UNIVERSITAT DE BARCELONA

Estructura funcional de la vegetació alpina dels Pirineus

Resposta de les comunitats als factors ambientals i als efectes del canvi global

Estela Illa Bachs

UNIVERSITAT DE BARCELONA

Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals
Programa de doctorat en Biodiversitat

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Memòria presentada per Estela Illa Bachs per optar
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Estela Illa Bachs	**M. Amparo Carrillo Ortuño**	**Josep M. Ninot Sugrañes**
doctoranda	directora/tutora de la tesi	co-director de la tesi

Agraïments

Ja fa molt anys, quan encara estudiava, pensava que això de venir a la universitat i només fer classes era una mica avorrit; tenia ganes d'aprendre més coses! I vaig pensar que la millor manera era col·laborant a un departament. Tot i que no tenia massa clar què era el que més m'agradava de la biologia, els cormòfits amb en Pep m'havien descobert un món que desconeixia, i em vaig decidir pel departament de botànica. Vaig entrar-hi de la mà d'en Toni Sànchez, ajudant-lo a l'herbari a les catacumbes de la facultat. Tot i que no he fet de botànica *sensu stricto*, el record de l'olor de plantes premsades no m'abandonarà mai. Més endavant en Pep ens va agafar a l'Artur i a mi per entrar dades de flora de la Vall d'Aran. Alhora, en Jordi, ens feia digitalitzar mapes a mà amb la pantalla digitalitzadora, i després a l'ordinador, on s'havia de jugar amb fletxetes amunt i avall per incorporar les línies a ArcInfo. No voldria passar per alt les maquetacions de mapes amb macros d'ArcPlot que em va ensenyar a fer l'Albert Ferré, llarguíssimes i complicades, gairebé tant com els scripts d'R. Va passar el temps, vaig acabar la carrera i en Jordi em va contractar per fer cartografia. Però tenia el cuquet de fer recerca, i vaig decidir fer el DEA. Aquí agraeixo a en Pep que em volgués dirigir. M'hagués agradat molt anar al Montsant a fer inventaris de boscos, però fer un treball sobre els trets i les estratègies de la vegetació alpina era més engrescador, i no en sabia ni un borrall, ni de trets, ni de plantes alpines... Per tant, m'hi vaig llençar de cap! També l'Empar, al cap de poc temps, em va embolicar a mostrejar congesteres amb l'Artur. Tornem-hi amb les plantes alpines, i aquesta vegada, amunt i avall, faci bo, plogui o nevi. Van ser uns estius genials, en un entorn genial! I als vespres, tots cap a la casa de Viella, on ecòlegs, limnòlegs, botànics... comentàvem els mostrejos respectius i la fèiem petar!

Al departament, amb molts companys (i amics!) hem fet camí junts durant aquests anys, i voldria agrair-vos la vostra companyia i amistat. Gràcies a totes i a tots, ha estat un plaer compartir tantes estones! A tots els amics i amigues, sobretot als masnovins, que ho heu viscut i patit en primera persona aquests dos últims anys, voldria agrair-vos la vostra ajuda en la logística familiar sempre que ha fet falta, i disculpar-me per les meves absències constants en trobades diverses. Us estic molt agraïda, i us prometo que quan tot s'acabi seré jo qui us recollirà nens a l'escola *in extremis*. A la meva mare li vull dedicar un agraïment especial. Gràcies per ser al meu costat sempre que t'he necessitat, per cuidar nens, per cuidar-me a mi, per obligar-me a descansar... Realment, com una mare no hi ha res! També vull agrair a l'Eloi i en Ferran les rialles i abraçades que m'han regalat cada dia, malgrat que no hagin tingut una mare tan dedicada a ells com segurament els hagués agradat. Espero que a partir d'ara puguin gaudir d'una vida familiar més normalitzada! Seria una desconsideració per part meva no agrair a en Bernat la paciència i resignació amb què ha afrontat les anades al Tonedor per baixar dades del data-logger, els mostrejos de congesteres i de matollars, el destriat de fulles, troncs i líquens a la taula del menjador, o les campanyes de camp de cartografia per tota la geografia catalana. Puc dir molt orgullosa que va aprendre a caminar sobre catifes de *Salix herbacea* i a anar en bicicleta entre brolles de *Genista biflora* al full 444 de Flix. Ets una joia, Bernat! Finalment, l'agraïment més sentit i profund és per l'Albert. Per acompanyar -me, per ajudar-me, per aconsellar-me, per animar-me, per encarregar-se de la família, per fer-me tocar de peus a terra, per exasperar-me (sí, això també de tant en tant!)... en definitiva, per ser-hi.

(…)
És sols lo començament
lo que prenies per terme.

L’univers és infinit,
pertot acaba i comença,
i ençà, enllà, amunt i avall,
la immensitat és oberta,
i aon tu veus lo desert
eixams de mons formiguegen.

Jacint Verdaguer, *Plus Ultra* (1903)

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Introducció general

Introducció

El paisatge de l'alta muntanya alpina és un dels menys antropitzats dels que ens envolten. Mostra per tant una elevada naturalitat i, sovint, un bon estat de conservació. També presenta forts gradients ambientals condicionats per l'elevada diversitat topogràfica, de manera que hostatja hàbitats molt diversos. A més, inclou zones amb un fort aïllament geogràfic, fet que ha propiciat una interessant barreja d'elements florístics i molta endemicitat. Tots aquests aspectes, juntament amb l'amenaça del canvi global, confereixen als ambients alpins un elevat interès científic.

El medi alpí i els vegetals

Els ecosistemes alpins i àrtics, tal com els descriuen Billings & Mooney (1968), són territoris que es troben per damunt del límit natural del bosc, de clima fred i dominats bàsicament per vegetació herbàcia o arbustiva. L'absència natural de boscos ha estat una característica constant a les parts altes de les serralades alpines (Elias 2001; Birks & Willis 2008), que durant els períodes interglacials han servit de refugi a espècies de procedència molt diversa que van poder migrar i colonitzar noves àrees durant les glaciacions (Schönswetter et al. 2006). Algunes d'aquestes espècies, poc competitives i amb una capacitat d'adaptació reduïda, han quedat confinades als ambients més desfavorables, i el seu aïllament geogràfic ha incentivat fenòmens d'especiació que han aportat un nombre considerable d'endemismes (Gómez et al. 2003; Loidi et al. 2015).

La flora total d'un territori ha de passar per una sèrie de filtres ambientals que se succeeixen jeràrquicament d'escala regional a escala local (de Bello et al. 2013), fent que només un nombre reduït d'espècies pugui viure a un ambient determinat. L'altitud, que és el principal agent modulador de les condicions climàtiques, és el primer d'aquests filtres ambientals. A les muntanyes de latituds mitjanes de l'hemisferi Nord, per cada 100 metres d'altitud la temperatura mitjana anual disminueix al voltant de 0,6 °C (Scherrer & Körner 2010). Tenint en compte el gran desnivell inherent a les zones d'alta muntanya, les temperatures i les precipitacions poden canviar substancialment en poca distància. Aquesta reducció tèrmica en alçada té efectes tant en les plantes com en els ecosistemes. Per exemple, les plantes alpines tenen alçades reduïdes que els permeten crear un microambient sota la capçada amb unes condicions microclimàtiques menys vinculades al clima general (Körner 2003). A nivell d'ecosistema, les taxes globals de descomposició de la matèria orgànica són molt baixes (Zhang et al. 2008), entre d'altres motius perquè les baixes temperatures no permeten l'activitat dels microorganismes del sòl durant bona part de l'any (Saccone et al. 2013). El resultat són sòls en general pobres en nutrients i ambients poc productius (Field et al. 1998).

En segon lloc trobem la topografia, que determina les condicions climàtiques locals i la presència dels sòls, i el tipus de roca mare. Pel que fa a les condicions climàtiques, la topografia afavoreix la formació de fenòmens convectius locals, que comporten un augment de precipitació respecte d'àrees veïnes. També condiciona el pas del vent, el qual redueix la temperatura i humitat ambientals i regula la distribució de la neu. Una neu que, precisament per la microtopografia particular de cada indret, presenta un patró de distribució a finals de primavera molt constant any rere any. Finalment, condiciona la radiació solar incident (Swanson et al. 1988), que en funció de l'orientació i del pendent dels vessants i de la microtopografia, té efectes tant en la temperatura i humitat ambientals (Scherrer & Körner 2011) com en la persistència de la neu. La radiació i la temperatura mesurades als vessants solells de l'hemisferi nord són molt superiors que les que es donen als vessants obacs, de manera que la neu hi fon abans i els vegetals disposen de períodes vegetatius més llargs però de menys humitat ambiental (Scherrer & Körner 2011). Pel que fa als sòls, la topografia en determina la presència i el gruix a través de processos de transferència o de dinàmiques d'acumulació de materials (Swanson et al. 1988). Per exemple, el relleu especialment abrupte de les zones més elevades de l'alta muntanya, on la meteorització de la roca i la gravetat són els principals agents ambientals de canvi, afavoreix l'acumulació dels materials a les parts baixes dels vessants o a les clotades. En aquestes situacions es poden formar sòls relativament profunds, favorables per a la retenció d'aigua i de nutrients, i per tant, per a l'establiment de la vegetació. Finalment, les característiques físico-químiques de la roca mare determinen la capacitat de retenció de l'aigua (Michalet et al. 2002) i la disponibilitat de nutrients per part de les plantes (Hobbie & Gough 2002; Arnesen et al. 2007).

Per tant, si al gran desnivell altitudinal de les zones d'alta muntanya s'hi afegeixen una topografia i microtopografia heterogènies i una certa varietat de substrats geològics, el resultat és una elevada diversitat d'ambients que hostatgen conjunts diferenciats d'espècies vegetals (Stanton et al. 1994; Onipchenko et al. 1998; Michalet et al. 2002; etc.) amb adaptacions concretes a les restriccions particulars de cada ambient. La vegetació alpina consisteix doncs en un mosaic de comunitats vegetals, on els forts gradients ambientals redueixen enormement la superfície de transició entre unes i altres, fet que en facilita l'estudi i la tipificació.

Les espècies capaces de viure en un ambient determinat interactuen entre elles amb relacions que poden ser positives (facilitació), negatives (competència) o neutres (tolerància). En bona part dels ambients alpins, sotmesos a molt estrès abiòtic, les relacions predominants són de facilitació entre espècies (Choler et al. 2001; Callaway et al. 2002). Quan la intensitat de l'estrès abiòtic es redueix, sobretot a altituds més baixes o en indrets protegits, la facilitació deixa pas a la competència. En aquestes situacions les espècies més competitives limiten la presència d'un cert nombre d'espècies o formes de creixement (Bråthen & Ravolainen 2015), ja sigui a través de l'ocupació de l'espai per mitjà d'estructures clonals (Pornon et al. 1997), de la monopolització dels recursos (Pornon & Lamaze 2007), o de la producció de matèria orgànica acidificant que impedeix l'establiment de moltes plàntules (Welling & Laine 2002). És un fet general doncs, que les espècies més competitives acabin fent-se dominants.

Finalment, espècies que no són excloses per competència també han de ser capaces de perpetuar-se en el temps. En el context impredictible de les condicions de l'alta muntanya, no tots els anys són favorables perquè les plantes puguin completar el seu cicle reproductiu (Bliss 1971, Lluent et al. 2013), produir un nombre elevat de llavors (Molau & Larsson 2000) o establir-se amb èxit després de la germinació (Forbis 2003). És per aquest motiu que en indrets àrtics i alpins històricament s'ha interpretat la clonalitat com l'estratègia més fiable de persistència i reproducció tant en l'espai com en el temps (Bliss 1971; Evette et al. 2009; etc.), tot i que Klimešová & Doležal (2011) destaquen que la clau de la persistència de les espècies d'ambients freds és la seva longevitat.

Trets adaptatius de les espècies

Només una part del conjunt potencial d'espècies d'un territori supera els filtres esmentats anteriorment a través d'una sèrie de trets adaptatius (Díaz et al. 1998) que els permeten afrontar les restriccions del medi, fent que sigui evident l'existència de vincles entre trets i condicions ambientals (Keddy 1992). El terme *tret* (en anglès *trait*) ha estat àmpliament utilitzat en diferents àrees d'investigació i s'ha fet servir tant a nivell d'espècie com a nivell de comunitat o d'ecosistema, de manera que el seu significat sovint no és evident (Violle et al. 2007). A nivell d'espècie, fa referència a qualsevol característica morfològica, fisiològica, fenològica o reproductiva mesurable a nivell individual i que no requereix informació externa a la planta. Els trets poden ser continus o categòrics, i cada valor que prenen en un indret o moment determinats s'anomena *atribut* (en anglès *attribute*), si bé fins a finals del segle XX sovint s'utilitzava com a sinònim de *tret*, i era habitual fer servir el mot *estat* (en anglès *state*) per definir els diferents valors o categories d'un tret (Semenova & van der Maarel 2000). Al conjunt de trets que tenen influència directa o indirecta en l'establiment, la supervivència i la reproducció de les espècies, és a dir, que tenen significació adaptativa o estratègica, se'ls anomena *trets funcionals* (Semenova & van der Maarel 2000; Reich et al. 2003). Quan són interpretables com a resposta de les espècies a les condicions ambientals es fa referència a *trets resposta* (o *adaptatius*), mentre que si tenen efecte en les propietats de l'ecosistema es parla de *trets efecte*. Un dels trets funcionals més àmpliament utilitzat en estudis d'ecologia vegetal són les *formes vitals* definides per Raunkiaer (1934), o les seves possibles subdivisions en *formes de creixement*.

Dins del camp de l'ecologia funcional s'han estudiat les relacions existents entre un bon nombre de trets funcionals i la fisiologia dels vegetals (Wright et al. 2004; Chave et al. 2009; Adler et al. 2014), les característiques ambientals a nivell global (Ordoñez et al. 2009) i regional (Díaz et al. 1998), o el funcionament de l'ecosistema (Cornwell et al. 2008). A més, diversos estudis recullen la variabilitat intra- i interespecífica dels atributs en funció de gradients ambientals com a factor determinant de la capacitat d'adaptació de les espècies al medi (Albert et al. 2010; Violle et al. 2012; etc.).

Conscients de la importància que ha pres l'ecologia funcional, diversos autors han intentat definir els trets més rellevants i estandarditzar-ne la mesura (Weiher et al. 1999; Cornelissen et al. 2003; Pérez-Harguindeguy et al. 2013). Un dels objectius bàsics d'aquests treballs ha estat seleccionar trets clau senzills de mesurar (*soft traits*) que sovint correlacionen amb processos fisiològics responsables de les respostes al medi o dels efectes sobre el medi, la mesura dels quals és complexa (*hard traits*). D'aquesta manera, s'han elaborat propostes de quins són els trets de fàcil mesura determinants per entendre la relació dels vegetals amb el medi (Westoby 1998).

No només hi ha hagut interès en estudiar els trets funcionals i la seva relació amb la fisiologia de les espècies, amb la seva capacitat de supervivència o amb el medi, sinó també en classificar les espècies en funció de les característiques biològiques que comparteixen, creant *grups funcionals*. Depenent dels objectius que es plantegin en cada cas, aquests grups funcionals poden reflectir respostes adaptatives i limitacions evolutives de les espècies (Leishman & Westoby 1992; Chapin III et al. 1993; Leishman et al. 1995; etc.), patrons adaptatius relacionats amb la resposta a la disponibilitat de recursos i a les pertorbacions (estratègies, Grime 1979) o amb el funcionament de l'ecosistema (*PFTs* o *plant functional types*, Box 1996; Chapin III et al. 1996; Woodward & Cramer 1996; etc.).

En ambients àrtics i alpins, l'estudi dels trets adaptatius de les espècies i dels seus efectes sobre el medi ha despertat l'interès de molts científics des de mitjan segle XX, amb els treballs pioners de Bliss (1956; 1962; 1971), de Billings (1974), o de Billings & Mooney (1968), als quals s'han d'afegir nombrosos treballs més recents (Choler 2005; Venn et al. 2011; Gutiérrez-Girón & Gavilán 2013; etc.). Les restriccions ambientals generals de l'estatge alpí comporten una sèrie de trets adaptatius similars en els vegetals, fent que majoritàriament presentin alçades reduïdes (Billings & Mooney 1968; Körner 2003), valors de biomassa subterrània força superiors que els valors de biomassa aèria (Billings & Mooney 1968; Webber & Ebert May 1977), o continguts de nitrogen foliar superiors que les espècies similars d'altituds més baixes (Körner 1989). Són les particularitats de cada ambient en concret les que seleccionen per trets més específics, on els que siguin avantatjosos permetran la dominància de les espècies que els posseeixen.

El paisatge supraforestal s'ha de considerar doncs com un àmbit molt singular, tant en l'aspecte evolutiu i filogenètic, com també en el de les adaptacions funcionals de les plantes al medi. En aquest sentit, un coneixement profund de les característiques adaptatives i reproductives de les espècies (capítols I, II) és essencial per entendre el funcionament de la vegetació i per valorar-ne la vulnerabilitat o la resistència davant dels processos actuals de dinàmica dels ecosistemes.

El salt d'espècie a comunitat

L'ecologia comparativa de plantes permet passar del coneixement profund d'unes poques espècies al coneixement extensiu de conjunts molt més amplis, com poden ser els grups funcionals, gràcies a la consideració de trets adaptatius, de síndromes o d'estratègies vitals. En un determinat ambient, la freqüència amb què es donen els trets adaptatius és altament informativa de les respostes específiques de les plantes al medi (Körner 2003). Així, l'estudi de les plantes i la vegetació a través dels seus trets esdevé una eina particularment útil, perquè estandarditza i simplifica la multiplicitat de respostes de les plantes, perquè permet anàlisis comparatives entre ecosistemes anàlegs però florísticament allunyats, i sobretot perquè permet relacionar la composició i el funcionalisme de la vegetació amb el seu medi, entès de la manera més àmplia.

Tant a nivell global com en medis alpins, les comunitats d'indrets amb condicions ambientals més benignes (a l'alta muntanya, les altituds més baixes i els llocs més abrigats) presenten valors de biomassa i de productivitat més elevats, i és alhora on s'observen relacions de competència més fortes (Kikvidze et al. 2005). D'aquí en resulta la clara dominància d'unes poques espècies que representen una proporció molt elevada de la biomassa total de la comunitat (Grime 1998; Smith & Knapp 2003). Per tant, l'estructura de la comunitat i el funcionament de l'ecosistema vénen determinats per les espècies dominants (Hobbie 1992; Walker et al. 1999). Canvis en l'abundància d'aquestes espècies comporten invariablement canvis en el processos de l'ecosistema, mentre que variacions en la riquesa específica de les espècies acompanyants no són rellevants a nivell funcional (Grime 1998), però sí que ho poden ser per l'estabilitat de les comunitats, ja que contribueixen a la resiliència de l'ecosistema (Walker et al. 1999).

En resum, les comunitats alpines són especialment adients per avaluar fins a quin punt la pressió ecològica que exerceix el medi sobre les espècies ha determinat les agrupacions dels vegetals (capítol I) i l'estructura i funcionament de les comunitats (capítols III, IV). A més, la clara preponderància que hi solen tenir una o poques espècies les fa molt sensibles als canvis ambientals, que quan afecten les espècies principals generen efectes en cascada que poden comportar la substitució de tota la comunitat.

Dinàmica de la vegetació

Canvis en la composició de les comunitats vegetals, sobretot en la proporció dels diferents grups funcionals (Hooper & Vitousek 1997), així com la substitució d'unes comunitats per unes altres, impliquen alteracions en el funcionament de l'ecosistema, particularment en la dinàmica del carboni i dels nutrients. En el context actual de canvi global, l'increment de CO_2 (determinant del canvi climàtic), les alteracions en els cicles biogeoquímics, els canvis en els usos del sòl o les invasions biològiques no només provoquen canvis en la composició de les comunitats, sinó que afavoreixen els processos de dinàmica de la vegetació. Actualment, alguns casos de dinàmica han esdevingut rellevants a l'alta muntanya, entre els quals destaca el desplaçament en altitud d'un bon nombre d'espècies vegetals (Klanderud & Birks 2003; Pauli et al. 2003; Parolo & Rossi 2008), i del propi límit forestal, o *treeline* (Dullinger et al. 2004; Rundqvist et al. 2011; Améztegui et al. 2016). Les zones de muntanya són especialment sensibles als canvis, pel fet que hostatgen un bon nombre d'espècies que es troben als seus límits de tolerància ambiental. Aquesta particularitat les converteix, però, en zones d'observació i d'experimentació privilegiades.

A les serralades alpines l'increment de les temperatures està provocant la reducció de les glaceres (Haeberli & Beniston 1998), i tots els models apunten a una disminució significativa de la coberta de neu hivernal durant el segle actual (Beniston et al. 2003; López-Moreno et al. 2009). Els Pirineus, una de les serralades alpines més meridionals d'Europa, estan per tant molt exposats a l'increment general de les temperatures i a la disminució de les precipitacions (Diaz & Bradley 1997; Engler et al. 2011). Certament, la freqüència de dies càlids ha augmentat i el gruix de la coberta nival ha disminuït durant les últimes dècades (López-Moreno 2005; Morán-Tejeda et al. 2013), i s'espera més irregularitat climàtica a la serralada (López-Moreno 2005; Esteban et al. 2009; López-Moreno et al. 2009), que pot afectar la distribució de la vegetació alpina.

La vegetació lligada a les congesteres forma part d'un dels ecosistemes de l'alta muntanya potencialment més sensibles al canvi climàtic. Són unitats de vegetació de dimensions reduïdes que es troben escampades als indrets on la neu s'acumula més temps, i que hostatgen espècies amb un elevat interès biogeogràfic. La vegetació de congestera (o quionòfila) depèn principalment de la durada i del gruix de la coberta de neu (Galen & Stanton 1995), però també de la distribució de l'aigua procedent de la fosa de la neu i del contingut en matèria orgànica del sòl (Stanton et al. 1994). La innivació prolongada d'aquests ambients fa que les plantes disposin d'un breu període vegetatiu i per tant d'una aportació limitada d'energia per completar el seu cicle (Lluent 2007; Illa et al. 2011), circumstàncies que exclouen la majoria de les espècies de l’alta muntanya. En contrapartida, les plantes no experimenten dèficit de nutrients, d’una banda perquè la neu a la primavera afavoreix la retenció de nitrogen atmosfèric (Bowman 1992), disponible per als vegetals amb l’aigua de fusió, i per altra banda perquè l’aïllament tèrmic de la neu permet l’activitat dels microorganismes del sòl durant l’hivern (Brooks et al. 1996). Tampoc no hi ha dèficit hídric, per la pròpia aportació d’aigua provinent de la fosa de la neu tardana (Lluent 2007) i de les precipitacions estivals. L’existència simultània de relacions de competència i de facilitació entre les espècies de congestera (Schöb et al. 2010) fa que hi hagi una certa estabilitat en les comunitats vegetals. Aquesta estabilitat és però especialment sensible a canvis en les condicions ambientals que afectin la durada i el gruix de la neu, ja que un allargament del període vegetatiu pot fer variar la disponibilitat de nutrients i d’aigua, provocant desajustos en les relacions entre les espècies. En aquest sentit, diversos autors alerten que una fosa primerenca de la neu pot afectar aquests ambients particulars permetent l’entrada de les espècies pradenques, més competitives, a partir dels prats veïns (Heegaard & Vandvik 2004; Björk & Molau 2007; Schöb et al. 2008).

Pel que fa als canvis d’usos del territori, els usos tradicionals a les zones agrícoles i de muntanya a Europa han estat abandonats progressivament durant la segona meitat del segle XX (Garcia-Ruiz et al. 1996; MacDonald et al. 2000; Otero et al. 2015). A les zones de muntanya s’ha donat una substitució del bestiar oví pel boví, la intensificació de la pastura als indrets més accessibles, la substitució de camps de cereals per prats a les valls i un abandonament de les zones de més difícil accés (Garcia-Ruiz & Lasanta-Martinez 1990). Aquests canvis en l’ús del territori han permès la recolonització dels prats pel bosc (Gellrich et al. 2007), incentivada també per l’augment de les temperatures (Gehrig-Fasel et al. 2007). En paral·lel a la reforestació, les comunitats arbustives han iniciat un procés de colonització de les comunitats pradenques, que es coneix com a *emmatament*. S’han dut a terme nombrosos estudis en zones àrtiques (Myers-Smith et al. 2011; Ropars & Boudreau 2012; Dumais et al. 2014; etc.) i alpines (Dullinger et al. 2003; Anthelme et al. 2007; Cannone et al. 2007), on s’ha comprovat que la cobertura arbustiva s’incrementa a expenses dels prats a taxes relativament elevades (Sturm et al. 2001; Cannone et al. 2007). La substitució de comunitats herbàcies per llenyoses comporta grans canvis, no només en la riquesa florística (Anthelme et al. 2007), sinó en l’estructura de la comunitat i en els processos a nivell d’ecosistema, entre els quals destaquen augments considerables de biomassa i d’acumulació de virosta, i canvis en el cicle dels nutrients (Formica et al. 2014).

Centrar-se en uns pocs casos d’estudi relatius a la dinàmica de la vegetació de l’alta muntanya (capítols V, VI) és rellevant per tal de poder avaluar els canvis que s’hi donen, els quals, en funció del grau de substitució de les espècies i de la superfície de territori que impliquin, poden tenir efectes lleus o notables sobre els ecosistemes. Per tant, per poder predir les conseqüències del canvi global a escala regional en sistemes alpins, convé conèixer amb detall els processos relacionats amb la dinàmica de la vegetació a escala local.

Àrea d'estudi

Fisiografia

L'àmbit d'estudi abraça el territori pirinenc situat dins els límits administratius de Catalunya i d'Andorra. Dins d'aquest àmbit, l'àrea d'estudi correspon a les altituds superiors als 2.200 m (Fig. 1), que ocupen en total 103.937 ha i es reparteixen de manera discontínua ocupant un espai d'aproximadament 140 km de longitud (E-W) i una amplada d'entre 5 i 50 km. Les cotes més elevades superen els 3.000 m d'altitud: en total hi ha 10 cims de més de 3.000 m –el més alt és la Pica d'Estats, amb 3.143 m– i al voltant de 30 cims es troben entre els 2.900 i els 3.000 m (Institut Cartogràfic i Geològic de Catalunya, www.icgc.cat).

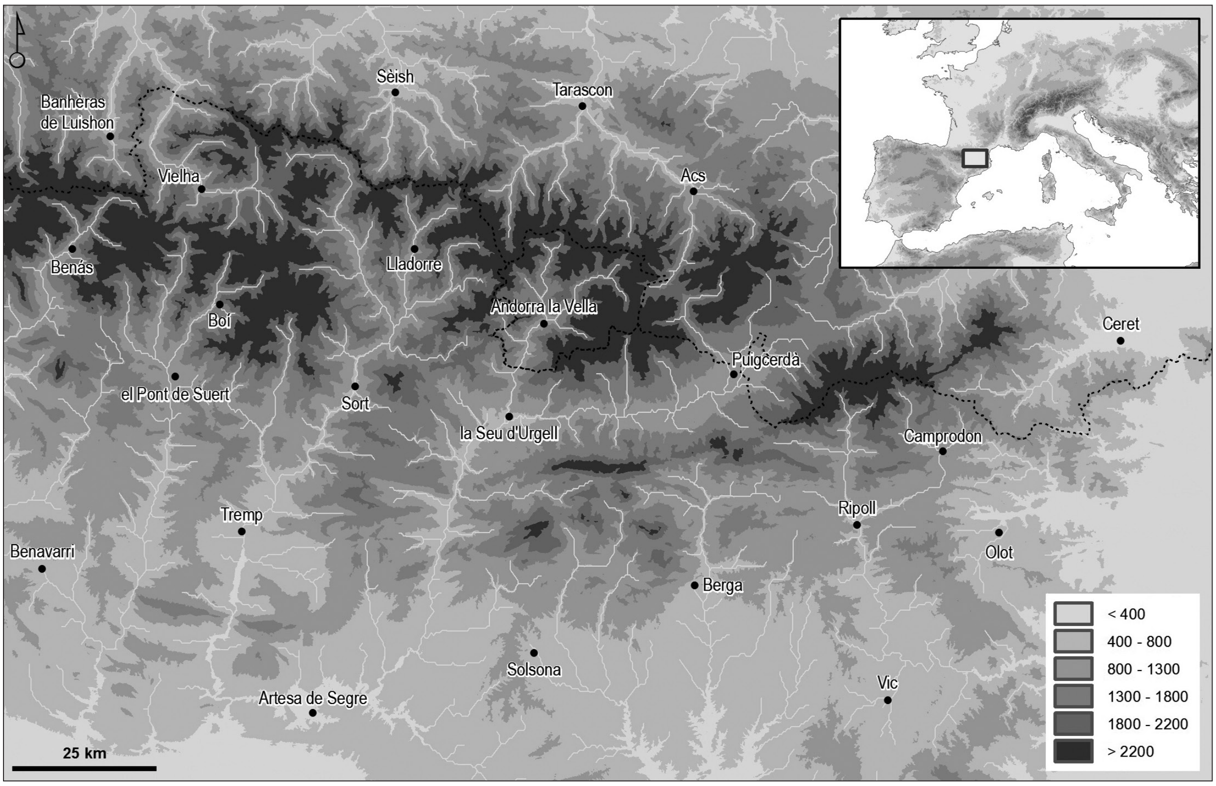

Fig. 1. Àmbit d'estudi, que inclou el territori pirinenc comprès dins els límits administratius de Catalunya i d'Andorra. Les tonalitats més fosques delimiten l'àrea d'estudi, per sobre els 2.200 m d'altitud.

La superfície ocupada per sobre els 2.200 m d'altitud no és contínua, sinó que forma illes de superfícies variables. Els dos sectors amb àrees contínues més extensos són el que inclou la part axial de la serralada entre el port de Salau a l'oest i la fossa de la Cerdanya a l'est, fronterer entre Catalunya, Andorra i França (45.000 ha), i el que inclou el parc nacional d'Aigüestortes i Estany de Sant Maurici i rodalies (34.000 ha). A través del port de Salau (2.085 m), gairebé hi ha continuïtat entre el sector axial pirinenc català-francès-andorrà i el sector axial pròpiament aranès (4.000 ha), el qual també està pràcticament connectat amb el sector del Montlude (1.700 ha) a través de la capçalera de la vall de Liat, a més de

2.150 m, i amb el tuc d'Arenho (1.350 ha) a través del coll de Varradòs, a 2.050 m d'altitud. D'altra banda, el port de la Bonaigua (2.075 m) gairebé uneix el sector d'Aigüestortes i el massís de Marimanha (amb aproximadament 5.000 ha). Així doncs, es pot parlar de dos grans sectors pràcticament continus per sobre dels 2.000 d'altitud, que junts ocupen al voltant de 91.000 ha. La resta de sectors amb cotes per damunt els 2.200 m d'altitud són de dimensions marcadament més reduïdes i queden relativament aïllats, tant al límit oriental de la serralada pirinenca com al límit meridional. Només el sector que conforma la capçalera de les valls del Ripollès, que té una extensió de 6.925 ha i un bon nombre de cims que superen els 2.700 m, la resta (Torreta de l'Orri, Cadí, Port del Compte, Pedraforca, Ensija, Moixeró, Tossa d'Alp, Puigllançada, etc.), són de dimensions més reduïdes i presenten altituds més modestes, en general per sota dels 2.500 m.

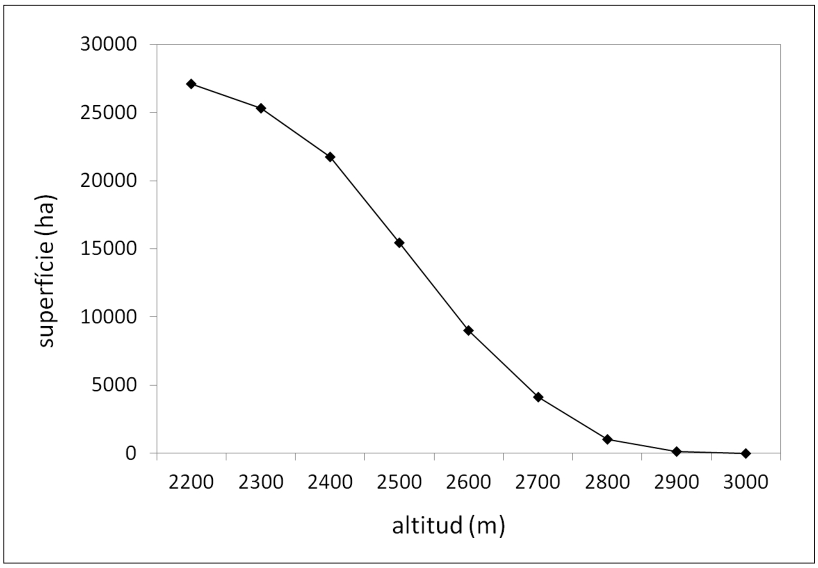

Fig. 2. Superfície (ha) que correspon als diferents intervals altitudinals de 100 metres entre els 2.200 i els 3.000 m d'altitud. Dades elaborades a partir del model d'elevacions derivat de la topografia de l'ICGC.

A mesura que augmenta l'altitud la superfície disponible disminueix dràsticament, a causa del relleu abrupte i els forts pendents que hi ha a les parts culminants de la serralada. A les cotes més baixes (entre 2.200 i 2.300 m) hi ha més de 50.000 ha, mentre que per sobre dels 2.800 m hi ha menys de 1.000 ha (Fig. 2).

Clima

Als Pirineus la temperatura mitjana anual de l'aire a 2.300 m és de 2,4 °C, i a 2.900 m és de -0,9 °C; i a partir dels 2.000 m d'altitud pot glaçar o nevar en qualsevol moment de l'any (Gómez et al. 2003). Al Pirineu català i andorrà coexisteixen dos climes principals. Per una banda trobem un clima oceànic o de tendència marítima a la vall d'Aran i a l'extrem oriental de la serralada (al Ripollès): a les valls les precipitacions hi són relativament abundants, especialment durant el període vegetatiu, i la vegetació hi és ufanosa i més semblant a la que es pot trobar al vessant francès i a l'extrem occidental pirinenc. Per altra banda trobem un clima majoritari marcadament continental, amb estius secs i calorosos i hiverns freds, i precipitacions que oscil·len al voltant dels 600-800 mm anuals a les valls a la part central i occidental dels Pirineus catalans (de la fossa de la Cerdanya fins a la Ribagorça). A les cotes altes que integren l'àrea d'estudi aquestes diferències climàtiques s'atenuen, i les precipitacions hi són de mitjana més elevades (al voltant dels 1.200 mm anuals) i més constants durant tot l'any (Fig. 3).

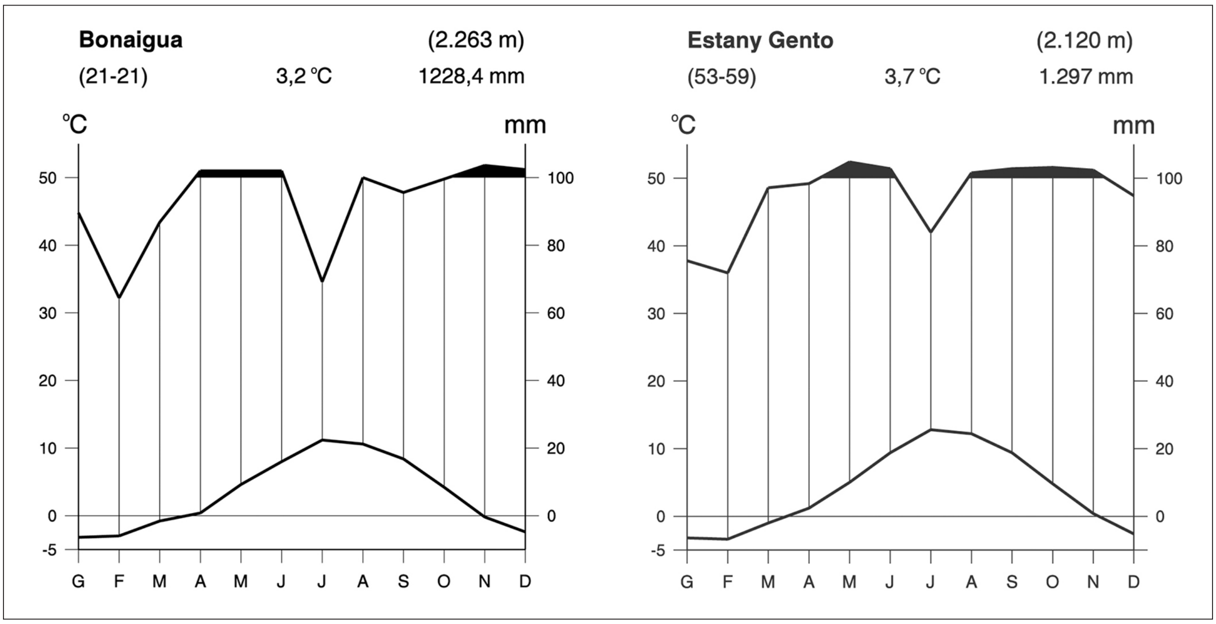

Fig. 3. Diagrames ombrotèrmics de les estacions meteorològiques de la Bonaigua (2.263 m) i de l'estany Gento (2.120 m).

