temperature and precipitation on *P. uncinata* recruitment dynamics in the alpine treeline ecotone (Danby & Hik 2007). But low or no significant relationships between recruits density and climate variables also occur, thus highlighting that this relation is not straightforward (Gamache & Payette

2005). For instance, many studies stated the importance of microsite environmental conditions for seedling suvivorship and performance at treeline (e.g. Germino et al. 2002, Smith et al. 2003, Akhalkatsi et al. 2006, Resler 2006). Seedlings' microclimate at ground level is dramatically different than adjacent adults climatic conditions, and its likely to be highly uncoupled from the atmospheric climate (Stayler & Noble 1992, Körner 1995, 2007). Furthermore, seed production, dispersal and quality may be also among the factors modulating recruitment dynamics. Overall, all these factors may explain the important differences detected in the recruitment age structures of the studied treelines compared to the similarity of ring width chronologies.

We cannot ascertain the scarcity of recently established seedlings at the study sites. We aknowledge that during the field sampling some of the small seedlings may have escaped our detection. In this sense, we restricted demographic structures to 1971-2000 period. Despite the mentioned problem of detectability, we are still confident that there is a real lack of newly established pines at the populations studied. Whether it is a result of recent adverse climatic conditions (e.g., increased drought stress), to increased climate variability (Camarero & Gutiérrez 2004) or to reproductive constraints remains uncertain. This emphasizes the need of medium-term monitoring of treeline populations and detailed studies of seed production and reproductive potential of different growth forms at treeline.

Main conclusions

In accordance with the traditional treeline paradigm, low temperatures during the growing season are among the factors limiting both tree radial growth and recruitment at treeline. Climate is one of the most important driving factors on tree growth as evidenced by the results presented here, which demonstrate that *P. uncinata* growth sensitivity at several treeline ecotones was regionally affected in a similar way by macroclimatic conditions. In contrast, although climate exert important influences on recruitment, recruits demographic age structure appears to be much more influenced by local and microclimate conditions leading to the no concordance in the periods of increased regeneration over the Pyrenean range studied. Species specific traits and the characteristics of alpine climate may be the cause of general climatic constraints affecting tree growth and regeneration at a regional scale. For example, positive responses of tree growth to May temperature of the growing year and November temperature of the year prior to growth, and negative effects of March temperature are observed in all the treelines studied. However, local climatic conditions modulate site specific growth-climate relationship leading to certain contrasted responses of tree growth under the same sub-regional climatic conditions. This is the case of July summer drought stress on radial growth detected in several treelines which was not previously evidenced neither for the Pyrenean nor for other European treelines. Recruitment may also suffer drought stress but due to warm falls. Hence, our results do not supportincreased seedling establishment and tree growth rate at Pyrenean treelines under the influence of the predicted climate change (increased temperature and reduced precipitation). We suggest that future warming can lead to reduced growth and diminished seedlings performance distorting the ongoing afforestation process at treeline.

Acknowledgements

We are grateful to all the people who helped us with the field work. This study was supported by the project REN2002-04268-C02 (Spanish Ministry of Research). Enric Batllori thanks the support of a MEC-FPU grant.

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Capítol V. Vegetation patterns at alpine treeline: the role of tree cover on abrupt changes in alpine communities species composition.

Resum

A les regions muntanyoses, el límit superior del bosc coincideix, per definició, amb la frontera entre els estatges subalpí i alpí. La sensibilitat d'aquesta zona de transició, o ecotò bosc subalpí-prats alpins, a l'actual canvi climàtic ha estat evidenciada en molts estudis que descriuen per exemple processos de densificació de l'ecotò en paral·lel a l'augment de la temperatura del segle XX. Aquestes respostes poblacionals poden comportar a mitjà termini la reducció i fragmentació de l'habitat de les espècies alpines, i per tant, comportar canvis importants en el paisatge supraforestal. L'anàlisi de l'estructura de la vegetació és molt important per poder predir de manera fiable la resposta i la vulnerabilitat de les espècies alpines en front dels possibles canvis del límit superior del bosc com a resultat del canvi global.

Tot i que els Pirineus representen l'enclau meridional de distribució de moltes espècies alpines, hi ha una manca d'estudis regionals de l'estructura de la vegetació a l'ecotò bosc subalpí-prats alpins. Aquest estudi va ser realitzat a 12 límits del bosc dominats per *Pinus uncinata* als Pirineus centrals i orientals (Pirineu català i Andorra). A cada ecotò es va delimitar una parcel·la rectangular, amb l'eix més llarg paral·lel al gradient altitudinal, incloent la transició des del bosc subalpí fins als prats alpins. L'àrea mostrejada varia entre 940 i 1900 m^2 en funció de les característqued de la transició de cada localitat. Es van realitzar inventaris de vegetació per determinar l'estructura de les comunitats vegetals i la seva diversitat al llarg del gradient altitudinal. L'efecte del recobriment de les capçades del *Pinus uncinata* sobre l'estructura de la vegetació es va analitzar mitjançant l'aplicació de *wavelets*, concretament es va utilitzar la CWT (continuous wavelet transform).

Els resultats mostren una gran similitud del bosc subalpí, a nivell estructural i de composició d'espècies, entre les localitats estudiades. Per contra, els mosaics de vegetació alpina, caracteritzats per canvis bruscs i irregulars de comunitats contrastades al llarg de tota la transició bosc subalpí-prats alpins, presenten una elvada variabilitat entre ecotons. Els resultats mostren una disminució gradual del recobriment de les capçades i un augment del número d'espècies i la diversitat al llarg de la transició bosc-prats alpins. Però tot i la influència negativa del recobriment de les capçades sobre la riquesa d'espècies i la diversitat, el límit del bosc en sentit estricte no implica canvis acusats en la diversitat de les formacions alpines. No s'han trobat comunitats intermèdies, en quant a composició específica, al llarg de l'ecotò.

La vegetació alpina de l'ecotò està determinada pel tipus de substrat i per l'heterogeneitat de les condicions ambientals arran de terra, emfatitzant la importància dels microambients en la fluctuació de les comunitats vegetals al llarg de l'ecotò. Les respostes retardades dels ecosistemes en front de les fluctuacions ambientals, juntament amb els diferents ritmes de resposta entre processos diferents (p.e., estructura del bosc, composició específica) i la inèrcia de les comunitats, explicarien la situació de no equilibri entre la posició de les fronteres de diversitat i el límit del bosc.

Vegetation patterns at alpine treeline: the role of tree cover on abrupt changes in alpine communities species composition.

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Article enviat a: *Journal of Vegetation Science*

Abstract

1. In mountain ranges, the upper limit of the forest coincides with the boundary between subalpine and alpine belts: the alpine treeline ecotone. The sensitivity of this ecotone to the ongoing global change is widely reported in terms of treeline shifts and/or ecotone afforestation. The consequent alpine habitat fragmentation and loss is expected to trigger important changes in the alpine vegetation. In this scenario, the analysis of vegetation structure is of primary importance to realistically forecast vegetation responses and the susceptability of alpine habitats to treeline changes. Despite the Pyrenees encompass the southermost distribution range of many endangered alpine species, there is a lack of regional detailed descriptions of plant communities structure at treeline.

2. We studied twelve alpine *Pinus uncinata* treeline ecotones on the Iberian eastern range of the Pyrenees. Rectangular plots ranging from 940 to 1900 m^2 were placed along the forest-grassland transition, from the closed forest to the treeless alpine area. To determine community structure and species distrubution at treeline ecotone, species variation along the forest-alpine grassland transition was sampled by means of relevés of 0.5 m^2 set every 2 m along the length of each plot. Fuzzy C-means clustering was performed to evaluate the transitional status of the relevés in

terms of species composition. The role of *P. uncinata* on the spatial pattern of vegetation was evaluated using the continuous wavelet transform analysis.

3. Irrespective of local characteristics, vegetation analyses revealed an important degree of uniformity of the subalpine forest among all the treeline ecotones studied. Contrastingly, the vegetation mosaic found upslope presented great variation between sites and was characterized by abrupt changes of plant communities along the treeline ecotone. Plant richness and diversity significantly increased along the treeline but tree cover and diversity boundaries were not spatially coincident.

4. Our results revealed that no intermediate communities in terms of species composition are present along the treeline ecotone. Ecotone vegetation reflected both bedrock type and fine-scale heterogeneity at the ground level, reinforcing the importance of microenvironmental conditions for alpine community composition. Tree cover did not appear as the principal driver of the alpine communities composition at treeline, which may evidence a non-equilibrium situation due to microclimate modifications by low shrubs and temporal lags of ecosystem response to environmental fluctuation.

Keywords: Plant diversity, Community structure, Ecotone, *Pinus uncinata*, Pyrenees, Tree cover, Treeline, Vegetation analysis, Wavelets

Introduction

In the Pyrenean range, like in the other mountain systems, an altitude zonation made up of contrasted vegetation belts occurs. In the upper parts of the Pyrenees, following the model of the Alpine ranges, a subalpine (or highest forest) belt and an alpine (supraforest) belt have been traditionally distinguished (Braun-Blanquet 1948, Ninot et al 2007). In the upper mountain ranges, the theoretical upper limit of the forest coincides, by definition, with the boundary between the subalpine and the alpine belts, also called timberline or treeline ecotone. Ecotones have been focus of scientific research for long and are defined as transition zones between adjacent ecological systems, but particularly considered as transitions between 'patches' (Hansen et al. 1988, van der Maarel 1990). Two types of transitions have been differentiated, 1) *ecotones* in a strict sense, where strong fluctuations occur creating contrasting but individually relatively homogeneous environments and 2) *ecoclines*, where gradual differences in at least one major environmental factor permit the occurrence of transitional states. In this study, if not specifically pointed, we use the term treeline ecotone (or merely treeline) in a broad sense to describe the transition between the subalpine forests and the alpine pastures (Körner 1998). This transition occurs through an elevational gradient of increasing adverse conditions that finally leads to the altitudinal limit of tree growth (treelimit), which marks a biological threshold for arboreal life (Körner 1999, 2007).

Treeline populations are regarded as very sensitive to climate variation (Hansen & di Castri 1992, Theruillat & Guisan 2001, Grace et al. 2002). Körner (1998) and Körner & Paulsen (2004) presented data supporting the hypothesis of a common thermal threshold that might explain the limits for forest growth at high elevation. According to the thermal explanation of treeline elevation and with the traditional treeline paradigm (Tranquillini 1979), great sensitivity of treelines to climate change is expected. Thus, in the context of global change, responses of polar and altitudinal treelines have become a major concern at an international level (Callaghan et al. 2002). Active scientific research on altitudinal and polar treelines documents important treeline population changes during the 20th century (e.g., Payette et al. 2001, Juntunen et al. 2002, Camarero & Gutiérrez 2004, Daniels & Veblen 2004, Kullman 2005, Danby & Hik 2007, Gehring-Fasel et al. 2007, Payette 2007). Such structural changes at treeline, including growth and regeneration responses which can lead to treeline shifts, are expected to trigger changes in the alpine vegetation (Holtmeier & Broll 2005). For example, several alpine plant species that are restricted above the treeline would experience severe habitat fragmentation and reduction, which may derive in increased regional extinction risk (Dirnböck et al. 2003). However, climate change is only one aspect of environmental variation at treeline (Holtmeier & Broll 2005). Other factors have to be considered, of which land use change may be the most important. In the Pyrenean range, as in many other Eurasian mountain systems (Körner 1999), human activities (e.g. seasonal farming) were common at treeline but they have decreased drastically during the 20th century, specially since 1950s (García-Ruiz et al. 1996). Consequently, during the second half of the 20th century climate changes have run in parallel with important land use changes. This may have contributed to the spatiotemporal variability of treeline response due to local treeline history and climatic characteristics (Daniels & Veblen 2003, Dalen & Hofgaard 2005), being difficult to forecast how current treeline dynamics will affect alpine flora in the global change context.

The analysis of vegetation structure, i.e. the identification of species composition as well as its temporal and spatial patterns, is of primary importance for the subsequent understanding and interpretation of its dynamics (Fortin 1994). In the global change context, changing environmental conditions might set the new distribution limits of species and communities. Thus, to define the susceptibility of alpine grasslands to potential tree colonization, we need a precise description of the spatial pattern of plant communities across treeline ecotones at local scales (Hofgaard 1997). Furthermore, due to a scarcity of quantitative descriptions of tree cover and plant richness boundaries at the treeline (Camarero et al. 2000), a better understanding of the influence of the spatial patterns of tree cover upon the spatial patterns of plant richness is required to predict the response of local alpine flora to potential treeline shifts (Camarero et al. 2006). Hence, plant diversity and community structure have to be examined together to assess the potential role of key structuring species (e.g., tree species), which may cause directional effects on the entire community (Hofgaard & Wilmann 2002). Individual trees change the environmental conditions under their canopy decreasing light availability and modifying soil nutrient and moisture conditions as well (Kembel & Dale 2006). Thus, estimates of canopy cover are a surrogate measure for the influence of the canopy on the understorey environment.