Vegetació

En base a criteris geobotànics, en tot l'àmbit d'estudi es pot considerar que l'estatge alpí comença entre els 2.200 m i els 2.450 m, en funció de l'exposició del vessant i de la situació dins la serralada (Carreras et al. 1996; Ninot et al. 2007). Les comunitats vegetals més àmpliament distribuïdes per damunt dels 2.200 m d'altitud són els prats, que ocupen més de dues terceres parts de la superfície total (Taula 1). Les tarteres i les roques, que presenten recobriments molt baixos de vegetació, són els següents hàbitats més àmpliament distribuïts al territori, si bé amb una ocupació que representa poc més de la meitat del que suposen els prats. Els boscos i matollars ocupen una superfície total gens menyspreable, tot i que majoritàriament es troben a les parts altes de l'estatge subalpí (que pot arribar fins els 2.450 m), on tenen el seu límit altitudinal superior (Ninot et al. 2007). La resta d'hàbitats són més aviat anecdòtics si només els valorem en base a la superfície que ocupen. Ara bé, en el sentit biogeogràfic tenen un gran interès. Per exemple, tant les molleres com les congesteres representen el límit meridional de tipus de vegetació típicament boreals i temperats (les molleres), o articoalpins (les congesteres). A escala pirinenca, aquestes comunitats es distribueixen reflectint el seu caràcter biogeogràfic: les molleres són sobretot subalpines, però s'estenen també força per l'estatge alpí, mentre que les congesteres es troben restringides a les cotes més elevades de la serralada.

La distribució altitudinal dels diferents tipus d'hàbitats és molt variable. Les comunitats pradenques i les subarbustives, que representen una part important de la vegetació estudiada en aquesta tesi, es distribueixen de manera poc equilibrada al territori alpí pirinenc. Entre els 2.200 i els 2.500 m d'altitud els prats ocupen un 50% o més de la superfície disponible, i van essent cada vegada més escasses a mesura que es guanya altitud. Les comunitats subarbustives queden restringides a la part inferior de l'estatge alpí (o part alta del subalpí en territoris continentals desforestats (Ninot et al. 2007), on la poca superfície que ocupen decreix en funció de l'altitud (Fig. 4a); i un patró semblant s'observaria en el cas de les molleres i dels boscos. Les congesteres representen un percentatge de superfície ocupada ínfim en comparació amb la resta de tipus de vegetació, i contràriament als altres tipus d'hàbitats, el seu patró de distribució és gaussià, amb un màxim d'ocupació a altituds intermèdies. Les roques i tarteres tenen poca extensió a les parts baixes de l'estatge alpí i són cada vegada més abundants a mesura que augmenta l'altitud. Només a les zones culminants les roques passen a ser l'hàbitat majoritari (Fig. 4b).

	superfície ocupada (ha)	superfície ocupada (%)
molleres	536,85	0,52
estanys	1.215,92	1,18
congesteres	1.365,61	1,33
boscos	6.733,32	6,54
matollars	6.790,31	6,60
roques	15.379,75	14,95
tarteres	19.879,10	19,32
prats	50.999,12	49,56

Taula 1. Superfície ocupada pels diferents tipus d'hàbitats en el conjunt del territori estudiat per sobre els 2.200 m. Dades elaborades a partir de la Cartografia dels Hàbitats de Catalunya (1:50.000) i d'Andorra (1:25.000).

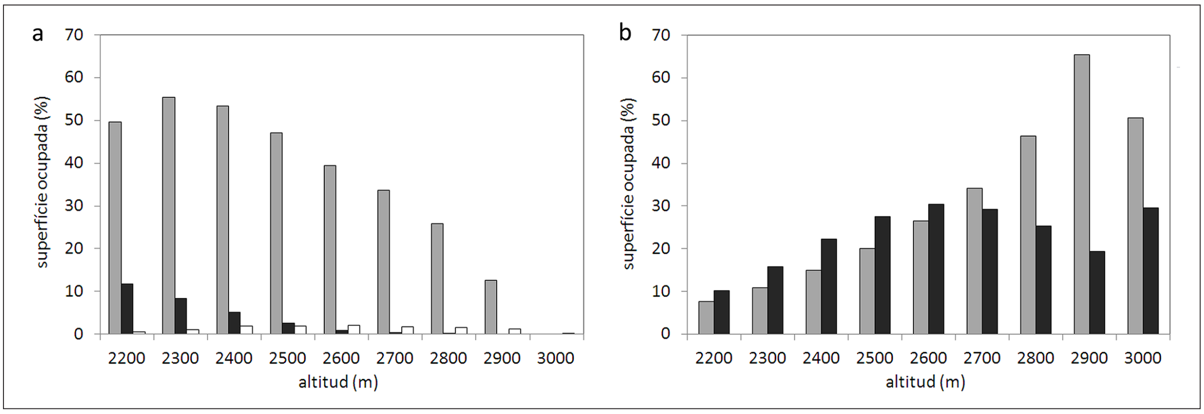

Fig. 4. Distribució en intervals altitudinals de 100 metres de la superfície ocupada pels hàbitats alpins als Pirineus catalans i andorrans. **a**-hàbitats amb un elevat recobriment de la vegetació: prats (gris), matollars (negre) i congesteres (blanc). **b**-hàbitats on la vegetació presenta poc recobriment: roques (gris) i tarteres (negre). Dades elaborades a partir de la Cartografia dels Hàbitats de Catalunya (1:50.000) i d'Andorra (1:25.000).

Antecedents: l'estudi de la vegetació a l'alta muntanya pirinenca catalana

L'estudi de la vegetació als Pirineus catalans (i andorrans) ha despertat l'interès de gran quantitat de científics, i compta amb nombroses obres des de mitjans del segle XX. Per una banda hi ha treballs que abracen grans àrees geogràfiques pirinenques, entre els quals destaca l'obra de Braun-Blanquet (1948), que va utilitzar la vegetació alpina com a base per al seu estudi fitocenològic precisament pels gradients sobtats i per la poca influència humana, que li van permetre delimitar i caracteritzar fidelment les comunitats vegetals a l'alta muntanya. També Grüber (1978) va prospectar la part central de la serralada. Per altra banda, a les darreries del segle XX s'han realitzat abundants estudis regionals (Carrillo & Ninot 1992; Carreras et al. 1993; Carreras 1993; Vigo 1996; Soriano 2001), que han permès tenir un bon coneixement tant de la flora com de la vegetació de la part central i oriental de la serralada. Pel que fa a la distribució de les comunitats, els mapes de vegetació a escala 1:50.000 (Carreras et al. 1997; Carrillo & Ninot 1998;

Carreras et al. 2000; etc.), la cartografia dels hàbitats de Catalunya a escala 1:50.000 (Carreras & Vendrell 2012) i d'Andorra a escala 1:25.000 (Carreras et al. 2012), i més recentment la cartografia dels hàbitats CORINE de parcs naturals a escala 1:10.000, han contribuït a la seva delimitació geogràfica. Durant els darrers anys, al coneixement florístic, sintaxonòmic i cartogràfic s'hi han d'afegir els treballs que estudien les relacions de la vegetació amb el medi, alguns d'ells centrats en ambients que presenten gradients ecològics molt marcats i que hostatgen comunitats vegetals tan especialitzades com són les congesteres (Lluent 2007; Domènech 2012) i les molleres (Casanovas 1991; Pérez-Haase 2015). Tot i això, l'estructura funcional i els processos a nivell d'ecosistema de bona part de les comunitats vegetals alpines pirinenques encara són força desconeguts. Així mateix, aquesta manca de coneixement impedeix fer prediccions ajustades de la dinàmica de les comunitats vegetals d'alta muntanya en el context d'un canvi global.

Objectius

L’objectiu general que es planteja en aquesta tesi és aprofundir en la caracterització funcional de les comunitats alpines pirinenques i els factors que la determinen dins del context actual de canvi global. Aquest objectiu genèric l’hem concretat en tres línies de recerca.

La primera pretén millorar el coneixement de la composició i estructura funcionals de les comunitats. En aquest sentit hem volgut caracteritzar la flora alpina dels Pirineus, determinar els grups funcionals de vegetació alpina en base als trets vegetatius i reproductius de les espècies (capítols I i II) i caracteritzar les comunitats pradenques i subarbustives alpines a nivell estructural (capítols III i IV).

En la segona línia de recerca ens hem proposat estudiar la influència dels factors abiòtics i biòtics en l’estructura de les comunitats (capítols III i IV), i en el cas dels matollars alpins, veure el seu efecte en el funcionament de l’ecosistema (capítol IV).

Finalment, des d’una perspectiva de la dinàmica de la vegetació lligada al canvi global, hem analitzat quins factors afavoreixen l’emmatament per subarbustos als prats supraforestals, en vista a les conseqüències d’aquest procés en el funcionament de l’ecosistema a escala pirinenca (capítol V), i hem valorat els canvis en la vegetació de congesteres a partir de l’anàlisi diacrònica de les comunitats i els factors abiòtics que les condicionen (capítol VI).

Informe dels directors de tesi del factor d'impacte dels articles publicats

Els Drs. Amparo Carrillo Ortuño i Josep Maria Ninot Sugrañes, com a co-directors de la tesi que porta per títol 'Estructura funcional de la vegetació alpina dels Pirineus. Resposta de les comunitats als factors ambientals i als efectes del canvi global', que ha dut a terme la doctoranda Estela Illa Bachs, emeten el següent informe relatiu a l'impacte científic i a la participació de la doctoranda en cadascun dels articles inclosos en la memòria de l'esmentada Tesi.

En cinc dels sis articles apareix com a primera autora, el que reflecteix el seu paper principal a totes les fases d'elaboració dels mateixos, i molt especialment en el mostreig de camp, l'obtenció i estructuració d'informació de bases de dades, el tractament de mostres i dades, i la preparació dels manuscrits.

Article 1: Patterns of plant traits in Pyrenean alpine vegetation, d'E. Illa, E. Carrillo i J.M. Ninot. Publicat a la revista *Flora* el 2006, amb índex d'impacte de 1,232, i situada en la posició 59 de 147 en la categoria *Plant Sciences*. Correspon a una anàlisi comparativa de la flora alpina catalana, a partir de nombrosos inventaris de vegetació i a través de trets adaptatius. El disseny fou conjunt amb els dos co-directors, i la doctoranda va realitzar la part principal de les tasques (des de l'obtenció i uniformització de les dades a partir de bases de dades, fins a la preparació dels resultats definitius i la discussió); i va contribuir substancialment en la redacció i edició de l'article.

Article 2: Functional plant traits and species assemblage in Pyrenaean snowbeds, de J.M. Ninot, O. Grau, E. Carrillo, R. Guàrdia, A. Lluent i E. Illa. Publicat a la revista *Folia Geobotania* el 2013, amb índex d'impacte d'1,565, i situada en la posició 83 de 197 en la categoria *Plant Sciences*. Aquí s'analitza la vegetació de congesteres i comunitats veïnes a través dels trets funcionals de les espècies, com a resposta a l'ambient. La doctoranda va aportar dades pròpies, i va contribuir substancialment en la interpretació dels resultats i en la discussió.

Article 3: Aportación al conocimiento de la estructura funcional de los pastos alpinos de los Pirineos catalanes, d'E. Illa i J.M. Ninot. Publicat a la revista *Bulletin de la Société d'histoire naturelle de Toulouse* el 2005, no indexada (es tracta d'una revista d'àmbit regional). En aquest treball es presenta i discuteix l'estructura funcional de la vegetació pradenca, en base a un mostreig extens de les comunitats més rellevants en el paisatge alpí. Les dades obtingudes i elaborades (biomassa dels diferents compartiments ecològics, estructura foliar de les espècies dominants…) són novedoses, i són punt de partida per altres recerques en el camp de l'ecologia alpina. La doctoranda va tenir un paper preeminent en totes les fases de la recerca, mentre que l'elaboració de l'article va ser conjunta amb l'altre coautor.

Article 4: The role of abiotic and biotic factors on functional structure and processes of alpine subshrub communities, d'E. Illa, J.M. Ninot, A. Anadon-Rosell & X. Oliva. Sotmès a la revista *Folia Geobota-*

nica. Es presenta i discuteix l'estructura funcional de les comunitats subarbustives alpines, mostrejades i analitzades a través dels seus trets funcionals; i s'estudia el paper determinant que hi tenen els factors fisiogràfics i l'espècie dominant. La doctoranda ha realitzat la major part de totes les tasques (mostreig, recopilació de dades, anàlisis, elaboració del manuscrit l'article); el segon coautor ha participat en totes aquestes fases, i els altres dos han contribuït en l'anàlisi estadística, interpretació de resultats i discussió.

Article 5: Shrub encroachment above the Pyrenean treeline: identifying the main factors and the potential effects on ecosystem processes, d'E. Illa, O. Grau, A. Ferré i J.M. Ninot. Està previst enviar-lo a la revista *Plant Ecology*. Aquí s'estudia la invasió de prats supraforestals per part de matollars durant els darrers 17 anys, a través d'imatges aèries i Sistemes d'Informació Geogràfica (ArcGis). La doctoranda ha dissenyat i executat tot l'estudi, des de la planificació, a l'obtenció i elaboració de dades, i a la redacció del manuscrit, amb la col·laboració dels altres coautors.

Article 6: Changes in snowbed vegetation as a response of climatic variability: a case study, d'E. Illa, A. Lluent i E. Carrillo, en procés d'edició (en premsa) a la revista *Bulletin de la Société d'histoire naturelle de Toulouse* el 2013, no indexada (es tracta d'una revista d'àmbit regional). El treball es basa en l'anàlisi comparativa de dos mostrejos complexos de vegetació de congesteres, realitzats amb 9 anys de diferència, seguint un disseny conjunt dels tres coautors. La doctoranda ha realitzat el mostreig junt amb el primer coautor, mentre que l'elaboració de dades i la redacció del manuscrit l'ha fet conjuntament amb la tercera coautora.

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Amparo Carrillo Ortuño
Departament de Biologia Evolutiva,
Ecologia i Ciències Ambientals
Universitat de Barcelona

Josep M. Ninot Sugrañes
Departament de Biologia Evolutiva,
Ecologia i Ciències Ambientals
Universitat de Barcelona

Discusió general

En aquesta tesi hem vist com l'espectre general de trets adaptatius de les plantes que es troben a l'estatge alpí respon a les condicions ambientals que es deriven del gradient d'altitud, i també com l'espectre s'aparta d'aquest patró general quan l'anàlisi se circumscriu a diferents grups de comunitats vegetals. En alguns d'aquests tipus de vegetació, hem constatat com els factors abiòtics exerceixen una clara influència no només en la composició i l'estructura de les comunitats vegetals, sinó també en el seu funcionament. A més, hem vist com el tipus funcional de l'espècie dominant en una comunitat en condiciona l'estructura, i té efectes tant en la riquesa específica i la singularitat funcional com en processos ecosistèmics de primer ordre lligats al cicle de la matèria orgànica. Finalment, hem comprovat com els canvis en els factors ambientals solen ser els desencadenants dels processos de dinàmica de la vegetació, però l'estructura espacial de la vegetació determina la capacitat colonitzadora d'unes comunitats o la susceptibilitat a la invasió d'unes altres.

Trets adaptatius de la flora alpina pirinenca

Els resultats del capítol I mostren que l'espectre general de trets adaptatius de la vegetació alpina pirinenca es caracteritza per la dominància dels hemicriptòfits, de les plantes que renoven el fullatge anualment, i de les espècies amb algun tipus de multiplicació vegetativa; trets molt sovint coincidents en les mateixes espècies. També és destacable la baixa freqüència de mecanismes específics de disseminació de les llavors. Tots aquests trets confereixen a la vegetació alpina una clara dinàmica estacional i força estabilitat espacial a mig termini.

Les proporcions en què es troben les diverses formes de creixement permeten fer-se una idea de les característiques ambientals de l'alta muntanya. La dominància d'hemicriptòfits, característica de les flores alpines (Gómez et al. 2003; Aeschimann et al. 2012), lliga amb la forta estacionalitat del medi alpí, ja que aquesta forma biològica mostra una gran eficiència en combinar la persistència en l'espai a través d'estructures subterrànies perennes amb la dinàmica estacional de regeneració de tiges i fulles, que els permet escapar als rigors hivernals especialment marcats per sobre el nivell del sòl. Dins els hemicriptòfits, el tipus graminoide mostra força menys diversificació taxonòmica que no pas el no-graminoide, però en canvi correspon molt sovint a la forma dominant a nivell de comunitat, de manera que en condiciona l'estructura i el funcionament. D'altra banda, els ambients limitants per a la vegetació, com ara superfícies rocalloses i tarteres, també tenen una importància destacable a l'estatge alpí, fet que es tradueix en l'abundància gens menyspreable de camèfits, ja que, sobretot els reptants i els pulviniformes, són indicatius de condicions ambientals desfavorables (Bliss 1971).

El predomini d'espècies que renoven el fullatge anualment indica que les fulles perennes constitueixen un atribut poc favorable a l'estatge alpí. El presenten sobretot espècies subarbustives formadores de matollars i camèfits diversos d'ambients rupícoles (annexos 1, 3). Bona part d'aquestes espècies a l'hivern queden desprotegides per la neu, i han de presentar adaptacions per resistir les glaçades, que suposen un risc per als teixits vegetals (Billings & Mooney 1968). Hem vist, per exemple, com d'entre tots els subarbustos, els perennifolis tenen els continguts de matèria seca foliar (leaf dry matter content, LDMC) més elevats (annex 7). És a dir, tenen fulles gruixudes i amb elements mecànics interns, trets que les fan més resistents als cristalls de gel (Neuner 2014), però menys eficients fotosintèticament, de creixement més lent (Givnish 2002) i més difícils de descompondre (Cornwell et al. 2008).

Pel que fa a la colonització de l'espai, l'expansió vegetativa a través de rizomes i estolons, que sobretot es realitza a distàncies curtes respecte dels brots ja establerts, és el mecanisme majoritari de multiplicació de les plantes, i és característic d'ambients alpins (Pokarzhevskaya 1995; Evette et al. 2009). Implica el manteniment d'individus vegetals longeus amb certa capacitat reproductiva i amb poca dinàmica a petita escala, com passa en moltes espècies quionòfiles (capítol II). A nivell reproductiu, en les espècies alpines i subàrtiques és habitual no presentar mecanismes específics de dispersió de les llavors (Welling et al. 2005; Vittoz et al. 2009). Al capítol I hem vist com aquest fet es dóna sobretot als ambients més limitants, on les diàspores de les plantes solen ser de dimensions reduïdes i tenen per tant facilitat per incorporar-se al banc de llavors del sòl (Thompson et al. 1993). D'aquesta manera contribueixen al manteniment de les poblacions germinant en indrets amb poca competència, a la colonització de nous indrets favorables propers a la població d'origen (Vittoz et al. 2009), o a la ràpida recolonització del medi després d'una pertorbació (Somson 1984; Lluent 2007). A més, a l'alta muntanya hi té molta incidència el transport lateral de les llavors, lligat a la dinàmica de vessant molt generalitzada i a la importància del vent en els hàbitats oberts (Chambers et al. 1991; Chambers & MacMahon 1994). Tant aquests fenòmens abiòtics com la preeminència de plantes longeves hauria desincentivat la selecció de mecanismes adaptatius de disseminació en les espècies.

Quan hem restringit l'anàlisi funcional de la vegetació a un determinat tipus d'ambients com són les congesteres, hem vist que no hi ha un patró aparentment avantatjós definit en base a les diferents formes de creixement i als trets de les llavors (capítol II), que té a veure amb el fet que, en termes generals, els trets reproductius estan clarament lligats a l'herència filogenètica de les espècies (Será & Serý 2004) i, per tant, desvinculats de les característiques del medi. Tot i això, quan hem analitzat només el conjunt d'espècies quionòfiles sí que hem detectat alguns patrons singulars en relació amb el caràcter general de la flora alpina. Així, un cert nombre d'espècies especialistes destaquen per la producció de gran quantitat de llavors de dimensions reduïdes i contorn més o menys isomètric, característiques que els confereixen la capacitat de persistir més temps al sòl en forma de banc permanent (Thompson et al. 1993; Cerabolini et al. 2003) i que els permeten colonitzar àrees adjacents, com hem vist al capítol VI. En canvi, es caracteritzen per ser colonitzadores poc eficients a una certa distància de la població d'origen (Vittoz et al. 2009). Altres espècies quionòfiles destaquen per la forta persistència d'individus longeus que disseminen les seves llavors anemocores a llarga distància i, per tant, pel seu potencial de colonització d'àrees allunyades de la població d'origen.

El paper dels factors abiòtics

Al capítol I hem vist com de l'ordenació de les comunitats alpines en base als trets adaptatius de les espècies emergeixen grups funcionals contrastats, cadascun dels quals està integrat per comunitats vegetals que viuen en hàbitats similars. Hem constatat, doncs, com els factors abiòtics exerceixen de filtre sobre els trets més adients i per tant sobre les espècies, seleccionant les més adequades per tal de bastir les comunitats en cada ambient (Díaz et al. 1998) i evidenciant l'existència de vincles entre trets i els factors ambientals (Keddy 1992).

Les àrees alpines estables, amb un mínim gruix de sòl i sotmeses a les condicions generals de l'alta muntanya, es troben ocupades principalment per prats, que presenten l'espectre de trets adaptatius força coincident amb l'espectre general alpí i inclouen una elevada riquesa específica local. En canvi, als ambients particulars on la vegetació està sotmesa a condicions menys favorables, ja sigui per estrès abiòtic o per pertorbació lligada a dinàmica de vessant, no només l'espectre de trets adaptatius és molt discordant, sinó que les comunitats presenten poca diversitat a nivell específic i de família, fet que posa de manifest que la riquesa d'espècies en moltes de les comunitats alpines està limitada per l'estrès abiòtic (Kammer & Möhl 2002). Les particularitats de cada tipus d'ambient seleccionen trets –i espècies– que en la resta d'hàbitats poden ser molt rars o inexistents. La rellevància que prenen els trets en els diferents grups funcionals de la vegetació alpina ajuda a entendre com la vegetació es troba acoblada als condicionants concrets de cada tipus d'ambient. Els ambients més limitants sovint concentren en el seu poblament vegetal trets que en general són rars a l'estatge alpí, i de retruc concentren tàxons singulars (famílies, gèneres, espècies): a les pedrusques de pedra menuda abunden relativament les plantes de cicle curt, a les formacions subarbustives s'hi concentren plantes de fulla perenne i endozoocores, i als llocs rocosos destaca la diversificació de plantes crasses (dels gèneres *Sedum*, *Saxifraga*... amb notables endemismes; Aeschimann et al. 2011; Aeschimann et al. 2013) i d'espècies pulviniformes. Les formes de creixement en pulvínul, per exemple, són les més ben adaptades tant als forts contrastos tèrmics que es donen a les roques com al sòl magre que limita la disponibilitat d'aigua i de nutrients, ja que amb la seva estructura compacta per una banda generen un microambient desvinculat del clima general que els fa molt resistents a les glaçades (Larcher et al. 2010), i per altra banda creen unes condicions locals de fertilitat retenint matèria vegetal en descomposició i elements minerals fins sota les capçades (Körner 2003), com corroboren els valors elevats de SLA que hem trobat en espècies com *Silene acaulis* o *Minuartia sedoides* (annex 6).

Dins d'un mateix grup funcional de vegetació també hem constatat com els factors abiòtics determinen la presència d'un tipus o altre de comunitats (capítols III i IV). Les diferents situacions topogràfiques resumeixen tota una sèrie de particularitats climàtiques i edàfiques que es tradueixen en la presència de comunitats vegetals contrastades, tant pel que fa a la seva composició florística i de trets funcionals com a la seva estructura i biomassa. Als vessants solells veiem com la vegetació assoleix valors de biomassa i producció primària elevats (Taula 2), principalment perquè són més càlids i el període vegetatiu hi és més llarg (Körner 2003; Scherrer & Körner 2011). L'elevada radiació incident, però, hi pot provocar episodis de sequera a l'estiu (Isard 1986), fet que comporta la presència de plantes amb fulles xeromorfes, de teixits gruixuts amb un elevat contingut de C i valors baixos de SLA (annexos 6, 7). D'altra banda, als forts pendents solells s'hi donen fenòmens de solifluxió que no permeten l'establiment de comunitats vegetals denses ni complexes estructuralment. En aquests casos hi dominen certes espècies graminoides, que tenen un sistema radical extens i molt resistent a la tracció (Pohl et al. 2011), que les fixa fermament al substrat (Braun-Blanquet 1948; Palmier et al. 1990) i contribueix a l'estabilització del vessant. No hi és rara la presència d'espècies llenyoses, moltes d'elles perennifòlies i amb capacitat d'expansió vegetativa a llargues distàncies, que és el mecanisme principal de colonització de l'espai en matollars alpins i subalpins (Pornon & Doche 1995; Welling et al. 2005). Als indrets més estabilitzats aquestes espècies subarbustives poden expandir-se i ser protagonistes de processos de dinàmica de la vegetació (capítol V), assolint taxes d'emmatament superiors que les espècies que viuen en situacions obagues, probablement per les condicions ambientals més favorables per al creixement dels vegetals que es donen als solells. Així com la producció primària és alta als solells, la velocitat de descomposició de la virosta hi és lenta, tant per les característiques foliars de les espècies dominants, tant arbustives com herbàcies (annex 6), com per l'activitat dels microorganismes del sòl, la qual resta limitada a l'estiu (Brooks et al. 1996) sempre que no hi hagi episodis de sequera (Bryant et al. 1998; Aerts 2006).

A les parts culminants obagues les condicions ambientals són estables, però les plantes estan sotmeses a un fort estrès abiòtic. En aquestes situacions s'hi dóna una coberta irregular de neu durant l'hivern, amb un gruix sovint reduït, de manera que la vegetació pot veure's temporalment descoberta i per tant exposada a temperatures extremadament baixes. També el sòl sovint hi és poc desenvolupat i pobre, fet que contribueix a limitar l'alçada de les plantes (Pellissier et al. 2010; Gutiérrez-Girón & Gavilán 2013) i, per tant, la seva biomassa i productivitat (capítols III, IV). Les restriccions ambientals d'aquests ambients més durs fan que les relacions de competència pels recursos no siguin el factor estructurador de les comunitats, de manera que hi conviuen diverses espècies i formes de creixement. La situació contrària la trobem a les parts més baixes dels vessants obacs i en clotades i zones planeres on s'hi acumula un bon gruix de neu durant l'hivern, que implica una certa disponibilitat de recursos hídrics durant els períodes de poca precipitació. Allà on hi ha una bona protecció nivosa a l'hivern, combinada amb un període vegetatiu relativament llarg, les comunitats semblen disposar de condicions favorables. Així ho indiquen els valors elevats de biomassa i producció primària dels prats i matollars mesòfils d'aquests ambients. En canvi, les comunitats més llargament innivades presenten valors de biomassa aèria i de productivitat molt baixos, deguts al breu període vegetatiu de què disposen i a la poca energia que acumulen durant aquest temps (Lluent 2007; Illa et al. 2011).

El paper de l'espècie dominant

A l'estatge alpí hem constatat la importància del tipus funcional de l'espècie dominant en condicionar l'estructura de la comunitat a través de la seva capacitat d'ocupació de l'espai, que es tradueix en les relacions que estableix amb les espècies acompanyants (capítols III i IV). Tal com indica Grime (1998), les espècies més competitives assoleixen els valors de biomassa més elevats, sobretot als matollars perennifolis i als prats densos, on la pròpia estructura de les espècies dominants contribueix a l'exclusió de la resta d'espècies i formes de creixement. Als matollars, els subarbustos perennifolis, independentment de les condicions abiòtiques a què estiguin exposats, generen unes condicions poc favorables per al desenvolupament de bona part de les espècies, no només amb la seva estructura densa, sinó també amb l'elevada acumulació de la seva virosta recalcitrant. En el cas dels prats, en canvi, hem vist com només les situacions topogràfiques més favorables (sense dinàmica de vessant ni fort estrès abiòtic) permeten la dominància d'una sola espècie, més competitiva, que propicia l'exclusió de la resta d'espècies i formes de creixement.

A nivell de funcionament de l'ecosistema, hem vist com el tipus funcional de l'espècie dominant condiciona la quantitat de virosta que s'acumula i la seva persistència (capítol IV). Les característiques foliars de les espècies arbustives perennifòlies (annexos 6, 7) comporten l'acumulació virosta recalcitrant, difícil de descompondre (Cornwell et al. 2008; Saccone et al. 2013), fet que es tradueix en sòls pobres en nutrients. En els casos d'emmatament per part d'arbustos perennifolis, aquests, amb la seva estructura i característiques foliars modifiquen les condicions microclimàtiques i edàfiques sota la seva capçada (Doche et al. 2005; Sundqvist et al. 2011; Myers-Smith & Hik 2013). Alhora, la seva virosta comporta una reducció en la taxa de descomposició de la matèria orgànica (Montané et al. 2010) i un empobriment dels sòls. La combinació d'aquests diversos factors dificulta el creixement de les espècies graminoides, heliòfiles i amb més requeriments nutricionals (Pornon & Lamaze 2007), incentivant encara més el domini de les espècies arbustives. En canvi, la virosta es descompon amb més facilitat a les comunitats arbustives caducifòlies, d'una banda perquè les característiques foliars de les espècies dominants (annexos 6, 7) faciliten la descomposició (Cornelissen et al. 1999; Cornwell et al. 2008), i per altra banda perquè la presència de diferents formes de creixement a la comunitat contribueix a una descomposició més ràpida de la matèria orgànica (Aerts 2006; Montané et al. 2013).

Efecte de l'estructura espacial de la comunitat

L'estructura espacial de les comunitats, sobretot referida a la biomassa que hostatgen els diferents compartiments funcionals, veiem que té un paper cabdal tant en la seva capacitat de colonització com en la seva resiliència o susceptibilitat a ser envaïdes. En el cas de l'emmatament (capítol V), en funció de l'estructura que presenta la població d'arbustos, que ve determinada per les seves característiques reproductives, canvia la capacitat de colonització sobre els prats veïns. L'espècie clonal *Rhododendron ferrugineum* principalment es troba formant taques grans de matollar, i és en aquestes situacions quan té més potencial d'invasió (Pornon et al. 1997), sigui per tancament de petites clarianes, sigui per expansió generalitzada del matollar. En canvi, *Juniperus communis* subsp. *alpina* bàsicament s'expandeix a través de l'establiment de nous individus, perquè la seva estratègia reproductiva es basa principalment en la regeneració per llavors (Thomas et al. 2007). Per tant , en funció de l'edat, les seves poblacions són heterogènies pel que fa a les dimensions de les taques d'arbust i a les proporcions d'individus aïllats, fet que es tradueix en creixements similars en els diferents tipus d'estructura de la població.

Així com en el procés d'emmatament l'estructura de la població de cada espècie arbustiva és important, l'estructura de les comunitats pradenques sobre les quals creixen no sembla tenir importància, contràriament al que han detectat altres estudis dels Alps i els Pirineus (Dullinger et al. 2003; Montané et al. 2007). Les proporcions de creixement arbustiu observades són semblants als prats densos, als prats culminants i als prats esglaonats, tot i que en aquests últims hi ha una tendència lleugerament superior a la resta. La interpretació que en fem és que els arbustos estudiats, que es troben al seu límit altitudinal, no tenen prou capacitat competitiva davant les espècies graminoides pradenques, més eficients a l'hora de competir pels nutrients (Pornon et al. 2007).

A les congesteres, l'estructura espacial de les comunitats quionòfiles determina la seva susceptibilitat a la invasió (capítol VI). Una sèrie d'anys amb precipitacions estivals més reduïdes que la mitjana sembla ha-ver afavorit les espècies graminoides generals als prats, que sobretot han colonitzat el *Gnaphalio-Sedetum candollei*, integrat per petits hemicriptòfits distribuïts en taques de dimensions variables, amb sòl nu entremig. En canvi l'*Anthelio-Salicetum*, que està format per tapissos vegetals densos del camèfit reptant *Salix herbacea*, tot i trobar-se més a prop dels prats, pràcticament no experimenta canvis en la freqüència de les espècies. En aquests casos s'evidencia com l'estructura del *Gnaphalio-Sedetum*, juntament amb una capacitat competitiva reduïda de les espècies no-graminoides que l'integren (Pohl et al. 2011), facilita l'entrada de plantes més competitives quan les condicions ambientals ho permeten.

Taula 2. Mitjanes i desviació estàndard dels paràmetres estructurals i funcionals de les comunitats estudiades. En negreta, valor mínim i màxim per a cada variable

	biomassa total (g/m^2)		biomassa aèria activa (g/m^2)		producció primària (g/m^2 any)*		virosta total (g/m^2)		persistència de la virosta (anys)*	
Pastures culminants										
Arenario-Fesucetum yvesii	**121,62**	± 81,35	**54,70**	± 24,77	**48,99**	± 17,67	**12,62**	± 11,48	0,23	± 0,16
Elyno-Oxytropidetum hallerii	206,48	± 74,17	167,00	± 40,82	166,05	± 40,95	77,58	± 94,96	0,40	± 0,46
Leontodo-Caricetum curvulae	159,83	± 39,31	120,14	± 20,44	119,57	± 19,79	67,54	± 26,75	0,58	± 0,24
Hieracio-Festucetum airoidis	312,56	± 39,30	222,40	± 82,11	220,77	± 83,07	91,58	± 39,55	0,42	± 0,19
Pastures denses										
Alchemillo-Nardetum	428,48	± 25,44	401,10	± 7,40	401,10	± 7,40	42,58	± 9,06	0,11	± 0,02
Festuco-Trifolietum thalii	202,71	± 0,65	156,12	± 19,62	156,11	± 19,63	16,59	± 10,02	0,10	± 0,06
Selino-Festucetum eskiae	645,04	± 266,34	524,96	± 200,50	**524,96**	± 200,50	298,79	± 242,33	0,56	± 0,45
Pastures esglaonades										
Carici-Festucetum eskiae	247,33	± 68,66	223,88	± 58,53	223,88	± 58,53	51,25	± 28,20	0,77	± 0,07
Festucetum eskiae	260,92	± 89,47	208,91	± 73,52	208,75	± 73,74	47,53	± 28,21	0,62	± 0,09
Festucetum scopariae	316,98	± 114,70	237,05	± 72,26	234,33	± 70,85	39,32	± 20,60	0,18	± 0,09
Matollars obacs culminants										
Dryas octopetala	559,60	± 61,00	234,17	± 32,06	234,17	± 32,06	777,39	± 252,80	3,29	± 0,89
Loiseleuria procumbens	606,24	± 100,59	259,14	± 61,44	107,28	± 31,00	325,81	± 92,71	3,06	± 0,56
Vaccinium uliginosum microph.	678,19	± 313,36	270,06	± 169,18	189,76	± 73,31	364,80	± 272,85	1,75	± 0,80
Matollars obacs nivosos										
Rhododendron ferrugineum	2034,96	± 657,75	406,96	± 145,93	175,19	± 42,24	766,76	± 493,38	4,46	± 2,54
Salix herbacea	152,41	± 53,79	80,17	± 23,00	79,01	± 24,62	79,16	± 96,33	0,85	± 0,85
Matollars de solell										
Arctostaphylos uva-ursi	1761,10	± 791,11	**817,05**	± 408,09	313,46	±139,31	**1773,98**	± 651,90	**5,94**	± 1,72
Juniperus communis alpina	**2483,13**	± 521,95	643,15	± 90,83	212,43	±21,60	975,21	± 327,96	4,60	± 1,51

*Els valors de producció primària i de persistència de la virosta de les comunitats pradenques s'han calculat a partir de les dades del capítol III amb la finalitat d'elaborar aquesta discussió

Conclusions

Els diferents estudis duts a terme en aquesta tesi doctoral permeten entendre millor el funcionament d'alguns tipus de vegetació alpins, avaluar-ne les adaptacions predominants en funció de les condicions ambientals particulars de cada ambient, i veure la influència dels factors abiòtics i biòtics en l'estructura, el funcionament i la dinàmica de les comunitats vegetals. Seguidament, enumerem les conclusions que hem extret dels diferents capítols:

Capítol I

- L'espectre general de trets adaptatius de la vegetació alpina pirinenca es caracteritza per un clar predomini dels hemicriptòfits i de les espècies amb capacitat d'expansió lateral.
- Les condicions particulars de cada ambient alpí seleccionen les espècies més idònies en cada cas a través de conjunts de trets específics que permeten la classificació de les comunitats alpines en grups funcionals, els quals corresponen en bona part a categories sintaxonòmiques d'alt nivell (ordres i classes) com són la vegetació rupícola, la vegetació glareícola, la vegetació higròfila, la vegetació arbustiva o els prats.
- Els espectres de trets adaptatius dels grups de vegetació que inclouen comunitats sotmeses a les condicions climàtiques generals de l'alta muntanya, principalment les pradenques, no difereixen gaire de l'espectre general alpí, mentre que els dels grups de comunitats restringides a indrets amb condicions ambientals més limitants són clarament discordants, i amb certa concentració de biotipus -i tàxons- singulars.
- La major part d'espècies que viuen en ambients molt limitants mostren clares adaptacions als seus hàbitats particulars en la seva morfologia funcional (camèfits pulviniformes, fulles crasses, llargs rizomes, etc.); però, no mostren mecanismes específics de disseminació de les llavors.