Although the Pyrenees encompass the southermost distribution range of many European alpine species, including endemic and endangered species (Bolòs & Vigo 1984; Ozenda 1985; Carreras et al. 1996a), only local studies concerning vegetation structure has been performed at treeline (Camarero & Gutiérrez 2002, Camarero et al. 2006). Thus, there is a lack of regional detailed descriptions of plant communitites across the treeline in the Pyrenean range. The main objective of the present study was to describe community structure and species distribution at the treeline ecotone in the Pyrenees at a regional scale, and to ascertain whether *Pinus uncinata* is a main influencing factor for vegetation spatial pattern along the forest-pasture transition. The following objectives were specifically addressed: 1) description of vegetation patterns at 12 treeline ecotones, 2) evaluation of plant richness, diversity and tree cover along the treeline, 3) characterization of the relationships between plant richness and diversity with tree cover, and 4) *post hoc* evaluation of the coincidence between species diversity and treeline boundaries (timberline and treelimit).

Methodology

Study area

In contrast to the Alps, in the studied range of the Pyrenees (central and oriental range of the Catalan Pyrenees and Andorra) there is essentially one tree species that inhabits the upper subalpine area: the mountain pine (*Pinus uncinata* Ramond ex DC.). This species forms most of the alpine treeline ecotones, on any substrate and at any exposure (Ninot et al. 2007). Other species such as silver fir (*Abies alba* Mill.), birch (*Betula pubescens*) and beech (*Fagus sylvatica* L.) are present in the subalpine belt but rarely dominating the treeline ecotone (Vigo 1979, Carrillo & Vigo 2002). Thus, the present study was conducted on *P. uncinata* dominated treeline ecotones of the eastern half range of the Spanish Pyrenees (Catalan Pyrenees) and Andorra (Fig. 1). *P. uncinata* is a highly frost-resistant and low-demanding species regarding the supply of nutrients and water (Ceballos & Ruiz de la Torre 1979), which makes it appropriate to be one of the most widespread alpine timberline species (Erschbamer and Wallnöfer 2007). Early phytosociological studies (Braun-Blanquet 1948, Rivas-Martínez 1968) described major differences in species occurrence between *P. uncinata* forests related to aspect (north- and south-facing) and substrate (acidic and lime-rich). Pine forests on acidic north-facing slopes are characterized by a dense understorey of the low shrubs *Rhododendron ferrugineum* and *Vaccicnium myrtillus* (*Rhododendro-Pinetum uncinatae* Rivas-Mart. 1968) whereas on south-facing slopes dominate the low shrubs *Juniperus communis* subsp. *nana* and *Arctostaphylos uva-ursi* (*Arctostaphylo-Pinetum uncinatae typicum* Rivas-Mart. 1968). Such differences are mainly mediated by the presence of an important and long-lasting snow cover in the north-facing slopes which allows *R. ferrugineum*, very sensitive to winter freezing, to develop. In lime-rich substrata and north facing slopes *Sesleria coerulea* and *Festuca gautieri* make a herbaceous understorey along with some particular species like *Pulsatilla alpina* subsp. *alpina* (*Pulsatillo-Pinetum uncinatae* Vigo 1974). Finally, in lime-rich south facing slopes, dominate communities more tolerant to drought events through the year, corresponding to open, irregular pinewoods with a xerophilous subshrub layer usually dominated by *Arctostaphylos uva-ursi* with *Rhamnus alpina* (*Arctostaphylo-Pinetum uncinatae rhamnetosum alpinae* Rivas-Mart. 1991).

Detailed studies of vegetation mapping and field surveys lead Carreras et al. (1996b) to draw the potential timberline for the Catalan Pyrenees mostly between 2.200-2.450 m, depending on continentality, exposure and landform. *P. uncinata* forests reaching the timberline exhibit lower canopy density and trees grown to smaller height due to adverse environmental conditions (Erschbamer and Wallnöfer 2007). At the timberline, open woods give way to a patchy area including small spots of dwarf-scrubs, pastures, tree islands and isolated trees. The vegetation above the timberline, in the alpine zone, forms a small-scale mosaic of structurally and floristically different plant communities (Illa et al. 2006, Vonlanthen et al. 2006) that include short pastures of *Festuca airoides* or *Carex curvula* (on acidic substrata) and pastures of *Kobresia myosuroides* or *Trifolium thalii* (in carbonated soils), ericaceous dwarf-scrubs (formed by *Rhododendron* *ferrugineum, Vaccinium uliginosum* subsp. *microphyllum, Loiseleuria procumbens, Dryas octopetala*, etc.), and sparse vegetation of rocky substrata and scree (Braun-Blanquet 1948; Carrillo & Ninot 1992).

Field methods

We combined field visits with aerial photographs interpretation (taken in 1956 and 2000) to select 12 sites (Fig. 1), including a progressive – though relatively sharp – treeline zonation. At each site we placed a rectangular plot at the upper treeline (transect of 10 m wide × variable length) parallel to the main slope and expanding from the subalpine forest up to the alpine grasslands. Plot area varied from 960 to 1900 m^2 depending on each transition characteristics (Table 1) to include the timberline (closed forest at high altitude) and the treelimit (uppermost elevation of upright trees with a minimum height of 2 m, *sensu* Kullman 2000, 2002). Keeping in mind the characteristics of the high subalpine Pyrenean forests of *Pinus uncinata*, in this study we defined the timberline position by a coverage threshold of 30-40 % (Holtmeier 2003) given by arboreal (at least 5 m height) pines (Smith et al. 2003).

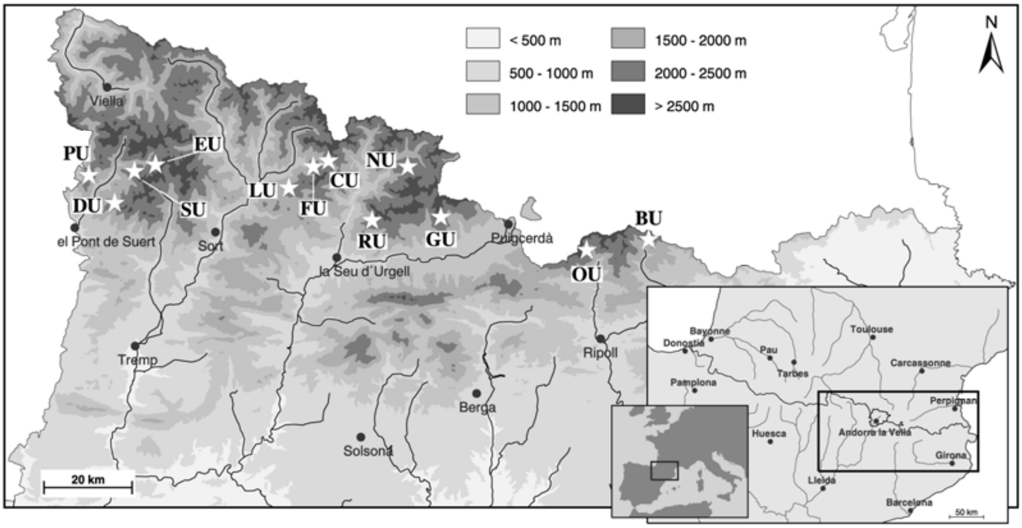

Figure 1. Location of the study sites in Catalan Pyrenees, NE Spain, and Andorra.

The study plots were placed on homogeneous slopes and avoiding major rocky outcrops, avalanche paths and other topographic irregularities. None of the areas studied is intensively grazed nowadays nor in the recent past decades, and five of them are located in protected areas. We restricted our study to *P. uncinata* ecotones on north-facing aspects since, as mentioned above, great differences occur between north- and south-facing ecotones in terms of vegetation structure and composition.

At each plot the location of all *P. uncinata* stems was noted using rectangular coordinate axes (*x*, *y*). For each tree an estimation of crown size was obtained by means of 4 crown radii measurements. Major and minor crown radii and their opposite radii, as well as aspect for each radius, were noted. Using ArcInfo (ArcGis 9.2) we calculated the crown projection area for each tree, properly orientated, and crown cover estimates were then computed for every 1 m along the length of each plot.

Table 1. Characteristics of the *Pinus uncinata* treeline ecotones sampled in the Catalan Pyrenees, NE Spain, and Andorra.

Code	Latitude	Longitude	Plot size (m^2)	Altitude (m a.s.l.)	Slope (º)	Aspect	Bedrock
PU	42º 31’	0º 45’	1400	2199 - 2268	28	N	lime
DU	42º 28’	0º 49’	1200	2010 - 2069	30	N	lime
SU	42º 32’	0º 53’	1500	2270 - 2338	27	NW	lime
EU	42º 33’	0º 56’	940	2299 - 2339	24	W	granodiorite
LU	42º 31’	1º 21’	1180	2363 - 2405	21	N	slate
FU	42º 33’	1º 23’	1900	2352 - 2435	24	NW	slate
CU	42º 33’	1º 25’	1160	2250 - 2297	26	NW	lime
RU	42º 26’	1º 32’	1650	2236 - 2271	24	W	slate
NU	42º 34’	1º 37’	980	2266 - 2314	29	N	lime
GU	42º 27’	1º 44’	1500	2312 - 2365	16	NE	slate
OU	42º 23’	2º 08’	1500	2241 - 2308	27	N	slate
BU	42º 24’	2º 19’	1500	2184 - 2241	22	N	slate

We sampled the species variation along the ecotone by means of relevés since plant richness estimates based on the point method (absence/presence measures) depend on plant size, which affects the probability of occurrence and leads to underestimations of species diversity (Fortin et al. 1999). Thus, given the characteristics of the alpine grasslands we used relevés of 0.5 m^2 (1 × 0.5 m) set at every 2 lineal m on the central axis of each plot. In each relevé, a list of all plant species present and their cover/abundance were noted using the Braun-Blanquet scale (Braun-Blanquet 1979, Choesin & Boerner 2002). Plants were identified to species in the field or collected and identified in the laboratory when necessary. Field sampling was conducted between 2003 and 2006 in summer months.

Data analysis

We analyzed the vegetation relevés using multivariate techniques, namely Fuzzy C-means (FCM) partitions (Bezdek 1981) and Principal Coordinate Analyses (PCoA), using the package GINKGO (de Cáceres et al. 2007). FCM is an iterative procedure that minimizes the within-cluster variability but allowing clusters to overlap (Bezdek 1981). Furthermore, such analyses combine the advantages of numerical partitions with an estimate of membership for each sample to the groups created. To perform the FCM partitions, the relevés data in each plot were converted to a distance matrix using the Chord distance to take advantage of the fact that the original data are relative species cover. Then relevés were partitioned in 2, 3 or 4 groups using a fuzzy exponent of 1.2 (de Cáceres 2005). The evaluation of the species composition and its membership to the groups created were used to determine the transitional status of the relevés and the number of communities present along the treeline in each study site. Finally, we constructed a new matrix containing the abundance of the species present in the communities identified in all the treelines studied. This matrix was converted to a distance matrix with the Chord distance, and PCoA analyses were used to evaluate the uniformity of forest and alpine communities among the 12 study plots. Two PCoA were performed, one including all the communities identified in the transects and one for the alpine communities only.

Linear regression methods were used to ascertain trends in tree cover, plant richness and diversity (Shannon index) along the treeline (increasing altitude gradient) as well as the relationships between plant richness and diversity with tree cover. Tree cover and diversity regressions were computed by means of linear models, whereas for plant richness regressions we used generalised linear models with a Poisson distribution (Faraway 2006). Finally we analysed the relationships between the spatial pattern of crown cover and species diversity variation at each plot using the continuous wavelet transform (CWT). The CWT analysis is the most commonly used in ecological studies involving wavelet analyses (Kembel & Dale 2006), and it presents some advantages compared to other spatial methods. For instance, moving split windows can ignore minor changes at small scales (Choesin & Boerner 2002) and the wavelet functions are also robust against nonstationarity (Bradshaw & Spies 1992). The CWT analysis consists of a particular wave form in a moving window of a fixed dimension (windowing function or 'wavelet'), which travels along the data sequence to assess the match between the analysing wavelet and the data at each point (Bradshaw & Spies 1992). This process is repeated for a range of wavelet sizes, providing a transformation of the data by the wavelet function at several scales. The CWT method permits the data analysis using different wavelet forms; in this study we choose the Haar wavelet since, given its resemblance to a step function, it is the most appropriate in the detection of edges and gradients (Bradshaw & Spies 1992). We examined the tree cover and species diversity relationship at several spatial scales, up to a maximum wavelet size equal to a 10% of the length of the sampled area in each plot (Camarero et al. 2006). We established a buffer zone at the extremes of each transect to avoid computing the CWT outside the sampled area. The wavelet coefficients were averaged over all scales for any particular position along each transect to obtain a position variance (Dale & Mah 1998). The position variance permited us to identify abrupt diversity changes and density transitions of the crown cover along the treeline ecotone. Due to the lack of tests of statistical significance for the wavelet transform, we calculated the wavelet variance from 1000 different randomizations of the diversity and crown cover original data. The 95th highest value of the position variance for each position along the treeline ecotone was used to ascertain the significance of the detected peaks at the $\alpha = 0.05$ level (Manly 1997). Following Kembel & Dale (2006) we calculated the covariance between the CWT of tree cover and species diversity at each scale in each plot. Covariances were preferred to correlations because it has been demonstrated that spatial correlations peak at spatial scales unrelated to the actual scale patterns in the data (Dale 1999). Linear regression and wavelet analysis were carried out in R 2.6.1 (R Foundation 2007), using for the latter the wavCWT routine of the wmtsa Package (Constantine & Percival 2007).

Results

Vegetation patterns

Two or three communities integrating the treeline ecotone transition at each plot were determined by means of FCM analysis (Fig. 2). We identified the species that behave as faithful to the communities in each transect (Table 2). Some of these species coincided with the characteristic taxa inferred by phytosociologists (Carrillo & Ninot 1992, Bolòs et al. 2005) whereas others reflected local particularities. In spite of noticeable crown heterogeneity among plots and a relatively poor understorey, the subalpine forest in all the study sites was still representative of the calcifuge subalpine *Rhododendro-Pinetum uncinatae* (Br.-Bl.) Rivas-Mart. 1968 in terms of structure and species composition. Such association is characterized by an arboreal layer of *Pinus uncinata*, usually presenting open canopy cover, accompanied by a low shrubby layer of *Rhododendron ferrugineum* and *Vaccinium myrtillus* interspersed with herbs as *Deschampsia flexuosa* and feather mosses (e.g. *Hylocomium splendens*).

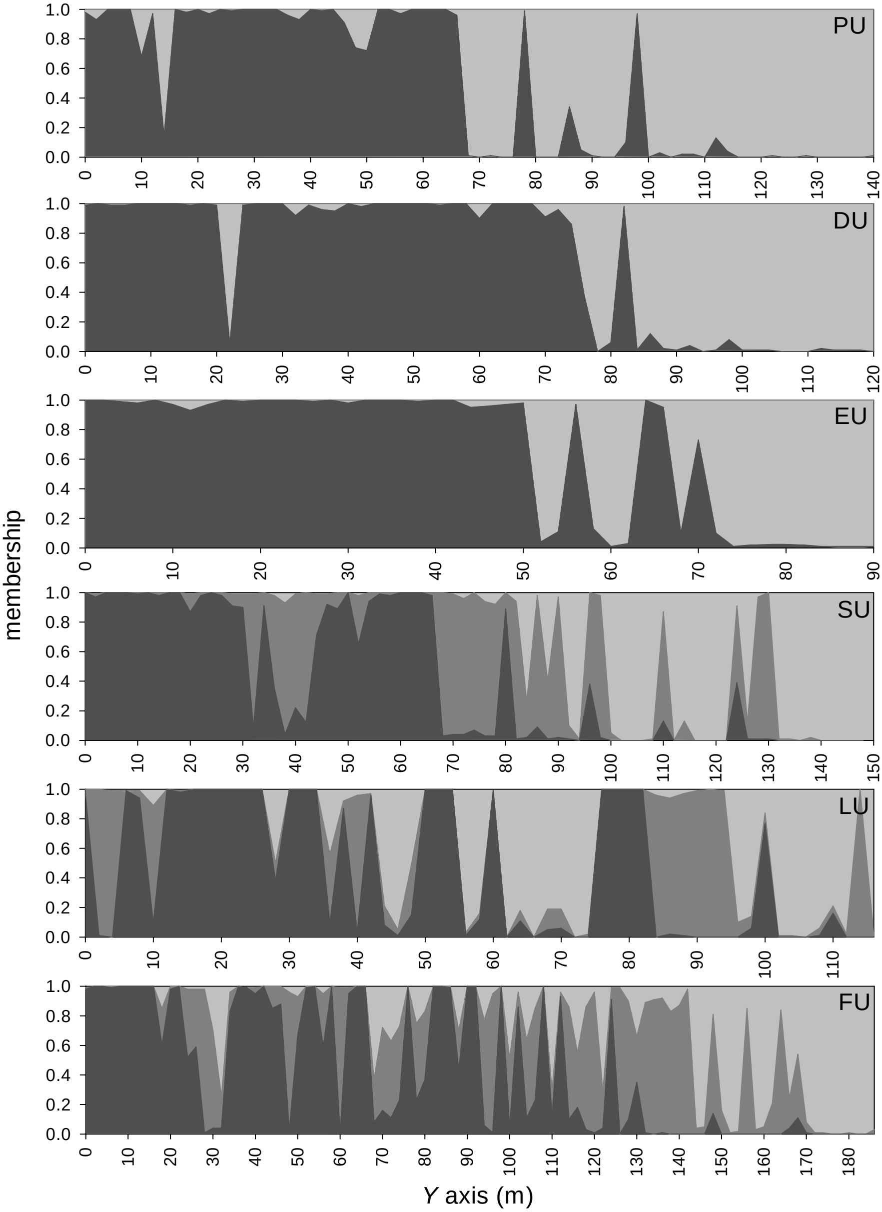

Figure 2. Vegetation structure along the treeline ecotone in the 12 plots studied, from the subalpine forest (left) to the alpine pastures (right), evidenced by the membership of the relevés defined by Fuzzy C-means analysis. Grey intensity, from dark grey to lightest grey, represents: the subalpine forest and different types of alpine formations. See table 2 for detailed communities description at each site.

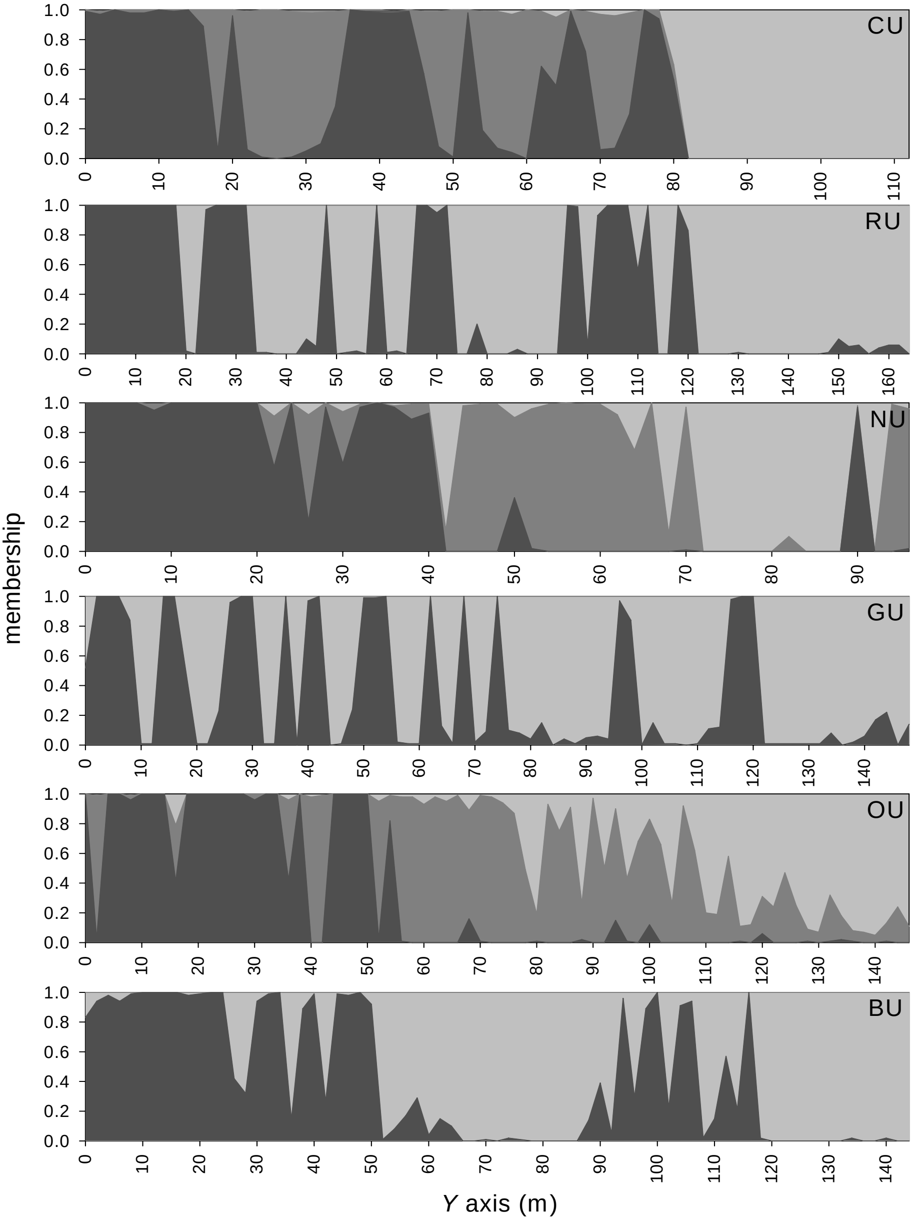

Figure 2. C*ontinued*

Table 2. Communities recognized in each transect. We list the species with higher membership and behaving as faithful to each community. Communities are ordered from left to right according to their dominance along the altitudinal gradient.