Capítol II

- En el conjunt d'espècies que conviuen als ambients de congestera no es detecta cap patró definit entre les formes de creixement i els trets de les llavors, però sí que s'aprecia una certa convergència de trets reproductius quan es comparen les espècies quionòfiles amb la resta. En el conjunt d'especialistes de congestera destaquen les espècies amb capacitat d'expansió vegetativa a llarga distància i amb capacitat de disseminació llunyana de les llavors, i les que formen bancs de llavors persistents al sòl.

Capítol III

- Les diferents situacions topogràfiques que ocupen els prats alpins generen condicions ambientals específiques que condicionen la diversitat de formes de creixement i de valors de biomassa aèria. En les situacions més favorables s'acumula molta biomassa aèria i hi ha una clara dominància dels hemicriptòfits graminoides, mentre que en condicions més desfavorables, ja sigui per pertorbació lligada a la dinàmica de vessant, ja sigui per estrès abiòtic, la biomassa de les comunitats es redueix alhora que les altres formes de creixement, especialment els camèfits, s'hi fan més abundants.

Capítol IV

- Els matollars alpins presenten valors de biomassa aèria molt contrastats segons el tipus funcional de l'espècie dominant, que és el principal responsable de l'estructura de la comunitat. L'hàbit perennifoli en l'espècie dominant correspon a situacions ambientals i valors de biomassa aèria més diversos, i limita l'abundància d'altres formes de creixement. En contrast, els subarbusts caducifolis mostren un espectre força més reduït en condicions ambientals però afavoreixen la diversitat de formes de creixement.
- Els factors abiòtics i biòtics tenen papers contrastats en el funcionament de les comunitats subarbustives. La productivitat ve determinada sobretot pels factors abiòtics, mentre que l'acumulació i la persistència de la virosta depenen simultàniament de les particularitats ambientals lligades a cada situació topogràfica i de les característiques del tipus funcional de l'espècie dominant.

Capítol V

- Per sobre del límit forestal pirinenc, tant *Juniperus communis* subsp. *alpina* com *Rhododendron ferrugineum* mostren ser espècies emmatadores, tot i que protagonitzen dinàmiques expansives molt diferents que depenen de la seva estructura poblacional i de la seva estratègia reproductiva i expansiva. *Rhododendron ferrugineum* mostra els percentatges de creixement més elevats quan forma taques grans, mentre que en *Juniperus communis* subsp. *alpina* es donen quan es troba en forma d'individus aïllats o de taques de dimensions reduïdes.
- L'emmatament per damunt del límit del bosc no depèn de manera general de la susceptibilitat dels diferents tipus de prats a ser envaïts, sinó probablement de la combinació d'aquesta amb l'estratègia de cada arbust. Dels casos analitzats, només els prats esglaonats de *Festuca eskia* mostren una tendència a ser més favorables per a l'emmatament per part de *Juniperus communis* subsp. *alpina*.
- El procés d'emmatament fa que augmentin considerablement la biomassa i l'acumulació de virosta, i per tant el carboni immobilitzat, mentre que comporta una reducció en la producció primària.

Capítol VI

- Les comunitats que se succeeixen al llarg del gradient de fusió de la neu a les congesteres demostren ser sensibles a les variacions climàtiques, i es detecten canvis tant en l'àrea ocupada per les zones de transició entre comunitats com en la distribució de les espècies. Algunes espècies quionòfiles redueixen la seva freqüència i es desplacen cap a l'interior de la congestera, mentre que espècies graminoides més generalistes incrementen la seva freqüència, principalment a la comunitat quionòfila del *Gnaphalio-Sedetum candollei*.

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Publicacions

Capítol I

Patterns of plant traits in Pyrenean alpine vegetation

Trets adaptatius de la vegetació alpina pirinenca

Estela Illa, Empar Carrillo & Josep M. Ninot

Flora 201 (2006): 528–546

Trets adaptatius de la vegetació alpina pirinenca

Resum

En aquest treball vam estudiar l'adaptació de les comunitats vegetals a les condicions ambientals de l'estatge alpí dels Pirineus catalans a través de l'anàlisi comparativa dels trets de les espècies. Per fer-ho, vam seleccionar gairebé 800 inventaris fitosociològics del Banc de Dades de Biodiversitat de Catalunya corresponents a 47 comunitats (associacions i subassociacions), que inclouen 683 tàxons. Per a cada comunitat vegetal vam estudiar onze trets, alguns dels quals fan referència a nivell de comunitat (recobriments mitjans, riquesa específica o diversitat de formes biològiques), i altres a nivell d'espècie però expressats com a recobriment relatiu a les comunitats (percentatges de formes de creixement, suculència, sempervirència, llenyositat, capacitat d'expansió lateral i tipus de disseminació). Els resultats obtinguts mostren com el paisatge alpí està format majoritàriament per hemicriptòfits, dels quals els graminoides dominen en recobriment i els no-graminoides en nombre d'espècies. L'elevada persistència representada per bases o tofes plurianuals, la renovació de tota la biomassa aèria a l'hivern, l'expansió lateral a curtes distàncies i una disseminació de les diàspores de tipus generalista completen els principals atributs de la vegetació alpina dels Pirineus i de la major part de flores alpines. Tot i això, hi ha percentatges considerables de tipus particulars de plantes (teròfits, diversos tipus de camèfits, espècies suculents, perennifòlies o productores de fruits carnosos) que contribueixen a una elevada diversitat a l'estatge alpí.

En base als diferents atributs, vam realitzar una classificació multivariant difusa (*fuzzy*) de les comunitats vegetals, que va donar com a resultat set grups principals de vegetació, i cinc subgrups dins el conjunt més ampli, el de les pastures. La major part dels grups coincideixen amb sintàxons d'alt nivell (classes i ordres) i corresponen als hàbitats principals de l'estatge alpí, que es troben definits per la situació topogràfica que ocupen i per seves particularitats edàfiques i microclimàtiques. Pel que fa a l'espectre de trets del conjunt de la flora alpina, els grups més diferenciats de comunitats corresponen a alguns dels hàbitats principals, tots ells relacionats amb condicions d'estrès (sòls magres, poc fèrtils o entollats). Aquestes comunitats tendeixen a tenir poca riquesa específica i percentatges relativament elevats d'alguns tipus particulars de plantes. Els grups menys diferenciats de l'espectre global corresponen a ambients més balancejats i inclouen sobretot comunitats riques en espècies i amb dominàncies més compartides dels atributs.

Mots clau: trets funcionals, hàbitats, comunitats vegetals, ordenació, alta muntanya

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Patterns of plant traits in Pyrenean alpine vegetation[☆]

Estela Illa, Empar Carrillo, Josep M. Ninot*

Grup de Geobotànica i Cartografia de la vegetació, Departament de Biologia Vegetal, Univ. de Barcelona, Av. Diagonal 645, E-08028 Barcelona, Spain

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Abstract

Here we studied the adaptation of plant communities to environment in the alpine belt of the Catalan Pyrenees through comparative analysis of plant traits. The starting point consisted of about 800 phytocoenological relevés from the Banc de Dades de Biodiversitat de Catalunya, which corresponded to 47 communities (associations and subassociations) and included 683 taxa. Eleven attributes were examined in each community. Some of these traits are directly referred to the community level (averages of cover, species richness or diversity of life forms) and others to species level, but expressed as the relative cover in the communities (percentages of life forms, succulence, evergreeness, woodiness, lateral spread ability, dissemination type). Alpine landscape is mainly made up of hemicryptophytes, of which graminoids dominate in terms of cover and non-graminoids in species number. Strong persistence via plurennial stocks or dense turfs, entire above-ground renewal over winter, lateral spreading over short distances and generalistic diaspore dissemination complete the main attributes of the High Pyrenees and most alpine floras. Nevertheless, considerable percentages of particular plant types (like therophytes, various kinds of chamaephytes, succulents, evergreens and berry-producers) give a highly diversified alpine belt.

On the basis of the attributes, we performed a fuzzy multivariate classification of plant communities, which gave seven main vegetation groups, and five subgroups in the largest category (pastures). Most of the groups coincided with high-level syntaxa (classes, orders) and corresponded to the main habitats of the alpine belt, defined in terms of topography and related soil and microclimate descriptors. With respect to the spectrum of attributes of the whole alpine flora, the most differentiated groups of communities corresponded to several main habitats, all of which associated with stress conditions (scarcity of soil, unfertile or waterlogged substrata). These plant communities tend to be species-poor and show relatively high percentages of particular types. Groups less differentiated from the global spectrum included mainly richer communities with more shared dominances, and correspond to more balanced environments.

Keywords: Functional attributes; Habitats; Plant communities; Ordination; High mountain

Introduction

Plants are subjected to several limiting constraints in alpine habitats: shortness of vegetation period, scarcity of soil, low levels of nutrients, strong daily thermal

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[☆] *Nomenclature*: Names of higher plants follow De Bolòs et al. (2005), and names of syntaxa are those stated in the Banc de Dades de Biodiversitat de Catalunya (Font 2005).

*Corresponding author.

E-mail address: jninot@ub.edu (J.M. Ninot).

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amplitudes and related processes (Billings and Mooney 1968; Braun-Blanquet 1948; Körner 1999; Onipchenko and Blinnikov 1994). These constraints determine the main feature of the alpine belt, i.e., the lack of forest development. Hence, alpine potentiality corresponds to pastures, which are diversified into various communities depending on microclimate and soil conditions. However, alpine landscapes include notable surfaces that offer extreme conditions for plant life, such as short growth period in snow beds, extreme winter temperatures in ridges and steep slopes, or waterlogging and infertility in the bottom of valleys. In these conditions, as well as on surfaces occupied by scree or rock, pastures are replaced by particular plant communities (Braun-Blanquet 1948; Carreras et al. 1993; Carrillo and Ninot 1992; Vigo 1996). Consequently, alpine vegetation is diversified into dense mosaics following heterogeneous ecological conditions. The boundaries between neighbouring communities are often sharp, and discriminate not only between distinct species sets but also between contrasting plant forms and functions (Körner 1999; Onipchenko 1994; Shaver et al. 1997).

Moreover, the alpine belt has not escaped human influence, although the effects of human activities are weaker than at lower altitudes. Pastures have been grazed for centuries by domestic livestock and have been extended downwards by means of clearing subalpine pinewoods. This process has strongly modified the transition zone above the timberline (De Bolòs et al. 2004; Pignatti et al. 1988), where scrubs and open krummholz formations previously prevailed and have since been replaced by pastures, which hold woody units only on rocky or abrupt surfaces. In addition, the structure and composition of the best alpine pastures are conditioned by increased grazing pressure of domestic cattle and sheep.

Like in other landscapes, alpine plant communities are dynamic assemblages, where changing events may produce considerable changes in species composition and structure. A notable part of the alpine landscape is subjected to non-equilibrium situations, species replacements may therefore involve substantial shifts in coarse vegetation structure and ecosystem function. Several examples of these shifts, caused by Quaternary climatic changes, have been documented from soil and lacustrine sediments over the last millenia (Blinnikov 1994; Carcaillet and Brun 2000; Montserrat 1992; Tinner and Theurillat 2003). The present coupling of climatic change and pasture abandonment is expected to contribute to further strong shifts.

In this context, and to increase our knowledge of vegetation dynamics, a comprehensive analysis of the alpine vegetation in terms of structure and function is crucial. Although several studies have addressed phytocoenological aspects in the Pyrenees, few functional studies have been performed. Therefore, a broad morpho-functional analysis of alpine vegetation is required, supported by phytocoenological data and by trait assessment of the species included. In this regard, the reductive analyses of flora and vegetation, such as the spectra of life forms (Raunkiaer 1934), growth forms (Barkman 1988), plant strategies (Grime 2001; Frey and Hensen 1995) and plant functional types (Box 1996; Chapin et al. 1996; Gitay and Noble 1997) contribute to our understanding of the ecological constraints of plants and their communities from scaling abstraction levels. These analyses involve accurate selection and evaluation of attributes, with a compromise between ecological significance and the possibility to assess the whole alpine flora. The community level has been identified as the most adequate for the study of specific adaptive responses to particular environments (Körner 1999, p. 2).

Here, we analyse plant adaptation to environmental conditions in the alpine belt, considering plants structured into communities, and evaluating them through their main morpho-functional traits or attributes. This study is a basic step, useful both per se as a standardised compilation of functional knowledge, and providing a starting point for further studies. In addition, the results can be applied for the conservation management of communities and landscapes.

Material and methods

Study area

The study was performed in the alpine belt of the Catalan Pyrenees, i.e., the high mountain areas where subalpine *Pinus uncinata* forests do not develop because of climatic constraints. The deforested higher part of the subalpine belt was not included, although at present it hosts plant communities that are very similar to those found in the alpine belt. According to Carreras et al. (1996), the alpine belt occurs from 2400 m a.s.l. upwards on south-facing slopes and from 2200 m a.s.l. upwards on north-facing exposures, flats or concavities. These altitudinal boundaries run about 100 m lower in the eastern part of the range and in the Aran valley, both areas subject to more maritime climates.

Although bioclimatic conditions are extremely variable over the alpine belt, there is a general trend, i.e., the length of the plant growth period decreases regularly in parallel with increasing altitude, from 88 days at 2300 m a.s.l. to 42 days at 2700 m a.s.l., and to 0–3 days at 3100 m a.s.l. (Gómez et al. 1997).

The study area, made up of alpine surfaces in Catalonia and Andorra (Fig. 1), is split into irregular units, corresponding to the higher slopes and summits of various ranges. The Pre-Pyrenean ranges appear as

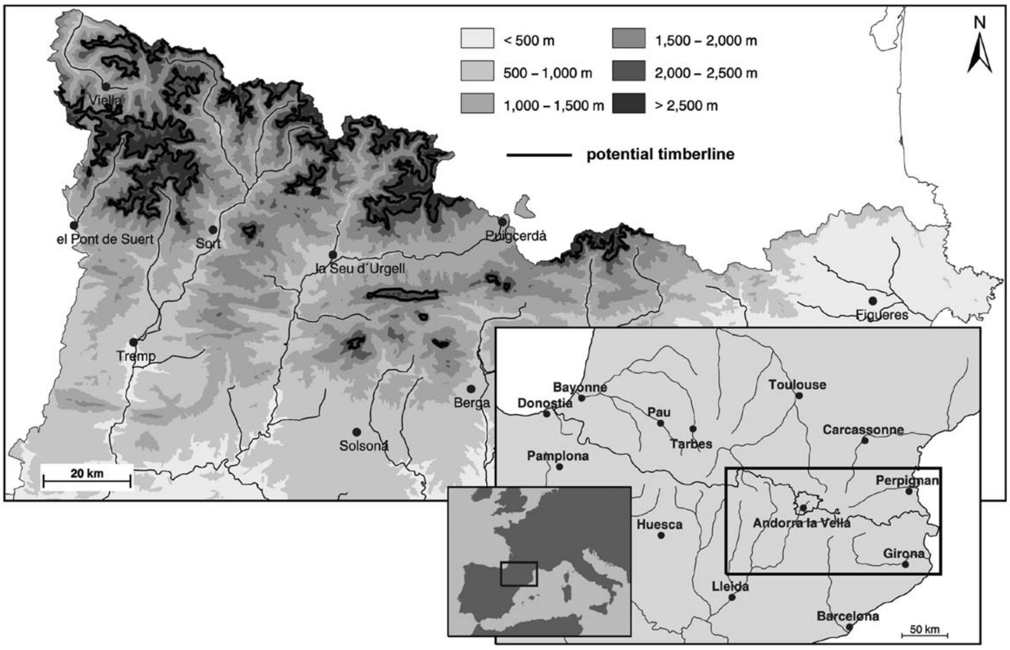

Fig. 1. Delimitation of the alpine belt in the Catalan Pyrenees.

small to medium-sized islands detached southwards from the main range, peaking between 2400 and 2600 m; their alpine vegetation is dominated by calcicolous taxa and includes several Mediterranean orophytes. From Puigcerdà eastwards, the eastern part of the main range also forms a unit, reaching altitudes of 2600–2800 (2909) m, and bearing floristic particularities and a maritime climate. In contrast, in the north-western corner, around Viella, is the Aran valley, with higher altitudes, also ranging from 2600 to 2800 (3014) m, and showing Atlantic influence from climatic to landscape aspects, as it is part of the north face of the main range. The rest comprises complex mountains and massifs (including a number of summits over 3000 m, and considerable surfaces above 2800 m), mainly acidic, abrupt, and under continental climatic influence.

The total surface projection of the study area is 735 km^2, of which the Pre-Pyrenees account for 37 km^2, the eastern Pyrenees 83 km^2 and the Aran valley 129 km^2 (Carreras et al. 1996). The area shows a clear dominance of acidic pastures, extensive rocky surfaces and scarcity of fens and scrubs (De Bolòs et al. 2004) (Table 1).

Table 1. Surface projection of the main habitats in the Catalan alpine belt

Habitats	Surface (km^2)	Percentage
Rhododendron scrub	15.0	2.0
Acidophilous pastures	432.6	58.9
Calcicolous pastures	53.6	7.3
Acidic rocks and screes	187.3	25.5
Calcareous rocks and screes	38.3	5.2
Fens	2.1	0.3
Lakes	5.7	0.8

Vegetation data

For this study, we used the relevés available for the alpine belt of the Catalan Pyrenees. Using a comprehensive list of the alpine plant communities known from there, we searched all the corresponding relevés which fulfil the "alpine" condition (as described in the previous section) in the data bank "Banc de Dades de Biodiversitat de Catalunya" (Font 2005). To ensure the significance of data, communities with less than five relevés were rejected. Therefore, a few specific associations were not studied, such as Cratoneuretum commutati or Gnaphalio-Sedetum hoppeani. We next retained 798 relevés, classified into 47 communities (43 associations, two of them split into subassociations; see Appendix A).

The compilation of the relevés and the following calculations were done using the "Quercus" processor, part of the "VegAna" package (De Cáceres et al. 2003). We changed the dominance/abundance indexes given in the original relevés to the mean cover values defined by Braun-Blanquet (1979) and we averaged the covers for each community and taxon in order to build a synthetic table. After some nomenclature unification and simplification of low-level taxonomy, the table included 683 taxa (× 47 columns), 560 of which were higher plants and 123 terricolous mosses, lichens or liverworts.

Statement of attributes

After a review of the literature on plant attributes (Barkman 1988; Box 1996; Gitay and Noble 1997; Grime et al. 1988; etc.) and taking into account the volume and nature of the data to be handled, we selected 11 easily measured traits which have been identified as potentially useful predictors of ecosystem functioning. These can be ordered into general community attributes and functional plant attributes. Community attributes are as follows:

(a) *Global cover* of the vegetation, i.e., the average of the covers given to the relevés of each community.
(b) *Cumulate cover*, i.e., the sum of the cover means of the taxa included in each community. This measure evaluates general cover and structure; values higher than 100 express above-ground overlapping or stratification.
(c) Mean of higher plant taxa included in the relevés as an evaluation of *species richness* of each community.
(d) Total *number of families* in the whole community, assuming this to be a rough evaluation of diversity, complementary to species richness.
The plant attributes selected were:
(e) Raunkiaer (1934) *life forms*, subdivided into narrower types following other sources (Halloy 1990; Körner 1999). The main cryptogam groups settling on soil were also considered. Thus, we obtained 11 types: nanophanerophytes, suffruticose chamaephytes (like *Vaccinium myrtillus*), diffuse chamaephytes (*Sideritis hyssopifolia*), pulviniform chamaephytes (or small cushions, like *Silene acaulis*), creeping chamaephytes (*Thymus nervosus*), graminoid hemicryptophytes, non-graminoid hemicryptophytes, geophytes, therophytes, bryophytes and lichens.
(f) *Diversity of life forms*, calculated through the Shannon–Weaver index, as follows:

$$\mathrm{SHDI} = -\Sigma(p_i \ln p_i),$$

where p is the partial cover of each life form over 1, and i is each life form. Higher values are expected for the communities with more life forms included, and these more evenly distributed.
(g) *Succulence* considers three levels: non-succulent, semi-succulent (some Liliaceae, Orchidaceae or Saxifragaceae) or succulent (Crassulaceae).
(h) *Evergreeness* considers fully evergreen taxa, partially evergreen taxa (like *Vaccinium myrtillus*) or plants that lack green parts in winter.
(i) *Woodiness*, expressed also as a three degree characteristic; semi-woody taxa correspond to some chamaephytes, mainly herbaceous but with a conspicuous woody basis.
(j) Capacity for *lateral spread* and clonal multiplication, evaluated as four possible states: lack of lateral expansion, spreading to short distance (few tillers closer than 2.5 cm to the mother plant), spreading to long distance (tillers farther than 2.5 cm caused by long rhizomes, or creeping, rooting twigs in some woody plants) or forming dense turfs.
(k) *Dissemination* type, or distance reached by diaspores, considering five states: very long distance (species with dust-like seeds or spores), long distance (as in Asteraceae with hairy or plumose achenes), short distance (species setting winged or membranous diaspores, like *Peucedanum ostruthium* or *Festuca* spp.), no apparent mechanism (*Rhododendron ferrugineum* or *Silene acaulis*) and endozoochory (a few dwarf shrubs with fleshy fruits). Finally, for analytical purposes, we merged categories one and two because they give similar results at the landscape scale.

The attributes that directly referred to plant communities (*a, b, c, d* and also *f*) were expressed as numerical values. Attributes *g*, *h* and *i*, each categorised into three states, were also expressed as a single value each per community, calculated as the relative cover of plants presenting the fully developed attribute plus half of the relative cover of plants partially bearing the attribute. Regarding the other attributes (*e, j* and *k*), the relative cover of the group of taxa bearing each attribute in each state was taken as a community descriptor (such as relative covers of nanophanerophytes, or of taxa with long-distance dissemination). In most of the proposed systems of plant attributes, characters of diverse type are combined and organised into a hierarchy (Barkman 1988; Box 1996; Halloy 1990, etc.); however, we considered all attributes at the same level, since there is not enough basis on which to give more relevance to particular ones (Orshan 1986; Semenova and Van der Maarel 2000). The combination of plant attributes into specific life histories results in plant strategies, which define the capacity of each taxon to persist and expand, disseminate and colonise, and also modify its environment. When combined at community level, these attributes define community functions and relationships with the environment, including responses of ecosystems to changing conditions (Lavorel and Garnier 2002).

Classification of communities and analysis of the vegetation groups

To study the segregation of attributes across alpine habitats, the classification of communities into groups should be done on the basis of these functional characters. However, community classification generates the transitional position of certain units between distinct groups, which reflects some of the progressive transitions of nature. Therefore, here we chose a fuzzy classification of communities. The main feature of this classification system is that one element's membership can be shared between two or more groups. Here we used Fuzzy C-means (Bezdek 1981), a classification method available in the statistical module "Ginkgo", part of the "VegAna" package (De Cáceres et al. 2003). One drawback of this method is that it requires the specification of the number of groups to be found. As a criterion to facilitate this decision, we used a non-parametric statistic of cluster isolation called "Silhouettes" (Rousseuw 1987).

Using the standardised data on community attributes, we built a similarity matrix, which was the reference matrix used for classification. The resulting fuzzy groups and subgroups of communities were considered units in the comparative analysis of attributes with respect to the main habitats in which they are found.

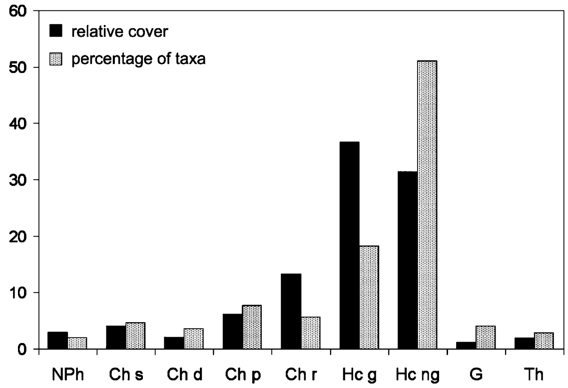

Fig. 2. Percentages of life forms of higher plants in the alpine vegetation of the Catalan Pyrenees, taken as the mean values across the communities recorded. NPh, nanophanerophytes; Ch s, suffruticose chamaephytes; Ch d, diffuse chamaephytes; Ch p, pulviniform chamaephytes; Ch r, creeping chamaephytes; Hc g, graminoid hemicryptophytes; Hc ng, non-graminoid hemicryptophytes; G, geophytes; Th, therophytes.

Results and discussion

General trends in the attributes of alpine vegetation

A first general characterisation of alpine vegetation may be attempted from the data summarised in the general table of Appendix B, which provides an average of the values of each attribute in the 47 communities studied.

The main structural aspect corresponds to the spectrum of life forms (Fig. 2), which showed a strongly uneven distribution, both in terms of number of taxa and plant cover. Two groups were dominant: graminoid and non-graminoid hemicryptophytes. These two groups showed opposite patterns. While graminoids accounted for more than one-third of mean cover across the alpine communities (36.6%), and a moderate 18.3% of the alpine taxa, forb hemicryptophytes exhibited a slightly lower mean cover (31.6%) but much more diversity (51.1% of total taxa). Similar patterns have been described in other alpine landscapes and in the arctic (Körner 1995; Komárková and McKendrick 1988). Together, these two groups reflected the strong prevalence of hemicryptophytes in the alpine belt (68.2% of mean cover, 69.4% of taxa), where plants are subjected to a clearly seasonal regime, in which the growing period, although rather short, is favourable (at least concerning light, temperature and water) and predictable.

All the subgroups of chamaephytes presented low percentages, but together accounted for 25.7% of mean cover and 21.7% of taxa. This significant presence is related to various stress conditions – mainly derived from infertile soils – and to low perturbation regimes, which enable plants to persist for many years with small above-ground perennial structures, which are frequently lignified (Gerdol et al. 2000a; Shaver et al. 1997). This situation is exemplified by the two main subgroups, creepers (13.3% of mean cover, 5.7% of taxa) and pulvinules (6.2%, 7.7%), both frequently found in rocky sites. Pulvinules are especially adapted to summits and other high mountain habitats. According to Körner (1999, p. 39), their fitness is related to thermal functioning caused by a compact form, which would not be functional in warmer lowland habitats, and to substrate improvement through retention of litter, water and soil fertility.

Therophytes, geophytes and nanophanerophytes are minor groups in alpine flora (Bliss 1971; Gómez et al. 1997; Körner 1999). In our study, the two former types presented lower cover percentages than species diversity, and were sparse in the whole belt. In contrast, nanophanerophytes showed greater cover than diversity and were restricted to the lower part of the belt.

Evergreeness, woodiness and succulence seem inadequate attributes under alpine conditions. Plants with each of these traits accounted, nevertheless, for about 7% of the taxa (Table 2). While evergreeness and woodiness are clearly more relevant at lower altitudes, succulence is more frequent in the alpine belt (Carrillo and Ninot 1992; Vigo 1996); according to Körner et al. (1989), this succulence pattern is a general feature in high mountain areas in temperate regions.

Table 2. Means of cover and occurrence percentages of taxa with the functional attributes considered in the whole Catalan alpine vegetation

	Cover (%)	Taxa (%)
Vegetative particularities		
Succulent taxa	6.8	7.2
Woody taxa	13.9	7.0
Evergreen taxa	10.9	6.8
Lateral spread		
Taxa without lateral spreading	3.6	4.3
Taxa spreading to < 2.5 cm	26.3	39.5
Taxa spreading to > 2.5 cm	29.6	30.3
Taxa forming dense turfs	40.5	25.9
Diaspore dissemination		
Taxa with dust-like diaspores	3.0	4.9
Taxa with hairy or plumose diaspores	13.7	13.0
Taxa with winged or membranous diaspores	34.4	24.7
Taxa with seeds lacking special mechanisms	44.2	54.3
Taxa with fleshy fruits (endozoochory)	4.7	3.1

Our data corroborate lateral spread and eventual clonal multiplication as useful attributes in alpine environments, as only 4.3% of taxa did not show lateral expansion (Table 2), which is consistent with the findings of other studies performed in alpine and arctic areas (Billings and Mooney 1968; Körner 1995). The development of these strategies may be attributed to generalised difficulties in completing life cycles under harsh arctic and alpine conditions (Bliss 1971). Vegetative expansion is the mechanism by which alpine plants achieve crown expansion and eventual dominance, and community structure is maintained (Forbis 2003). The same capacity is shown by arctic vegetation and has been related to the space and time heterogeneity encountered by plants (Carlsson et al. 1990). In our study, the most efficient expansion mechanism seems to combine persistence in microsites with slow expansion through nearby offspring, as most of the alpine flora (65.4%) expanded a short distance from the mother plant (Table 2). This is achieved through dense turfs, mainly in dominant graminoids, or by means of few sprouts, in less dominant plants.

Temporal and spatial colonisation is achieved through diaspores, which, in addition, accomplish sexual reproduction. These ecosystem functions are uneven and even hazardous under alpine conditions because of climatic constraints. Thus, the supply of diaspores aimed to regeneration of populations and colonisation of new habitats must be accomplished in the few years with good seed production (Molau and Larsson 2000). Our observations indicate that only a few plants are related to zoochory: no species showed clear adaptations to ectozoochory, and only 3.1% were endozoochorous (some Ericaceae and *Juniperus communis* ssp. *alpina*). Even in this case, the production of fleshy fruit is more related to phylogeny than to function, as this dissemination mechanism in *Vaccinium* species shows low efficiency (Vander Kloet and Hill 1994). More than half the taxa do not show apparent mechanisms for dispersing diaspores, which are generally small and isometric, a typical feature of plants that have the capacity to persist in soil seed banks (Thompson et al. 1993). Thus, most of these taxa would be able to recover their populations in situ after perturbations, such as vegetation dieback and soil erosion, or the opening of small gaps. Long-distance dissemination was observed in almost 18% of taxa with plumose or dusty diaspores, which may dominate the colonisation of newly open habitats, like moraines uncovered by ice, snow beds or stream banks (Ozinga et al. 2004). Moreover, in spite of the low percentages of specialised modes of dispersal, frequent and long-distant diaspore dissemination is common in arctic and alpine landscapes (Tollesfrud et al. 1998). This may become significant in case of climatic change, as main governing factor of changes in composition and structure of varying communities (Molau and Larsson 2000).

Grouping alpine communities in function of plant attributes

The ordination of the communities on the basis of attributes is shown in Fig. 3 using the first two axes. In this ordering, we took the fuzzy partition into seven groups, since it yielded the highest value of silhouette average within the range from four to 11 groups. This classification is also meaningful with respect to vegetation physiognomy and functioning:

1. Evergreen scrubs: from dwarf, creeping *Loiseleuria* carpets to medium-sized heaths (numbers 43–46 of Appendix A).
2. Deciduous scrubs: woody snow bed communities and similar dwarf scrubs (39, 41, 42).
3. Hygrophilous communities: herbaceous carpets developing in and around rivulets and springs (1, 2, 11).
4. Rock communities: disperse fissuricolous communities (6–10, 15) and one open, transitional pasture (33).
5. Therophytic scree communities: sparse communities formed by annuals and perennials, settling on small- to medium-textured scree (14, 16, 17) or on gravel- and sand-rich snow beds (40).
6. Perennial scree communities: sparse communities of perennials, settling on medium- to coarse-textured scree (12, 13, 18, 19).
7. Pastures, in broad sense.

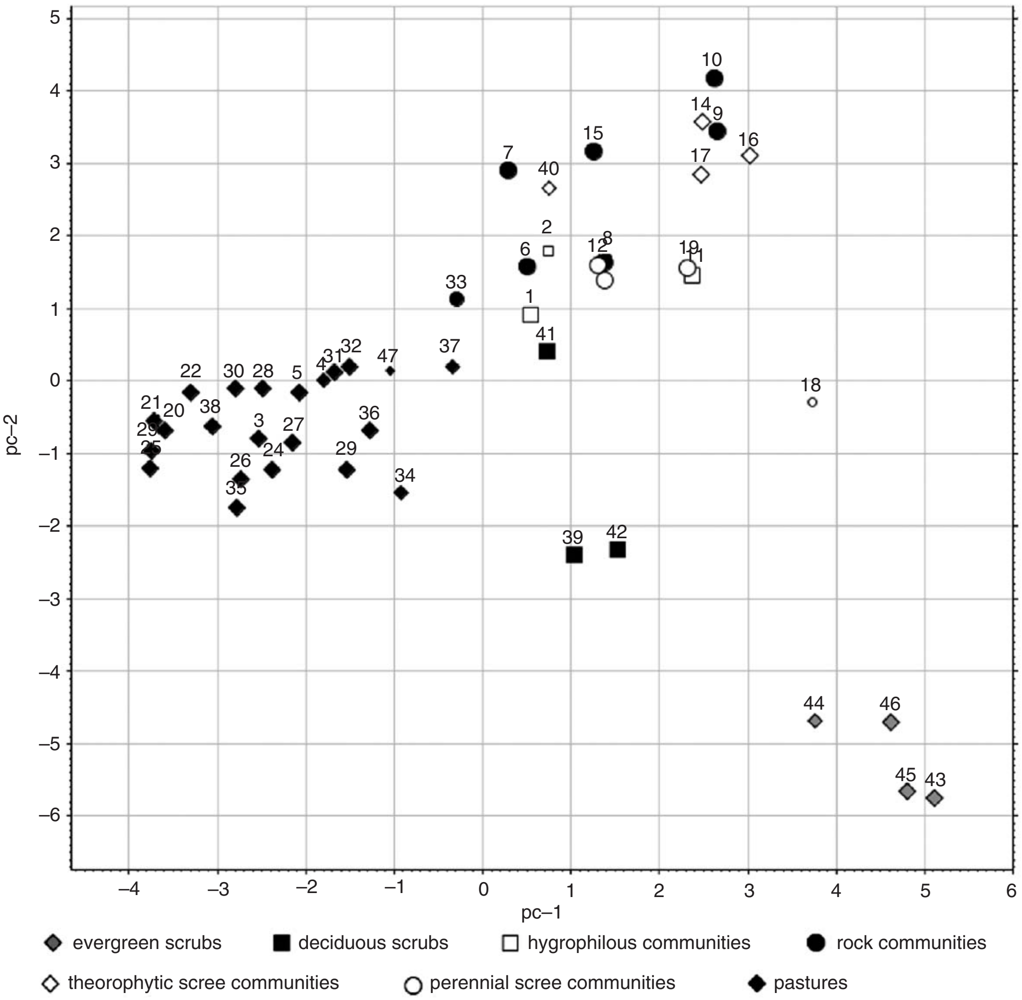

Fig. 3. Fuzzy C-means ordination of the communities studied on the space defined by the two first axes (23.96% and 19.42% of variance). The size of the symbols indicates the membership degree of each community to the corresponding group. Numbering of communities is given in Appendix A.

As expected, the group of pastures was much larger (22 communities) than the other categories. Thus, we performed a second analysis restricted to pastures and took the cut-off level of five subgroups, as this was the most meaningful from a physiognomic and functional viewpoint (Fig. 4):

7a. Dense pastures (numbers 20–23, 25, 30, 38).
7b. Summit open pastures (26–29, 31, 34).
7c. Sloping open pastures (24, 32, 35–37).
7d. Fens (3–5).
7e. Tall-herb community (47).