Site			
PU	***Rhododendro-Pinetum uncinatae*** *Deschampsia flexuosa, Oxalis acetosella, Pinus uncinata, Rhododendron ferrugineum, Vaccinium myrtillus*	***Arenario grandiflorae-Festucetum yvesii*** *Arenaria grandiflora, Festuca gautieri, Festuca yvesii, Helictotrichon sedenense, Hieracium breviscapum, Lotus corniculatus* subsp. *alpina, Plantago monosperma, Potentilla crantzii, Thymus nervosus, Vitaliana primuliflora*	
DU	***Rhododendro-Pinetum uncinatae*** *Deschampsia flexuosa, Oxalis acetosella, Pinus uncinata, Rhododendron ferrugineum, Vaccinium myrtillus*	***Festuco-Trifolietum thalii*** *Alchemilla alpina, Festuca nigrescens, Galium pumilum, Helictotrichon sedenense, Hieracium lactucella, Lotus corniculatus* subsp. *alpina, Plantago monosperma, Potentilla crantzii, Thymus nervosus, Trifolium alpinum*	
SU	***Rhododendro-Pinetum uncinatae*** *Deschampsia flexuosa, Hieracium murorum, Pinus uncinata, Rhododendron ferrugineum, Vaccinium myrtillus*	***Festuco-Trifolietum thalii*** *Carex ornithopoda, Festuca gr. rubra, Helictotrichon sedenense, Potentilla crantzii, Thymus nervosus*	***Oxytropido-Elynetum with Dryas*** *Agrostis alpina, Dryas octopetala, Oxytropis campestris, Luzula lutea, Minuartia verna, Polygonum viviparum, Saxifraga paniculata*
EU	***Rhododendro-Pinetum uncinatae*** *Pinus uncinata, Rhododendron ferrugineum, Vaccinium myrtillus*	***Hieracio-Festucetum supinae*** **with** ***Calluna vulgaris*** *Calluna vulgaris, Festuca nigrescens, Hieracium breviscapum, Jasione crispa, Thymus nervosus*	
LU	***Rhododendro-Pinetum uncinatae*** *Pinus uncinata, Rhododendron ferrugineum, Vaccinium myrtillus*	***Cetrario-Loiseleurietum procumbentis*** *Hieracium breviscapum, Jasione crispa, Leontodon pyrenaicus, Loiseleuria procumbens, Vaccinium uliginosum*	***Hieracio-Festucetum supinae*** *Agrostis rupestris, Antennaria dioica, Carex ericetorum, Festuca airoides, Juncus trifidus, Luzula spicata, Pedicularis pyrenaica, Plantago monosperma*
FU	***Rhododendro-Pinetum uncinatae*** *Festuca gr. rubra, Pinus uncinata, Rhododendron ferrugineum, Vaccinium myrtillus*	***Cetrario-Loiseleurietum procumbentis*** *Cardamine resedifolia, Loiseleuria procumbens, Minuartia recurva, Nardus stricta, Vaccinium uliginosum* subsp. *microphyllum*	***Hieracio-Festucetum supinae*** *Agrostis rupestris, Arenaria grandiflora, Carex ericetorum, Festuca airoides, Luzula spicata, Pedicularis pyrenaica, Pulsatilla vernalis, Thymus nervosus*
CU	***Rhododendro-Pinetum uncinatae*** *Deschampsia flexuosa, Festuca gautieri, Pinus uncinata, Rhododendron ferrugineum, Vaccinium myrtillus*	***Festuco-Trifolietum thalii*** *Bellardiochloa violacea, Cerastium arvense, Festuca nigrescens, Galium pumilum, Phleum alpinum, Potentilla crantzii, Trifolium pratense, T thalii*	***Oxytropido-Elynetum with Dryas*** *Daphne cneorum, Euphrasia salisburgensis, Helianthemum oleandicum* subs. *alpestre, Helictotrichon sedenense, Kobresia myosuroides, Koeleria vallesiana, Oxytropis campestris, Thymus nervosus*
RU	***Rhododendro-Pinetum uncinatae*** *Carlina acaulis, Deschampsia flexuosa, Juniperus communis subsp. nana, Pinus uncinata,*	***Arenario grandiflorae-Festucetum yvesii*** *Arenaria grandiflora, Festuca gautieri, Galium pyrenaicum, Helictotrichon sedenense, Hieracium breviscapum, Potentilla crantzii, Ranunculus parnassifolius, Thymus nervosus*	
NU	***Rhododendro-Pinetum uncinatae*** *Pinus uncinata, Rhododendron ferrugineum*	***Oxytropido-Elynetum*** **with** ***Salix retusa*** *Euphrasia salisburgensis, Helianthemum nummularium, Kobresia myosuroides, Minuartia verna, Potentilla crantzii, Salix retusa*	***Oxytropido-Elynetum with Dryas*** *Dryas octopetala, Festuca glacialis, Gentiana verna, Oxytropis campestris, Saxifraga oppositifolia*
GU	***Rhododendro-Pinetum uncinatae*** *Pinus uncinata, Rhododendron ferrugineum*	***Arenario grandiflorae-Festucetum yvesii*** *Festuca gautieri, Galium pyrenaicum, Helictotrichon sedenense, Hieracium breviscapum, Jasione crispa, Minuartia recurva, Thymus nervosus*	
OU	***Rhododendro-Pinetum uncinatae*** *Deschampsia flexuosa, Pinus uncinata, Rhododendron ferrugineum*	***Hieracio-Festucetum supinae*** *Carex ericetorum, Euphrasia minima, Luzula lutea, Pedicularis pyrenaica, Pulsatilla vernalis*	***Hieracio-Festucetum supinae (elynetosum)*** *Agrostis rupestris, Antennaria dioica, Erigeron aragonense, Festuca airoides, Helictotrichon sedenense, Kobresia myosuroides, Potentilla crantzii*
BU	*Rhododendro-Pinetum uncinatae* *Carex caryophyllea, Deschampsia flexuosa, Festuca gr. rubra, Phyteuma hemisphaericum, Pinus uncinata*	***Arenario-Festucetum yvesii*** *Arenaria grandiflora, Festuca airoides, Helictotrichon sedenense, Hieracium breviscapum, Oxytropis campestris, Thymus nervosus*	

In the stands studied on siliceous bedrock the alpine pasture was the short, tussock-like grassland *Hieracio-Festucetum supinae* Br.-Bl. 1948 (LU, FU and OU) or an open grassland dominated by *Festuca gautieri* (*Arenario grandiflorae-Festucetum yvesii* Baudière & Serve 1975) (GU and BU) but with very similar floristic trends (Fig. 2, Table 2). Between pinewood and pasture, two of these ecotone examples (LU, FU) included small patches of *Rhododendron ferrugineum,* dwarf formations of *Vaccinium uliginosum* subsp. *microphyllum* or spots of the creeping, dwarf-shrub *Loiseleurietum procumbentis*. The alpine pasture in EU, where upper parts of the treeline are dominated by granitic rocky outcrops, was the tussok-like grassland *Hieracio-Festucetum supinae* with high coverage of heather (var. of *Calluna vulgaris*). In lime-rich plots (PU, DU, SU, CU, NU) only the pinewood was calcifuge while the alpine communities were clearly calcicole (Fig. 2, Table 2). In PU and RU the alpine pasture was an open grassland of *Festuca gautieri* (*Arenario grandiflorae-Festucetum yvesii*) and in DU the mesophilous grassland *Festuco-Trifolietum thalii* Br.-Bl. 1948. In SU, CU and NU two alpine communities were identifyed. The alpine pasture in these three stands was a short grassland mixed with spots of *Dryas octopetala* carpets (*Oxytropo-Elynetum* with *Dryas* Chouard 1943), and between the forest and the alpine pastures the NU site presented important patches of *Oxytropido-Elynetum* with *Salix retusa* whereas SU and CU included the rich mesophilous grassland *Festuco-Trifolietum thalii* Br.-Bl. 1948.

The PCoA analysis of all the plant communities identified at the stands discriminated between forest and alpine communities (Fig. 3a). Furthermore, the described uniformity of the pinewoods in the lower part of the plots and the high variability of the alpine vegetation mosaics were clearly reflected. The first two PCoA coordinate loadings were significant representing 27% and 14.7% of the total variance. The PCoA analysis of the alpine communities (without the forest) revealed 3 groups of communities depending on species composition (Fig. 3b). The first three PCoA coordinates were significant, representing 20.2%, 17.1 % and 14% of the total variance, respectively. Acidophilous and calcicole communities appeared clearly separated, and the third group corresponded to the dwarf shrub carpet.

Tree cover and diversity variations

Linear regression results showed that plant richness and diversity present significant increases along the treeline, through the altitudinal gradient, in the vast majority of the plots studied (Table 3). Although this altitudinal trend was also observed, plant richness increase in BU and diversity increases in EU and NU were not significant. In contrast, as expected, *Pinus uncinata* tree cover presented a significant reduction with altitude in all the treelines studied (Table 3). Even though 87.5% of the linear fits were significant at $p < 0.001$, the explained variance of the models was rather low. The relationship between plant richness and diversity with tree cover was significant and negative in all the study plots except for BU and SU, where the same negative relation was observed but it was not significant at $\alpha = 0.05$ (Table 4).

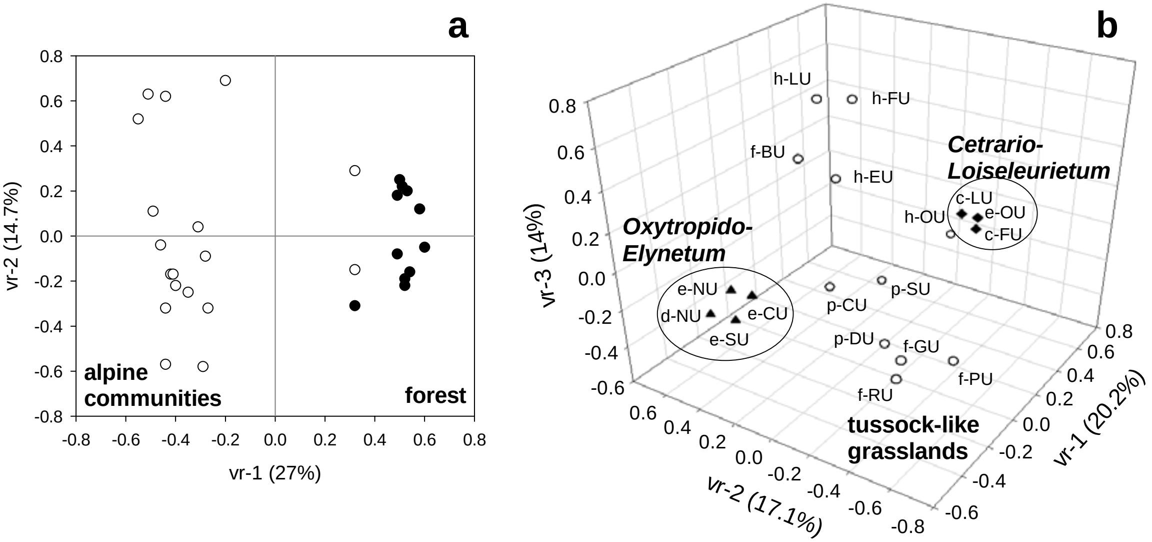

Figure 3. Scatter plots of the PCoA coordinate loadings of the plant communities identified in the 12 plots studied. a) Two first PCoA loadings from all of the plant communities; filled dots represent the forests and open dots the alpine communities. b) Three first PCoA loadings of the alpine communities, each spot represents the group of relevés corresponding to: dots – tussock-like grasslands; diamond – *Cetrario-Loiseleurietum*; triangles – *Oxytropido-Elynetum*. In the codes, lower-case letters indicate the plant community: *c*, *Cetrario-Loiseleurietum*; d, *Oxytropo-Elynetum* with *Salix retusa*; e, *Oxytropo-Elynetum* with *Dryas*; f, *Arenario grandiflorae-Festucetum yvesii*; h, *Hieracio-Festucetum*; p, *Primulion*. Capital letters identify the study sites, see Table 1 for codes.

Wavelet analysis of *P. uncinata* crown cover along the altitudinal gradient highlighted that in none of the plots studied occurred a single and clear tree cover boundary coincident with the timberline location (Fig. 4). Instead, multiple significant crown cover fluctuations can be observed in the lower and middle parts of the plots of which one, not necessarily the strongest or widest, corresponded with the timberline position. Beneath the timberline, cover fluctuations indicated the presence of multiple gaps in the canopy layer. Upslope, above the forest limit, the more or less isolated significant crown cover fluctuations observed through the ecotone revealed the presence of sparse individuals forming tree islands in the transition zone. Except for the GU plot, the treelimit position was not associated with significant cover fluctuations in none of the study plots. Wavelet analysis of species diversity along the treeline ecotone revealed significant sharp changes in species composition in the vast majority of plots (Fig. 4). Only DU, EU and OU did not present abrupt significant changes in species diversity, nevertheless important fluctuations in species richness can also be observed in these treeline ecotones. Multiple significant changes in community diversity, not aggregated in space, were detected in 7 of the 12 study plots (PU, SU, LU, FU, RU, NU, BU) (Fig. 4).

Table 3. Results of linear regressions fit to tree cover, plant richness and diversity along the ecotone at the 12 treelines studied. The values of *a* and *b* correspond to the intercept and the slope of the linear regression (e.g. tree cover = $a + b \cdot$ altitude). See Table 1 for the altitudinal range at each plot. Tree cover and diversity regressions were computed by means of linear models, whereas for plant richness regressions generalized linear models with a Poisson error distribution were used.

Site code	Tree cover			Plant richness			Diversity		
	a	b	r^2	*a*	*b*	r^2	*a*	*b*	r^2
PU	31.41***	-0.56***	42.84	1.802***	0.013***	30.50	1.396***	0.026***	35.66
DU	48.40***	-0.83***	34.28	1.532***	0.019***	34.86	1.588***	0.035***	38.03
SU	29.35***	-0.45***	35.46	2.165***	0.008***	13.65	2.687***	0.015***	16.01
EU	31.76***	-0.58**	16.19	1.408***	0.016**	21.10	1.505***	0.014	4.82
LU	13.65***	-0.34***	18.18	1.753***	0.016***	21.97	2.312***	0.024***	19.38
FU	10.97***	-0.16***	16.04	1.732***	0.011***	35.38	1.627***	0.016***	21.17
CU	38.43***	-0.77***	30.9	1.972***	0.019***	36.84	1.526***	0.041***	47.25
RU	42.27***	-0.76***	45.56	1.562***	0.012***	26.23	1.491***	0.019***	18.36
NU	38.12***	-0.95***	35.56	1.973***	0.011***	15.56	1.852***	0.016	5.89
GU	27.00***	-0.88***	28.33	1.096***	0.020***	10.09	0.958***	0.032**	11.36
OU	21.99***	-0.44***	59.88	1.557***	0.022***	66.35	1.062***	0.040***	70.86
BU	29.37***	-0.63***	36.4	2.112***	0.003	3.48	1.946***	0.010*	5.90

*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$

The spatial location of noticeable changes in species composition were not restricted to the vicinity of the timberline nor to the abrupt crown cover fluctuations. The majority of significant abrupt changes in species diversity (74%) occurred in the area between timberline and treeline, namely the ecotone. However, at three of the study sites (PU, FU and RU) significant changes in species composition were observed beneath the timberline, and only in NU an abrupt diversity shift occurred above the treelimit. Patterns of wavelet covariance between tree canopy cover and species composition (Table 5) revealed weak relations, and no general trends are apparent across the studied range of scales.

Table 4. Results of linear regressions fit to the tree cover vs. plant richness or diversity relationship at the 12 treeline ecotones studied. The values of *a* and *b* correspond to the intercept and the slope of the linear regression (e.g. plant richness = *a* + *b* · tree cover). Diversity regressions were computed by means of linear models, whereas for plant richness regressions generalized linear models with a Poisson error distribution were used.

Site code	Plant richness			Species diversity		
	a	*b*	r^2	*a*	*b*	r^2
PU	2.469***	-0.019***	36.86	2.601***	-0.028***	28.75
DU	2.462***	-0.015***	31.17	3.201***	-0.024***	32.99
SU	2.493***	-0.004	2.57	3.304***	-0.007	1.11
EU	1.993***	-0.012**	16.90	2.119***	-0.016**	14.95
LU	2.205***	-0.016**	11.58	2.983***	-0.020*	6.57
FU	2.285***	-0.020***	12.26	2.393***	-0.026**	7.29
CU	2.705***	-0.014***	31.90	2.995***	-0.024***	29.81
RU	2.122***	-0.009***	15.07	2.424***	-0.018***	20.51
NU	2.393***	-0.011***	26.16	2.420***	-0.012*	9.73
GU	1.548***	-0.014**	10.59	1.724***	-0.018**	9.74
OU	2.586***	-0.042***	54.52	2.765***	-0.052***	38.69
BU	2.234***	-0.004	7.29	2.322***	-0.008	3.12

*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$

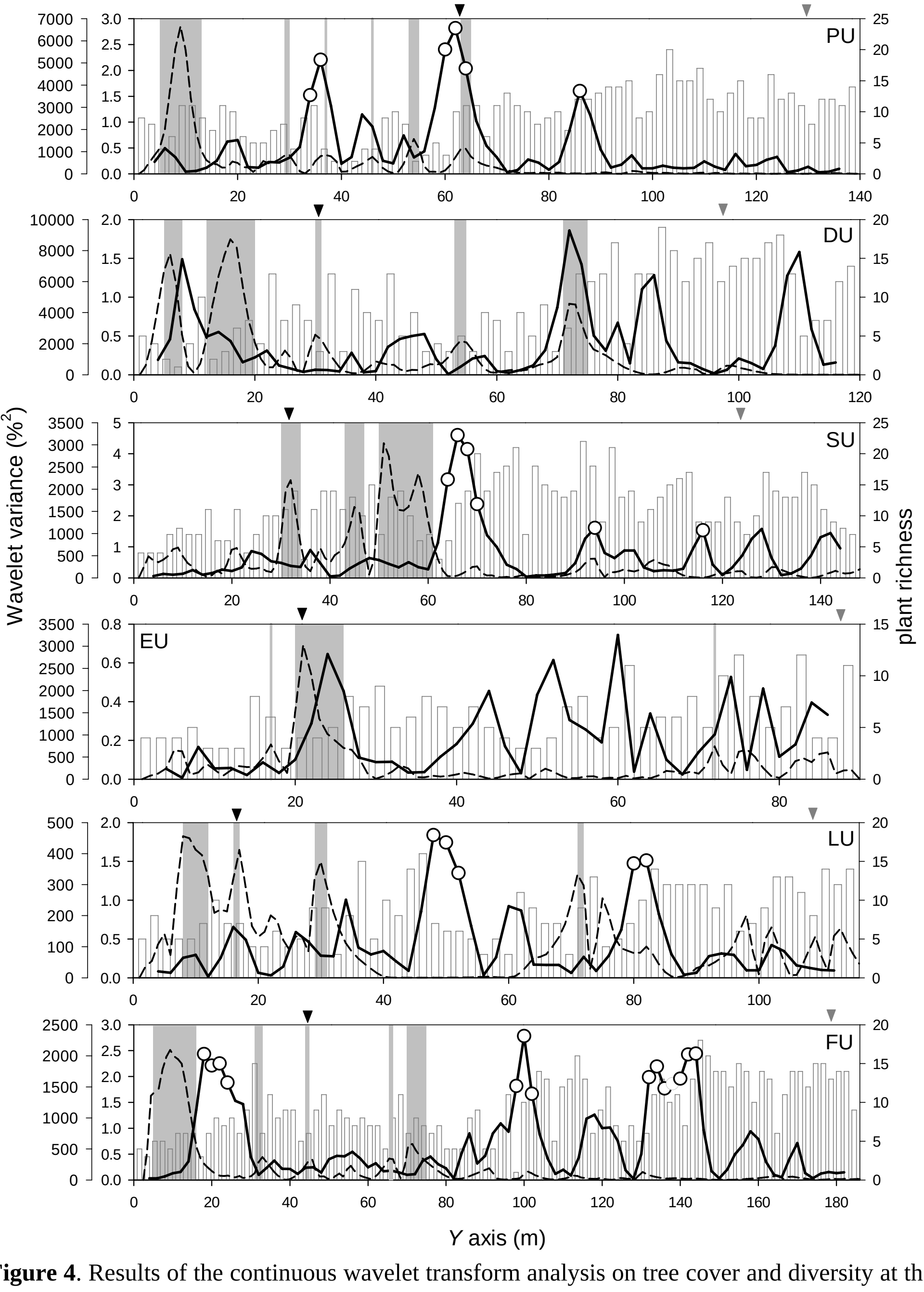

Figure 4. Results of the continuous wavelet transform analysis on tree cover and diversity at the 12 studied treelines. Discontinuous line - wavelet position variance (WPV) for tree cover, left offset axis; black line - wavelet position variance for diversity, left axis; grey areas - significant values of the WPV for tree cover; open symbols - significant values of the WPV for diversity; bars – plant richness; upper black arrow – timberline position; upper grey arrow – treeline position.

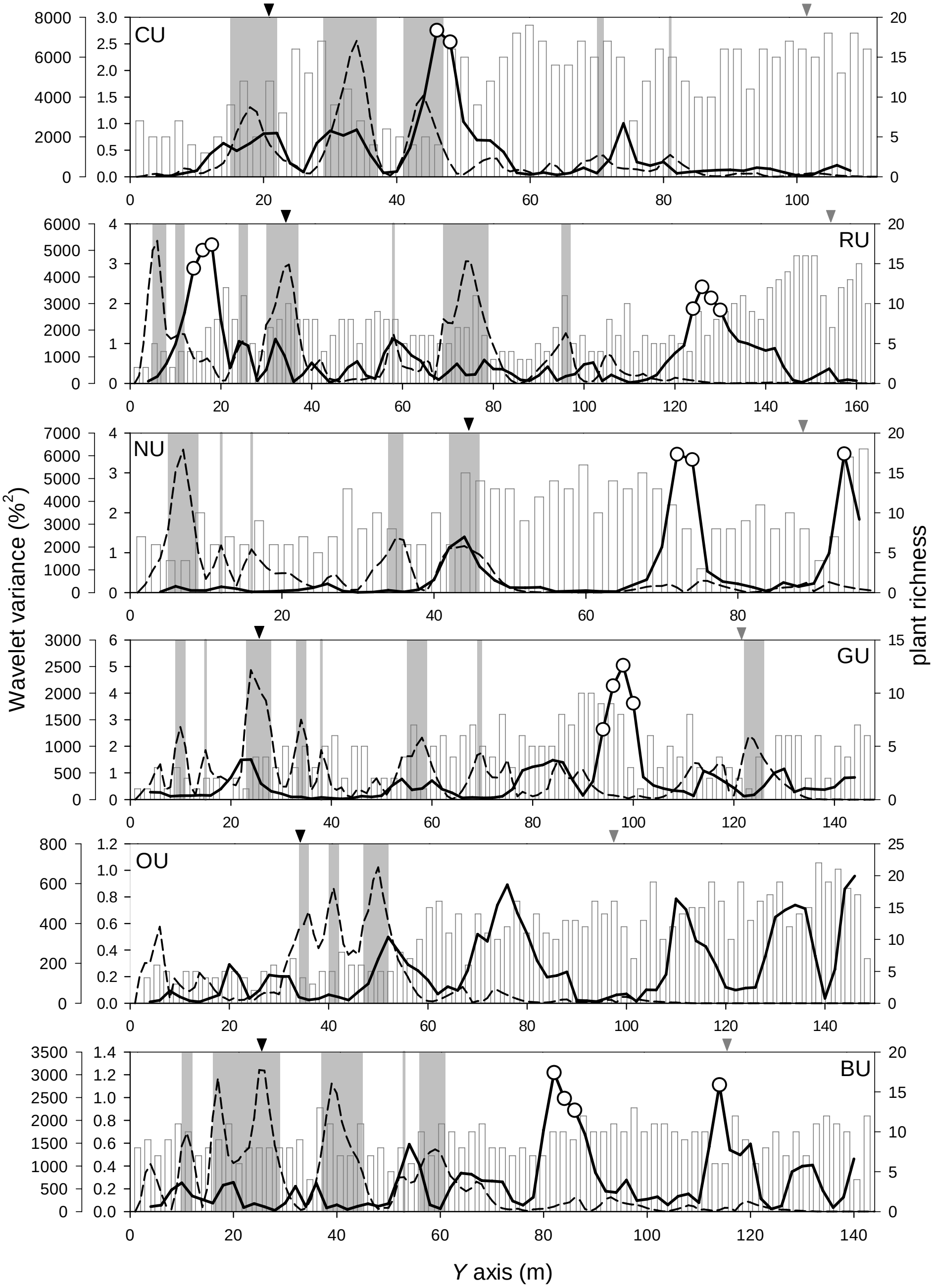

Figure 4. *Continued*

Table 5. Wavelet covariance versus spatial scale for relationships between tree cover and alpine communities diversity in the 12 treelines studied.

Site code	CWT scale of analysis								
	1	2	3	4	5	6	7	8	9
PU	-0.561	-2.901	-5.429	-6.810	-4.281	-2.527	-	-	-
DU	0.457	1.392	2.493	4.352	7.723	12.132	-	-	-
EU	1.199	2.359	1.965	2.685	3.403	-	-	-	-
SU	0.379	0.763	0.762	1.045	1.333	1.543	1.698	1.524	-
LU	0.120	0.333	0.785	1.035	1.215	1.223	-	-	-
FU	-0.173	-0.543	-0.435	-0.069	0.142	-0.189	-0.873	-1.782	-2.755
CU	-0.513	-2.869	-5.681	-7.952	-10.004	-10.928	-	-	-
RU	-0.882	-3.584	-6.208	-6.704	-4.959	-3.157	-2.382	-2.635	-
NU	0.101	0.937	2.941	5.129	6.983	-	-	-	-
GU	0.259	1.107	2.529	4.173	4.866	4.741	4.488	-	-
OU	0.013	0.097	0.277	0.409	0.386	0.148	-0.204	-	-
BU	0.321	1.027	0.596	-0.251	-0.486	-0.542	-0.818	-	-

Discussion

Vegetation patterns

Vegetation analyses revealed an important degree of uniformity of the subalpine forest between the 12 treelines studied irrespective of the bedrock type of each site. Contrastingly, great variation can be observed among plots in the mosaic found upslope, which may reflect the microscale heterogeneity in environment conditions at the ground level (Körner 1995). At the alpine treeline, exposition, soils, mineral nutrients, water availability and microclimate change over short distances, which translates into small-scale mosaics of varying life conditions (environmental micro-fragmentation). Moreover, a complex pattern of interferences between species may also contribute to important vegetation changes at small scale (Grabherr et al. 1995). Accordingly, our results of clustering analyses (FCM) done in the set of relevés of each plot evidenced that the transition from subalpine to alpine communities was not a smooth and gradual change where plant species shifted individually from pinewood to pasture. This was evidenced by the very high membership values of the vast majority of relevés to one or other plant communities in all the treelines studied. Two or three contrasting plant communities (pinewood, dwarf heath and pasture) replaced one another sharply and irregularly along the altitudinal gradient. Thus, no typical intermediate communities in terms of species composition were found along the forest-grasslands transition.