Most of these groups and subgroups coincided with high-level syntaxa (classes, orders), in some cases with small differences, such as the inclusion of Saxifrago-Minuartietum (33) in rock communities, or Gnaphalio-Sedetum (40) in communities on fine scree, which is related to strong functional particularities of both associations within their phytocoenological classes. The attribute-based classification did not reflect differentiation between calcicolous or calcifuge communities, which results in distinct orders or classes in the floristic-based, phytocoenological system. However, it assembles in the same group functionally related communities, such as sloping pastures, or dense pastures. The attribute-based ordination and classification reflect the main habitats of the alpine belt, defined in terms of topography and related soil and microclimate descriptors (Fig. 5). As a general rule, the vegetation groups most coincident with syntaxa (1, Vaccinio-Piceetea; 3, Montio-Cardaminetea; 4, Asplenietea; 7d, Scheuchzerio-Caricetea; 7e, Betulo-Adenostyletea) are more associated with certain

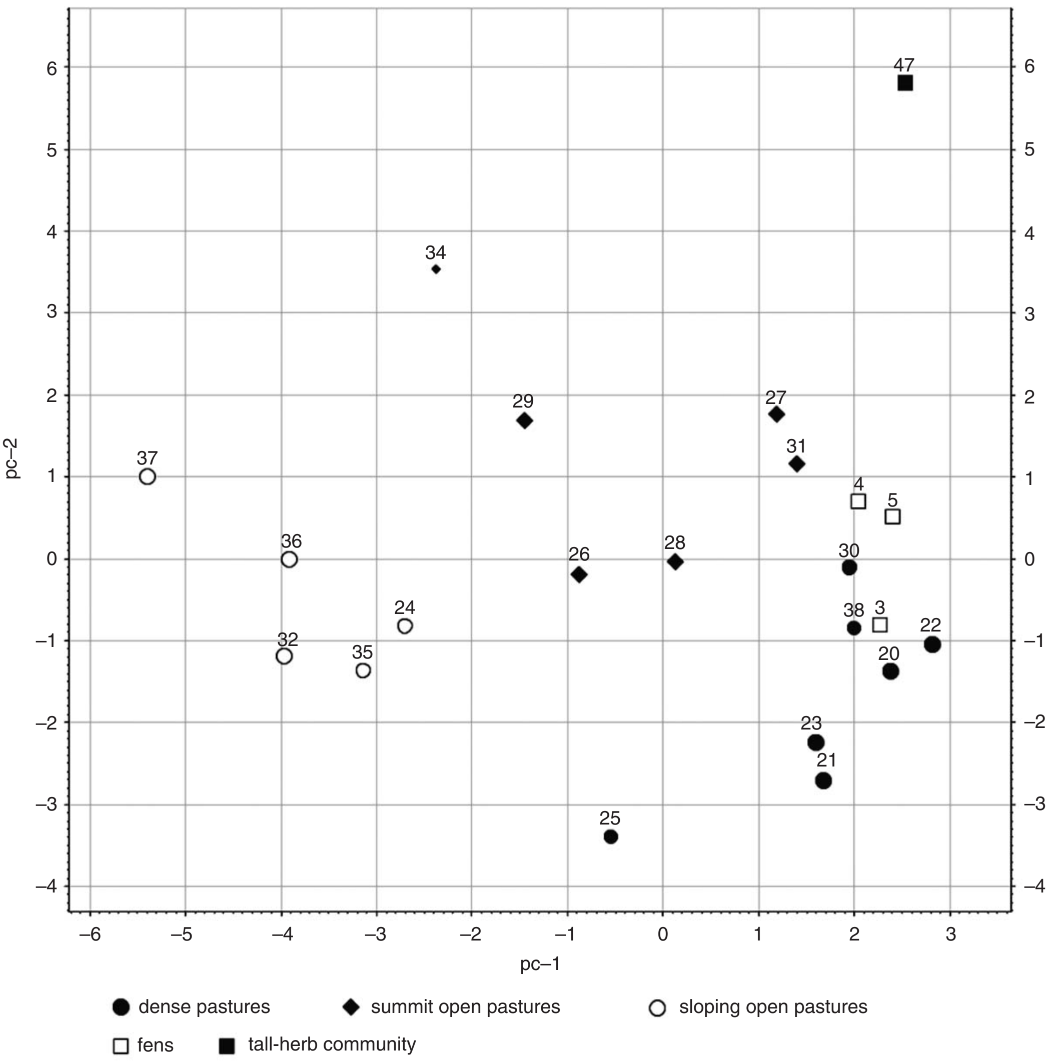

Fig. 4. Fuzzy C-means ordination of the pasture communities on the space defined by the two first axes (26.26% and 16.64% of variance). The size of the symbols indicates the membership degree of each community to the corresponding group. Numbering of the communities is given in Appendix A.

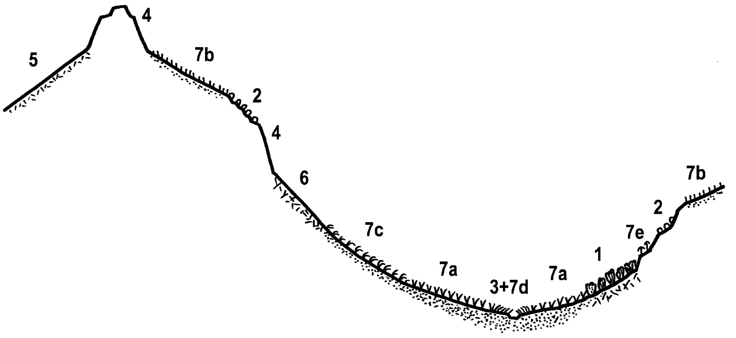

Fig. 5. Catenal situation of vegetation groups in main habitats of the alpine belt. (1) evergreen scrubs, (2) deciduous scrubs, (3) hygrophilous communities, (4) rock communities, (5) therophytic scree communities, (6) perennial scree communities, (7a) dense pastures, (7b) summit open pastures, (7c) sloping open pastures, (7d) fens, (7e) tall-herb community.

conditions, which implies particular environment stress, such as waterlogging, soil scarcity or low fertility (Braun-Blanquet 1948; Carreras et al. 1993; Carrillo and Ninot 1992). Therefore, the corresponding communities are mainly species-poor, and clearly dominated by one or a few species, thereby strongly influencing the spectra of that particular community.

Defining traits of alpine vegetation groups

It has been widely reported that the spectra of plant life forms are good descriptors of functional morphology. They may express the strong determinism of differentiated microclimates and soils within small surfaces typical of alpine and arctic landscapes. This space heterogeneity is related to strong variations in several ecosystem descriptors, like primary production, total biomass or soil organic matter (Shaver et al. 1997). In our study, strong spectra differentiation occurred between the seven main vegetation groups (Fig. 6); even pastures were noticeably differentiated at this level (Fig. 7). The average values of the other attributes (functional attributes: Tables 3 and 5; community attributes: Tables 4 and 6) also define the characteristics of each vegetation group, and hence indicate preference for particular environmental conditions. However, elsewhere, group averages masked considerable differences between communities in the same group when referring to a single attribute, which is reflected in the tables as high scores of standard error (Tables 5 and 6).

Woody vegetation (groups 1 and 2)

Scrubs included the most apparent woody plants, which attained distinct coverage in the two groups: woodiness reached 64.3% in evergreen scrubs and 27.8% in deciduous scrubs. In the former, this strong woody dominance was shared mainly by nanophanerophytes (22.5%) and suffruticose (13.6%) and creeping (33.0%) chamaephytes. This codominance is related to the varied physiognomy of the communities included, which may be erect (*Rhododendron ferrugineum* scrub), diffuse (*Arctostaphylos uva-ursi* carpets) or creeping (*Loiseleuria procumbens* dwarf carpets). Other characteristics of evergreen scrubs were the lowest cover percentage of non-graminoid hemicryptophytes (11.3%), and the highest cover reached by terricolous lichens (5.7%). These cryptogams are absent in the *Rhododendron* and in the *Juniperus communis* subsp. *nana* scrubs (0.9% and 0.3%, respectively), but cover noticeable surfaces in the *Loiseleuria* and in the *Empetrum nigrum* subsp. *hermaphroditum* carpets (15.0% and 6.7%).

Evergreeness is the most characteristic attribute of evergreen scrubs, which was due to several taxa (*Rhododendron, Loiseleuria, Empetrum, Juniperus*) that have adapted to cold environments and poor soils (Bliss 1971). Evergreen shrubs are the only plants that can build complex epigeous structures. They must face the energetic costs involved in the maintenance of evergreeness under alpine conditions, probably because whole foliage sprouting is not viable in plants of this size, in spite of their mycorrhizae symbioses and considerable stem and root stocks (Lamaze et al. 2003).

In deciduous scrubs, creeping, semi-woody chamaephytes were dominant (*Salix* spp., *Dryas octopetala*; 46.7%), and the two types of hemicryptophytes accounted for 40.2% of the cover, which indicates the transitional position of these communities between scrubs and pastures. It is interesting to note that while evergreen scrubs are restricted mainly to the lower part of the alpine belt, deciduous ones were spread across the belt, and were especially abundant in the places with most snow (Braun-Blanquet 1948; Carrillo and Ninot 1992). According to Tieszen et al. (in Komárková and McKendrick 1988), the higher efficiency of deciduous arctic chamaephytes in winter storage compared with evergreen shrubs allows them to sprout faster at the beginning of summer and to escape from winter desiccation caused by leaf transpiration when the soil is frozen. The strategy of deciduous chamaephytes involves greater resource dynamics, related to habitat quality and to higher herbivorous interaction, while evergreen scrubs occupy and maintain poorer substrata (Chapin et al. 1996; Gerdol 2005; Gerdol et al. 2000b).

These two scrub types showed high percentages of long-distance vegetative expansion from the mother plant. Most dominant shrubs and subshrubs show layering via lateral rooting branches, which may result in phalanx colonisation and clonal spreading over sizable surfaces (Albert et al. 2005; Pornon et al.1997). Regarding diaspore dissemination, endozoochory is exclusive to evergreen scrubs, where berry-producers account for more than half the cover. In contrast, deciduous scrubs showed by far the highest percentage (78.9%) of long-distance dispersion, which is attributed to the dominance of subshrubs that bear plumose diaspores (*Salix* spp., *Dryas octopetala*).

Communities of particular habitats (groups 3, 4, 5 and 6)

Rock and scree surfaces strongly limit plant colonisation because of the scarcity and space dispersion of soil, which, in addition, implies lower water and nutrient reserves. Low vegetation cover is a clear expression of these constraints (Burga et al. 2004). Rock communities

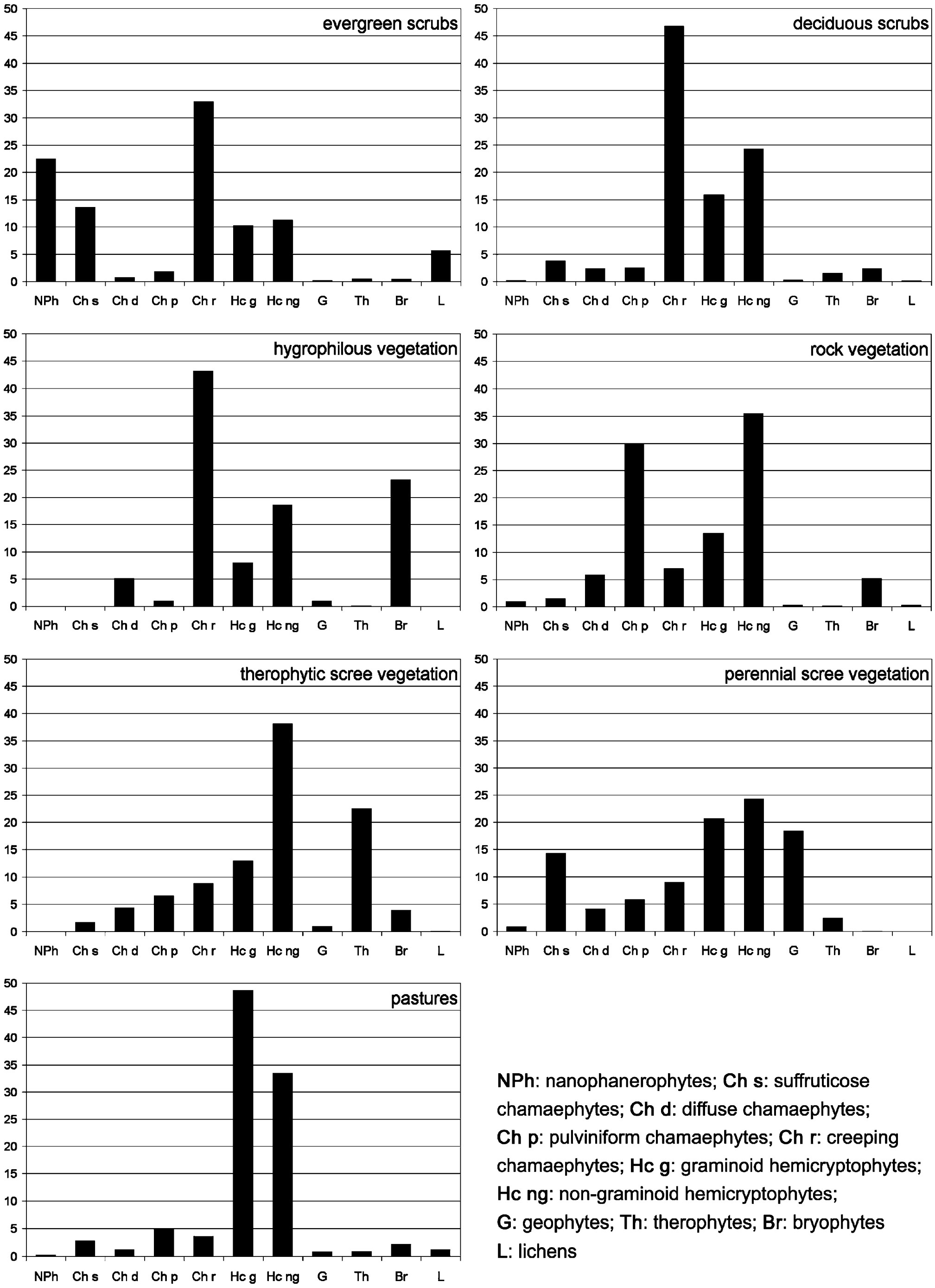

Fig. 6. Relative cover values of life forms in the vegetation groups. The bars correspond to the mean covers of each life form across the communities included in each group.

were characterised by a very high percentage of pulvinules (29.9%, much higher than in the other groups), which codominated with non-graminoid hemicryptophytes (35.5%). The relative cover of pulvinules, other chamaephytes (14.3%) and bryophytes (5.2%), together with evergreeness (17.9% of cover, 27.9% of

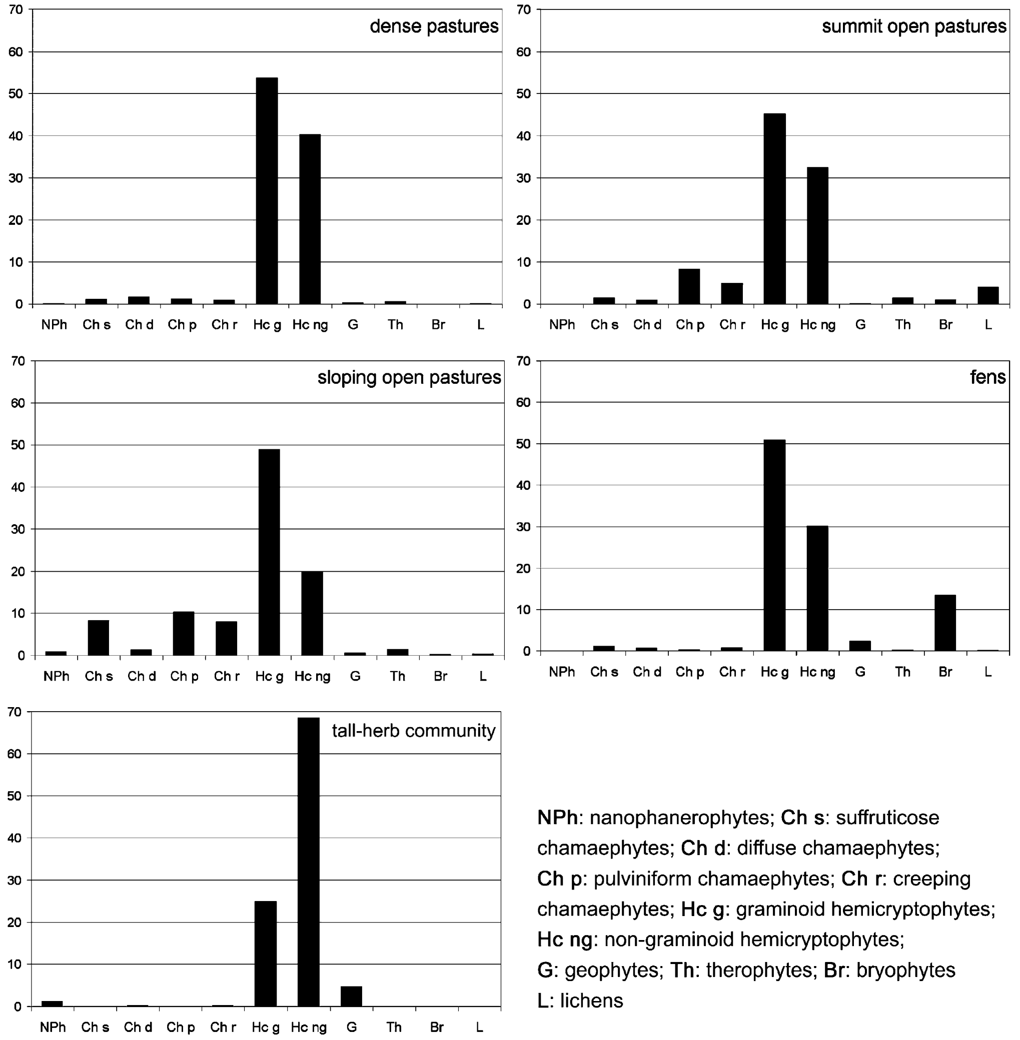

Fig. 7. Relative cover values of life forms in each subgroup of pasture communities.

taxa) and succulence (8.8%, 11.8%) indicates environmental stress conditions, which lead to slow growth and low turnover (Bliss 1971).

Perennial glareicolous communities are mainly related to scree of medium-sized to large pieces, even to huge blocks. Slope sliding is there a minor constraint compared to the scarcity of soil. This is frequently reduced to small, remote interstices among rock material, in the form of soil pockets conserved by the dense root systems of specialised plants, which can thus survive land movements (Somson 1984). These scree surfaces are good niches for a number of geophytes (several mountain ferns and forbs: *Cryptogramma crispa* – cf. also Tomaselli et al. (2005), *Crepis pygmaea*), which accounted for 18.4% of the relative cover. Together with these, hemicryptophytes (graminoid and non-graminoid, 20.7% and 24.3%, respectively) comprise the bulk of the communities. A high percentage of long-distance lateral expansion (67.7%) is related to the irregularity of the substrate, which leads plants to produce long rhizomes or to resprout after being covered by rock debris.

The significant presence of annuals was the most distinctive trait of the therophytic communities that settle on scree and in some acidic snow beds. Their relative cover (22.6%), which was much higher than their average cover in alpine vegetation (2.0%), indicates that these substrata provide an adequate habitat for such short-lived plants (*Galeopsis pyrenaica* var. *nana, Iberis spathulata, Mucizonia sedoides*). These substrata comprise generally small to medium-sized rock pieces, which periodically slide. However, beneath these gravel, there are less conspicuous matrixes of fine earth (Somson 1984), which may harbour considerable seed banks. In this regard, these scree communities also

Table 3. Cover percentages (and ±SE) of taxa with the functional attributes considered in the vegetation groups

	Evergreen scrubs	Deciduous scrubs	Hygroph. veg.	Rock veg.	Theroph. scree	Perenn. scree	Pastures
Vegetative particularities							
Succulence	0.2±0.1	1.2±0.5	28.0±6.4	8.7±2.0	7.2±5.3	2.4±1.0	1.6±0.2
Evergreeness	50.7±4.5	1.4±0.2	0.9±0.3	17.9±3.7	1.7±0.7	11.5±5.8	1.8±0.3
Woodiness	64.3±3.6	27.8±2.4	0.0±0.0	3.6±1.8	0.7±0.1	1.3±0.8	2.9±0.6
Lateral spread							
Absent	0.0±0	0.0±0.0	0.0±0.0	0.8±0.8	33.8±3.7	1.2±1.2	1.1±0.8
<2.5 cm	2.4±1.4	40.3±29.9	31.2±16.3	47.8±8.0	21.9±13.4	6.6±3.7	25.0±3.1
>2.5 cm	95.4±1.8	56.1±28.1	35.1±20.2	9.6±2.5	33.0±16.2	67.7±12.3	10.5±3.1
Dense turf	2.2±2.2	3.6±1.8	33.6±26.7	41.8±8.6	11.3±4.3	24.5±8.9	63.4±2.8
Diaspore dissemination							
Long distance	0.0±0.0	78.9±5.9	5.8±3.8	11.5±4.5	22.2±11.5	52.2±16.1	6.9±2.1
Short distance	2.2±2.2	8.2±8.2	9.2±4.5	16.9±3.8	9.3±3.6	19.0±9.7	63.0±5.6
No dissemin.	45.6±13.0	12.9±3.0	85.0±8.1	71.5±5.2	68.5±13.4	28.8±6.6	30.2±4.7
Endozoochory	52.2±12.2	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0

Table 4. Mean values (and ±SE) of community attributes in the vegetation groups

	Evergreen scrubs	Deciduous scrubs	Hygroph. veg.	Rock veg.	Theroph. scree	Perenn. scree	Pastures
Global cover	93.4±1.3	91.7±2.0	84.6±3.6	14.0±8.1	30.6±12.0	19.1±5.5	81.6±3.9
Cumulate cover	154.3±10.0	139.9±8.7	120.1±7.8	57.2±16.2	65.1±15.9	45.2±4.7	155.4±6.4
Species richness	14.4±0.9	17.6±1.5	9.7±1.6	12.1±1.2	9.7±0.9	9.9±1.4	18.0±1.0
Number of families	24.5±1.8	29.0±2.9	17.7±1.2	18.1±2.3	18.5±2.5	17.0±2.6	25.4±1.2
Shannon diversity index	1.6±0.1	1.4±0.0	1.2±0.1	1.4±0.1	1.6±0.1	1.6±0.1	1.2±0.1

Table 5. Cover percentages (and ±SE) of taxa with the functional attributes considered in the subgroups of pastures

	Dense pastures	Summit pastures	Sloped pastures	Fens	Tall-herb com.
Vegetative particularities					
Succulence	1.3±0.4	2.1±0.4	1.0±0.4	2.4±0.0	0.5
Evergreeness	0.6±0.1	3.0±0.4	2.9±0.6	0.9±0.3	1.1
Woodyness	0.9±0.3	3.7±1.5	6.0±0.6	1.5±0.8	1.3
Lateral spread					
No spreading	0.0±0.0	0.0±0.0	4.8±3.0	0.0±0.0	0.0
<2.5 cm	34.1±5.0	29.4±5.8	10.1±3.1	24.6±3.9	11.2
>2.5 cm	0.7±0.7	9.3±5.9	15.8±1.8	11.0±6.9	58.0
Dense turf	66.3±5.2	61.3±2.9	69.3±5.6	64.3±5.8	30.8
Diaspore dissemination					
Long distance	3.6±1.4	13.9±3.6	0.0±0.0	1.9±1.9	37.3
Short distance	83.4±3.6	43.3±9.6	74.9±6.2	46.3±18.9	27.8
No dissemination	13.0±3.1	42.7±8.4	25.2±6.2	51.9±20.2	35.0

showed high cover percentages of plants that lack lateral expansion (33.8%) mainly annuals. Nevertheless, this scree type was dominated by non-graminoid hemicryptophytes (38.1%, the highest relative cover of this type), which produce long rhizomes that can resprout after being covered by debris, moved or even fragmented (*Viola lapeyrousiana, Veronica nummularia, Galium cometerrhizon*; Somson 1984).

The communities related to running waters showed the highest bryophyte cover (23.3%) and the lowest presence of graminoid hemicryptophytes (8.0%). The dominance corresponded to creeping herbaceous

Table 6. Mean values (and ±SE) of community attributes in the subgroups of pastures

	Dense pastures	Summit pastures	Sloped pastures	Fens	Tall-herb com.
Global cover	93.6±3.0	85.0±1.9	52.4±6.3	91.6±2.8	94.0
Cumulate cover	161.0±7.0	170.7±7.7	117.5±15.4	178.7±3.1	144.5
Species richness	17.2±1.3	21.7±1.4	18.9±2.8	12.8±1.4	12.2
Number of families	25.6±1.8	24.7±2.9	27.6±2.5	25.7±3.8	17.0
Shannon diversity index	0.9±0.1	1.4±0.0	1.5±0.1	1.2±0.1	0.8

chamaephytes (43.2%), generally one of these species per relevé (*Saxifraga aquatica, S. stellaris, Epilobium alsinifolium*). Curiously, these communities showed the highest values for succulence (28% of cover, 14% of taxa). Hygrophylous communities include some succulent (*Sedum villosum, Saxifraga aizoides*) and also semi-succulent plants (*Saxifraga* spp., *Dactylorhiza* spp.), a few of which may be abundant. Since succulence indicates particular resource niches, and not necessarily water scarcity (Shmida and Burgess 1988), in our study this trait may be related to various stress factors, namely low water and nutrient supply in rocky habitats and nutrient deficiency in waterlogged soils. Alternatively, succulence may partially reflect phylogenetic links expressed by taxa excluded from better habitats.

In general, communities related to rocks, scree and running waters showed low diversity, at least when expressed as number of species and number of families. This trend reflects that the constraints of these habitats exclude most of the alpine flora and, at the same time, favour a number of taxonomic groups (families, genera) in each case. The density of endemics and other particular taxa (Braun-Blanquet 1948; Küpfer 1974) show that these stressful habitats have been a suitable arena both for persistence of paleoendemics and for geographic and ecologic selection at the species level.

Pastures (group 7)

Although this group is the most diversified into associations, its coarse physiognomy is quite uniform and gives the main feature of the alpine belt. This group showed the highest percentage of one life form, namely grasses and related plants, which accounted for almost half the cover (48.6%). The presence of non-graminoid hemicryptophytes was also high (33.4%), while all the other types presented much lower percentages (<5%). This observation indicates that, excluding extreme substrata (scree, rock, water-saturated soils, etc.), hemicryptophyte form and function is the most efficient type in alpine vegetation. The combination of persistence, ensured through strong below-ground structures, and dynamics, performed by seasonal leaves and shoots, suits contrasting alpine seasonality.

Given the generalised dominance of hemicryptophytes, the subgroups of pastures showed only small particularities (Fig. 6). Only the tall-herb community differed clearly; the prevalence of forb hemicryptophytes with respect to graminoids (68.5 vs. 25.0%) is related to particular conditions (i.e., fertile soils with good water supply, in the lower alpine belt) that enhance rapid growth and crown competition for light. Fens stand out at this level because of the high cover of bryophytes (13.5%). The characteristics of the environment these communities occupy (waterlogged soil) were hardly reflected by the percentages of life forms observed, as the general graminoid dominance was maintained through sedges instead of grasses. Among the typical pastures, hemicryptophytes reached the highest percentage in the subgroup of dense communities, which settle on flats or gentle slopes with relatively good soil (deep, stable, neither flooded nor drying out), mainly in the lower alpine belt (Carreras et al. 1993; Carrillo and Ninot 1992). Other life forms find there low possibilities, as reflected by the very low cover recorded. In the two subgroups of open pastures, chamaephytes (creeping, suffruticose, pulvinules) reached significant values (most between 5–10%), mainly at the expense of non-graminoid hemicryptophytes, which, in sloped pastures, had the lowest abundance within the group (19.9%). Summit pastures were characterised by the relatively high presence of terricolous macrolichens (4%). According to Onipchenko (1994), in typical alpine pastures, lichens benefit from the smaller lateral extension shown by main grasses and dwarf shrubs above ground than in the root system. At the community level, the presence of these cryptogams together with that of pulvinules and creepers indicate hard conditions (stoniness, dryness, erosion) and a certain degree of community stability.

The dominant grasses and sedges also define the regenerative strategies of the group of pastures. The type of dense turfs reaches its maximum resulting into slow, massive lateral expansion of most plants, typical of habitats with limited fertility. The dissemination type of these main graminoids is to short distances, through flattened or membranous diaspores. According to Semenova and Onipchenko (1994), most of the dominant plants of well-established alpine communities do not make permanent seed banks, as their persistence is ensured by perennial roots and bases. On the contrary, non-dominant species in these communities, and most plants in communities of unfavourable habitats (scree, rock, water), are more dependent on permanent seed banks, as their persistence is more related to disturbance and opening of gaps (‘‘explorative’’ taxa, sensu Onipchenko et al. 1998).

Synthesis of main trends and conclusions

In the Catalan alpine landscape, hemicryptophytes are dominant, both at the species level (69.4%) and as mean of cover percentages (68.2%), which reflects the appropriateness of this life form for general alpine conditions. Other very dominant features of plants in this vegetation belt include the lack of green parts in winter, the capacity for lateral spreading to short distances and the absence of disseminating mechanisms. Nevertheless, the general spectrum of attributes includes diversity of types which, although showing low general percentages, are significant in particular environments. Hence, the communities most differentiated from the general alpine spectrum settle on a variety of unbalanced habitats, mainly associated with stress conditions (scarcity of soil, nutrient-poor or waterlogged substrata). These communities tend to be species-poor and with relatively high percentages of particular types. Groups less differentiated from the global spectra, i.e., with great dominance of hemicryptophytes, included richer communities, with more shared dominances, and correspond to more balanced environments. Like in other landscapes, richer alpine communities become classified into richly hierarchised syntaxa (Elyno-Seslerietea, Juncetea trifidi), and show gradual transitions among them and towards other peripheral syntaxa (Thlaspietea, Scheuchzerio-Caricetea), a scheme similar to that shown at physiognomic and functional levels.

Communities of several harsh habitats show mainly low diversity at species and family levels, together with high taxonomic specialisation. The lowest values are found in scree and water communities (less than 10 species per relevé) and also fens (12.3 taxa/relevé). Limiting conditions are also reflected by plant cover, most strikingly in rock and scree communities, but also in hygrophilous communities and in extreme pastures on rocky areas or sliding slopes. In contrast, scrubs and pastures have the highest covers (global and cumulative) and number of species per relevé. Although there is a strong dominance of one or few species in most of these communities, the poor above-ground plant stratification and the microtopographic irregularities favour the settlement of many subordinate species. Therefore, in alpine communities, a general positive correlation is observed between species richness and cover values. However, the lowest structural diversities are found in dense pastures and fens, while scree and rock communities exhibit the highest heterogeneity (i.e., high number of life forms, evenly distributed). Hence, this sparse vegetation would be less sensitive to environmental changes at the community level.

The capacity of plants to spread laterally, mainly over small distances, is very general in alpine flora. Moderate foraging and displacement is combined in most species with strong persistence of plurennial bases. This strategy is most evident in dominating turfs of pastures and fens, and also in small cushions. In addition, more loose chamaephytes and nanophanerophytes follow the same strategy, but on a larger scale. Concerning dissemination, snow bed carpets and perennial scree communities include high percentages of long-distance types. In other stressful habitats, such as rocks, waters and fine screes, most plants show no apparent dissemination mechanism. These trends, together with dominant short distance dissemination in pastures and zoochory in scrubs indicates that the coarse dissemination types observed here may be more related to phylogeny than to function. In alpine landscapes, selection pressure on dispersal mechanisms is low or random because of various ecological features, mainly generalised difficulties in setting seeds, low chance of seedling or juvenile establishment and intense slope dynamics. Therefore, the major plant strategy consists of strong persistence and moderate regeneration, which is for the most part short distance offspring, and eventually the setting diaspores over space or via the soil bank.

The typical alpine geomorphology produces highly heterogenous landscapes in terms of microclimates and substrata, thereby leading to dense, contrasting land mosaics. Thus, while alpine pastures depend principally on general bioclimates and become finely diversified at the floristic level, neighbouring plant communities bear strong differentiation and are tightly related to a wide scope of specific environments. In particular, the morphology and functioning of these plant communities show adaptive persistence of various plant sources at the cost of coupling with various stress conditions. Therefore, while vegetation dynamics is not a significant cause of diversity in alpine landscapes, the abundance of particular species richness at these altitudes is the result of a broad spectrum of habitats that are stressful, extended and conservative.