Recent works (Vonlanthen et al. 2006) highlight the importance of soil pH and daily maximum temperature on species richness, both directly and via their effects on other environmental variables. Accordingly, the alpine vegetation mosaics above the timberline described in this study present important differences related to main substrata among plots. Major and well acknowledged differences between alpine pastures on siliceous and lime-rich bedrocks are observed in terms of species composition (Braun-Blanquet 1948). Furthermore on siliceous bedrocks the spatial distribution of dwarf heath communities, where present, is related to the duration of snow cover through relief irregularities. In the LU and FU treeline ecotones *Loiseleuria procumbens*, the most frost-tolerant species, settled on convexities, whereas *Rhododendron ferrugineum*, the most frost-sensitive, remained in concavities where snow lasted for longer (Braun-Blanquet 1948; Körner 1999; own data). Similarly, on lime-rich substrata, where *Oxytropido-Elynetum* is present (NU, CU and SU), the mesophilous grassland settled on gentle slopes or concavities and *Dryas octopetala* formed creeping carpets on rocky exposed landforms. In these cases, the spatial distribution of communities may be related both to the snow cover and to the soil quality (Carrillo & Ninot 1992).

Tree cover and diversity variations

The presence of multiple canopy gaps beneath the timberline, evidenced by the CWT analysis, is reflected by the presence in the lower part of the ecotones (forest relevés) of alpine grassland species (e.g., *Festuca airoides*, *Helictotrichon sedenense*, *Leontodon pyrenaicus*, *Luzula lutea*) and the low presence of species indicative of closed forest environments (e.g., *Hieracium murorum*, *Oxalis acetosella*, *Pyrola secunda*). Overall, this reflects the low canopy cover typical of the *Pinus uncinata* forests reaching the treeline (Ninot et al. 2007). The frequency of alpine species in the forest relevés did not exceed ca. 15%, except in LU where *Luzula lutea* and *Festuca airoides* are present in ca. 30% of the forest inventories. Closed forest species only appeared in some of the study sites ranging between 3.5% and 16.4% of the forest inventories. Finally, the presence of montane and subalpine grassland species (e.g., *Alchemilla hybrida*, *Carex umbrosa*, *Carlina acaulis*, *Trifolium pratense*) was detected in 4 of the treelines studied (DU, CU, RU and BU) with a very low frequency (< 5% of the forest relevés). These results evidence an interchange of species between the subalpine forests and the adjacent non-forest communities.

Plant richness increases significantly along the treeline ecotone in all, except BU, stands studied. However, great differences in the number of species can be observed among contiguous relevés reinforcing the important shifts in vegetation composition at small scales. Since alpine species are generally of a relatively small size, fine-scale environmental heterogeneity became an important determinant for abrupt differences in plant richness (Körner 1999). Similarly, species diversity along the treeline ecotone presents a significant relationship with altitude, increasing from the forest to the alpine pastures. Furthermore, the CWT analysis of diversity variation along the treeline ecotone shows important fluctuations tied to the plant richness small-scale variations. The described diversity patterns do not agree with the overall reduction of species richness with increasing altitude (Grabherr et al. 1995). But to ascertain the general trends of plant richness and species diversity with altitude, longer transects (from the valley bottom to the summit) should be set and vegetation sampling must be not restricted to single units like here. Furthermore, the sampling method used gives important underestimations of forest plant richness and diversity estimates due to the area of the relevés (0.5 m^2), that should be much greater (> 25 m^2) to properly gather vegetation composition of the forest community. Hence, the small scale and grain of our study do not reflect forest heterogeneity while the rapid shifts in alpine community composition are precisely recorded. Finally, at the studied scale the interchange of species between forest and alpine communities at treeline ecotone (mass effect) is also reflected, this contributes to cause richness to increase at altitudes corresponding to the forest-limit as well (Grytnes 2003).

Tree cover presents opposite trends than plant richness and species diversity, showing a significant decrease from the forest to the alpine pastures. The relationship between plant richness and diversity with tree cover reflects the negative influence of tree cover for alpine species occurrence. These results, in accordance with Grytnes (2000), emphasize the importance of light availability in influencing the species-richness pattern in alpine vegetation. But plant community diversity and composition at small spatial scales are controlled by numerous factors, including light availability, temperature, soil nutrient and moisture availability, pH, dispersal limitation, competition, and herbivory (Ehrlén & Eriksson 2000, Kembel & Dale 2006, Vonlanthen 2006). This may explain the general low variance accounted for by the linear fitted models, which may mainly reflect the increasing light availability through the altitudinal gradient.

Despite the general negative relation between plant richness and diversity with tree cover along the treeline, the wavelet analysis reveals that tree cover is not a driving factor for abrupt changes in alpine communities species composition at alpine treeline. Furthermore, the absence of clear peaks or shoulders in the covariance between tree canopy cover and species composition indicates no relationship between the spatial patterns of the analysed variables. Thus, in accordance with Camarero et al. (2006), tree cover significant changes are not spatially overlaped with abrupt changes in species diversity. Hence the timberline position does not involve, in the vast majority of treelines studied, significant abrupt changes in species diversity. Above the timberline multiple abrupt diversity changes occur reflecting the upslope increase in local environmental heterogeneity, which greatly determines the species composition at small spatial scales (Körner 1995, Camarero et al. 2006). The spatial pattern of low shrubs (e.g., *Rhododendron ferrugineum*), which have the potential to modify microenvironmental conditions (Akhalkatsi et al. 2006), may be a very important factor in determining species occurrence. The effect of low shrubs may contribute to weaken the relationship between tree cover and species diversity. Besides, due to community inertia and resilience, structural and compositional adjustments of ecosystems to environmental changes may present important temporal lags, resulting in non-equilibrium situations between current environmental conditions and species distribution (Noble 1993). Furthermore, distinct adjustment rates to environmental variations are expected when considering different processes such as tree cover dynamics, low shrub expansion or forest faithful-species establishment or loss. Thus, community responses to past climate and land use changes may have weakened the expected correlation between species distribution and vegetation structure (e.g., timberline) (Hofgaard & Wilmann 2002).

At this point it is important to mention, as stated by Armand (1992), that "any natural boundary is in reality a transition zone [...] So localization of a natural border is in principle inexact and therefore determined by convention". Moreover, detection of a distinct natural boundary line becomes more difficult as change becomes more gradual (Choesin & Boerner 2002). This is the case of the treeline ecotones studied, where the boundary between subalpine forest and alpine pastures is often unsharp and fragmented over several tens meters of altitude (Körner 1995). The inherent arbitrariness in boundary delineation may also explain part of the weak correlation between timberline and treeline with plant richness and community diversity. Our results highlight the occurrence of a gradual transition of the tree population from forest to alpine pastures coinciding with the general increase in climate conditions harshness. This transition is coupled with important fluctuations of environmental conditions at ground level, creating great variability of microclimates, which triggers abrupt plant richness and diversity variations. Hence, although the general view of the plots studied gives the impression of a gradual transition and thus could be regarded as *ecoclines*, the sharp and irregular oscillations of contrasted communitites and the lack of intermediate communtites in terms of species composition observed at finer scale are more associated with *ecotones* characteristics (van der Maarel 1990). Overall reinforces the importance of the scale when analysing and interpreting transition chatacteristics.

Main conclusions

Pinus uncinata treeline ecotones present an important degree of uniformity concerning the *Rhododendro-Pinetum uncinatae* subalpine forest in terms of structure and species composition. Contrastingly, great differences occur in the mosaic found upslope between sites, reflecting both bedrock type and microscale heterogeneity at the ground level. Such fine-scale environmental heterogeneity triggers abrupt changes in community composition and plant richness along the treeline ecotone. Despite the negative influence of tree cover on plant richness and diversity, *P. uncinata* crown cover does not appear as a driving factor of the observed abrupt changes in alpine community composition. This partly explains the lack of uncoupling between tree cover and species composition boundaries. Microclimate modifications by low shrubs and community dynamics and resilience, which translate into important temporal lags in ecosystems adjustments to environmental fluctuations, may also contribute to non-equilibrium situations between the alpine species distribution and tree population structure. The progressive decline upslope of the tree population is overlapped with strong fluctuations of community composition at ground level, which may indicate both the ecocline or ecotone character of the alpine treeline depending on the scale considered.

Acknowledgements

We are grateful to all the people who helped us with the field work. Especially to J. Carreras and A. Ferré who, besides performing some of the field analyses of vegetation, produced the figure 1 and helped us with tree cover calculations. This study was supported by the project REN2002-04268-C02 (Spanish Ministry of Research). Enric Batllori thanks the support of a MEC-FPU grant.

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Discussió general

L'estructura demogràfica de les poblacions estudiades evidencia que la dinàmica de regeneració a la zona del límit superior del bosc es caracteritza per processos de reclutament episòdics (Cullen et al. 2001, Walther et al. 2005). Les limitacions d'interpretació de les estructures d'edat estàtiques per inferir processos de dinàmica poblacional han estat clarament exposades per Johnson et al. (1994). Per tant, els pics de reclutament observats en l'estructura demogràfica de les poblacions poden ser deguts a augments d'establiment d'individus, a taxes de mortalitat més baixes, o a la combinació de tots dos processos. Tot i que el mètode utilitzat no serveix per fer descripcions detallades dels processos poblacionals, sí que permet detectar episodis favorables per al reclutament d'individus i analitzar-ne la seva coincidència entre les diferents poblacions. Aquest seria el cas de la densificació de la zona de l'ecotò al llarg del segle XX que s'ha observat al límit superior del bosc de *Pinus ucinata* a escala regional dels Pirineus. Processos de densificació aparents també han estat descrits en d'altres poblacions al seu límit de distribució altitudinal o latitudinal durant aquest mateix període (p.e. Payette i Filion 1985, Scott et al. 1987, Payette i Lavoie 1994, Sceicz i MacDonald 1995, Kullman 1997, MacDonald et al. 1998, Stöcklin i Körner 1999, Payette et al. 2001, Juntunen et al. 2002, Shiyatov 2003, Camarero i Gutiérrez 2004, Kullman 2005, Danby i Hik 2007, Gehring-Fasel et al. 2007). Als Pirineus, l'augment del caràcter forestal de la zona de l'ecotò ha estat molt marcat des de la dècada de 1950s, i s'ha observat al 92% de les poblacions estudiades. Però és durant els últims 30 anys (des de la dècada de 1970) quan s'observa un increment més alt en el reclutament (present al 83% dels ecotons) coincidint amb un augment marcat de la temperatura als sistemes muntanyosos d'Europa (Diaz i Bradley 1997).

Però són aquestes respostes poblacionals realment atribuïbles a un canvi climàtic? Als Pirineus, com a la majoria de les muntanyes alpines, l'aprofitament de la zona del límit superior del bosc, sobretot, per guanyar terrenys de pastura, a suposat la seva antropització des de molts segles enrera (Walter 1976, Körner 1999). Però al llarg del segle XX, la despoblació de les zones de muntanya a comportat una disminució de les activitats agropecuàries tradicionals, molt acusada a partir de 1950s (García-Ruiz et al. 1996). En d'altres límits altitudinals d'Europa, s'ha descrit que la resposta dels ecotons ha estat més influenciada pel canvi d'usos del sòl que no pas pel canvi climàtic (Hofgaard 1997, Gehring-Fasel et al. 2007). La manca de dades concretes de la pressió antròpica de les 12 localitats estudiades ha fet que s'hagin buscat indicadors indirectes per tal d'inferir quin factor, canvi climàtic o d'usos del sòl, és el responsable de les respostes observades al límit supeior del bosc. En absència de pertorbacions antròpiques i naturals (allaus, vents extrems, caiguda de roques, etc.) la transició de l'edat i mida dels indivius des del bosc fins al prats alpins és gradual (Holtmeier i Broll 2005, Körner 2007). Per aquest motiu, s'ha utilitzat el patró de la transició de l'edat i la mida dels arbres al llarg de l'ecotò com a indicador de la presència de perturbacions antròpiques. Així, les transicions amb canvis bruscs (en forma d'esgraó) en l'edat i/o mida dels arbres al llarg de l'ecotò haurien estat recentment afectades per l'activitat humana. Per tant, els canvis poblacionals detectats en aquests ecotons respondrien fonamentalment a la disminució de la càrrega ramadera, sota unes condicions climàtiques favorables. Per contra, les localitats on la transició en l'edat i la mida dels arbres és gradual al llarg de l'ecotò no haurien estat afectades recentment per l'home, i la seva dinàmica hauria estat principalment influenciada pel canvi climàtic. Però sigui quina sigui la causa última de les tendències observades al llarg del segle XX, sota les previsions del mantingut canvi climàtic (IPCC 2007) i la poc probable recuperació de les activitats ramaderes tradicionals, els límits altitudinals antropitzats passarien a ser cada vegada més sensibles a les variacions climàtiques (Holtmeier i Broll 2005). Per tant, entendre els efectes del clima sobre la dinàmica d'aquestes poblacions és imprescindible per poder-ne inferir possibles dinàmiques a mitjà termini.