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Appendix A. Syntaxonomic scheme of the communities treated

- Montio-Cardaminetea Br.-Bl. et Tüxen ex Klika et Hadac 1944
  - Montio-Cardaminetalia Pawl. 1928
    - Cardamino-Montion Br.-Bl. 1926
      1. **Saxifragetum aquaticae** Br.-Bl. 1948
      2. **Montio-Bryetum schleicheri** Br.-Bl. 1925
- Scheuchzerio-Caricetea fuscae Tüxen 1937
  - Caricetalia fuscae Koch 1926
    - Caricion fuscae Koch 1926
      3. **Caricetum fuscae** Br.-Bl. 1915
      4. **Narthecio-Trichophoretum** Br.-Bl. 1948 **primuletosum integrifoliae** Ninot et al. 2000
  - Caricetalia davallianae Br.-Bl. 1949
    - Caricion davallianae Klika 1934
      5. **Swertio-Caricetum nigrae** Vigo 1984
- Asplenietea trichomanis (Br.-Bl.) Oberd. 1977
  - Potentilletalia caulescentis Br.-Bl. 1926
    - Saxifragion mediae Br.-Bl. 1934
      6. **Saxifragetum mediae** Br.-Bl. 1934 1948
      7. **Sileno borderei-Potentilletum nivalis** (G. Monts.) Ninot et Soriano 1996
  - Androsacetalia vandellii Br.-Bl. 1934
    - Androsacion vandellii Br.-Bl.1926
      8. **Saxifrago-Androsacetum vandellii** Carrillo et Ninot 1986
      9. **Saxifragetum iratianae** Nègre 1969
      10. **Saxifragetum pubescentis** Br.-Bl. (1934) 1948
- Thlaspietea rotundifolii Br.-Bl. 1948
  - Thlaspietalia rotundifolii Br.-Bl. 1926
    - Iberidion spathulatae Br.-Bl. 1948
      11. **Saxifragetum praetermissae** Br.-Bl. 1948
      12. **Festucetum glaciali-pyrenaicae** Rivas-Mart. 1977
      13. **Crepidetum pygmaeae** Br.-Bl. 1946
      14. **Iberidetum spathulatae** Br.-Bl. 1948
  - Androsacetalia alpinae Br.-Bl. 1926
    - Androsacion alpinae Br.-Bl 1926
      15. **Oxyrio-Doronicetum viscosae** (Chouard) Gruber 1978
    - Senecion leucophylli Br.-Bl. 1948
      16. **Violetum diversifoliae** Fern. Casas 1970
      17. **Galeopsio-Poetum fontqueri** Br.-Bl. 1948
      18. **Senecietum leucophylli** Br.-Bl. 1948
    - Dryopteridion oreadis Rivas-Mart. 1977
      19. **Cryptogrammo-Dryopteridetum abbreviatae** Rivas-Mart. 1970
- Juncetea trifidi Hadac 1944
  - Caricetalia curvulae Br.-Bl. 1926
    - Nardion strictae Br.-Bl. 1926
      20. **Alchemillo-Nardetum strictae** Gruber 1975 **nardetosum strictae** Carrillo et Ninot 1990
      21. **Selino-Nardetum** Br.-Bl. 1948
      22. **Trifolio-Phleetum gerardi** Br.-Bl. 1948
      23. **Selino-Festucetum eskiae** Nègre 1968 (= Ranunculo-Festucetum eskiae Nègre 1974)
    - Festucion eskiae Br.-Bl. 1948
      24. **Festucetum eskiae** Br.-Bl. 1948
      25. **Carici-Festucetum eskiae** Rivas-Mart. 1974
    - Festucion supinae Br.-Bl. 1948
      26. **Hieracio-Festucetum supinae** Br.-Bl. 1948 **typicum**
      27. **Hieracio-Festucetum supinae juncetosum trifidi** Br.-Bl. 1948
      28. **Hieracio-Festucetum supinae caricetosum curvulae** Baudière et Serve 1975
      29. **HieracioFestucetum supinae kobresietosum myosuroidis** Carrillo et Vigo 1993
      30. **Gentiano-Caricetum curvulae** Nègre 1969
      31. **Leontodonto-Caricetum curvulae** Br.-Bl. 1948
      32. **Arenario-Festucetum yvesii** Baudière et Serve 1975
      33. **Saxifrago-Minuartietum sedoidis** Carrillo et Ninot 1989
- Elyno-Seslerietea Br.-Bl. 1948
  - Elynetalia Oberd. 1957
    - Oxytropido-Elynion Br.-Bl. 1949
      34. **Elyno-Oxytropidetum hallerii** Br.-Bl. 1948
  - Seslerietalia caeruleae Br.-Bl. 1926
    - Festucion scopariae Br.Bl. 1948
      35. **Festucetum scopariae** Br.-Bl. 1948
      36. **Oxytropido-Caricetum humilis** Carrillo et I. Soriano 1997 **typicum**
      37. **Oxytropido-Caricetum humilis helictotrichetosum sedenensis** (Carreras et Carrillo) Carrillo et al. 2000
    - Primulion intricatae Br.-Bl. ex Bolòs 1970
      38. **Festuco-Trifolietum thalii** Br.-Bl. 1948
      39. **Dryado octopetalae-Salicetum pyrenaicae** Vanden Berghen 1970 (incl. Alchemillo-Dryadetum I. Soriano 2001)
- Salicetea herbaceae Br.-Bl 1948
  - Salicetalia herbaceae Br.-Bl. 1926
    - Salicion herbaceae Br.-Bl 1926
      40. **Gnaphalio-Sedetum candollei** Br.-Bl 1948
      41. **Salici-Anthelietum juratzkanae** Br.-Bl 1948
    - Arabidion coeruleae Br.-Bl. 1926
      42. **Carici parviflorae-Salicetum retusae** (Br.-Bl.) Rivas Mart. 1969
- Vaccinio-Piceetea Br.-Bl. 1939
  - Piceetalia Pawl. 1928
    - Juniperion nanae Br.-Bl. et al.1939
      43. **Genisto-Arctostaphyletum** Br.-Bl. (1939) 1948
    - Loiseleurio-Vaccinion Br.-Bl. 1926
      44. **Cetrario-Loiseleurietum** Br.-Bl. 1926
    - Rhododendro-Vaccinion G. et J. Br.-Bl. 1931
      45. **Saxifrago-Rhododendretum** Br.-Bl 1939 **typicum**
      46. **Empetro hermaphroditi-Vaccinietum uliginosi** Br.-Bl. 1926
- Betulo-Adenostyletea Br.-Bl. et Tüxen ex Br.-Bl. 1948
  - Adenostyletalia G. et J. Br.-Bl. 1930
    - Adenostylion alliariae Br.-Bl 1926
      47. **Peucedano-Luzuletum desvauxii** Br.-Bl. 1948

Appendix B. Values of attributes of the communites treated

	Alchemillo-Nardetum	Arenario-Festucetum	Caricetum fuscae	Carici-Festucetum	Carici-Salicetum	Cetr.-Loiseleurietum	Crepidetum pygmaeae	Crypt.-Dryopteridetum	Dryado-Salicetum	Elyno-Oxytropidetum	Empetro-Vaccinietum	Ferstucetum eskiae	Festucetum gl.-pyren.	Festucetum scopariae	Festuco-Trifolietum	Galeopsio-Poetum	Gen.Arctostaphyletum	Gentiano-Caricetum	Gnaphalio-Sedetum	Hier.-Festuc. caricet.	Hier.-Festuc. juncet.	Hier.-Festuc. kobresiet.	Hier.-Festuc. typicum
Global cover	98.4	35.2	95.0	78.8	87.8	92.8	11.2	10.6	92.5	82.2	90.0	67.5	20.5	60.8	100	30.0	95.0	90.1	64.8	82.0	88.3	93.0	82.0
Cumulate cover	174.6	79.0	184.8	154.2	126.5	152.1	44.9	32.3	156.2	161.1	138.3	128.6	54.2	166.3	196.0	73.4	143.7	150.3	106.1	169.5	196.6	188.2	163.5
Mean of higher plant taxa	19.6	12.6	11.4	18.7	19.8	14.8	13.2	7.3	18.3	21.6	15.5	17.0	11.2	28.5	22.9	9.5	11.8	16.6	11.1	20.3	26.5	22.8	23.0
Total number of families	25	25	29	25	34	29	23	11	29	37	24	32	15	35	28	15	20	25	25	20	21	20	30
Nanophanerophytes	0.0	0.1	0.1	0.3	0.1	0.6	0.0	3.5	0.6	0.1	7.5	2.5	0.0	0.4	0.0	0.0	38.1	0.1	0.0	0.0	0.0	0.0	0.1
Suffruticose chamaephytes	0.0	0.8	0.3	3.7	3.4	0.6	3.4	1.8	7.9	2.8	24.0	9.7	0.0	6.6	0.7	1.9	10.9	0.1	0.1	0.1	0.2	4.2	1.6
Diffuse chamaephytes	1.7	1.7	0.4	0.6	1.3	0.5	6.0	0.0	0.1	1.8	2.0	0.7	4.4	3.3	7.0	1.4	0.3	0.7	3.9	0.6	1.4	0.0	0.8
Pulviniform chamaephytes	0.4	15.3	0.5	0.4	1.7	2.5	10.8	0.0	4.3	5.6	1.1	2.0	8.7	9.9	2.8	1.0	1.7	4.1	0.4	11.2	9.7	7.1	8.2
Creeping chamaephytes	1.7	9.5	1.3	1.0	51.6	57.6	12.8	0.0	43.7	17.0	38.8	2.6	18.3	9.6	0.8	6.5	23.0	2.0	3.7	1.8	1.6	4.8	3.4
Graminoid hemicryptophytes	49.5	56.6	51.7	67.3	12.5	11.7	21.6	14.2	22.9	40.4	7.5	49.2	31.1	46.1	45.5	8.7	13.4	45.8	18.1	48.9	43.7	51.0	46.1
Non graminoid hemicrypt.	46.3	13.6	18.6	24.9	24.6	10.8	24.5	39.8	18.2	27.4	11.0	30.9	20.4	22.8	41.5	45.5	11.1	45.8	41.6	34.2	35.2	25.0	33.6
Geophytes	0.4	0.1	5.0	0.7	0.2	0.0	18.8	40.7	0.4	0.4	0.0	0.7	12.3	0.4	0.3	2.6	0.7	0.0	0.0	0.0	0.0	0.0	0.1
Therophytes	0.0	2.1	0.2	1.1	0.6	0.9	2.1	0.0	1.8	1.4	0.6	0.7	4.8	1.0	1.0	32.5	0.6	0.8	16.3	2.7	0.8	1.7	1.8
Bryophytes	0.0	0.0	21.9	0.0	3.8	0.0	0.0	0.0	0.0	0.7	0.7	1.0	0.0	0.0	0.1	0.0	0.0	0.1	15.7	0.3	0.9	0.0	0.5
Lichens	0.1	0.1	0.0	0.0	0.4	14.9	0.0	0.0	0.0	2.4	6.7	0.0	0.0	0.0	0.1	0.0	0.3	0.5	0.2	0.1	6.4	6.3	3.8
Diversity of life forms	0.9	1.3	1.3	0.9	1.4	1.3	1.9	1.2	1.5	1.6	1.7	1.4	1.8	1.5	1.2	1.4	1.6	1.0	1.6	1.2	1.4	1.4	1.4
Succulence	0.5	1.0	3.0	0.3	1.9	1.7	4.3	0.0	0.6	1.8	1.7	2.2	1.8	1.3	1.5	2.8	0.0	5.6	23.6	4.2	4.0	1.8	2.4
Evergreeness	0.1	3.8	0.5	1.0	1.0	48.9	3.0	10.2	1.4	1.7	39.7	4.6	4.5	2.5	0.3	0.3	61.0	1.2	2.7	3.0	2.6	4.6	3.1
Woodiness	0.8	4.5	0.5	2.5	49.8	58.8	0.3	3.5	33.8	9.7	57.4	5.8	0.5	5.5	0.8	1.1	71.0	1.2	0.6	1.0	0.9	6.9	3.4
No lateral spread	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.8	0.0	0.0	42.5	0.0	0.0	29.2	0.0	0.0	0.0	0.0
Lateral spread < 2.5 cm	39.8	13.5	18.5	8.6	13.2	5.5	6.0	3.5	7.7	9.4	4.0	6.3	17.1	0.0	39.4	0.0	0.0	47.1	54.6	39.7	40.4	21.0	20.8
Lateral spread > 2.5 cm	0.0	12.7	9.5	0.0	81.4	94.5	50.3	81.2	87.0	37.0	96.0	15.4	43.9	17.4	4.7	57.5	91.2	0.0	0.0	0.0	0.0	7.6	11.2
Dense turf	60.2	73.8	72.0	91.4	5.4	0.0	43.7	15.3	5.3	53.6	0.0	78.2	34.3	82.6	55.9	0.0	8.8	52.9	16.3	60.3	59.6	71.5	68.0
Long distance dissemination	0.0	0.0	5.6	0.0	87.3	0.0	33.8	82.7	67.6	28.8	0.0	0.0	16.6	0.0	4.7	45.7	0.0	9.0	38.2	10.5	21.0	7.1	8.5
Short distance dissemination	82.7	73.8	72.0	92.0	0.0	0.0	33.4	0.0	24.7	20.0	0.0	84.6	37.7	91.2	74.2	7.2	8.8	69.1	16.3	60.2	33.7	20.2	79.2
No space dissemination	17.3	26.2	22.4	8.0	12.7	73.1	32.8	17.3	7.7	51.2	51.0	15.4	45.7	8.8	21.1	47.1	27.4	21.9	45.5	29.3	45.4	72.8	12.2
Endozoochory	0.0	0.0	0.0	0.0	0.0	26.9	0.0	0.0	0.0	0.0	49.0	0.0	0.0	0.0	0.0	0.0	63.8	0.0	0.0	0.0	0.0	0.0	0.0

	Iberidetum spathulatae	Leontodo-Caricetum	Montio-Bryetum	Narth.-Trichophoretum	Oxyrio-Doronicetum	Oxytr.-Caricetum helict.	Oxytr.-Caricetum typ.	Peucedano-Luzuletum	Salici-Anthelietum	Saxifragetum aquaticae	Saxifragetum iratianae	Saxifragetum mediae	Saxifragetum praeter.	Saxifragetum pubesc.	Saxifr. –Androsacetum	Saxifr. –Minuartietum	Saxif.–Rhododendretum	Selino-Festucetum	Selino-Nardetum	Senecietum leucophylli	Sileno-Potentilletum	Swertio-Caricetum	Triolio-Phleetum	Violetum diversifoliae
Global cover	15.2	82.2	89.0	86.1	7.2	40.0	58.3	94.0	94.6	87.3	1.0	7.8	77.5	4.0	7.0	62.1	96.0	89.1	99.2	34.0	9.0	93.8	99.5	12.3
Cumulate cover	45.6	145.2	132.5	175.7	53.7	90.4	123.3	144.5	137.2	105.8	32.3	52.9	122.1	27.0	37.4	151.7	183.1	160.8	142.7	49.3	45.2	175.5	147.9	35.3
Mean of higher plant taxa	10.9	15.9	7.9	11.4	13.3	15.0	21.2	12.2	14.8	8.3	8.2	13.3	13.0	9.3	12.6	17.9	15.4	14.5	14.0	8.2	9.9	15.6	13.9	7.3
Total number of families	20	20	17	30	21	22	24	17	24	20	11	29	16	13	18	21	25	34	18	19	14	18	24	14
Nanophanerophytes	0.0	0.0	0.0	0.1	0.0	0.6	0.5	1.2	0.0	0.0	0.0	1.4	0.0	2.5	3.2	0.0	43.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Suffruticose chamaephytes	5.1	0.0	0.0	2.4	0.0	10.3	14.1	0.0	0.0	0.0	0.0	1.1	0.0	4.3	3.2	0.0	18.9	2.6	0.5	51.9	1.5	0.7	0.1	0.0
Diffuse chamaephytes	9.1	1.1	2.1	0.5	13.2	0.7	0.0	0.3	5.6	0.3	6.5	0.4	13.0	13.0	3.2	2.8	0.0	0.3	0.5	6.1	2.0	1.0	0.8	3.1
Pulviniform chamaephytes	11.1	8.0	1.5	0.0	18.3	18.4	5.8	0.0	1.5	0.7	43.0	26.8	0.7	29.6	25.7	39.5	2.1	0.4	0.0	3.7	26.0	0.2	0.5	13.5
Creeping chamaephytes	8.9	1.1	8.2	0.7	7.0	13.2	5.1	0.3	44.9	69.2	9.6	10.8	52.2	0.0	13.9	4.4	12.4	0.5	0.0	4.8	2.9	0.2	0.5	16.0
Graminoid hemicryptophytes	14.3	41.0	7.3	55.9	16.6	44.2	49.1	25.0	12.4	11.2	8.7	8.5	5.4	4.9	19.3	25.2	8.2	54.2	64.9	15.9	11.5	45.0	49.0	10.7
Non graminoid hemicrypt.	28.0	39.5	18.4	33.3	34.5	10.2	22.0	68.5	30.0	13.6	7.4	50.7	23.6	45.7	30.5	23.5	12.3	41.1	33.4	12.3	56.0	38.5	48.9	37.4
Geophytes	1.2	0.0	0.1	2.2	0.6	0.8	0.8	4.7	0.2	0.2	0.0	0.2	2.5	0.0	1.1	0.0	0.2	0.6	0.2	1.9	0.0	0.0	0.1	0.0
Therophytes	22.3	0.5	0.1	0.0	0.0	1.6	1.5	0.0	2.3	0.0	0.0	0.2	0.0	0.0	0.0	1.0	0.1	0.2	0.6	3.0	0.0	0.5	0.2	19.2
Bryophytes	0.0	3.9	62.2	4.5	9.8	0.0	0.0	0.0	3.2	4.8	24.8	0.0	2.7	0.0	0.0	1.8	1.2	0.0	0.0	0.3	0.0	14.0	0.0	0.0
Lichens	0.0	5.0	0.0	0.4	0.0	0.0	1.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.8	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Diversity of life forms	1.9	1.3	1.2	1.1	1.6	1.5	1.7	0.8	1.4	1.0	1.5	1.3	1.3	1.4	1.7	1.5	1.6	0.9	0.7	1.5	1.2	1.1	0.8	1.6
Succulence	1.9	4.1	18.3	10.1	8.4	0.2	0.3	0.5	3.2	40.0	6.8	7.3	26.8	17.3	7.2	15.7	0.2	0.7	1.0	3.7	0.5	5.2	4.2	0.9
Evergreeness	3.2	2.8	1.4	1.4	10.1	2.2	1.3	1.1	1.0	0.4	27.8	17.1	0.3	30.6	24.6	9.9	53.3	0.3	0.1	28.1	5.5	0.5	0.2	0.6
Woodiness	0.4	0.8	0.0	3.0	0.1	6.2	8.1	1.2	23.1	0.0	0.0	6.8	0.0	5.2	13.6	0.5	70.1	0.7	0.2	0.8	0.7	0.9	0.2	0.6
No lateral spread	37.4	0.0	0.0	0.0	0.0	10.3	13.8	0.0	0.0	0.0	0.0	0.0	0.0	5.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	26.2
Lateral spread < 2.5 cm	32.9	45.3	63.1	32.0	72.4	12.6	17.9	11.2	100	9.2	52.6	38.6	21.4	77.8	28.7	22.2	0.0	35.5	25.0	0.0	42.5	23.4	43.2	0.0
Lateral spread > 2.5 cm	10.6	0.0	28.6	0.0	11.5	21.9	11.6	58.0	0.0	3.9	16.0	18.1	73.0	4.0	12.3	5.1	100	0.0	0.0	95.3	0.0	23.6	0.0	64.0
Dense turf	19.2	54.7	8.4	68.0	16.1	55.2	56.7	30.8	0.0	86.9	31.4	43.3	5.6	12.7	59.0	72.6	0.0	64.5	75.0	4.7	57.5	53.0	56.8	9.8
Long distance dissemination	5.1	7.6	13.0	0.0	0.0	0.0	0.0	37.3	81.8	4.4	0.0	28.8	0.0	17.5	11.5	0.0	0.0	0.0	7.1	75.9	23.0	0.0	4.4	0.0
Short distance dissemination	13.7	46.8	18.2	9.3	26.4	55.6	69.1	27.8	0.0	3.9	11.3	21.9	5.6	0.0	28.7	19.8	0.0	93.0	92.9	4.7	10.4	57.5	80.3	0.0
No space dissemination	81.3	45.6	68.8	90.7	73.6	44.4	30.9	35.0	18.2	91.8	88.7	49.3	94.4	82.5	59.8	80.2	62.3	7.0	0.0	19.4	66.6	42.5	15.3	100
Endozoochory	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	37.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0

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Capítol II

Functional plant traits and species assemblages in Pyrenean snowbeds

Trets funcionals i agrupació de les espècies en les congesteres pirinenques

Josep M. Ninot, Oriol Grau, Empar Carrillo, Roser Guàrdia,
Artur Lluent & Estela Illa

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Trets funcionals i agrupació de les espècies en les congesteres pirinenques

Resum

A les muntanyes de latituds mitjanes les congesteres sovint consisteixen en unitats de vegetació alpina de dimensions reduïdes i fragmentades que hostatgen un bon nombre d'espècies amb un elevat interès biogeogràfic. La majoria de les espècies de congestera són plantes poc competitives, i estudiar-ne la capacitat de disseminació i de persistència de les seves llavors és important per entendre millor les seves dinàmiques poblacionals. Aquest estudi va analitzar la flora de congesteres dels Pirineus centrals fent servir onze trets morfo-funcionals, la major part d'ells relacionats amb la llavor. Les llavors de la majoria d'espècies que viuen a les congesteres són petites o molt petites, tenen formes ovoides o el·líptiques i no presenten atributs relacionats amb la dispersió. Quan només es tenen en compte les espècies especialistes de congestera es fan evidents tres grups: a) plantes anuals o paucianuals que produeixen un nombre elevat de llavors de dimensions reduïdes que s'acumulen al sòl; b) camèfits o hemicriptòfits que produeixen llavors anemòcores; i c) altres espècies perennes, principalment hemicriptòfits, sense trets específics en la llavor. Les espècies que pertanyen als dos primers grups mantenen les poblacions ja sigui a través de l'existència d'un banc de llavors permanent al sòl, ja sigui a través de la persistència vegetativa i la dispersió. La manca de trets específics al tercer grup suggereix que aquestes espècies poden ser més sensibles a l'exclusió competitiva per part de les espècies no quionòfiles en un context de canvi climàtic, en el qual les plantes quionòfiles tenen tendència a desaparèixer.

Mots clau: vegetació alpina, dispersió, estratègies vegetals, *Salicetea herbaceae*, banc de llavors del sòl

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Functional Plant Traits and Species Assemblage in Pyrenean Snowbeds

**Josep M. Ninot · Oriol Grau · Empar Carrillo ·
Roser Guàrdia · Artur Lluent · Estela Illa**

Abstract In mid-latitude mountains, snowbeds often consist of small, scattered alpine belt units that host many plants of high biogeographic interest. Because most snowbed species are weak competitors, it is important to study the dissemination and persistence of their seeds to better understand their population dynamics. This study analyzed the snowbed flora of the Central Pyrenees using 11 morpho-functional traits, mostly related to seed function. The seeds of most plants found in snowbeds are small or very small, they have ovoid to elliptical shapes, and have no attributes related to dispersal. When only snowbed specialists (i.e., with a phytosociological optimum in snowbed habitats) are considered, three strategy groups become apparent: *i*) annuals or pauciennials producing abundant small seeds prone to accumulate in the soil; *ii*) chamaephytes or hemicryptophytes that produce anemochorous seeds; and *iii*) other perennials – mainly hemicryptophytes – with no specific seed traits. In the first two groups, the extant populations are maintained either by permanent soil seed banks or by means of vegetative persistence and dispersal. The lack of specific traits in the third group suggests that these plants could be more sensitive to direct competitive exclusion from non-chionophilous species under a changing climatic scenario in which snowbeds tend to disappear.

Keywords Alpine vegetation · Dispersal · Plant strategies · Salicetea herbaceae · Soil seed bank

Plant nomenclature Bolòs et al. (2005)

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J. M. Ninot (✉) · O. Grau · E. Carrillo · A. Lluent · E. Illa
Group of Geobotany and Vegetation Mapping, Department of Plant Biology, University of Barcelona,
Av. Diagonal 643, E-08028 Barcelona, Catalonia
e-mail: jninot@ub.edu

R. Guàrdia
Centre de Documentació de Biodiversitat Vegetal, University of Barcelona, C/ Baldiri Reixac 2,
E-08028 Barcelona, Catalonia

Introduction

High-altitude mountains, typically the alpine belt, are a suitable environment to investigate the relationships between environmental constraints, species pools and adaptive plant traits (Körner 2003: 2). Snowbeds are a particularly interesting habitat in the alpine belt, because long-lasting snow cover adds specific constraints over the general restrictions associated with altitude. Snowbeds are mainly characterized by a very short growing period. Plants living there undergo marked physical disturbance as a consequence of snow accumulation (on the plant carpet and soil) and intense soil leaching during the long snowmelt period (Komárková 1993; Körner 2003: 47–62). Notwithstanding, plants settling on snowbeds benefit from efficient thermal insulation during winter and spring, and from an abundant water supply during the growing season (Björk and Molau 2007; Lluent 2007).

Several plant communities in the snowbeds of alpine mountains have been described in relation to the environmental constraints of these habitats (e.g., Braun-Blanquet 1948; Onipchenko 2004; Choler 2005). Such communities are clearly different in terms of species composition and their functional structure and dynamics from those in neighbouring grasslands. Moreover, different snowbed communities can be found within a short transect (just a few meters) from an alpine grassland to the almost bare ground in the center of the snowbed, because the length of the growing season causes a steep gradient that affects snowbed communities. The substrate type (e.g., lime rich *vs* siliceous, soil texture) is also a determinant of the plant communities' composition.

The most common plants growing in snowbeds correspond to Arctic-Alpine taxa, which occur in rather isolated localities across the Pyrenees, where most of them have their southernmost populations in Europe (Bolòs et al. 2005). Most snowbed specialists are poor competitors (Kudo et al. 1999; Onipchenko and Semenova 2004; Schöb et al. 2010). They may occur in small gaps in alpine grasslands with abundant snow cover in winter, but they only develop optimally where long-lasting snow cover (i.e., snowbeds) hampers the establishment of grassland species. Also, a number of grassland plants settle on snowbeds from neighbouring mother-plants, and form scattered populations (Galen and Stanton 1995; Volkova et al. 2005).

The seed phase is important in a plant's life cycle because colonizing new sites and regenerating extant populations promotes gene flux. In relation to seed morphology, production and functioning in the particular snowbed environment, we hypothesize that seed dispersal across the landscape and persistence in the soil seed bank could have shaped to some extent the composition of snowbed communities. According to this, some snowbed species have been identified as opportunistic in other alpine ecosystems because of their regenerative strategies (Scherff et al. 1994; Semenova 2004), mostly in relation to their seed traits that ensure long persistence in the soil (Thompson 1993b; Cerabolini et al. 2003). However, other plant traits related to life history could also be responsible for the particular plant assemblage occurring in snowbeds.

Our aim is to assess the extent to which the species pool found in Pyrenean snowbeds supports this hypothesis. Thus, we analyze these species in terms of morpho-functional traits, mostly related to the seed function in this particular environment; we also highlight and discuss the main trends found in snowbed specialists – plants with their optimum in snowbed communities – compared to the remaining taxa – plants more frequent in pastures and rocky places, but also found in snowbeds. This comparison may help to explain the present and future fate of both groups, in the context of present interannual snow-cover variation and of future hypothetical reduction and disappearance of most Pyrenean snowbeds.

Material and Methods

Study Area and Vegetation

The study was performed in the Aigüestortes i Estany de Sant Maurici National Park, in the Central Pyrenees, in Catalonia (NE Iberian Peninsula). The alpine landscape of the area is highly representative of the Central Pyrenean high mountains. It consists of varied plant formations covering from exposed rocky surfaces to gentle slopes and valley bottoms with fens and lakes. The core of the study area is formed by a massive granodiorite batholith, although a few calcareous and slate outcrops are also found surrounding it.

Snowbed vegetation is widespread in the alpine belt, from (2,000)2,300 m a.s.l. to 2,700(2,900) m a.s.l., and includes most of the Pyrenean plant communities of the class Salicetea herbaceae (Carrillo and Ninot 1992). The abrupt relief given by granodiorite and lime leads to the formation of snowbeds mainly on footslopes of cliffs and other glacial geoforms. As such, chionophilous vegetation is restricted to small, irregular patches where concavities or gentle landforms favor some soil formation. In the most developed examples, distinct plant communities make clear graded catenas; these are modulated by substrate characteristics and by the length of the snowmelt period, which varies from the edges to the center of the snowbeds.

On siliceous soils the vegetation gradient goes from bryophyte carpets in the center of the snowbed, where snow lasts until mid-July and summer radiation is at its minimum, to Gnaphalio-Sedetum and *Salix herbacea* formations at the edges, which give way to grasslands with moderate snow cover and higher radiation (Trifolio-Phleetum gerardii Br.-Bl. 1948, Selino-Festucetum eskiae Nègre 1969). In calcareous areas, snowbeds are usually found at lower altitudes in the alpine belt, coinciding with particular, rocky north-facing slopes. In most cases, chionophilous vegetation consists of a dwarf-shrub community of *Salix reticulata* and *S. retusa*, which covers skeletal soils with protruding bedrock. The calcicole Potentillo-Gnaphalietum hoppeani and a moderately calcifugue *Salix herbacea* formation (Salici-Anthelietum thalictretosum) are found only where fine-textured soil covers gentle slopes. Outside the snowbed, this chionophilous vegetation contacts with the calcicole grasslands – Festuco-Trifolietum thalii Br.-Bl. 1948 in slight-snowpack zones, and Oxytropido-Elynetum myosuroidis Chouard 1943 in early-melting areas. More precise information on the snowbed vegetation is given in Table **S1** in Electronic Supplementary Material and in Carrillo and Ninot (1992).

Given the small area covered by snowbeds in most cases and the marked changes in topography and snow conditions of these surfaces, the whole set of snowbed plant communities may occur within a few meters. In addition, snowbed communities frequently include species more characteristic of neighbouring grasslands and of rocky places. Also, these grasslands offer good conditions for some plants typical of snowbeds (*Gnaphalium supinum*, *Sagina saginoides*, *Sibbaldia procumbens*), which frequently settle in small gaps. Moreover, interannual variability of snow cover causes small changes in the location and nature of the boundaries between plant communities (Lluent et al. 2006; Lluent 2007).

Analyses

We investigated the Spermatophyta occurring in the snowbeds of the Aigüestortes i Estany de Sant Maurici National Park, namely the species or subspecies found in at least 5 % of 233 phytosociological relevés of Salicetea herbacea taken in the area, for a particular monitoring program (reported in Lluent et al. 2006). Then, we added to this list a few other taxa considered characteristic of this vegetation class that were less frequent or were not sampled due to their local or regional rarity. This provided a list of 81 taxa, including species or subspecies that were strictly chionophilous, or typical of alpine habitats other than snowbeds, or even ubiquitous. The nomenclature used follows that given in Bolòs et al. (2005).

We selected a set of seed traits corresponding to morpho-functional aspects, five referring to seed characteristics (following the proposal of Thompson 1993a), and two measuring seed production and size of the soil seed bank (Table **1**). Seed is here understood as the diaspore unit or dispersule, i.e., including the walls of indehiscent fruits and the appendages (awns, pappi) or bracts attached to it during dispersal. Only in the case of seed mass do we refer to the germinule (i.e., excluding bracts, pappi or other attachments), because this trait is examined with the aim of evaluating the chance of emerging and settling on a new site.

The seed traits were analyzed from a specific collection of seeds and fruits sampled in the study area from 2006 to 2010, and kept in the Herbarium of the University of Barcelona (BCN). Morphological aspects were observed under a stereoscopic microscope at 10–40-fold magnification. The measurements correspond to the mean of ten seeds, and seed mass was calculated from five samples of at least 50 air-dried seeds each, weighed to the nearest mg. Exceptionally, for the few taxa that were not well documented from this collection, data were obtained or complemented from a few sources (particularly Bojňanský and Fargašová 2007; Castroviejo et al. 1986–2009; and Liu et al. 2008), under the assumption that these morphological data are relatively constant among populations of the same species living in different areas.

We evaluated the dispersal mode from seed morphology, assuming barochory for the seeds with no apparent dispersal attributes, short-distance anemochory (or zoochory) for seeds with awns or small wings (or small elaiosomes), and long-distance anemochory for seeds with pappi. Seed production was estimated after multiplying mean values of the number of seeds per fruit, and then fruits per infructescence, and infructescences per ramet, which were assessed from a minimum of ten cases during the specific sampling mentioned above.

The estimation of the seed-bank size was based on greenhouse germination experiments of soil samples obtained from the study area. The data on seed germination were recorded from more than 100 samples of different snowbed communities, and synthesized as the average densities for surface area from the samples where each

Table 1 Plant traits considered and data structure

Traits	Data structure	Units or categories
Seed length, width and breadth (including appendages)	quantitative	mm
Weight of germinule	quantitative	mg
Number of seeds per ramet	quantitative	–
Seed surface	categorized	1, smooth
		2, rugose, muricate
		3, striate
		4, hairy
Seed appendices	categorized	1, absent
		2, beak or hook
		3, wing(s)
		4, (hygroscopic) awn
		5, elaiosome
		6, persistent pappus
Seed morphology	categorized	1, sphaerical
		2, ovoid, rhomboidal
		3, tigonous, triquetrous
		4, lenticular, reniform, elliptical, subulate
		5, cylindrical, fusiform, ligulate
		6, conical, clavate
Density of seeds in the soil bank	categorized	1, <3 per m^2
		2, from 3 to 29 per m^2
		3, from 30 to 299 per m^2
		4, >300 per m^2
Lateral expansion	categorized	none
		few tillers, to short distance (<2.5 cm)
		many tillers, to short distance (dense turf)
		few tillers, to long distance (>2.5 cm)
Life form	categorized	therophyte
		non-gaminoid hemicryptophyte
		gramidoid hemicryptophyte
		diffuse chamaephyte
		pulvinular chamaephyte (small cushions)
		creeping chamaephyte

species occurred in the standing vegetation (methodology and results reported in Lluent 2007). Only in the few cases in which we could not collect enough reliable data from our experiments did we take density data from literature specific for snowbeds or alpine vegetation (Cerabolini et al. 2003; Semenova 2004; Welling et al. 2004; Marcante et al. 2009).

The seed analysis was complemented with the evaluation of two traits related to plant performance, namely lateral expansion and life-form (Table **1**). We sorted the taxa into six life-forms and into four categories of lateral expansion, as stated in Illa et al. (2006).

To define the distinct ecological groups and classify the plants analyzed, we synthesized the information about species ecological preferences assessed in the phytosociological studies by Carrillo and Ninot (1992) and in Bolòs et al. (2005) and created three distinct categories, i.e., three main habitats, in relation to the duration of snow cover: *i*) snowbeds (species characteristic of Salicetea herbaceae and included syntaxa, or typical of grasslands of late-melting sites); *ii*) grasslands (taxa from sites with medium snow duration, mainly typical of the alpine grassland classes Juncetea trifidi or Elyno-Seslerietea); and *iii*) rocky sites (plants from rock crevices, screes or fellfields, mainly thriving on early-melting surfaces). In the case of the first group, we distinguished the snowbed specialists by taking into account the phytosociological information from the BDBC data bank (Font 2009); from a pool of 1,600 relevés taken in the alpine belt of the Catalan Pyrenees, we considered to be snowbed specialists those taxa with at least 30 % of their occurrence in relevés of the class Salicetea herbaceae (i.e., more than 28 occurrences over 96 relevés). Although this threshold may seem a bit low, it allowed us to define a broader ecological group, which included locally rare snowbed species and also weakly chionophylous species. Among the non-specialist taxa, we defined the grassland species by using the same threshold (at least 30 % of occurrence in relevés of Caricetea curvulae or Elyno-Seslerietea). The inclusion of species into the third group, i.e., ecological preference for rocky sites, was based only on literature sources (Carrillo and Ninot 1992; Bolòs et al. 2005), given that most of them have a narrow ecological niche (e.g., humid crevices, lime-rich scree) although making a rather diverse group.

The data were organized in a rectangular table (81 species × 11 traits) to summarize the general spectra of the species found in the Pyrenean snowbeds. From this table we categorized the distribution of seed measurements or trait categories in the species pool investigated, and drew comparative analyses between the three ecological groups defined, based on species percentages of each trait category.

A general assessment of the functional diversification of the seeds was derived from a multivariate ordination of the species according to the traits stated in Table **1**. Data were analyzed in a Principal Component Analysis (PCA) using R.2.8.0 (R Development Core Team 2011). In the qualitative traits the categories were arranged in order of their functional significance and scored accordingly as qualitative traits (as ordered in Table **1**). The quantitative data were transformed logarithmically to normalize the distribution of the observations. Then, all variables were standardized so as to facilitate the comparison of different scales and units. To test the significance of the multivariate statistics, we ran a multivariate-ANOVA with 999 permutations (PERMANOVA test, Anderson 2001), using the 'vegan' package in R (Oksanen 2009).

Results

Trait Spectra in the Species Pool

Seeds of snowbed species are mostly very small: in 25 % of species the germinule weighs less than 0.1 mg, and in 75 % less than 0.6 mg (Table 2; Fig. S1a in Electronic Supplementary Material). The number of seeds produced per ramet is in general moderate or low. For instance, in 36 % of species this value is lower than 40, and in 60 % it is lower than 80 (Fig. S1b in Electronic Supplementary Material). However, because most of the plants considered are small and have ramets that occupy an area of a few cm^2, these seed yields are relatively high at population or community levels.

As for the soil seed bank, the obtained values of viable seed density also gave a power distribution among species (more detailed data in Lluent 2007), with a few species (*Sagina saginoides*, *Murbeckiella pinnatifida*, *Cardamine bellidifolia*) concentrating the vast majority of viable seeds. 57 % of the species were apparently absent or almost absent in the soil seed bank, whereas the rest of the species were evenly distributed among the other density categories established (Table 2).

68 % of the species had slightly longer than wide seeds, i.e., varying from ovoid to elliptical (Fig. S1c in Electronic Supplementary Material), with a smooth surface (78 %) and without appendages (58 %). However, 14 % of the species had pappi (Asteraceae, Salicaceae) that are more or less efficient in wind dispersion; and 17 % had awns – mostly short – or narrow wings, which may play some role in seed dispersal. No species had clear adaptations to zoochory (i.e., fleshy fruits, hooked dispersule, etc.), except for the small elaiosomes present in three *Luzula* species.

Of the life-forms considered, the most commonly observed in the snowbeds were hemicryptophytes (72 %), most of which were non-graminoid (Fig. S1d in Electronic Supplementary Material), as is generally the case in alpine vegetation (Illa et al. 2006). Chamaephytes made up the second group (22 %), including three woody creeping species of *Salix*. Therophytes were rare and geophytes were absent. In terms of ecological preference, we included 23 species in the group of snowbed specialists, and distributed the remaining species into the groups of grasslands (45 taxa) and rocky sites (13 taxa), as described in the methods section.

Relationships between Seed Traits and Species

The first PCA based on the seed traits revealed strong correlation between width, breadth, length and weight, and between these traits and the type of appendix. To avoid an over-biased ordination, we performed a second analysis rejecting some of the most correlated traits (seed breadth, mostly correlated with seed width, and seed shape, also dependent on the three seed dimensions). Among the remaining traits, correlation within pairs in absolute values ranged from almost zero (weight and surface) to about 0.71 (length and width) as shown in Table 3.