Els processos recents d'establiment massiu d'individus de *P. uncinata* (durant la segona meitat del segle XX) s'han caracteritzat per increments sobtats en la densitat de la classe regeneradora, que es produeixen amb un fort patró d'agregació espacial a distàncies curtes (fins a 3 m). Aquests resultats, reflexen la importància dels processos de retroalimentació positiva en la dinàmica temporal i espacial de la regeneració a la zona de l'ecotò. Els individus establerts modifiquen les condicions locals (microambient) afavorint així l'establiment de nous individus (Smith et al. 2003, Resler 2006), fet que deriva en l'agregació en l'espai de la classe regeneradora. Aquests processos de retroalimentació positiva, podrien ser en part, responsables del clar caràcter episòdic de la regeneració al límit superior del bosc, que mostra un comportament equiparable a processos determinats per certs llindars climàtics. És important mencionar, que l'alta densitat actual de plançons en comparació amb les dels estadis més avançats del cicle vital (pinetons, joves i adults) podria indicar una elevada mortalitat inicial de l'espècie. Però ja que la mortalitat instantània (nº plançons morts/total de plançons; Lloyd i Fastie 2003) detectada per la classe regeneradora ha estat molt baixa (promig d'un 2.63%), és raonable concloure que els increments observats en el reclutament durant les últimes dècades representen una densificació real de l'ecotò en la gran majoria de les poblacions estudiades. Tot i això, el fet que en dos dels ecotons estudiats no s'ha detectat un increment del reclutament en les últimes dècades (des de 1970s), juntament amb l'estabilitat del límit de l'arbre des del 1950 observada només en la meitat de les localitats estudiades, posa de manifest la presència de dinàmiques poblacionals diferencials a nivell regional (Dalen i Hofgaard 2005, Payette 2007). El comportament del límit de l'arbre ha estat avaluat per l'edat dels individus que marquen la posició d'aquesta frontera, i en la meitat de les poblacions està determinat per individus establerts després de 1950. Així, tot i la importància de la inèrcia d'aquesta frontera degut a la longevitat i plasticitat fenotípica dels individus (Noble 1993), els resultats obtinguts en aquest estudi evidencien també l'alta sensibilitat climàtica que pot tenir el límit de l'arbre sota les condicions climàtiques actuals. L'individu més jove que determina la posició d'aquesta frontera en les poblacions estudiades s'ha establert després del 1980, fet que corrobora la gran capacitat de resposta del límit de l'arbre en algunes circumstàncies.

La diversitat específica dels mosaics de vegetació que hi ha per sobre el límit del bosc està determinada per l'elevada heterogenitat microambiental a nivell del sòl. I tot i que la posició del límit del bosc no coincideix amb canvis significatius de diversitat específica al llarg del gradient altitudinal, sí que s'ha detectat una influència negativa entre el recobriment de les capçades i el número d'espècies i la diversitat de les formacions alpines. Això és deu a que els arbres modifiquen les condicions del sotabosc (disponibilitat de llum i nutrients, modificació del pH del sòl, etc.). Per tant, una de les conseqüències que podria comportar la densificació i migració del límit superior del bosc és la fragmentació i reducció de l'hàbitat de les espècies alpines (Luckman i Kavanah 2000). L'abandó de les activitats ramaderes tradicionals podria ocasionar una més ràpida densificació de la zona de l'ecotò incrementant els efectes negatius sobre l'hàbitat de les espècies alpines (Dirnböck et al. 2003). Per això, la migració altitudinal de les espècies alpines ha estat també tema d'estudi. Recentment, Holtzinger et al. (2008) han descrit tendències generals de migració altitudinal de la vegetació alpina cap a l'estatge subnival als Alps. Metre que d'altres estudis evidencien respostes no lineals de certes comunitats a les variacions climàtiques, evidenciant la presència de respostes específiques dabant d'un canvi regional comú (Gavin i Brubacker 1999). Dit d'altre manera, hi hauria espècies que no serien capaces de migrar altitudinalment. En aquest context, Dirnböck et al. (2003) proposen que les polítiques de gestió dels usos del sòl a la zona del límit superior del bosc, per exemple mantenint certa càrrega ramadera, són una eina molt important per mantenir l'hàbitat actual de les espècies alpines, algunes d'elles relictuals i amenaçades actualment. Però s'ha de tenir en compte, que la distribució actual de les espècies alpines als Pirineus, i a moltes muntanyes europees, respon en molts casos a "l'alpinització" del límit superior del bosc degut a les perturbacions antròpiques històriques (Walter 1976). L'increment de l'àrea de pastura va comportar una reducció de les masses forestals al límit superior del bosc, modificant la distribució potencial de la vegetació i permetent, per tant, l'establiment de comunitats alpines a menor altitud. Així, només en ecotons naturals i situats a l'altitut potencial, la possible migració altitudinal del límit superior del bosc comportaria una reducció real de l'hàbitat de les espècies alpines. Tot i que en el context dels Pririneus l'ecotò superior no és en cap cas natural, entendre la seva dinàmica és imprescindible per avaluar quin pot ser el comportament dels límits naturals. Entre d'altres factors, la resposta dels ecotons als canvi global pot estar influenciada per la seva capacitat d'invasió de les formacions vegetals alpines, la possibilitat de respostes diferencials entre ecotons, així com la resposta de la regeneració i el creixement dels individus en front de les prediccions climàtiques (IPCC 2007). Aquests factors es comenten tot seguit en base als resultats presentats.

La descripció del patró espacial de la regeneració mostra que l'establiment massiu d'individus des de 1950s ha tingut lloc preferencialment a la zona de l'ecotò en sentit estricte, és a dir entre el límit del bosc i el límit de l'arbre. La distribució dels plançons a l'interior de l'ecotò pròpiament dit no presenta agregació significativa a petita escala amb els individus de mida més gran (pinetons, joves i adults) ni amb els arbres potencialment reproductors (els que presenten pinyes al moment del mostreig), i tampoc forma agregats de regeneració d'edat homogènia en l'espai. La interacció entre els planços i els individus reproductors a mitja distància (10-17 m) s'ha atribuït a la dispersió de les llavors. A més a més, el reclutament durant els períodes 1950-1974 i 1975-1999 no s'ha produït de manera segregada al llarg de la transició. Aquests patrons espacials en el reclutament, en base al patró de la transició de l'edat i la mida dels individus, són comuns entre els ecotons on la dinàmica recent és deguda al canvi d'usos del sòl i en aquells on la seva resposta està lligada al clima. Aquests resultats tenen una sèrie d'implicacions. Primer, fa palès el caràcter heliòfil i colonitzador de l'espècie (Ceballos i Ruiz de la Torre 1979). Segon, indiquen que la producció, qualitat i dispersió de les llavors no seria un factor limitant per la dinàmica de regeneració de *P. uncinata* (Dalen i Hofgaard 2005). Tercer, evidencia el potencial invasor de *P. uncinata* sobre les comunitats vegetals alpines de la zona de l'ecotò. I quart, posen de manifest la similitud de les característiques microambientals entre localitats (Resler 2006). Limitacions en la dispersió i la regeneració, fortament condicionada per la "invasibilitat" de la vegetació alpina, semblen ser factors determinants per la dinàmica del límit superior del bosc (Dullinger et al. 2004). Per tant, els resultats presentats en aquest estudi indicarien que la dinàmica de la regeneració recent de l'ecotò superior de *P. uncinata*, a escala regional dels Pirineus, no ha estat condicionada per limitacions reproductives de l'espècie sota les condicions climàtiques actuals ni per una manca d'hàbitat favorable per a l'establiment de nous individus. La vegetació existent per sobre del límit del bosc pròpiament dit, a la zona típicament alpina, està formada per petits mosaics de comunitats florística i estructuralment diferents (Vonlanthen et al al. 2006), amb una elevada presència de petites clapes sense vegetació (Illa et al. 2006). La constant fluctuació en l'espai de la composició de les formacions vegetals alpines, reflexa la gran heterogeneitat de les condicions microambientals a nivell del sòl (Körner 1999) així com els diversos graus d'interacció (p.e. competència) entre les diferents espècies (Grabherr et al. 1995). En base als resultats de la caracterització del nínxol de regeneració de *P. uncinata*, aquesta heterogeneitat i distribució de la vegetació sembla crear els microambients idonis per la germinació i l'establiment de nous individus de l'espècie. Els plançons s'estableixen principalment sobre terra fina i graves en zones amb una cobertura laxa de vegetació herbàcia (p.e., *Festuca* sp., *Trifolium alpinum*) o subarbustiva (p.e. *Vaccinium uliginosum* subsp. *microphyllum*, *Loiseleuria procumbens*, *Dryas octopetala*). Els arbustos com el neret (*Rhododendron ferrugineum*) i el ginebró (*Junniperus communis* sups. *nana*), tot i constituir un hàbitat molt desfavorable per a l'establiment dels plançons (Pornon i Doche 1996), semblen tenir un paper molt important en la modificació de les condicions microambientals del seu entorn, fent-les favorables per al reclutament de *P. uncinata*. Les petites formacions del microrelleu i les roques també generarien microclimes que afavoririen l'establiment i el creixement de nous individus de l'espècie. Aquests resultats, estan en concordància amb d'altres estudis que emfatitzen la gran importància dels processos de facilitació a petita escala per a la dinàmica de la regeneració al límit superior del bosc (Ball et al. 1997, Germino i Smith 1999, Germino et al. 2002).

Els resultats de la supervivència dels plançons de la plantació experimental realitzada a la zona del Serrat de Capifonts, indiquen que les condicions hivernals són un dels factors més limitants per a la supervivència i creixement de l'espècie. Per tant, els processos de facilitació exercits tant per individus prostrats de la mateixa espècie (*krummholz*), com per arbustos, formacions del microrelleu o roques, modificarien el microambient suavitzant les condicions ambientals a nivell del sòl augmentat, així, la supervivència dels plançons. Els efectes beneficiosos de la facilitació semblen estar molt relacionats amb la redistribució del mantell nival (Smith et al. 2003), on el vent hi juga un paper molt important. Així, l'agregació espacial dels plançons descrita a petita escala, seria deguda als processos de retroalimentació que augmenten els efectes de la facilitació derivats del paper del vent en l'acumulació diferencial de la cobertura de neu (Malanson 1997, Alftine i

Malanson 2004). De la mateixa manera, els resultats obtinguts fan pensar que la diferent intensitat en l'espai d'aquests processos de facilitació, és una part fonamental dels mecanismes responsables de patrons de distribució típics del límit superior del bosc com són les ones i llengües de regeneració (Bekker 2005). Patrons de regeneració en ones al llarg de l'ecotò han estat detectats a tres de les localitats estudiades. Però tot i els efectes beneficiosos de la protecció de la neu, els resultats experimentals presentats suggereixen que un excés del gruix de neu pot exercir efectes negatius en la supervivència i creixement dels plançons degut a la reducció del període de creixement (Hättenschwiler i Smith 1999). Per tant, les pròpies característiques dels plançons (p.e., l'alçada) modularien la intensitat dels processos de facilitació, la importància dels quals, varia també d'acord amb les fluctuacions climàtiques interanuals. Tot plegat, mostra la gran complexitat de processos, i les interaccions entre ells, que determinen la supervivència i el desenvolupament dels plançons al límit superior del bosc.

Ja que els resultats presentats indiquen que no hi ha limitacions reproductives ni d'invasibilitat, el patró espacial dels plançons a la zona de l'ecotò respondria a la distribució dels llocs segurs de reclutament de l'espècie, que són determinats, en part, per la distribució espacial dels elements responsables dels processos de facilitació. Per sobre de l'ecotò, la densitat de plançons establerts naturalment és molt baixa, i els resultats de la plantació experimental han evidenciat una elevada mortalitat (90%). Això fa pensar, que les característiques de la vegetació i del microrelleu més amunt de l'ecotò no són favorables per la regeneració de l'espècie per la manca de llocs segurs de reclutament (*safe sites*), probablement degut a la manca de processos de facilitació que afavoreixin la supervivència dels plançons. Per tant, no hi ha indicis que facin pensar que s'està produïnt, o es pugui produir a curt termini, una invasió massiva de les comunitats alpines per sobre de l'ecotò.