The species ordination shown in Fig. 1a highlights the trade-off between seed mass and seed production, i.e., from taxa producing a few big seeds (in the upper central part: e.g., *Trifolium alpinum*, *Androsace carnea*, *Arenaria purpurascens* or *Galium pyrenaicum*) to those bearing large numbers of tiny seeds (in the lower right corner: e.g., *Gentiana nivalis*, *Saxifraga moschata*, *S. aizoides* or *Veronica alpina*). Most of

Table 2 Characterization of the taxa analyzed according to nine traits (see Table 1) and to habitat preference: Longitude and Width of the dispersule (mm), Weight of the germinule (mg), Number of seeds per ramet, Surface type (1–4, from smooth to hairy), Appendices of the dispersule (1–6, from none to pappus), Seed Bank density in the soil (1–4, from <3 to >300 of seeds * m^{-2}), Lateral Expansion (1 – none; 2 – few tillers to short distance; 3 – many to short distance; 4 – few to long distance), Life Form (Th – therophyte; Hng – non-graminoid hemicryptophyte; Hg – graminoid hemicryptophyte; Chd – difuse chamaephyte; Chp – pulvinular chamaephyte; Chr – creeping chamaephyte), and Habitat preference relating snow duration (Sb – snowbeds; Gld – grasslands, Rk – rocky places)

	Long	Width	Weight	Nmb	Srf	App	S-B	L-E	L-F	Hab
Agrostis alpina	6.4	0.5	0.070	30	3	4	1	3	Hg	Gld
Agrostis rupestris	3.6	0.6	0.080	40	3	4	3	3	Hg	Gld
Alchemilla fissa	1.5	0.9	0.400	18	1	1	1	4	Hng	Sb
Alchemilla pentaphyllea	1.3	0.8	0.336	6	1	1	1	4	Hng	Sb
Alopecurus alpinus	5.2	0.8	0.260	60	4	4	1	3	Hg	Sb
Androsace carnea	2.5	1.5	1.532	10	2	1	1	2	Hng	Gld
Antennaria carpatica	4.5	2.0	0.080	100	1	6	1	2	Hng	Gld
Arenaria biflora	0.8	0.7	0.133	144	2	1	3	4	Chr	Sb
Arenaria purpurascens	1.7	1.2	1.056	12	1	1	1	3	Chp	Gld
Armeria alpina	5.5	1.2	0.928	15	3	4	1	3	Hng	Gld
Astrantia minor	4.0	1.6	0.796	120	3	3	1	2	Hng	Rk
Campanula scheuchzeri	0.8	0.4	0.043	75	1	1	1	2	Hng	Gld
Cardamine bellidifolia subsp. *alpina*	1.3	1.0	0.198	40	1	1	4	2	Hng	Sb
Cardamine resedifolia	1.3	1.0	0.200	184	1	3	1	2	Hng	Rk
Carex atrata subsp. *nigra*	3.3	1.6	0.490	96	1	2	3	3	Hg	Gld
Carex curvula subsp. *curvula*	4.8	1.6	1.304	20	1	2	3	3	Hg	Gld
Carex pyrenaica	3.8	0.9	0.336	16	1	2	3	3	Hg	Sb
Cerastium cerastoides	1.1	0.9	0.166	26	2	1	4	2	Chr	Sb
Epilobium anagallidifolium	8.2	3.5	0.075	130	1	6	3	2	Hng	Sb
Euphrasia minima	1.3	0.5	0.110	70	1	1	1	1	Th	Gld
Festuca eskia	7.4	1.4	1.292	140	3	4	1	3	Hg	Gld
Festuca glacialis	5.0	0.8	0.510	18	3	4	1	3	Hg	Rk
Festuca nigrescens	7.0	1.0	0.980	80	3	4	3	3	Hg	Gld
Galium pyrenaicum	1.5	1.2	1.400	12	1	1	1	3	Chp	Rk
Gentiana alpina	0.9	0.3	0.200	50	2	1	1	2	Hng	Gld
Gentiana nivalis	0.9	0.5	0.078	1250	2	1	1	1	Th	Gld
Gentiana verna	0.9	0.5	0.090	625	2	1	1	2	Hng	Gld
Gnaphalium hoppeanum	4.9	2.5	0.090	96	4	6	2	2	Hng	Sb
Gnaphalium supinum	5.0	2.7	0.107	96	4	6	4	2	Hng	Sb
Helictotrichon sedenense	18.0	1.3	1.800	56	1	4	3	4	Hg	Gld
Hieracium lactucella	4.8	1.7	0.093	25	3	6	1	2	Hng	Gld
Kobresia myosuroides	2.5	1.0	0.690	14	1	1	3	3	Hg	Gld
Leontodon pyrenaicus	9.0	1.0	0.768	30	1	6	2	2	Hg	Gld
Leucanthemopsis alpina	3.0	1.0	0.400	30	3	3	1	2	Hng	Gld
Linaria alpina	1.8	1.6	0.160	140	1	1	1	2	Chr	Rk
Lotus corniculatus subsp. *alpinus*	1.9	3.1	1.608	60	1	1	1	2	Hng	Gld

Table 2 (continued)

	Long	Width	Weight	Nmb	Srf	App	S-B	L-E	L-F	Hab
Luzula alpinopilosa	1.2	0.6	0.210	108	1	5	1	2	Hg	Sb
Luzula lutea	1.4	0.7	0.360	108	1	5	2	2	Hg	Gld
Luzula spicata	1.1	0.7	0.356	57	1	5	2	2	Hg	Gld
Minuartia sedoides	0.9	0.8	0.260	75	2	1	1	3	Chp	Rk
Minuartia verna	1.2	1.0	0.312	85	2	1	1	2	Chp	Gld
Mucizonia sedoides	0.5	0.2	0.030	40	1	1	3	1	Th	Sb
Murbeckiella pinnatifida	1.1	0.5	0.122	280	1	3	4	2	Hng	Rk
Myosotis alpestris	1.8	1.1	0.540	192	1	1	1	2	Hng	Gld
Nardus stricta	10.4	0.9	0.380	15	3	4	3	3	Hg	Gld
Oreochloa disticha subsp. *blanka*	3.9	1.3	0.340	11	4	1	1	3	Hg	Gld
Oxytropis pyrenaica	2.2	1.7	2.000	48	1	1	3	2	Hng	Gld
Pedicularis kerneri	2.2	1.0	0.202	120	3	1	1	2	Hng	Gld
Phyteuma hemisphaericum	1.1	0.4	0.150	500	1	1	1	2	Hng	Gld
Plantago alpina	2.1	0.9	0.544	75	1	1	2	2	Hng	Gld
Plantago monosperma	3.3	1.6	2.990	15	2	1	3	2	Hng	Gld
Poa alpina	3.2	0.8	0.350	100	3	1	3	3	Hg	Gld
Polygonum viviparum	2.6	1.5	2.500	20	2	1	3	2	Hng	Gld
Potentilla brauneana	1.1	0.9	0,320	12	1	1	1	2	Hng	Sb
Primula elatior subsp. *intricata*	1.6	1.1	0.850	288	2	1	1	2	Hng	Gld
Primula integrifolia	1.5	1.0	0.200	159	1	1	2	2	Hng	Gld
Pritzelago alpina	1.7	0.7	0.236	30	3	3	4	2	Chd	Rk
Ranunculus alpestris	2.2	0.9	0.408	40	1	2	4	2	Hng	Sb
Ranunculus pyrenaeus	2.7	1.5	1.040	25	1	2	1	2	Hng	Gld
Sagina saginoides	0.4	0.3	0.020	450	1	1	4	2	Chd	Sb
Salix herbacea	4.0	3.0	0.510	20	1	6	1	2	Chr	Sb
Salix reticulata	3.2	2.7	0.050	96	1	6	1	4	Chr	Sb
Salix retusa	5.5	2.7	0.050	70	1	6	1	4	Chr	Sb
Saxifraga aizoides	0.7	0.4	0.050	600	2	1	2	2	Chd	Rk
Saxifraga androsacea	0.6	0.3	0.050	80	1	1	3	2	Hng	Sb
Saxifraga moschata	0.6	0.3	0.030	432	2	1	3	3	Chp	Rk
Saxifraga oppositifolia	1.1	0.5	0.110	258	3	1	2	4	Chr	Rk
Sedum alpestre	0.7	0.3	0.030	225	1	1	3	2	Chd	Sb
Sedum atratum	0.8	0.3	0.040	50	3	1	1	1	Th	Rk
Selinum pyrenaeum	4.5	3.0	1.580	300	3	3	1	2	Hng	Gld
Sibbaldia procumbens	1.2	0.9	0.470	48	1	1	3	2	Hng	Sb
Silene acaulis	1.2	1.0	0.316	21	2	1	1	3	Chp	Rk
Soldanella alpina	1.0	0.8	0.228	60	1	1	1	2	Hng	Gld
Taraxacum alpinum	11.0	4.0	0.450	30	3	6	1	2	Hng	Gld
Taraxacum dissectum	10.3	4.0	0.416	30	3	6	1	2	Hng	Gld
Thalictrum alpinum	3.1	1.1	0.432	30	3	1	1	2	Hng	Gld
Thymus nervosus	0.7	0.5	0.130	48	1	1	1	4	Chr	Gld

Table 2 (continued)

	Long	Width	Weight	Nmb	Srf	App	S-B	L-E	L-F	Hab
Trifolium alpinum	2.7	2.3	5.300	8	1	1	1	2	Hng	Gld
Trifolium thalii	1.4	1.2	0.840	30	1	1	1	2	Hng	Gld
Veronica alpina	0.9	0.6	0.040	170	1	1	4	2	Hng	Sb
Veronica aphylla	1.1	0.9	0.090	63	1	1	1	2	Hng	Sb

the species studied are spread along the area between these two extremes, with those with more rounded, unappendaged, smoother seeds located near the upper right edge. In contrast, dispersules with more conspicuous appendages and higher dimensions appear from the central part of the field to the lower left corner. This extreme consists of Asteraceae, Salicaceae and analogous types (e.g., *Gnaphalium supinum*, *G. hoppeanum*, *Salix retusa*, *S. reticulata*, *Taraxacum alpinum* or *Epilobium anagallidifolium*).

Species Groups

Life-forms show no obvious pattern in relation to seed traits. The most abundant type, hemicryptophytes, occupies almost all the area defined by the PCA (Fig. 1a). Among these, while non-graminoids are widespread, graminoids remain mostly reduced to the central-left part of the cloud. Therophytes and short-lived chamaephytes tend to be found at the lower right part, and pulvinules are mainly placed in the upper central part.

The ecological groups also overlap in the area defined by the PCA, although snowbed specialists are mostly concentrated in peripheral parts of the species cloud (Fig. 1b). The PERMANOVA test gives statistical support (*P*-value 0.018) to separate the two ecological groups shown in the figure (snowbed specialists *vs* non-specialists). Besides, two sub-groups of snowbed specialists may be observed in rather extreme positions (right and lower left), whereas the others are spread within the main core (upper central part).

Table 3 Pearson's product moment correlations between the variables measured: Numb – number of seeds per ramet; Width & Long – dimensions of the dispersule; Weight – weight of the germinule; Append – appendage type of the dispersule; Soil – density of seeds in the soil bank; Surf – surface type of the dispersule. * – statistically significant at $P<0.05$

	Numb	Width	Long	Weight	Append	Soil
Width	−0.3082*					
Long	−0.3442*	0.7071*				
Weight	−0.4961*	0.5247*	0.455*			
Append	−0.0497	0.4919*	0.6766*	−0.0492		
Soil	0.0918	−0.1812	−0.0689	−0.1503	−0.0484	
Surf	−0.0255	0.1342	0.4067*	0.0086	0.2699*	−0.0861

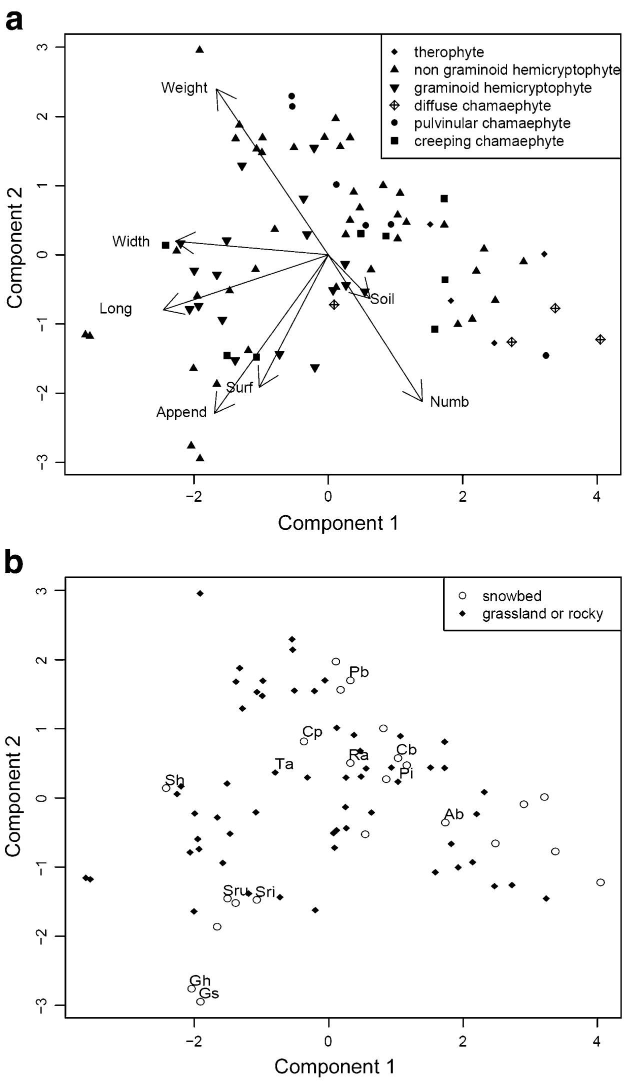

Fig. 1 Ordering of the taxa on the first two components (variance: 40.21 % and 20.15 %, respectively) given by the PCA, with the continuous variables transformed to $\log_{10}$: **a** Direction and relative weight of the traits in the analysis (abbreviated as in Table 3) indicated by the direction and size of the arrows, and life-form of the taxa; **b** Position of the snowbed specialists within the total pool considered, with the main species (Table S1 in Electronic Supplementary Material) abbreviated as follows: Ab – *Arenaria biflora*; Cb – *Cardamine bellidifolia*; Cp – *Carex pyrenaica*; Gh – *Gnaphalium hoppeanum*; Gs – *Gnaphalium supinum*; Ms – *Mucizonia sedoides*; Pb – *Potentilla brauneana*; Ra – *Ranunculus alpestris*; Sb – *Salix herbacea*; Sru – *Salix retusa*; Sri – *Salix reticulata*; Sp – *Sibbaldia procumbens*; Ss – *Sagina saginoides*

The distinct distribution of traits in each ecological group is illustrated in Fig. 2, which refers to three crucial aspects of plant life: vegetative expansion, soil seed bank, and dispersal. The group of snowbed specialists is similar to the grassland group in terms of general spectra, but is differentiated by the noticeable presence of species forming dense soil seed banks, by fewer turf-forming species and by more stoloniferous or long-rhizomatous plants. The snowbed group includes most of the long-distance disseminators; short-distance anemochory is less frequent than in grasslands, whereas barochory is more common, although clearly less so than in rocky places.

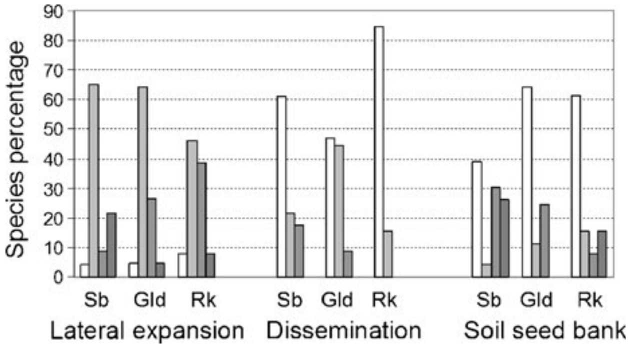

Fig. 2 Species percentages for three crucial traits in the three ecological groups considered (Sb – Snowbed specialists; Gld – Grasslands; Rk – Rocky places). The categories in each trait are indicated as growing grey intensities, in the following order: *i*) Lateral expansion: none, few tillers to short distance, dense turf, few tillers to long distance; *ii*) Dispersal mode: barochory, anemochory to short distance, anemochory to long distance; and *iii*) Density in the soil seed bank: from absent or very low to very high

Discussion

The Effect of Snowbed Constraints on the Flora

Snowbeds are particular habitats within alpine landscapes, in which plants are limited by various environmental constraints. Our results, together with other studies (Cherednichenko 2004; Choler 2005; Illa et al. 2006) show that snowbeds harbor less diversity of plant traits than do less restrictive habitats, and that they promote greater frequency of specific types or traits, such as deciduous woody chamaephytes, long stolons or rhizomes, or higher N content in leaves (Choler 2005). The snowbed species pool studied here includes no zoochorous species (producing fleshy fruits, or hooked or adherent seeds) nor geophytes. The seeds are mostly reduced to low-weight values and to ovoid or elliptical shapes (Fig. **S1** in Electronic Supplementary Material). A similar distribution of mass values has been found in other alpine assemblages (Zhang et al. 2004; Navarro et al. 2009), whereas in temperate floras the modal seed weight is one order of magnitude higher (Cerabolini et al. 2003).

A few plant types acquire particular relevance in snowbeds, more in terms of dominance than of species numbers. This is the case of deciduous chamaephytes (i.e., *Salix* spp.), and of therophytes and pauciennials, which produce large numbers of persistent seeds (*Mucizonia sedoides, Sagina saginoides*). In fact, the density of seeds found in the soil has been identified as a good surrogate for seed persistence in some snowbed ecosystems (Cerabolini et al. 2003; Semenova 2004; Lluent 2007).

These weak tendencies become stronger if the 23 snowbed specialists are considered as a unit (Fig. **2**). This is partly related to the particular taxonomical composition of this group, in which the richer families in the alpine flora (i.e., Asteraceae, Poaceae, Brassicaceae, Caryophyllaceae and Fabaceae; Körner 2003: 14) are poorly represented (Table **S2** in Electronic Supplementary Material). The rarity of Poaceae among snowbed specialists may be related to seed traits, because most grasses produce moderate numbers of seeds, which disseminate over a short distance and have low persistence in soil. Although these limitations are of minor importance in grasslands, they seem to become disadvantageous in snowbeds, where most species produce seeds that are persistent in the soil bank or are easily air-dispersed (Onipchenko and Semenova 2004). The relative decline of the other families mentioned above seems to be related to other biological features, because their seeds show no clear trends in relation to snowbed function. In fact, the relative increase of other taxa in the group of snowbed specialists (*Salix*, Crassulaceae) could explain the increase of co-occurring plant traits derived from their phylogenetic signal, which do not necessarily enhance their adaptation to snowbeds. Thus, the ecological filtering of plant traits in snowbeds seems to have shaped the chionophilous assemblage at the family level, because seed traits are rather dependent on these taxonomic entities (Šerá and Šerý 2004).

Diversification into Snowbed Microhabitats

It should be taken into account that snowbed specialists thrive in rather different microhabitats. Not only the duration of the period with snow cover, but also substrate properties affect them. Thus, chionophilous plants may be included in a few contrasting types and strategies, some of which involve specific seed traits. The morpho-functional analyses presented in this study (Fig. **1**) reveal three main strategy groups: *i*) annuals or short-lived perennials producing relatively small and abundant seeds, mostly without any dispersal aptitudes, which tend to accumulate in the soil bank up to high densities; *ii*) woody chamaephytes (ex. *Salix* spp.) or hemicryptophytes producing medium-to-high numbers of anemochorous seeds, thus ensuring vegetative persistence and wide wind dispersion; and *iii*) other perennials with no specific seed traits (medium production, low or no seed bank, barochory). In the first group, the maintenance of populations is based on the occupancy of patches with lower competition, which may generally develop in the late-melting parts of snowbeds or in small gaps of other snowbed parts or of neighbouring pastures (Semenova 2004; Welling et al. 2004; Lluent et al. 2006; Schöb et al. 2010). Favourable years would lead to a strong increase in the soil seed bank of these species in the areas where they normally or exceptionally thrive. In the second group, population maintenance is more ensured through perennial habit, mostly in the case of woody chamaephytes, and through annual seed rain facilitating occasional recolonization of favorable sites (Choler 2005; Lluent et al. 2006). Because the climatic conditions affecting snowbeds follow a very irregular pattern between years, species of the first two groups will presumably persist better if the decrease in areas occupied by snowbeds in the Pyrenees persists in the future (López-Moreno et al. 2009) under the expected warmer climate at regional scale (Esteban et al. 2010). Comparatively, the third group seems to face a more uncertain future; dispersal and persistence in soil are very limited (Scherff et al. 1994; Welling et al. 2004) and, in the cases of poorer tillering, vegetative performance may not ensure strong persistence.

Long-Term Persistence of Snowbed Plants

When estimating the nature of the soil seed bank in snowbeds, it should be taken into account that the persistence of viable seeds in natural conditions is only partially known. The few specific studies done on this subject (Molau and Larsson 2000; Semenova 2004) and our data neglect the presence of viable seeds of taxa with specific germination requirements, which cannot be reproduced in non-natural conditions. Most of the species pool investigated fulfils the morphological template proposed by Thompson (1993b; reviewed in Fenner and Thompson 2005: 82–86), which predicts that small seeds (<1 mg) with a fairly isometric shape (variance among dimensions <0.18) would persist easily in the soil (Fig. **3**). This hypothesis has been supported by case studies on distinct species pools. However, these morphological traits do not ensure seed viability (Cerabolini et al. 2003). In our study, most of the species considered, and most of the snowbed specialists, fall in the graphic area (Fig. **3**) that is characteristic of persistent seed banks. The only exceptions within these specialists are *Alopecurus alpinus* and *Carex pyrenaica*. However, a few non-chionophilous species with variance values higher than 0.18 were found in the soil bank (i.e., *Poa alpina*, *Helictotrichon sedenense*, *Nardus stricta*, *Kobresia myosuroides* and *Carex atrata* subsp. *nigra*). All these exceptions belong to Poaceae and Cyperaceae, whose bare fruits fulfil the shape conditions and may thus incorporate into the soil after losing the attached bracts or utricles. Moreover, the coarse soils found in snowbeds facilitate seed trapping, even for grasses and sedges, as experimentally found in sandy alpine soils (Chambers et al. 1991; Marcante et al. 2009).

Several snowbed specialists combine medium-to-high seed production with medium-to-high density of their soil seed bank, a trend also found in other snowbed ecosystems (Semenova 2004). Even some species producing only moderate seed numbers form large soil banks (*Sibbaldia procumbens*, *Sagina saginoides*, *Mucizonia sedoides*), which may progressively accumulate through time (Semenova 2004; Lluent 2007).

It has been hypothesized that snowbed specialists will be negatively affected under a scenario of rising temperatures because of the greater competitiveness of grassland species, which are favored by longer growing seasons (Schöb et al. 2009). More precisely, Björk and Molau (2007) envisage a stronger effect on chionophilous grasses and sedges than on chionophilous chamaephytes or forbs. In our case, only two species of these taxonomic groups are snowbed specialists, while others are weakly chionophilous. The seeds of these graminoids cannot ensure persistence in the

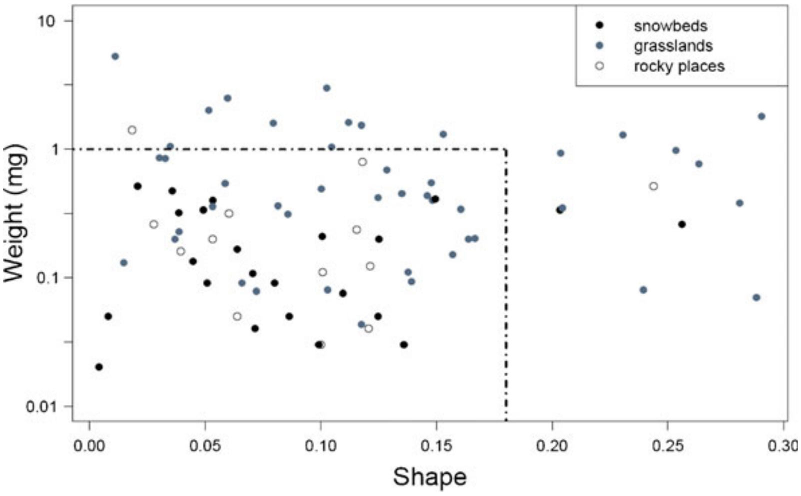

Fig. 3 Ordering of the taxa according to seed weight and seed shape coefficient (variance between dispersule length, width and breadth). The area hypothesized for species with persistent soil seed bank (seeds slighter than 1 mg, and with shape coefficient lower than 0.18) includes most of the snowbed specialists, and all the species well represented in the soil seed bank

soil or re-colonization from distant sites if they are displaced by more competitive alpine graminoids. More generally, snowbed specialists belonging to the third strategy group mentioned above seem to be prone to suffer more directly from competitive exclusion, in a scenario of a warmer climate (Esteban et al. 2010) and fluctuating or vanishing snowbeds. Their competitive disadvantage in respect to grassland species may not then be compensated by seed traits that favor their success in finding spatial or temporal ecological windows.

Concluding Remarks

As hypothesized, seed function seems to have played a noticeable role in the ecological selection of the extant snowbed plant assemblage in the Pyrenees. The group of snowbed specialists clearly shows some trait convergence in terms of seed types compared to the whole alpine flora. However, it still includes a few contrasting strategy sub-groups, whose persistence and regeneration in snowbeds depend on specific seed morphology and function combined with other plant traits.

The ecological filtering occurring in snowbeds has positively or negatively selected some taxonomic groups (families, genera) through the selection of some functional plant traits inherent to phylogeny (e.g., fruit type and vegetative tillering in grasses, or seed and habit in *Salix*).

The ongoing climate warming in the Pyrenees may reduce the chionophilous flora at regional scale, and we predict that it will have a stronger effect on those species that lack the specific morpho-functional traits associated with snowbeds.

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Electronic Supplementary Material

Fig. S1 Characterisation of the species pool found in the snowbeds, in terms of number of species per category in four traits: **a** Seed weight; **b** Number of seeds per ramet; **c** Seed morphology (sphaerical, ovoid, trigonous, lenticular, cylindrical, conical); **d** Life-form (therophytes, non-graminoid hemicryptophytes, graminoid hemicryptophytes, diffuse chamaephytes, pulvinular chamaephytes, creeping chamaephytes)

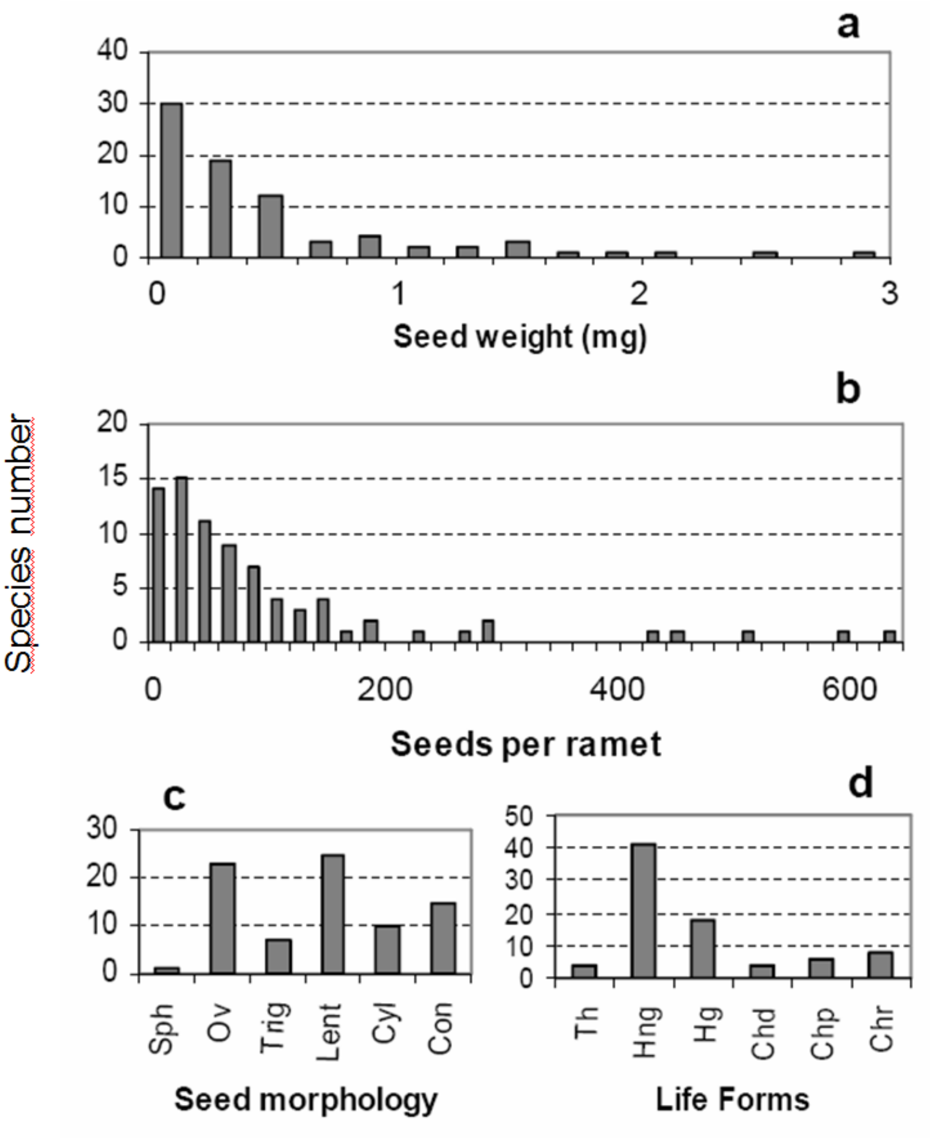

Table S1 Main characteristics of the snowbed communities (class Salicetea herbaceae Br.-Bl. 1948) found in the study area. Data synthesised from Braun-Blanquet 1948; Carrillo and Ninot 1992; and Lluent et al. 2006

Plant communities	Main species (* dominant)	Physiognomy	Substrate	Location in the snowbed
Polytrichetum sexangularis Br.-Bl. 1948	*Polytrichum sexangulare**	Bryophyte carpet	Siliceous; Sand and gravel with a thin humic layer	The innermost, latest-melting zone
Gnaphalio supini-Sedetum candollei Br.-Bl. 1948 (incl. Carici pyrenaicae-Cardaminetum alpinae Rivas Mart. et al. 1991)	*Gnaphalium supinum* *Cardamine bellidifolia* ssp. *alpina* *Mucizonia sedoides* *Arenaria biflora* *Carex pyrenaica*	Patched herbaceous carpet	Siliceous; Skeletal soils, rich in gravel or sand	Late-melting zone
Salici-Anthelietum juratzkanae Br.-Bl. 1948 (incl. subass. thalictretosum alpini E. Carrillo et Vigo 1992)	*Salix herbacea** *Gnaphalium supinum* *Sibbaldia procumbens* *Sagina saginoides*	Dense herbaceous carpet	Siliceous or lime leached; Dense, humus-rich, fine soils	Medium-melting zone
Potentillo dubiae-Gnaphalietum hoppeani Br.-Bl. 1948	*Ranunculus alpestris* *Potentilla brauneana* *Gnaphalium hoppeanum*	Patched herbaceous carpet	Calcareous; Fine-textured, deep soil	Late-melting zone
Carici parviflorae-Salicetum retusae Rivas Mart. 1969	*Salix reticulata** *Salix retusa**	Dense dwarf-shrub formation	Calcareous; Gravel-rich, irregular soils on rocky slopes	Medium-melting zone

Table S2 Main families found in the snowbeds, evaluated by the number of species in the total pool, and by the number of specialists

Family	total pool	snowbed specialists
Poaceae	10	1
Asteraceae	8	2
Caryophyllaceae	7	3
Scrophulariaceae	5	2
Brassicaceae	4	1
Cyperaceae	4	1
Fabaceae	4	0
Primulaceae	4	0
Rosaceae	4	4
Saxifragaceae	4	1
Crassulaceae	3	2
Gentianaceae	3	0
Juncaceae	3	1
Ranunculaceae	3	1
Salicaceae	3	3
Other	12	1
Total	81	23

Capítol III

Aportación al conocimiento de la estructura funcional de los pastos alpinos de los Pirineos catalanes

Aportació al coneixement de l’estructura funcional dels prats alpins dels Pirineus catalans

Estela Illa & Josep M. Ninot

Bull. Societé Histoire Naturelle Toulouse 141 (2005): 175-182

Aportació al coneixement de l'estructura funcional dels prats alpins dels Pirineus catalans

Resum

L'objectiu d'aquest treball és l'anàlisi comparativa de l'estructura funcional de les comunitats dominants a l'estatge alpí: els prats. A partir d'inventaris bibliogràfics vam obtenir dades estructurals de les deu associacions més freqüents i extenses, i vam recol·lectar-ne 38 mostres per estimar els seus patrons de fitomassa aèria (subdividida en compartiments funcionals), d'estructura foliar i de potencialitat productiva (LAI). Els resultats mostren unes tendències que permeten diferenciar tres grans grups de comunitats. Els prats densos (tres associacions) són molt uniformes a nivell estructural i presenten els valors més elevats de biomassa, de necromassa i de virosta no fragmentada. Els prats esglaonats (tres associacions) tenen biomasses moderades i inclouen alguns camèfits, fet que indica certes condicions d'estrès. Finalment, els prats rasos culminants (quatres associacions) tenen valors de biomassa entre moderats i baixos, i hi creixen líquens terrícoles i camèfits reptants i pulviniformes, relacionats amb les dures condicions ambientals que s'hi donen. El pes específic foliar de les 32 espècies analitzades va donar valors relativament elevats (5-13,5 mg/cm^2), i va permetre calcular índexs de LAI força heterogenis (entre 0,6 i 4,7) per a les diferents associacions.

Mots clau: prats, vegetació alpina, Pirineus, fitomassa, LMA, LAI

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Bull. Soc. Hist. Nat., Toulouse, 141-2, 2005, 175-182

Aportación al conocimiento de la estructura funcional de los pastos alpinos de los Pirineos catalanes

por E. Illa & J.-M. Ninot

Grup de Geobotànica i Cartografia de la Vegetació, Universitat de Barcelona, Av. Diagonal 645, E-28028 Barcelona.
e-mail : estelailla@ub.edu

RESUMEN

El objetivo de este trabajo es el análisis comparativo de la estructura funcional de las comunidades dominantes en el piso alpino, los pastos. De las 10 asociaciones más frecuentes y extensas, obtuvimos datos estructurales de los inventarios bibliográficos, y recolectamos 38 muestras para estimar sus patrones de fitomasa aérea (subdividida en compartimientos funcionales), de estructura foliar y de potencialidad productiva (LAI). Los resultados nos muestran unas tendencias que permiten distinguir tres grandes grupos de comunidades. Los pastos densos (3 asociaciones) son muy uniformes en su estructura y presentan los valores más elevados de biomasa y de necromasa y mantillo. Los pastos en gradería (3 asociaciones) muestran biomasas moderadas e incluyen algunos caméfitos, lo que indica ciertas condiciones de estrés. Finalmente, los pastos ralos culminantes (4 asociaciones) dan valores de biomasa entre moderados y bajos, y contienen líquenes terrícolas y caméfitos reptantes y pulviniformes, en relación con las duras condiciones a que se hallan sometidos. El peso específico foliar de 32 especies analizadas dio valores relativamente altos (5-13,5 mg/cm^2), y permitió evaluar índices de LAI bastante heterogéneos (0,6-4,7) para las distintas asociaciones.

Palabras clave : Pastos, vegetación alpina, Pirineos, fitomasa, LMA, LAI.

ABSTRACT

A contribution to the structure and functioning knowledge of Alpine pastures of the Catalan Pyrenees

This paper is aimed to the comparative analysis of the functional structure in the dominant communities of the Alpine belt. With respect to the 10 commonest associations, we obtained structure data of all the published relevés and yielded 38 representative field samples. From these samples, we have evaluated above-ground phytomass patterns and partitioning, leaf structure, and community LAIs. On the basis of the results, the Alpine communities analysed may be ordered into three main groups. Dense pastures (3 associations) are strongly dominated by hemicryptophytes and show the highest values of biomass, necromass and litter. Sloping pastures (3 associations) are more irregular, show moderate biomass values and include some chamaephytes, related to more stressing conditions. The last group, short pastures of summits and high slopes (4 associations), yielded moderate to low biomass amounts and noticeable percentages of lichens and low chamaephytes, which would indicate the strong constraints typical of their habitats. The leaf mass per area indexes measured in 32 species gave moderate to quite high values (5-13.5 mg/cm^2), and LAIs of the associations drew a rather broad range (0.6-4.7).

Key words : Pastures, Alpine vegetation, Pyrenees, phytomass, LMA, LAI.

INTRODUCCIÓN

En el paisaje de las altas montañas, el piso alpino destaca por su potencialidad pratense, condicionada por diversas constricciones ambientales genéricas : brevedad de periodo vegetativo, suelos de escaso desarrollo y con bajas dosis de fertilidad, cubierta nivosa y bajas temperaturas en invierno, dinámica de vertiente, etc. Por otro lado, la topografía diversa, a menudo abrupta, produce una gran variedad de situaciones a pequeña escala, que se expresan en forma de interesantes e intricados mosaicos de comunidades vegetales. Entre todas ellas, destacan especialmente los pastos, por ser el tipo de vegetación más genuinamente alpino, y también por la notable diversidad específica y funcional que muestran, tras su aparente homogeneidad. Al lado de comunidades relativamente maduras (algunas asumidas como potenciales) que ocupan suelos estables, se extienden pastos discontinuos que dependen de solifluxión activa en amplias vertientes, o densos tapices meso-higrófilos en hondonadas con suelo lixiviado, incluso con hidromorfía. Un buen número de estudios han abordado la descripción de los aspectos anteriores en los Pirineos (Braun-Blanquet 1948, Nègre 1969, Rivas-Martínez 1974, Carrillo & Ninot 1992, etc). En cambio, poco se sabe de los aspectos funcionales de las plantas y de las comunidades del piso alpino pirenaico, en comparación con comunidades alpinas de otros macizos (Cernusca 1989, Körner 1999, Onipchenko & Blinnikov 1994). No disponemos ni siquiera de aproximaciones a cuestiones funcionales de gran trascendencia, por ejemplo relativas a dinámica de la fitomasa, o del carbono y de nutrientes, a la potencialidad de producción primaria, o al uso del agua edáfica. Un análisis de la estructura funcional de los pastos alpinos permitiría una primera aproximación a dichas cuestiones, y también extrapolaciones a escala de paisaje, mediante el tratamiento de la cartografía de la vegetación de que ya se dispone (Carreras et al. 2004), o planificar estudios experimentales más específicos en el campo de la ecofisiología vegetal.