Tot i la similitud de les característiques microambientals al límit superior del bosc (Resler 2006), tant importants pels processos de regeneració, els pics de reclutament de les diferents localitats estudiades no presenten una marcada sincronització. Això queda palès tant en l'estructura d'edat de tota la població dels diferents ecotons, com en l'estructura demogràfica dels processos de regeneració recents (període 1971 - 2000). És a dir, tot i que hi ha períodes favorables de reclutament i tendències poblacionals observades a escala regional, en general els pics de regeneració no són significativament sincrònics entre localitats, fet que evidencia la importància de les condicions locals per la dinàmica de l'ecotò. Els períodes coincidents d'augment en el reclutament d'individus en les localitats estudiades, per exemple dècades 1830s-1860s i a partir de 1950s, evidencien l'existència de condicions macroclimàtiques regionals com serien l'acabament de la petita edat del gel (Piovesan et al. 2003) o l'augment de les temperatures de la segona meitat del segle XX (Diaz i Bradley 1997, Büntgen et al. 2006). Aquesta influència macroclimàtica, queda molt palesa en la correlació positiva i significativa de les sèries de creixement radial entre les localitats estudiades pel període 1955 – 2000. El fet que la sincronització entre ecotons sigui molt més aparent en el creixement radial dels individus que en l'estructura demogràfica, evidencia: que els processos demogràfics són molt més complexes que els processos de creixement dels individus, i la relativa homogeneitat en les condicions atmosfèriques (a uns de 2 m d'alçada) entre localitats. La duresa de les condicions ambientals al límit superior del bosc fa que no hi sigui possible la formació de masses forestals denses, degut a una elevada mortalitat dels individus reclutats, i per tant el creixement dels individus està principalment influenciat per les condicions climàtiques cosa que contribueix a la sincronització en el creixement entre localitats (Paulsen et al. 2000, Pfeifer et al. 2005). Per contra, la complicada topografia de les zones de muntanya, i la interacció de la meso- i la macro-topografia, fa que les condicions locals a petita escala (p.e., arran de terra) puguin arribar a ser molt diferents entre localitats (Resler 2006). Aquest fet explicaria que tot i la presència de factors macroclimàtics comuns, la resposta en la dinàmica de regeneració fos força específica de cada localitat.

Una altre causa que contribueix a les diferències en els pics de reclutament entre ecotons, són els processos de mortalitat diferencial dels individus de cada localitat que contribuirien a desdibuixar al llarg del temps els episodis sincrònics de reclutament. Tot i que no s'han presentat dades per estadis vitals avançats (joves i adults), la taxa de mortalitat "instantània" dels plançons (Lloyd i Fastie 2003) varia del 0% al 14% entre localitats. El període crític per a la supervivència dels individus, sembla tenir lloc en el moment que sobrepassen l'alçada del gruix de neu hivernal (Smith et al. 2003). Just a sobre de la coberta de neu és on els efectes de l'abrasió són més importants degut a l'elevada concentració que hi ha de petits cristalls de gel arrossegats pel vent. Per tant, fins i tot en els llocs segurs de reclutament, la supervivència dels plançons depèn d'una sèrie consecutiva d'anys favorables (p.e., hiverns suaus i estius no eixuts) que els permetin superar l'alçada on els efectes de l'abrasió són més intensos. La complexa micro- i meso-topografia de cada localitat pel que fa al pendent i al relleu, juntament amb el règim de vent de cada ecotò, deriva en les taxes diferencials de mortalitat no sols entre localitats sinó entre zones de cada localitat. Això explicaria que el patró espacial de distribució dels individus no es mantingui al llarg dels diferents estadis del cicle vital (Bunn 2004), agregat en la classe regeneradora i sense un patró significatiu pels individus joves i adults.

Les anàlisis de la relació del creixement radial amb el clima a cada localitat, han fet palesa la importància de les característiques biològiques de l'espècie i la presència de l'esmentat efecte macroclimàtic. Contràriament, les relacions entre el reclutament dels individus i les variables climàtiques són més febles i molt més variables entre localitats. Aquest fet emfatitza el clar desacoblament que hi ha entre les condicions climàtiques atmosfèriques i les condicions microambientals a nivell de terra (Körner 2007), fent palesa la gran complexitat a l'hora d'avaluar la resposta del límit superior del bosc en front del canvi climàtic. A més a més, la importància de les condicions microambientals per la regeneració faria que aquesta no estigués relacionada significativament amb el creixement radial, modulat per les condicions atmosfèriques.

Les relacions significatives del creixement radial amb el clima comunes a totes les localitats d'estudi, mostren que les característiques climàtiques de l'ambient d'alta muntanya condicionen el creixement dels individus. Però els resultats presentats, també evidencien la importància de les condicions locals en el creixement dels individus, fent paleses un cop més, respostes diferencials de les poblacions del límit superior del bosc als Pirineus a escala regional. El creixement radial del *P. uncinata* a l'ecotò està, en general, limitat per les baixes temperatures. Això queda palès en les relacions positives que s'han trobat entre el creixement radial i les temperatures de primavera (maig), estiu (període juny-agost) i tardor (setembre). Però tot i això, en algunes localitats s'ha detectat un efecte negatiu de temperatures elevades al més de juliol, juntament amb limitacions del creixement degudes a la baixa precipitació. Aquest resultat posa de manifest l'estrés hídric al que està sotmès el creixement radial dels individus (Barber et al. 2004, Wilmking et al. 2004), que està determinat per condicions climàtiques locals. De manera semblant, els processos de reclutament d'individus estan generalment relacionats positivament amb la temperatura. Però també s'ha detectat la influència negativa de temperatures massa elevades, sent a la tardor quan apareixen els efectes de l'estrés hídric en algunes de les localitats d'estudi. Aquesta influència negativa de la temperatura de tardor sembla que podria ser important per la supervivència a mitja termini dels plançons. Així, tot i que els resultats de la plantació experimental realitzada mostren una mortalitat molt baixa de plançons fora dels mesos hivernals, les relacions entre la regeneració natural i el clima evidencien la importància que pot tenir també l'estrés hídric en la dinàmica de reclutament. El seguiment a llarg temini dels individus transplantats, és doncs necessari per poder determinar la importància dels diversos factors climàtics sobre la supervivència de la classe regeneradora al límit superior del bosc. En vista dels resultats obtinguts, una datació més precisa de la classe regeneradora, que només es pot obtenir mitjançant mètodes destructius, és necessària per poder analitzar les relacions entre el reclutament i el clima a escala anual. Això permetria obtenir unes dades que manquen per al *P. uncinata* i que són molt importants de cara a poder modelitzar futures dinàmiques de regeneració, i en últim terme dels ecotons, en base a les previsions climàtiques.

L'evidència de la sequera estival en el creixement dels individus al límit superior del bosc no havia sigut fins ara descrita ni als Pirineus ni a d'altres sistemes muntanyosos d'Europa. Però són varis els estudis sobre límits de distribució altitudinals a Alaska que han descrit una disminució del creixement radial relacionat amb altes temperatures al mes de juliol (Lloyd i Fastie 2002, Wilmking et al. 2004, Wilmking i Juday 2005). La influència negativa de l'estrés hídric en el processos de regeneració al límit superior del bosc als Pirineus, ja havia estat reconeguda per Camarero i Gutiérrez (2004). Els resultats aquí presentats, corroboren la importància que pot tenir el balanç entre la temperatura i la precipitació en les dinàmiques poblacionals dels ecotons a mitjà termini. Per exemple, la presència d'estrés hídric en algunes de les poblacions estudiades, emfatitza la possibilitat de futures respostes contràries a les esperades segons el paradigma tradicional de les limitacions tèrmiques per als processos poblacionals i de creixement al límit superior del bosc (Tranquillini 1979, Grace i Norton 1990, Körner i Paulsen 2004). Així, el previsible increment dels fenòmens d'estrés hídric a escala regional al sud d'Europa (IPCC 2007), degut a augments de temperatura sense anar acompanyats d'augments en el règim de precipitació, poden aturar els processos de densificació de la zona de l'ecotò observats durant el segle XX i fins i tot revertir-los degut a increments en la mortalitat. Sumat als efectes de l'estrés hídric, hi hauria els efectes negatius de la probable disminució de la precipitació en forma de neu a les zones de muntanya d'Europa (IPCC 2007). Els processos de regeneració es veurien molt afectats per la disminució de la supervivència hivernal, però també el creixement dels individus podria patir possibles augments de fenòmens de sequera hivernal i cavitació (Mayr 2007). Per tant, s'ha de contemplar la possibilitat que, degut a les condicions climàtiques futures, es podria acabar desencadenant en alguns ecotons un procés de retroalimentació invers al que s'ha produït al llarg del segle XX que comportaria taxes elevades de mortalitat d'individus i una disminució de la regeneració. Per tant, les poblacions del límit superior del bosc podrien iniciar un procés de retrocés. De fet, a totes les poblacions estudiades s'ha detectat una tendència negativa recent en l'establiment d'individus (últims 6 anys) que no pot ser només atribuida a limitacions metodològiques degut a una menor detectabilitat dels plançons més petits (d'1 a 3 anys). Tot i que no s'ha pogut determinar quina és la causa d'aquesta davallada en el reclutament d'individus, es fa aparent que es pot haver produït un canvi en les condicions que havien afavorit l'increment del caràcter forestal de la zona de l'ecotò en la majoria de poblacions fins al moment. El seguiment de les poblacions estudiades és doncs necessari per poder detectar si hi ha una reversió de la dinàmica del límit superior del bosc. Això, complementat amb estudis amb resolució anual de les relacions amb el clima, permetria una modelització més fiable en base a les prediccions climàtiques de la dinàmica del límit superior del bosc i dels possibles efectes que això tindrà sobre la vegetació alpina.

Conclusions

Tot i la importància de les condicions locals en la dinàmica del límit superior del bosc, s'ha detectat una sincronització en el creixement radial i, en menor mesura, en el reclutament d'individus entre localitats a escala regional. Aquest fet evidencia la presència d'un factor comú extern, el macroclima, que modula la dinàmica d'aquestes poblacions.

La densificació del límit superior del bosc a escala regional durant la segona meitat del segle XX s'ha produït en paral·lel a l'increment de les temperatures (canvi climàtic). Però en base al patró de la transició en l'edat i la mida dels individus, el canvi d'usos del sòl hauria estat el factor determinant de l'augment del caràcter forestal en alguns dels ecotons.

Tot i la densificació regional de la zona de l'ecotò des de 1950s, l'estructura demogràfica recent (1971-2000) i la dinàmica del límit de l'arbre evidencien l'existència de respostes diferencials a curt termini entre localitats. Aquest resultat emfatitza la importància de les condicions locals en la dinàmica dels ecotons.

El patró espacial de la regeneració està determinat per la distribució dels llocs segurs de reclutament, que estan condicionats per la distribució espacial dels elements responsables dels processos de facilitació a nivell microambiental.

L'agregació espacial dels plançons a distàncies curtes, i els increments sobtats en la densitat de la classe regeneradora, corroboren la importància dels processos de retroalimentació positiva en la dinàmica de la regeneració al límit superior del bosc.

La dinàmica de la regeneració recent a l'ecotò superior de *Pinus uncinata*, a escala regional dels Pirineus, no ha estat condicionada per limitacions reproductives de l'espècie ni per una manca d'hàbitat favorable per a l'establiment de nous individus.

L'estructura de la vegetació al límit superior del bosc presenta una situació de no-equilibri entre les fronteres estructurals dels arbres i els canvis més acusats en la diversitat de les comunitats alpines. Aquest fet evidencia els diferents ritmes de resposta que presenten diferents processos de l'ecotò a la variació ambiental.

La vegetació alpina al llarg de l'ecotò es caracteritza per canvis bruscs i irregulars de comunitats que estan estretament relacionats amb l'heterogeneitat del substrat i de les condicions microambientals. No hi ha comunitats intermèdies, pel que fa a composició específica, al llarg de la transició bosc-prats alpins.

El previsible increment dels fenòmens d'estrés hídric a escala regional al sud d'Europa (IPCC 2007), degut a augments de temperatura sense anar acompanyats d'augments en el règim de precipitació, i la probable disminució de la precipitació hivernal en forma de neu, poden aturar i revertir els processos de densificació de la zona de l'ecotò observats durant el segle XX.

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