En este contexto, nuestro primer objetivo es obtener información de base sobre aspectos estructurales de las formaciones más típicamente alpinas, los pastos. A partir de su análisis comparativo, discutiremos los rasgos funcionales que derivan de ellos y la diversificación ecológica observada en las comunidades pratenses y en sus especies protagonistas.

EL ÁREA DE ESTUDIO

Nos centramos en el piso alpino de los Pirineos de Cataluña y Andorra, que se desarrolla por encima de los 2.400 m s.n.m. en las solanas y de los 2.200 m en umbrías, rellanos y concavidades. Dichos límites descienden unos 100 m en el extremo oriental de la cordillera y en el valle de Arán, debido a sus bioclimas más marítimos (Carreras et al. 1996). Como situación media, puede asumirse que el periodo vegetativo, que decrece al aumentar la altitud, dura unos 88 días a 2.300 m s.n.m y tan sólo 42 días a 2.700 m (Gómez et al. 1997). En la práctica, a partir de los 2.600-2.700 m los pastos bien desarrollados resultan ya sumamente raros y exiguos, debido no ya a aspectos climáticos, sino principalmente a la escasez de situaciones topográficas y edáficas adecuadas (Vigo & Ninot 1987).

Así definido, el piso alpino muestra una superficie proyectada de 735 km^2, de contorno muy irregular e incluyendo algunas pequeñas áreas prepirenaicas aisladas. En su mayor parte está formado por rocas ácidas (esquistos y granitos) que dan relieves bastante abruptos, principalmente en la parte central de la cordillera axial, donde diversos picos sobrepasan los 3.000 m de altitud. Las áreas rocosas (gleras, morrenas, cantiles, etc.) representan alrededor del 30% del total, siendo especialmente extensas hacia la parte alta del piso. En el resto dominan ampliamente las comunidades pratenses, de las cuales las acidófilas representan el 59% y las calcícolas el 7% (Bolòs et al. 2004 y datos propios). En estos pastos se han sustentado desde tiempos remotos importantes poblaciones de herbívoros domésticos, que fueron desplazando la fauna silvestre original. Aunque en las últimas décadas el uso pastoral ha disminuido fuertemente, podemos suponer que su influencia sigue pesando de forma diferencial, principalmente en los pastos de más calidad del piso alpino inferior.

MATERIAL Y MÉTODOS

Tomamos las asociaciones más características y extendidas, dejando de lado las de distribución local y las que cubren superficies muy pequeñas. Como primera aproximación, calculamos sus espectros de formas vitales de Raunkiaer, subdivididas en los tipos morfológicos propuestos por Körner (1999), a base de promediar los valores de todos los inventarios disponibles en el banco de datos BDBC (Font 2004).

Para cada asociación realizamos entre 2 y 6 muestreos de fitomasa, según fueran de distribución parcial o más general. Procuramos que las muestras correspondieran a pares procedentes de las partes alta y baja del piso alpino (o de posición topográfica superior e inferior de vertiente) y, en las asociaciones más extendidas, las distribuimos a lo largo de la cordillera. Elegimos ejemplos representativos de cada asociación, de acuerdo con los datos bibliográficos, y aparentemente poco o nada pastados. Dichos muestreos se realizaron con la vegetación bien desarrollada, entre mediados de julio y principios de septiembre. La mayoría tuvieron lugar en 2003, y menos en 2004 ; unos pocos muestreos se repitieron ambos años en la misma parcela, con el fin de evaluar la variabilidad interanual.

En cada localidad muestreada levantamos un inventario fitocenológico. Luego cortamos la fitomasa aérea a ras de suelo, en 5 pequeñas superficies cuadradas, ordenadas linealmente y separadas una de otra por la distancia del lado de los cuadrados. En las comunidades con notable irregularidad (pastos en gradería) o formadas por plantas robustas usamos un cuadrado de 50 x 50 cm, mientras que en pastos de menor talla o más regulares el cuadrado fue de 25 x 25 cm. También recogimos en los mismos cuadrados la materia orgánica caída poco fragmentada (subhorizontes orgánicos L y F, en adelante mantillo), y medimos el grosor del resto del horizonte orgánico (subhorizonte H). Todas las muestras se dejaron secar lo más pronto posible, y luego se dividieron en las siguientes 6 submuestras, o compartimientos funcionales :

a) tallos leñosos

b) bases más voluminosas de plantas herbáceas

c) hojas (y otras estructuras fotosintéticas)

d) estructuras reproductoras (flores, frutos) más conspicuas

e) plantas en pulvínulo denso

f) líquenes y musgos

Secamos las muestras a 50°C hasta peso constante y las pesamos con precisión de 0,001 mg. En algunas submuestras representativas de hojas, separamos las totalmente verdes de las senescentes y amarillentas, para extrapolar luego su proporción. Igualmente, en algunos pulvínulos evaluamos el porcentaje en peso que representaban las hojas verdes. A partir de los datos obtenidos de las distintas submuestras y réplicas, calculamos las medias de cada compartimiento funcional para cada muestreo, y luego para cada asociación.

Fijamos como objetivo obtener el peso específico foliar (LMA, *leaf mass per area*) de las plantas dominantes o codominantes, como mínimo de las que presentaban valores de 2 (recubrimiento del 10-25%) o superiores en algún muestreo. Recolectamos de cada una de ellas un mínimo de 20 hojas, a poder ser de 2 o más parcelas (de hasta 6, para las especies más generales o emblemáticas), y las prensamos cuidadosamente. En el caso de graminoides de hoja estrecha, multiplicamos la longitud total de hojas de cada muestra por la anchura media foliar, medida en corte al microscopio con ocular micrométrico. Con las dicotiledóneas, y también con algunas especies de *Carex* de hoja ancha, usamos el programa de tratamiento de imágenes "Image", que permite el cálculo directo de superficies. Una vez establecida la superficie foliar de cada muestra de hojas, las secamos a 50°C, y las pesamos inmediatamente (precisión : 0,0001 mg).

Posteriormente calculamos el índice foliar (LAI, *leaf area in dex*) de cada comunidad, a partir de los valores de biomasa de hojas de cada muestra y de los valores de LMA de sus especies dominantes, combinados en función del recubrimiento de dichas especies.

4. Resultados y discusión

4.1. Fisonomía funcional

Hemos tratado 10 asociaciones, caracterizándolas a través 289 inventarios bibliográficos. Teniendo en cuenta sus aspectos fisonómicos (recubrimiento, espectros de formas vitales) y sinecológicos, pueden distribuirse en tres grupos : pastos densos, que tapizan relieves suaves, con suelo estable y relativamente húmedo, principalmente en la parte inferior del piso alpino (3 asociaciones) ; pastos irregulares, que cubren extensas vertientes en forma de gradería, sometidos a solifluxión (3 asocs.) ; y pastos de vertientes altas y de áreas culminantes, de aspecto más o menos ralo, en suelos estables pero bajo condiciones más duras (4 asocs.). La tabla 1 indica esta agrupación, y sintetiza los aspectos más básicos de su ecología y distribución.

	Si	Ca	Ds	Gr	Rl	Ai	As	Pc	Po	Rec
Alchemillo-Nardetum strictae Gruber 1975	+		+			+		+	+	98
Selino-Festucetum eskiae Nègre 1968	+		+			+	+	+		89
Festucetum eskiae Br.-Bl. 1948	+			+		+	+	+	+	68
Carici-Festucetum eskiae Rivas-Mart. 1974	+			+		+	+	+		79
Hieracio-Festucetum supinae Br.-Bl. 1948	+				+	+	+	+	+	82
Leontodo-Caricetum curvulae Br.-Bl. 1948 (incl. *Gentiano-Caricetum* et *Oreochloo-Caricetum*)	+				+	+	+	+	(+)	88
Festuco-Trifolietum thalii Br.-Bl. 1948		+	+			+		+	+	100
Festucetum scopariae Br.-Bl. 1948		+		+		+	+	+	+	61
Elyno-Oxytropidetum hallerii Br.-Bl. 1948		+			+	+	+	+	+	82
Arenario-Festucetum yvesii Baudière et Serve 1975	+	+			+		+	(+)	+	35

Tabla 1. Principales características de las asociaciones tratadas : carácter silicícola (Si) o calcícola (Ca) ; aspecto uniformemente denso (Ds), en gradería (Gr) o ralo (Rl) ; distribución alpina inferior (Ai), alpina superior (As), pirenaica central (Pc) o pirenaica oriental (Po) ; y recubrimiento global medio (Rec).

Los espectros de formas vitales (fig. 1) muestran que en todos los casos el protagonismo corresponde a hemicriptófitos graminoides, en general centrados en una especie en cada caso, unas pocas en total. Los hemicriptófitos no graminoides muestran coberturas relativas algo menores en los pastos densos, y bastante más bajas en el resto, a pesar de presentar mayor diversidad. Los caméfitos juegan un papel ínfimo en los pastos densos, aumentan sensiblemente en los pastos en gradería y consiguen valores notables en los pastos ralos. En estos últimos también destacan las criptógamas terrícolas, que se benefician de la menor dominancia de las graminoides. Criptógamas y caméfitos pulviniformes responden a la vez a condiciones de estrés y de cierta estabilidad ; difícilmente pueden establecerse en los pastos densos, a causa de la activa competencia ejercida por los hemicriptófitos, ni en los pastos en gradería, ya que su crecimiento más bien escaso no es compatible con los movimientos de solifluxión.

4.2. Biomasa aérea

Obtuvimos en el campo 38 muestras de pastos, de las cuales 5 fueron repeticiones en dos años sucesivos (tabla 2; nomenclatura según Bolòs et al. 1993). La mayor parte dieron valores de biomasa aérea relativamente bajos, que oscilan entre 160 y 314 g/m^2 (tabla 3, fig. 2) ; quedan dentro de este intervalo la mayoría de pastos ralos y los pastos en gradería. En todos los casos sobresale ampliamente el compartimiento de hojas, al que sigue a gran distancia el de estructuras basales.

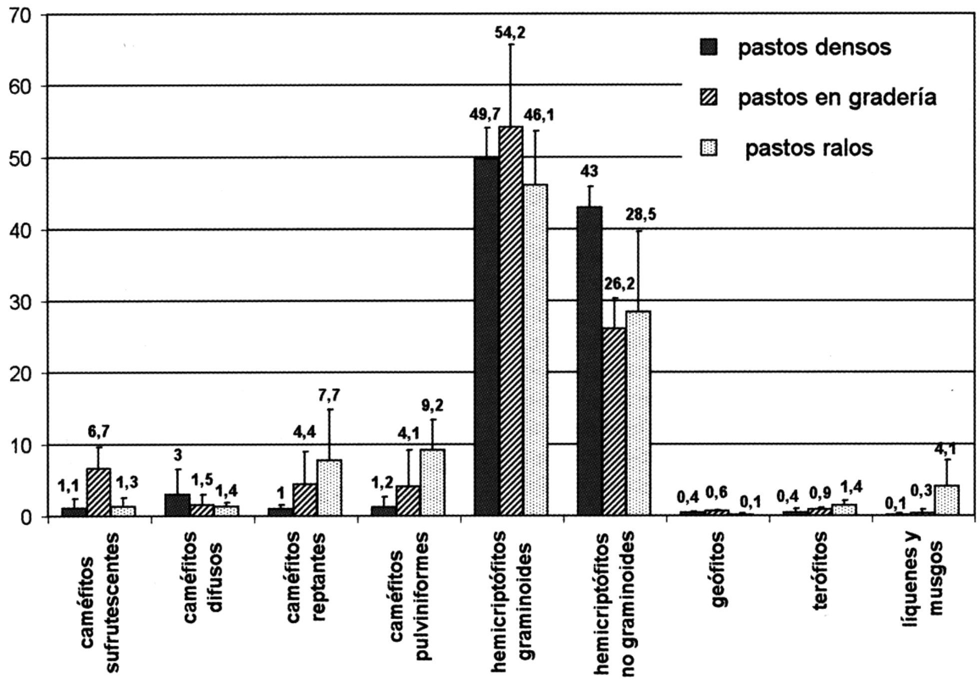

Figura 1. Espectros de formas vitales de los tres grupos de pastos tratados, expresados como promedios de las asociaciones incluidas en cada uno (ver tabla 1).

El grupo de los pastos densos presenta lógicamente los valores más altos, si bien muestra una gran heterogeneidad. En comparación con el *Alchemillo-Nardetum,* que corresponde a la media del grupo, el *Selino-Festucetum eskiae* sobresale notablemente por su elevada biomasa (645 g/m^2), debida a la mayor densidad y robustez de las hojas de la especie dominante, *Festuca eskia,* frente a las de *Nardus stricta.* En cambio, el *Festuco-Trifolietum thalii* dio valores mucho más bajos (203 g/m^2), quizá en parte a causa de pastoreo, pero más bien por la menor talla de las plantas dominantes. Esto puede interpretarse como expresión de que en suelos eutróficos las especies no acumulan tanta biomasa en forma de bases robustas o de hojas recias, como ocurre en los pastos oligotróficos anteriores.

Los tres tipos de pasto en gradería presentan valores totales moderados (247-314 g/m^2), ya que en ellos se compensan los recubrimientos de la vegetación relativamente bajos con la robustez de las gramíneas dominantes *(Festuca eskia, Festuca gautieri).* Destacan los elevados porcentajes de partes basales, lo que muestra la estrategia de dichas gramíneas, consistente en formar fuertes macollas entretejidas para persistir frente a la solifluxión. Esta tendencia es menor en el *Carici-Festucetum eskiae,* probablemente por la menor dinámica de vertiente que se da en los sustratos graníticos que ocupa.

Los pastos culminantes dieron pesos relativamente bajos (115-310 g/m^2), algo menores que los de comunidades vicariantes de los Alpes (*Caricetum firmae, Caricetum curvulae, Elynetum* : 160-400 g/m^2), según datos recogidos por Galland (1982). En nuestro caso destacan el *Hieracio-Festucetum supinae,* dada la relativa robustez de la gramínea dominante, y el *Arenario-Festucetum,* a causa de su bajísimo recubrimiento, no compensado por la notable presencia de estructuras perennes (bases, pulvínulos). Un aspecto diferencial de los pastos ralos es que incluyen una cierta biomasa de líquenes. Como indican Onipchenko (1994) y Grabherr (in Onipchenko & Blinnikov 1994), las plantas pratenses responden a la dureza de las condiciones en zonas culminantes con una mayor extensión del aparato radical que de las estructuras aéreas, lo cual se traduce en pequeños claros entre las macollas, que son ocupados por líquenes y musgos terrícolas.

4.3. Necromasa y horizonte orgánico

La necromasa y los subhorizontes L y F (mantillo) siguen un patrón similar al de las hojas (fig. 2). Los pastos ralos muestran una tendencia a acumular proporcionalmente más mantillo, lo que indicaría una mineralización de la materia orgánica más deficiente. El porcentaje es aun mayor en el *Selino-Festucetum,* en este caso quizá en relación con la mayor consistencia de las hojas de *Festuca eskia.*

En cuanto a la materia orgánica más finamente particulada (subhorizonte H), a pesar de haberse evaluado someramente, destaca como más abundante en los pastos densos (grosores de 2-3 cm). En los pastos en gradería, la fuerte irregularidad

Asociaciones silicícolas:	*Alch. -Nrd.*		*Selino-Festucetum*				*Festucetum eskiae*				*Car.-Fest.*		*Hieracio-Festucetum sup.*						*Leontd.-Caricet.*		
Campanula scheuchzeri s.l.			2				2			2											
Carex curvula curvula																			3	3	3
Carex ericetorum																	2				
Carex sempervirens pseudotr.											3	2									
Festuca airoides													5	4		4	3	4			
Festuca eskia			5	5	5	5	3	3	4	3	4	4									
Festuca gr. *rubra*															3						
Gentiana alpina															3				2	2	
Hieracium lactucella									2	2						2					
Juncus trifidus															3						
Leontodon pyrenaicus																					2
Nardus stricta	5	5		2		2													2		
Pulsatilla vernalis																				2	
Salix herbacea																					2
Thymus nervosus								2									2	2			
Trifolium alpinum	2	2			3						3								3		3
Vaccinium uliginosum															2			3		2	
Veronica fruticulosam s.l										2											

Asociaciones calcícolas:	*Festuco-Trifolietum*		*Festucetum scopariae*				*Elyno-Oxytropidetum*				*Arenario-Festucetum*	
Arenaria grandiflora												2
Campanula scheuchzeri					2							
Dryas octopetala							2			3		
Festuca gautieri			3	3	3	3						
Festuca yvesii			3	3							3	2
Festuca nigrescens	3	3										
Helictotrichon sedenense			2		2		2					
Kobresia myosuroides							4	4	4	3		
Thymus nervosus				2		2		2				
Trifolium thalii	4	5										
Vaccinium uliginosum										2		
Vitaliana primuliflora						2						

Tabla 2. Principales especies de las muestras de pastos, evaluadas según los índices fitocenológicos de dominancia. Las asociaciones se exponen en el mismo orden que en la tabla 1.

	A-N	**S-F**	**F-T**	**Fe**	**C-F**	**Fs**	**H-F**	**L-C**	**E-O**	**A-F**
Bases	27,4	119,7	32,3	45,9	14,5	54,0	50,4	16,8	16,2	15,2
Tallos leñosos	0,0	0,0	2,4	4,9	8,9	6,5	5,6	16,9	18,3	1,4
Hojas verdes	399,4	524,7	148,1	207,2	223,0	230,3	218,4	118,2	162,7	48,1
Pulvínulos (global)	0,0	0,0	0,1	1,2	0,0	19,4	11,7	4,0	6,8	40,8
Pulvn. (hojas/tallos)			0/0,1	0,2/1		2,7/16,7	1,6/10	0,6/3,5	0,9/5,8	5,7/35,1
Flores y frutos	1,7	0,3	8,0	1,5	0,9	4,0	2,4	1,4	3,4	0,9
Líquenes y musgos	0,0	0,4	11,9	0,0	0,0	0,0	21,7	1,8	10,8	8,8
Necromasa	266,2	349,8	98,8	138,1	148,7	153,6	145,6	78,8	108,4	32,1
Mantillo	42,6	298,8	16,6	47,5	51,2	39,3	91,6	67,5	77,6	12,6

Tabla 3. Peso seco (g/m^2) de los compartimientos considerados en cada una de las 10 asociaciones en estudio : *Alchemillo-Nardetum, Selino-Festucetum, Festuco-Trifolietum, Festucetum eskiae, Carici-Festucetum, Festucetum scopariae, Hieracio-Festucetum, Leontodo-Caricetum, Elyno-Oxytropidetum* y *Arenario-Festucetum.*

edáfica condiciona que se alcancen grosores notables (1,7-2,8 cm) debajo y alrededor de las macollas, contrastando con su ausencia en los claros. Teniendo en cuenta el recubrimiento de las macollas, esta distribución heterogénea corresponde a unos grosores medios de 1-2 cm en los pastos en gradería, que es el mismo intervalo que se midió en los pastos ralos, en forma de subhorizonte más uniforme.

4.4. Estructura foliar

El colectivo de especies analizadas en este aspecto (32) es bastante representativo de la flora de los pastos alpinos, además de incluir las especies más dominantes en general (tabla 4). Las dimensiones foliares son en la mayoría de los casos muy pequeñas, dando superficies de entre 10 y

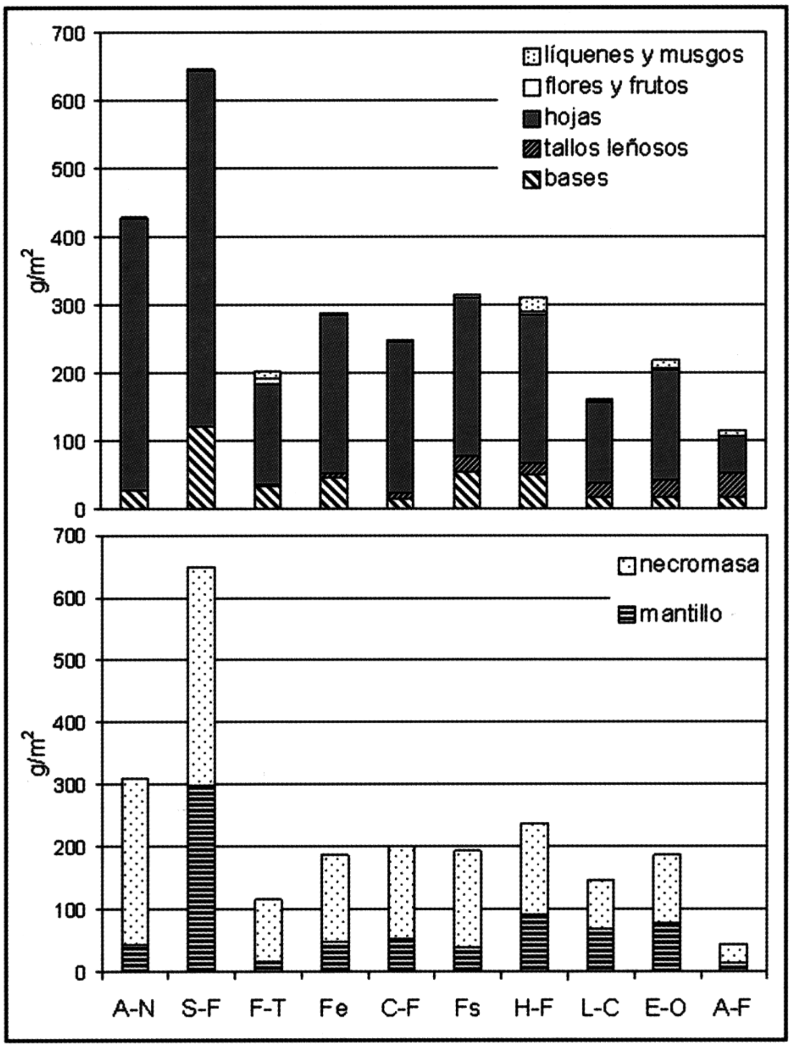

Figura 2. Promedios de biomasa (arriba) y necromasa y mantillo (abajo) de las asociaciones estudiadas (abreviaturas y ordenación como en la tabla 3).

100 mm^2 por hoja, con cierta independencia de la morfología foliar y del tipo biológico. Sobrepasan dicho intervalo varias graminoides ; las más robustas *(Festuca eskia, F. yvesii, Carex sempervirens* ssp. *pseudotristis, Helictotrichon sedenense)*, de hoja larga y relativamente ancha (2-3 mm), alcanzan valores de 200-450 mm^2. En cambio, destacan por debajo de los 10 mm^2 varios caméfitos reptantes y pulviniformes, con diminutas hojas lineares u oblongas, en algún caso de apenas 1 mm^2 *(Minuartia recurva).* Por todo ello, graminoides y caméfitos muestran una fuerte diversidad interna en dicho aspecto, mientras que los hemicriptófitos no graminoides son algo más uniformes. De todas formas, hay que tener en cuenta que las superficies dadas tienen un valor tan sólo indicativo, dada la variabilidad de tamaño foliar que presentan muchas especies, tanto dentro de poblaciones como entre ellas.

En cuanto al peso específico foliar, los tres grupos considerados dan promedios muy similares e intervalos de valores igualmente equivalentes, siendo algo menor el de los caméfitos. En general, los valores van desde 5-6 mg/cm^2 en especies de hoja tenue *(Festuca nigrescens, F. gautieri, Campanula scheuchzeri)* hasta 12-14 para las de hoja más tenaz *(Festuca eskia, Pulsatilla vernalis, Gentiana alpina).* En conjunto, se trata de pesos bastante más altos que los dados por Körner et al. (1989) para un grupo de forbias del piso subnival de los Alpes, que se mueven entre 2,5 y 10 mg/cm^2. Pero hay que tener en cuenta que éstas se encuentran en ambientes muy innivados, en los que el periodo vegetativo es sumamente breve y sin restricciones hídricas, mientras que las plantas pratenses de nuestro estudio suelen soportar, a lo largo del verano, al menos algunos episodios de sequía. Bastantes de ellas presentan hojas algo gruesas y con abundante esclerénquima, lo que puede interpretarse como adaptación a hábitats con limitación hídrica *(Festuca eskia, F. yvesii, Pulsatilla vernalis, Vitaliana primuliflora)* o de nutrientes *(Nardus stricta, Carex ericetorum).*

En cuanto al LAI de las distintas asociaciones (tabla 5), a pesar de la importante variabilidad entre ellas, e incluso entre los tres grupos fisonómicos, podemos subrayar que mayoritariamente (6 asociaciones) se dan índices de entre 1,5 y 2,9, intervalo bastante coincidente con el recogido por Körner (1999) de algunos pastos alpinos de los Alpes. Superan estos valores dos de los pastos densos, hecho explicable por hallarse en ambientes relativamente favorables del piso alpino inferior ; y se halla muy por debajo el *Arenario-Festucetum.*

5. SÍNTESIS Y CONCLUSIONES

En los pastos alpinos son generales los tamaños de hoja pequeños (mayoritariamente, entre 10 y 100 mm^2) ; los pesos específicos foliares relativamente altos (5-14 mg/cm^2) siendo plantas herbáceas de hoja no perenne ; las cantidades de biomasa moderadas y las de necromasa y mantillo elevadas, lo que indica mineralización lenta ; y los índices foliares de las comunidades relativamente elevados (1,5-4,7), teniendo en cuenta su escasa estructura vertical. Entre muestras de la misma asociación y entre asociaciones muestran una notable heterogeneidad a diversos niveles. A pesar de ello, los aspectos tratados tienden a diferenciar grupos de comunidades, y son explicables en términos sinecológicos.

Los pastos densos, que ocupan los ambientes más favorables, se distinguen por su elevada densidad, debida casi en exclusiva a hemicriptófitos, y por sus biomasas e índices foliares también elevados. Otros aspectos parecen responder al hábitat más indirectamente, a través de la morfología y funcionalismo de las especies dominantes, como son los elevados valores de necromasa y de mantillo del *Selino-Festucetum,* oligotrófico y dominado por la robusta *Festuca eskia,* al revés de lo que ocurre con el *Festuco-Trifolietum,* de suelos carbonatados y formado por plantas de menor talla y persistencia.

En los pastos en gradería dominan también los hemicriptófitos, sobresaliendo más los graminoides por encima de las forbias, y los subarbustos adquieren cierta importancia. La solifluxión de las vertientes que ocupan limita el papel de dominantes a unas pocas especies de graminoides robustas, capaces de formar fuertes macollas discontinuas, de forma que la biomasa aérea de estos pastos presenta valores intermedios dentro del conjunto. En el *Festucetum scopariae,* calcícola, se consiguen índices foliares bastante más altos que en las dos asociaciones silicícolas, dominadas por *Festuca eskia,* a pesar de su recubrimiento global inferior y de las biomasas de hojas equivalentes. Esta aparente disparidad debe relacionarse en parte con la estructura foliar más tenue de las plantas dominantes en el *Festucetum scopariae,* y en parte con su mayor densidad de especies y de tipos biológicos.

Los pastos ralos de áreas culminantes ocupan ambientes relativamente estables pero a la vez más limitantes. Ello se

	Superficie (mm^2)	Peso específico (mg/cm^2)
Hemicriptófitos graminoides		
Carex curvula (3)	97	7,9 (3,2)
Carex ericetorum (2)	91	11,6 (3,6)
Carex sempervirens (2)	447	10,3 (0,8)
Festuca airoides (3)	51	7,2 (1,4)
Festuca eskia (6)	294	13,5 (2,9)
Festuca gautieri (2)	79	5,7 (2,0)
Festuca nigrescens (2)	57	5,8 (1,8)
Festuca yvesii (4)	184	9,5 (1,2)
Helictotrichon sedenense (3)	212	7,3 (0,6)
Juncus trifidus: global (2)	-	4,9 (0,1)
Juncus trifidus: hojas	51	-
Juncus trifidus: tallos	184	-
Kobresia myosuroides (2)	129	5,6 (0,6)
Nardus stricta (3)	101	9,4 (1,1)
	149 (119)	**8,6 (3,3)**
Hemicriptófitos no graminoides		
Campanula scheuzcheri (2)	80	5,1 (1,3)
Gentiana alpina (2)	51	14,2 (0,1)
Gentiana verna (2)	80	12,0 (2,1)
Hieracium lactucella (2)	48	10,4 (0,8)
Leontodon pyrenaicus (1)	82	7,3 (—)
Primula integrifolia (2)	91	9,3 (3,6)
Pulsatilla vernalis (2)	46	12,1 (0,6)
Trifolium alpinum (4)	84	6,9 (0,9)
Trifolium thalii (2)	18	8,9 (0,4)
	64 (25)	**9,6 (2,9)**
Caméfitos		
Dryas octopetala (2)	75	10,4 (2,1)
Helianthemum nummularium (2)	53	10,6 (3,0)
Jasione laevis (2)	24	9,3 (2,8)
Minuartia recurva (1)	1	9,2 (—)
Salix herbacea (2)	120	7,2 (1,0)
Silene acaulis (1)	2	5,8 (—)
Thymus nervosus (2)	4	8,8 (1,8)
Thymus pulegioides (1)	9	6,3 (—)
Vaccinium uliginosum (2)	43	7,1 (0,6)
Veronica fruticulosa (2)	15	10,6 (2,6)
Vitaliana primuliflora (1)	4	11,5 (—)
	32 (38)	**8,8 (1,9)**

Tabla 4. Superficie foliar y peso específico foliar (y desviación estándar) de las especies estudiadas (entre paréntesis, número de poblaciones) agrupadas por formas vitales, para las cuales se da el promedio (y desviación estándar). La superficie se refiere en graminoides al limbo foliar, y en *Pulsatilla* y *Trifolium* a un foliolo.

	LAI	
Alchemillo-Nardetum (2)	4,5	(0,09)
Selino-Festucetum eskiae (4)	4,7	(2,11)
Festuco-Trifolietum thalii (2)	2,1	(0,02)
Festucetum eskiae (4)	2,0	(0,77)
Carici-Festucetum eskiae (2)	2,0	(0,86)
Festucetum scopariae (4)	3,3	(1,02)
Hieracio-Festucetum supinae (6)	2,9	(1,20)
Leontodo-Caricetum curvulae (3)	1,5	(0,29)
Elyno-Oxytropidetum halleri (4)	2,5	(0,38)
Arenario-Festucetum yvesii (2)	0,6	(0,26)

Tabla 5. Índice foliar (LAI, m^2/m^2) de las asociaciones estudiadas. Para cada una, se indican entre parénesis el número de muestras y la desviación estándar.

expresa en la notable presencia de líquenes terrícolas, que ocupan los pequeños claros dejados por las graminoides dominantes, y de caméfitos pulviniformes y reptantes, que aseguran su persistencia a costa de crecer muy lentamente. Dejando de lado el *Arenario-Festucetum,* los valores de biomasa aérea y los índices foliares no difieren notablemente de los del grupo anterior, y son algo inferiores a los de los pastos densos. Aquella asociación, en cambio, destaca por su escasa biomasa y por sus bajísimos recubrimiento e índice foliar, lo que se corresponde con los ambientes que ocupa, a la vez limitantes y sujetos a erosión.

De todo ello, puede concluirse que los aspectos estructurales y funcionales sobresalientes de las comunidades se relacionan directamente con aspectos ecológicos generales, por encima de su composición florística. Pero a más detalle, aparentes irregularidades en aquellas correlaciones se deben al protagonismo de unas u otras especies, que modulan la respuesta a las condiciones del medio, a través de su capacidad de competencia.

En el aspecto metodológico, dentro de cada parcela se dio una notable heterogeneidad en los diversos aspectos tratados, manifestada como variabilidad entre réplicas, principalmente en los pastos en gradería. También se evidenció bastante diversidad dentro de cada asociación y de cada grupo, así como en la estructura foliar de cada especie, a través de las desviaciones estándar de las correspondientes variables. En otro sentido, la repetición de unos pocos muestreos en 2 años sucesivos reflejó en general cambios pequeños, pero en algún caso se dieron variaciones más notables y en sentidos dispares, de interpretación poco evidente. Por ésto, los datos obtenidos deben ser tomados como una primera aproximación al conocimiento funcional de los pastos alpinos pirenaicos.

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Capítol IV

The role of abiotic and biotic factors on functional structure and processes of alpine subshrub communities

El paper dels factors abiòtics i biòtics en l'estructura i el funcionament de comunitats subarbustives alpines

Estela Illa, Josep M. Ninot, Alba Anadon-Rosell & Francesc Oliva

Folia Geobotanica (enviat)

El paper dels factors abiòtics i biòtics en l'estructura i el funcionament de comunitats subarbustives alpines

Resum

Als ambients alpins la presència de les espècies està determinada per les limitacions ecològiques particulars de cada indret, relacionades sobretot amb la situació topogràfica i el tipus de substrat geològic. Els trets adaptatius de les espècies no només reflecteixen les adaptacions a les condicions ambientals, sinó que també dirigeixen l'estructura i el funcionament dels ecosistemes. El nostre objectiu en aquest treball va ser estudiar la influència que exerceixen els principals factors abiòtics i biòtics (és a dir, la situació topogràfica i el tipus de substrat geològic, i el tipus funcional de l'espècie dominant, respectivament) en l'estructura i el funcionament de comunitats subarbustives alpines. A cada localitat d'estudi vam mesurar trets foliars per a tots els subarbustos presents, i vam recol·lectar la virosta i la biomassa. La biomassa es va separar en grups funcionals de vegetació, dels quals en vam separar els compartiments estructurals i fotosintètics. Posteriorment vam caracteritzar l'estructura de la comunitat en funció de la biomassa dels diferents grups funcionals, vam estimar la producció primària de fulles i la persistència de la virosta, i vam realitzar anàlisis de la variància per veure si hi havia diferències entre les categories dels factors considerats. Els resultats obtinguts mostren que a les comunitats subarbustives el tipus funcional de l'espècie dominant, juntament amb el tipus de substrat geològic, són els principals responsables de l'estructura de la comunitat. Pel que fa als processos a nivell d'ecosistema, la producció primària respon principalment a variables abiòtiques, mentre que la persistència de la virosta depèn simultàniament de les particularitats ambientals de cada situació topogràfica i del tipus funcional de l'espècie dominant.

Mots clau: tipus funcional, situació topogràfica, substrat geològic, producció primària, persistència de la virosta, Pirineus

The role of abiotic and biotic factors on functional structure and processes of alpine subshrub communities

Corresponding author: Estela Illa
Biodiversity Research Institute (IRBio) & Department of Evolutionary Biology, Ecology
and Environmental Sciences
University of Barcelona, Av. Diagonal 643, E-08028, Catalonia, Spain.
Telephone number: +34 93 402 14 76. E-mail address: estelailla@ub.edu

Josep M. Ninot
Biodiversity Research Institute (IRBio) & Department of Evolutionary Biology, Ecology
and Environmental Sciences
University of Barcelona, Av. Diagonal 643, E-08028, Catalonia, Spain.
Telephone number: +34 93 402 14 76. E-mail address: jninot@ub.edu

Alba Anadon-Rosell
Biodiversity Research Institute (IRBio) & Department of Evolutionary Biology, Ecology
and Environmental Sciences
University of Barcelona, Av. Diagonal 643, E-08028, Catalonia, Spain.
Telephone number: +34 93 402 14 75. E-mail address: a.anadon@ub.edu

Francesc Oliva
Department of Genetics, Microbiology and Statistics
University of Barcelona, Av. Diagonal 643, 08028 Barcelona, Catalonia, Spain.
Telephone number: +34 93 403 58 97. E-mail address: foliva@ub.edu

Abstract

In alpine environments species occurrence is subjected to the particular ecological constraints of each site, related mainly to topographical situations and bedrock type. Species traits not only reflect the adaptations to environmental conditions, but also drive the structure and functioning of ecosystems. Our aim was to study the influence exerted by the main abiotic and biotic factors, i.e. the topographical situation and the bedrock type, and the functional type of the dominant species, respectively, on functional structure and processes of alpine subshrub communities. We measured the leaf traits of all sub-shrub species present at each study site, and collected raw litter and aboveground biomass. Biomass was sorted into functional groups which, in turn, were separated into photosynthetic and structural compartments. Then, we characterised community structure in terms of biomass allocation of the different functional groups, estimated values of leaf primary production and litter persistence, and performed analyses of variance to look for differences between the categories of the factors considered. Our results showed that in alpine subshrub communities the functional type of the dominant species and the bedrock type were the main drivers of community structure. Primary production responded to abiotic variables and litter persistence was related to the combination of topographical situation and functional type of the dominant species.

Keywords: plant functional type, topographical situation, bedrock, primary production, litter persistence, Pyrenees

Introduction

In alpine environments species occurrence is subjected to the particular ecological constraints of each site, namely extreme low temperatures, wind desiccation, poorly developed or unstable soils and scarcity of nutrients (Körner 2003), which lead to low net global rates of productivity (Field 1998) and litter decomposition (Zhang et al. 2008). Abrupt and heterogeneous topography at high elevations provides contrasting environments for plant life where the distribution of species and communities is mainly regulated by snow cover dynamics and soil moisture (Isard 1986; Körner 2003). In northern hemisphere, southern slopes experience higher radiation and temperatures than northern slopes, translating into lower snowpack –i.e. longer growing season for plants– and moisture availability. Bedrock type, in combination with topographically related hydrochemistry, determine soil variables (Arnesen et al. 2007), which also influence plant distribution and performance. Contrasted bedrock types, through differences in water retention capacities (Michalet et al. 2002; Körner 2003) and soil nutrient availability (Hobbie and Gough 2002), influence species richness (Arnesen et al. 2007) and community composition (Hobbie et al. 2002). Besides environmental characteristics, biotic interactions, mediated by the dominant species traits, also drive community structure and processes (Grime 1998). Among plant traits, growth form and leaf characteristics are basic descriptors of plant strategies and adaptations to environmental conditions (Grime 1998). Plant growth form is related to plant size and structure, and the proportion of different growth forms or functional groups at a given site results into particular biotic interactions, community structure and effects on ecosystem. Leaf characteristics are mainly related to plant physiology, and can be summarised in two leaf habits (evergreen and deciduous) or finely described by plant traits such as leaf dry matter content (LDMC), specific leaf area (SLA) and leaf nitrogen content (LNC), all of them related to the strategy of resource acquisition (Garnier et al. 2001) and photosynthetic efficiency (Pérez-Harguindeguy et al. 2013). These physiological traits affect also ecosystem functioning (Cornelissen et al. 1999), being thus simultaneously 'response traits' (they respond to environmental factors) and 'effect traits' (they influence ecosystem properties), as defined by Lavorel and Garnier (2002). Then, community structure and processes are driven not only by abiotic, but also by biotic factors.

Many studies in alpine and Arctic environments include relevant data on community structure related to the biomass of functional groups. Some of them are descriptive (Shaver and Chapin III 1991; Walker et al. 1994; Onipchenko et al. 1998; Illa and Ninot 2005), whereas others concern manipulative experiments of some specific vegetation types (Bowman et al. 1993; Chapin III et al. 1995; Gough and Hobbie 2003). The effects of dominant species on community structure and dynamics (Klanderud and Totland 2005; Bråthen and Ravolainen 2015) and the influence of the topographical situation and bedrock on plant traits (Choler 2005; Gutiérrez-Girón and Gavilán 2013; Opedal et al. 2015), biomass (Michalet et al. 2002; Epstein et al. 2008), productivity (Fisk et al. 1998) or litter decomposition (Baptist et al. 2010) have also been studied in alpine and Arctic areas. In the last years, some authors have studied the effects of both biotic and abiotic factors on community structure or ecosystem processes in mountain vegetation (Sebastià 2004; Gracia et al. 2007; Ameztegui and Coll 2013; Klanderud et al. 2015). We focused on high elevations subshrub communities, which are usually heavily dominated by one or few species, either nanophanerophytes (i.e. woody species with regenerative buds above 0.5 m height) or chamaephytes (i.e. woody species with buds below 0.5 m). As a general rule, nanophanerophytes are restricted to the lower alpine belt, and as elevation or snowpack increase they are replaced by creeping and pulvinular chamaephytes (Körner 2003). In mountain areas there is an increasing interest on some of these communities due to their prominence in different processes related to global change, for instance shrub encroachement into grasslands (Dirnböck et al. 2003; Anthelme et al. 2007; Brandt et al. 2013). However, they have been rarely studied in terms of functional structure and processes at high elevations (but see Montané et al. 2007). Understanding how the main abiotic factors and the dominant species through their traits and interactions, shape community structure and control ecosystem processes, can be thus useful in predicting future shifts in vegetation and ecosystems.

Our study is an approach to the knowledge of subshrub communities at high elevations and the factors that influence their structure and processes. Our main aim was to investigate if some common patterns concerning community structure –understood here as the biomass allocated in the different functional groups– and ecosystem processes emerged depending on the particular environmental conditions given by different topographical situations or bedrock types, and the influence exerted by the functional type of the dominant species.

Methods

Study area and vegetation

The study area comprised the alpine belt of the south-eastern Pyrenees, namely the part of the Pyrenean range lying in Catalonia and Andorra above 2,400 m a.s.l. on south-facing slopes and above 2,200 m a.s.l. on north-facing slopes (Ninot et al. 2007), which occupies about 104,000 ha. This part of the range gains elevation from east to west, where the highest summit reaches 3,143.4 m a.s.l. Bedrock is mainly acidic, comprising siliceous schist and granite, with calcareous schist occurring in small areas along the axial range and calcareous rocks restricted to pre-Pyrenean summits. In the Pyrenean alpine belt woody vegetation occupies a reduced area (Ninot et al. 2013), and shrub species richness is low (Grau et al. 2012).

In the study area we selected seven contrasted subshrub communities concerning their canopy height and coverage, and their environmental requirements. More specifically, we studied heaths dominated by the evergreen nanophanerophytes *Juniperus communis* subsp. *alpina* (*Cytiso-Arctostaphyletum* Br.-Bl. 1948) or *Rhododendron ferrugineum* (*Saxifrago-Rhododendretum* Br.-Bl., Sissingh et Vlieger 1939), heaths of the deciduous diffuse –i.e. with woody erect stems– chamaephyte *Vaccinium uliginosum* subsp. *microphyllum* (*Empetro-Vaccinietum* Br.-Bl. 1926), carpets dominated by the evergreen creeping chamaephytes *Arctostaphylos uva-ursi* (*Cytiso-Arctostaphyletum* Br.-Bl. 1948) or *Loiseleuria procumbens* (*Cetrario-Loiseleurietum* Br.-Bl. 1926) and carpets of the deciduous creeping chamaephytes *Dryas octopetala* (*Dryado-Salicetum* Chouard ex Vanden Berghen 1970) or *Salix herbacea* (*Salici-Anthelietum* Br.-Bl. 1948). Hereafter we refer to each community with the genus of the dominant species. Nomenclature of taxa follows Bolòs et al. (2005).

Vegetation sampling

We sampled 24 sites, four for each *Rhododendron*, *Arctostaphylos* and *Vaccinium* communities, and three for each of the remaining communities. With the aim of encompassing the regional variability, sampling sites were established along the study area on different bedrock types except *Dryas* community, which was only found on calcareous schist (Online Resource, Table S1). In each site we selected an area with high and homogeneous coverage of a dominant subshrub species, we noted its coverage and mean height, and we listed all vascular taxa. We then harvested the aboveground biomass and collected the floor litter of five detached squares, hereafter subsamples, of 50 x 50 (or 25 x 25 cm in the cases of small-sized dominant species, i.e. *Loiseleuria* and *Salix*) separated from each other by squares of the same size. Sampling was performed between 2007 and 2013 during the peak of the growing season in mid or late summer.

We performed an ecological characterization of each sampling site in terms of the Ellenberg ecological indicator values, modified for the French flora by Julve (2014). At each sampling site we assigned to all species present the corresponding values of temperature, atmospheric moisture, soil moisture, soil nutrients and soil pH, and computed the average value. To characterise community ecological requirements, we computed the simple mean of the indicator values for the sampling sites belonging to each community type (Online Resource, Table S2).

Community structure and processes

In the laboratory we sorted the aboveground biomass of each subsample into functional groups (dominant subshrub, companion subshrubs, pulvinules, graminoids, forbs, bryophytes and terricolous lichens). The functional groups belonging to vascular plants were sorted again into photosynthetic (leaves) and structural (stems of woody species and thick bases of forbs and graminoids) functional compartments. Concerning the litter, we only kept the part retained by a 2 mm mesh sieve, assuming that smaller particles were soil components or already fragmented litter. However, for *Loiseleuria* and *Juniperus* subsamples we used a 1 mm mesh sieve to avoid the loss of their small leaves. Once functional compartments were sorted and litter processed, we dried them at 60 ºC for 72 hours and weighed them.

We used the dry weight values of each functional compartment to evaluate structural and functional characteristics of the different subsamples. To characterise community structure we calculated the biomass of the non-dominant functional groups (companion subshrubs, graminoids, forbs, bryophytes, lichens). We also used biomass values of the different functional compartments to infer some processes related to ecosystem functioning, namely leaf primary production and litter persistence. We assumed as approximate leaf primary production the amount of photosynthetic structures that are renewed yearly (mainly leaves). Deciduous subshrubs, graminoids and forbs were assumed to renew all their leaves yearly, whereas for evergreen subshrubs we assumed a leaf lifespan of 2.75, 2.70 and 2.20 years for *Loiseleuria*, *Arctostaphylos* and *Rhododendron* respectively (Karlsson 1992; Pornon and Lamaze 2007), and of 4 years for *Juniperus* (pers.obs.), which translates into 36%, 37%, 45% and 25% of green-leaf biomass falling each season, respectively. To estimate litter persistence we used the proportion of litter with respect to the yearly-renewed structures. Values close to 1 mean low litter persistence (all structures falling one season are processed and incorporated into the soil yearly), whereas values higher than 1 mean higher litter persistence and thus low decomposition rates. We assumed that, although deciduous communities experience a certain grazing pressure compared with evergreen communities, the real values of litter persistence would be similar than those obtained in our study, as our field experience showed that at the end of the growing season deciduous subshrubs still had the majority of their leaves.

Leaf functional traits

In order to support the classification of the dominant species into functional types, we analysed their leaf traits at each study site, and we related leaf traits at community level (based on all subshrub species present at each site) to the same factors that we used for community structure and processes. For all subshrubs present at each sampling site we collected well developed leaf-bearing twigs of five individuals (understood as distant ramets), kept them in sealed plastic bags with a saturated atmosphere and rehydrated them once in the laboratory (following Pérez-Harguindeguy et al. 2013). We measured the fresh weight from a set of at least five mature and well developed leaves from each individual, and obtained their area by scanning them and processing the image through IMAGEJ software (http://imagej.nih.gov). After performing fresh measurements of leaves, we dried them at 60 ºC for 72 hours and weighed them. With fresh and dry weight values, and leaf area, we calculated the leaf dry matter content (LDMC, the ratio between dry and fresh biomass) and specific leaf area (SLA, the ratio between leaf area and dry weight) of each species at each site. We also measured the leaf nitrogen (LNC) and carbon (LCC) concentrations of all subshrub species –dominant or not– using a Flash 1112 Elemental Analyzer (Carbo Erba, Milan) at CCiT of Univerity of Barcelona.

Factors studied

We summarised the environmental variables used in the ecological characterisation of sampling sites and communities in two abiotic factors, i.e. topographical situation and bedrock type. To objectively classify subshrub communities into topographical situations we first obtained data of their present distribution at the study area using the existing cartographies of habitats at scale 1:50,000 for Catalonia (Carreras and Vendrell 2012) and at scale 1:25,000 for Andorra (Carreras et al. 2001). These cartographies include up to three different vegetation units per polygon, with their respective percentage cover. Then, we combined these cartographies with a Digital Terrain Model (DTM) of 20 x 20 m grid, we selected all the polygons containing the studied communities and we obtained their distribution on the different aspects (Online Resource, Fig. S1). Finally, we based on the results obtained through the analysis of cartographies and also on the existing botanical knowledge in the Pyrenees (Braun-Blanquet 1948; Grüber 1978; Carrillo and Ninot 1992), to establish the different topographical situations for this study. Specifically, we defined southern slopes early uncovered by snow (*Arctostaphylos* and *Juniperus* communities), northern slopes subjected to fluctuations of snowpack and occasionally non-protected by snow in winter (*Dryas*, *Loiseleuria* and *Vaccinium* communities) and northern slopes permanently protected by snow in winter (*Rhododendron* and *Salix* communities). We considered two situations on northern slopes due to the known effects of permanent snow cover in winter on vegetation, namely thermal insulation and wind protection (Neuner et al. 1999). The other abiotic factor considered, bedrock type, consisted also in three coarse categories: granite, siliceous schist and calcareous schist. In this case, each subshrub community was sampled at least once in each bedrock type, except *Dryas*, which is only found on calcareous bedrock types.

We also considered one main biotic factor as potentially influencing community structure and processes, the functional type of the dominant subshrub species, which is related to the competitive ability (through its height and space occupancy, explained by its growth form) and to physiological processes (synthesised through its leaf habit). The resulting classification comprised three functional types, concretely evergreen nanophanerophytes (*Juniperus* and *Rhododendron*), evergreen creeping chamaephytes (*Arctostaphylos* and *Loiseleuria*) and deciduous chamaephytes (*Dryas*, *Salix* and *Vaccinium*).

Statistical analyses

In the first level of analysis we looked for differences between the categories of the abiotic and biotic factors considered on community structure. We applied a fourth root transformation to biomass data of the different functional groups considered (companion subshrubs, graminoids, forbs, bryophytes and lichens) due to its asymmetric distribution. Despite the transformation, some of the subsamples contained many zero values, so normality could not be reached and we required non-parametric techniques. Thus, we used PERMANOVA tests to analyse our data. To evaluate how the categories of each studied factor affected community structure, we modelled three tests, one for each factor. Topographical situation, bedrock type or functional type were specified as fixed effects factors in their respective models, and community type was considered a fixed effects factor nested to topographical situation or functional type (in their respective models), and was crossed with bedrock type in the bedrock model. In all cases we considered sampling site as random effects factor. For topographical situation and functional type tests we considered all available subsamples (111), and for bedrock we used 97 subsamples after the exclusion of *Dryas*. For each factor, we first performed an overall model considering all non-dominant functional groups together, and computing the Bray-Curtis distance between all subsamples. After that, we performed an individual model for each non-dominant functional group separately by computing the Euclidean distance between subsamples. All PERMANOVA tests were carried out with 9999 permutations, and post-hoc pair-wise comparisons were performed when necessary. PERMANOVA tests were executed with Permanova+ (version 1.0.1.) from PRIMER-E.

We also performed a distance-based Redundancy Analysis (dbRDA) to get an ordination of the sampling sites by relating community structure to explanatory environmental and biotic variables. The abiotic variables considered were the Ellenberg indicator values of soil pH, temperature, soil nutrients, soil moisture and atmospheric moisture. The biotic variables included in the analysis were structural characteristics (height and coverage) of the dominant species and total litter, related to space and light availability at the ground level. Height and coverage of the dominant subshrub were square-root transformed, total litter was log transformed and, as in the PERMANOVA analyses, biomass values of the non-dominant functional groups were fourth-root transformed. After that, explanatory variables were normalised. Finally, we computed the Bray-Curtis distance between samples and performed the dbRDA. This analysis was also executed with PRIMER-E.

A second level of analysis concerned ecosystem processes. In this case, to fulfil the requirements of the analysis of variance, a fourth root transformation was applied to leaf primary production and to litter persistence values. As in the analysis of community structure, we included all the subsamples in the tests for the effects of topographical situation and functional type of the dominant species, and 97 subsamples in the test of bedrock type. Therefore, to evaluate the effect of the categories of each studied factor we used generalised linear models (GLM) with the same model structure as in the PERMANOVA explained above. When significant effects ($p < 0.05$) were found, we ran the post-hoc Tukey test to look for differences between factor levels.

Finally, regarding leaf traits, to study the leaf characteristics of the main species driving community structure and processes at each sampling site, i.e. all subshrub species present, we computed the community-weighed mean (cwm) for each leaf trait ($\mathrm{trait}_{\mathrm{cwm}}$) as follows:

$$\mathrm{trait}_{\mathrm{cwm}} = \sum (t_i\, b_i) / b_{site}$$

where t_i is the trait value of the i-th species, b_i is the leaf biomass of the i-th species, and b_{site} is the total leaf biomass at the sampling site. Values of community-averaged leaf traits fulfilled the requirements of normality and homogeneity of variances. The effect of the study factors on community-averaged leaf traits was tested using two-way ANOVA. In this case, community-averaged values were computed for each sample, not for each subsample. Topographical situation, bedrock type or functional type were specified as fixed effects factor in their respective models, and community type was considered a fixed effects factor nested to topographical situation or functional type (in their respective models) and was crossed with bedrock type in the bedrock model. For the topographical situation and functional type models we used all the 24 samples, whereas for the bedrock type model we used 21 samples after the exclusion of *Dryas*. When significant effects ($p < 0.05$) were found, we ran the post-hoc Tukey test. Analyses related to ecosystem processes and community-averaged leaf traits were conducted with Minitab 16.

Results

Community structure

Communities with highest biomass values were dominated by *Juniperus*, *Rhododendron* and *Arctostaphylos*, whereas the community with the lowest values (more than 10-fold less biomass) was that dominated by *Salix* (Table 1). In all cases, the dominant subshrub species reached the highest biomass values, which represented more than 85% of total biomass in evergreen-dominated communities (Fig. 1). Whereas evergreen-dominated communities were very homogenous concerning their structure, the most heterogeneous was that dominated by *Salix*, with 47.08% of the biomass belonging to a wide range of functional groups. In general, non-dominant functional groups had very low and heterogeneous biomass values (Table 1), which translated into approximately the same variability due to differences between- and within-sites for all studied communities, except in *Loiseleuria* and *Vaccinium*, which had biomass values more homogenous within-sites and more than 70% of variability was explained by differences between-sites (Online Resource, Table S3). Companion subshrubs were practically absent in *Dryas* and *Salix* communities, and reached the highest biomass values in *Rhododendron* sites (Table 1) and the highest proportion of biomass in *Vaccinium* sites (Fig. 1). Pulvinules were only found in *Salix* and *Loiseleuria* communities, with relatively low biomass values (Table 1). Graminoids and forbs reached the highest proportions of biomass in deciduous-dominated communities (Fig. 1), although in terms of absolute biomass these functional groups also had relatively high values in *Juniperus* and *Rhododendron* communities (Table 1). Bryophytes were scarce in all communities except in those dominated by *Rhododendron* or *Salix*. In these communities they had similar absolute biomass values but in *Salix* community the proportion of bryophytes respect to total biomass was 10-fold higher than in *Rhododendron* sites (Fig. 1). Lichens had the lowest biomass values in the latter communities, and reached their highest biomass in *Loiseleuria* sites (Table 1).

The particular conditions of the different topographical situations considered had some effects on community structure (Table 2, Fig. 2). The overall model showed significant differences between situations permanently covered by snow in winter and the rest ($p < 0.05$). When non-dominant functional groups were analysed separately, we found significantly lower forb biomass values in southern slopes ($p < 0.05$), whereas north-facing situations non-permanently covered by snow in winter showed a non-significant trend towards higher biomass values of forbs. Lichen biomass was very low, although non-significant, in situations with permanent snow cover in winter. On the contrary, these situations favoured the presence of bryophytes, where they reached significantly higher values of biomass ($p < 0.05$).

Concerning bedrock type, granite supported less graminoid and lichen biomass than the other substrata did (Fig. 2).

The functional type of the dominant species had a significant effect on the whole community structure ($p < 0.05$) and on some of the coexisting functional groups, except companion subshrubs and lichens (Table 2, Fig. 2). Communities dominated by evergreen creeping chamaephytes had significantly lower biomass values of graminoids and bryophytes than communities dominated by evergreen nanophanerophytes ($p < 0.05$ in both cases) and by deciduous chamaephytes ($p < 0.05$ and $p < 0.1$, respectively). Forb biomass was significantly higher in deciduous-dominated communities ($p < 0.05$ between deciduous and evergreen nanophanerophytes, and $p < 0.005$ between deciduous and evergreen creeping chamaephytes).

The dbRDA showed how environmental and biotic variables had some influence on the biomass of non-dominant functional groups, namely forbs and bryophytes, which were negatively related to total litter, and positively related to soil moisture and nutrients (Fig. 3). The two first axes explained the 36% of the global variation, which represented 86.26% of the fitted space. Axis 1 scores were positively correlated with temperature and negatively to soil nutrient and soil moisture requirements, whereas axis 2 scores were negatively correlated with atmospheric moisture requirements. The first axis sorted the sampling sites according to the functional type of the dominant species. More precisely, the sites followed a gradient from the bottom-left (sites dominated by deciduous species) to the upper-right (sites with dominance of evergreen species) corners.

Ecosystem processes

The most productive community was that dominated by *Arctostaphylos*, followed by those dominated by *Dryas* and *Juniperus*, whereas the less productive were *Salix* and *Loiseleuria* communities (Fig. 4). Regarding litter accumulation, *Arctostaphylos* accumulated on average twice as much litter as *Juniperus*, which was the next community with highest litter values. *Salix* community, on the contrary, accumulated more than 20-fold less litter than *Arctostaphylos*, and 4-fold less litter than the next communities with lowest values, which were those dominated by *Loiseleuria* and *Vaccinium* (Table 1). Surprisingly, although *Dryas* community had 3- to 4-fold less biomass than *Rhododendron*, they accumulated similar amounts of litter (Table 1). The results on litter accumulation are related with the results obtained for litter persistence, with the highest values in *Arctostaphylos*, followed by *Juniperus* and *Rhododendron* communities, and the lowest found in *Salix*, preceded by *Vaccinium* and *Loiseleuria* communities (Fig. 4).

The three topographical situations analysed had significantly different values of leaf primary production ($p < 0.005$; Table 2, Fig. 5). The lowest values were found at permanently snow-covered sites in winter and the highest at southern slopes. We also found significant effects of the topographical situation on litter persistence ($p < 0.05$) although in this case significant differences were between southern slopes and the other two situations. Bedrock type had a significant effect on leaf primary production (Table 2), with calcareous schist having significantly lower values than siliceous schist (Fig. 5). We did not find any effect of bedrock type on litter persistence. Finally, concerning the effects of the functional type of the dominant species, we did not find significant differences in leaf primary production; although deciduous-dominated communities showed a non-significant trend towards lower values (Table 2, Fig. 5). Regarding litter persistence, we found significant differences between communities dominated by deciduous subshrubs, which had the lowest values, and the two types of evergreen-dominated communities ($p < 0.05$).

Plant traits

Environmental characteristics of the distinct topographical situations clearly determined the presence of particular functional types. In this sense, we found that northern slopes (both permanently covered by snow in winter or not) and communities dominated by deciduous species discriminate in a similar way for more productive leaves, i.e. leaves with higher values of SLA and LNC, and low values of LDMC (Fig. 6).

All community-averaged leaf traits except LCC differed significantly between northern slopes and southern slopes, whereas we did not find significant differences between bedrock types (Table 2). We also found differences between the functional types of the dominant species: LDMC and LCC increased from deciduous- to evergreen-dominated communities, in contrast to SLA and LNC, which showed the opposite trend (Table 3). Within evergreen communities, those of creeping chamaephytes had lower values of LNC than those of nanophanerophytes, which turned into higher C/N ratios. Differences in leaf traits between dominant functional types were significant (Table 2), not only between deciduous- and evergreen-dominated communities, but also within evergreens (Fig. 6).

Discussion

Contrasted effects of topographical situations

Contrasted environmental conditions given by the different topographical situations certainly influenced the distribution of species, which entailed different community traits, as found in other studies (Sebastià 2004; Choler 2005; Gutiérrez-Girón and Gavilán 2013). Whereas the topographic situation seemed to slightly influence community structure, it was the main driver of ecosystem processes.

Southern slopes showed the highest values of aboveground biomass and leaf primary production. In these situations, vegetation experiences a longer growing period with higher daily temperatures (Scherrer and Körner 2011), which favour higher soil organic carbon (SOC; Garcia-Pausas et al. 2007), and allow the presence of more productive communities (Berdanier and Klein 2011; Gutiérrez-Girón and Gavilán 2013). In southern slopes in our study area we only found communities dominated by evergreen subshrubs, which besides the longer growing season experienced in these situations, they also benefit from longer photosynthesizing periods than deciduous subshrubs due to the presence of active leaves early in the season (Givnish 2002). However, the highest incident solar radiation in southern slopes of northern hemisphere results in faster drying soils (Isard 1986). Our results showed that the species pool growing on south-facing communities had on average the lowest indicator values for soil moisture, therefore being more likely to suffer from drought. In fact, even winter droughts may occur where snow cover is irregular and leaves the vegetation unprotected, allowing leaf transpiration during soil frost (Brodribb et al. 2012). This explains the low community SLA and high LDMC we found in these situations. The increase found in LNC from communities of southern slopes to communities of sites permanently covered by snow in winter responds to a gradient of increasing soil moisture and nutrient availability. Thus, under the particular microclimatic conditions of southern slopes, where decomposing activity may be chiefly restricted to summer (Saccone et al. 2013), xeromorphous and N-poor leaves of the dominant species become harder to decompose, which in turn contributes to the local scarcity of soil nutrients (Ninot et al. forthcoming date). These drier and poorer soils, together with the high cover and biomass of the dominant species, constrained the role of other functional groups in the community, especially forbs and bryophytes.

North-facing areas (either permanently covered by snow in winter or not) experience lower air and soil temperatures than southern slopes, as the amount of incident radiation is lower. On these energy-limited sites total biomass and leaf primary production are generally low, as was also reported by Kikvidze et al. (2005). Certainly, a lower energy budget clearly limits plant growth, as shown by King et al. (2013) when comparing the same community on contrasting aspects in the Alps. Where snow is swept away by wind, or under shallow and variable snow cover, winter temperatures can reach extremely low values (Körner 2003). We found that subshrub species able to survive in these environments were either deciduous, which avoid freezing temperatures by losing their leaves in winter, or evergreen prostrate, which decouple their own microclimate from the general ambient conditions and accumulate more heat in the leaf canopy (Körner 2003). When communities are protected by a thick snowpack in winter, plants not only gain protection from severe winter conditions (Neuner et al. 1999) but also do not experience water restrictions during the growing season, as supported by the highest abundance of bryophytes in these situations. However, the more reduced energy budget received in these sites further constrained leaf primary production. Regarding litter persistence in situations with a permanent snowpack in winter, although near zero winter temperatures do not prevent litter decay because microorganisms remain active (Brooks et al. 1996; Brooks and Williams 1999), we found contrasted values between *Rhododendron* and *Salix* communities, which evidenced the prevalent role of the leaf structural properties in decomposition processes, in agreement with the findings of Baptist et al. (2010).

Effects of bedrock type

Leaf primary production was significantly lower on calcareous than on siliceous schist. In terms of aboveground biomass, Michalet et al. (2002) found an increase from calcareous to siliceous alpine communities in the French Alps, a trend that we did not find in our communities (unpublished data). They related the differences in biomass values to differences in water availability between the different bedrock types. Our lower primary production values on calcareous sites could be related to lower water availability too. They could also be related to differences in nutrient availability, although opposed results have been reported regarding this subject. For instance, whereas Hobbie and Gough (2002) found higher nitrogen values in acidic substrates in the Arctic tundra, Garcia-Pausas et al. (2007) found null effects of bedrock type on SOC in grasslands of high elevations. Michalet et al. (2002) did not find differences in nutrient availability between bedrock types, but on the contrary, they found that nutrient availability was correlated with microtopography and the duration of snow cover. Moreover, in our study sites, at least under evergreen subshrub canopies, soil may become more acidic due to the large amounts of hardly decomposable litter, partially decoupling the effects of bedrock on vegetation. Thus, despite the limitations of our analysis on the bedrock role, we point to the effect of differential water availability in the different bedrock types as the main factor constraining leaf primary production.

The role of dominant functional types

Besides the particular environmental effects mainly related to each topographical situation considered, the functional type of the dominant species was also a relevant factor determining community functional structure and processes in our study sites. Evergreen subshrubs limited the presence of other species and functional groups, in contrast with deciduous subshrubs. The lower density of deciduous subshrub canopies, and the fact that their leaves develop later in the growing season, allow light to reach the ground and thus, allow other functional groups to develop. Forbs were particularly scarce in subshrub communities, as found by other authors (Shaver and Chapin III 1991). Moreover, they were practically absent when the dominant species were evergreen, where close canopies and high amounts of litter appeared to be very unfavourable for them. Among evergreen functional types, creeping chamaephytes excluded all other functional groups, as their low, dense canopy with overlapping horizontal stems leave no gaps for the growth of other species. Among evergreens, only some *Loiseleuria* sites bore terricolous lichens. Belowground competition in these sites, with rocky or shallow soils, causes vascular plants to leave gaps on the surface, which are appropriate for lichen growth (Onipchenko et al. 1998). Nanophanerophytes seemed to be in an intermediate situation. On the one hand they allowed the presence of graminoids, which may profit gaps between subshrubs where incident radiation is enough for their growth but not for the smaller alpine forbs. On the other hand, they also favoured bryophytes, which may find not only place to grow but also certain environmental moisture below their canopies.

Ecosystem processes were also differently affected by the functional type of the dominant species. Although deciduous-dominated communities were chiefly found in rich, well-watered soils, their intrinsic delay in the beginning of the photosynthesizing period with respect to evergreens (Givnish 2002), and their situation in northern slopes generally constrained leaf primary production. In these communities litter persistence was the lowest, implying higher decay rates, which may be favoured not only by leaf characteristics of the dominant species (Cornwell et al. 2008), with high SLA and LNC and low LDMC values, but also by the relatively high proportion of graminoids and forbs, as litter decay has been proved to be enhanced by the mixture of growth forms (Aerts 2006). The opposite situation was found in evergreen-dominated communities, which tended to be more productive but produced leaves with low LNC and SLA values. Taking into account that nutrient resorption from senescent leaves appears to be more efficient in evergreen shrubs (Hobbie and Gough 2002), the resulting poor-quality litter turns into slow decay and nutrient mineralization rates in their communities (Cornelissen et al. 1999; Cornwell et al. 2008).

Concluding remarks

Our results evidenced that the main drivers of community structure across the different alpine subshrub communities studied are the functional type of the dominant species and the bedrock type. Ecosystem processes respond more diversely, since they seem to be differently regulated by abiotic and biotic factors. For instance, leaf primary production is mainly dependent on abiotic variables, whereas litter persistence appears to be regulated by the combination of environmental characteristics related both to topographical situation and plant traits.

In the context of a changing climate, the present distribution of alpine species and thus, communities, is expected to shift, leading to changes in community composition, structure and functioning. Models predicting community distribution and ecosystem processes must take into account the effects of both small-scale abiotic factors and plant traits of the dominant species, since they are the basis of vegetation strategies to mitigate environmental changes or to get adapted to them.

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Table 1. Mean and standard deviations (in parentheses) of biomass of functional compartments, total biomass and litter (in g m^{-2}) in each studied community, computed by within-site averages. In bold, minimum and maximum values for each category

		Arctostaphylos	*Dryas*	*Juniperus*	*Loiseleuria*	*Rhododendron*	*Salix*	*Vaccinium*
dominant subshrub	stems	880.18 (407.42)	295.04 (31.66)	**1,788.34** (447.81)	286.09 (36.98)	1,542.90 (581.44)	**36.90** (11.25)	364.67 (198.79)
	leaves	**777.11** (396.75)	149.16 (12.76)	562.92 (90.34)	236.26 (50.09)	257.81 (91.67)	**47.05** (14.36)	91.58 (39.57)
companion subshrubs	stems	52.13 (50.70)	2.78 (2.59)	33.88 (33.13)	12.68 (20.13)	**127.97** (147.92)	**0.99** (1.72)	91.81 (133.87)
	leaves	25.42 (23.46)	1.44 (1.18)	7.54 (9.41)	12.46 (20.85)	14.81 (15.56)	**1.07** (1.85)	**30.15** (20.62)
graminoids	bases	4.51 (5.49)	**17.23** (14.68)	14.91 (9.06)	**2.84** (2.67)	14.04 (9.87)	4.15 (1.75)	13.36 (3.86)
	leaves	13.69 (11.17)	39.38 (36.60)	59.31 (16.31)	**7.90** (5.27)	42.27 (33.73)	17.68 (10.60)	**59.71** (45.46)
forbs	bases	0.00 (--)	0.00 (--)	0.57 (0.98)	0.00 (--)	**2.46** (4.93)	0.00 (--)	0.28 (0.56)
	leaves	**0.83** (1.16)	**44.18** (36.45)	5.07 (5.21)	1.87 (1.08)	3.43 (2.63)	12.56 (8.84)	13.18 (7.95)
pulvinules		0.00 (--)	0.00 (--)	0.00 (--)	4.65 (6.66)	0.00 (--)	**8.32** (13.87)	0.00 (--)
bryophytes		**0.56** (1.12)	4.00 (4.58)	2.75 (2.58)	0.58 (0.62)	**23.30** (13.57)	22.30 (30.64)	2.28 (3.67)
lichens		6.68 (13.32)	6.38 (7.95)	7.85 (7.92)	**40.92** (59.28)	3.06 (4.52)	**0.74** (1.28)	11.46 (22.55)
total biomass		1,761.10 (791.11)	559.60 (61.00)	**2,483.13** (521.95)	606.22 (100.59)	2,034.96 (657.75)	**152.47** (53.71)	678.46 (313.36)
total litter		**1,773.98** (651.90)	777.39 (252.80)	922.97 (327.96)	325.81 (92.71)	766.75 (493.38)	**79.16** (96.34)	364.80 (272.85)

Table 2. Results obtained from PERMANOVA tests for community structure and from ANOVA tests for ecosystem processes and leaf traits. In bold, results for the community structure analysed as a whole. Predictors are in columns and response variables in rows

	topographical situation			bedrock type			functional type of dominant species		
	F	*p-value*		*F*	*p-value*		*F*	*p-value*	
Community structure	**2.26**	**0.0307**	*	**9.67**	**<0.001**	***	**3.23**	**0.0071**	**
comp. subshrubs	0.02	0.9766	n.s.	1.66	0.1976	n.s.	1.03	0.3736	n.s.
graminoids	0.33	0.7183	n.s.	4.97	0.009	**	5.02	0.0172	*
forbs	5.93	0.0104	*	7.10	0.0013	**	13.72	<0.001	***
bryophytes	9.55	0.0016	**	1.53	0.2334	n.s.	3.57	0.0521	.
lichens	2.22	0.1343	n.s.	24.21	<0.001	***	0.47	0.6332	n.s.
Ecosystem processes									
leaf primary prod.	9.78	0.001	**	5.77	0.005	**	1.17	0.334	n.s.
litter persistence	10.13	0.001	**	0.34	0.716	n.s.	11.37	0.001	**
Leaf traits									
SLA	32.27	<0.001	***	0.29	0.749	n.s.	74.96	<0.001	***
LDMC	20.75	<0.001	***	0.15	0.859	n.s.	66.79	<0.001	***
LNC	27.14	<0.001	***	0.27	0.769	n.s.	52.59	<0.001	***
C	0.97	0.401	n.s.	0.16	0.854	n.s.	18.43	<0.001	***
C/N	29.82	<0.001	***	0.17	0.845	n.s.	59.88	<0.001	***

*** $p < 0.001$ ** $0.001 \le p < 0.01$ * $0.01 \le p < 0.05$. $0.05 \le p < 0.1$ n.s. not significant

Table 3. Mean and standard deviation (in parenthesis) of community-weighed leaf traits in the communities studied. In bold, minimum and maximum values for each trait. Communities are identified by the initials of the dominant species: Au, *Arctostaphylos uva-ursi*; Do, *Dryas octopetala*; Jc, *Juniperus communis* subsp. *alpina*; Lp, *Loiseleuria procumbens*; Rf, *Rhododendron ferrugineum*; Sh, *Salix herbacea*; Vu, *Vaccinium uliginosum* subsp. *microphyllum*

	SLA (mm^2 mg^{-1})		LDMC (mg g^{-1})		LNC (%)		LCC (%)		leaf C/N	
Au	**4.45**	(0.28)	448.18	(22.58)	**0.79**	(0.06)	50.70	(1.75)	64.77	(7.12)
Do	12.27	(2.63)	**356.58**	(6.70)	1.54	(0.20)	48.21	(1.67)	31.73	(4.75)
Jc	6.00	(0.71)	**502.73**	(13.72)	0.92	(0.15)	49.70	(1.92)	52.22	(10.08)
Lp	5.48	(1.08)	486.38	(36.06)	0.86	(0.10)	**53.61**	(0.91)	**64.91**	(7.65)
Rf	7.59	(0.78)	456.56	(17.86)	1.27	(0.19)	52.25	(0.52)	42.13	(5.86)
Sh	**16.01**	(2.24)	362.44	(24.68)	**2.07**	(0.29)	**46.00**	(0.47)	**22.54**	(3.12)
Vu	14.04	(2.36)	392.52	(11.26)	1.84	(0.31)	49.85	(1.43)	30.57	(6.93)

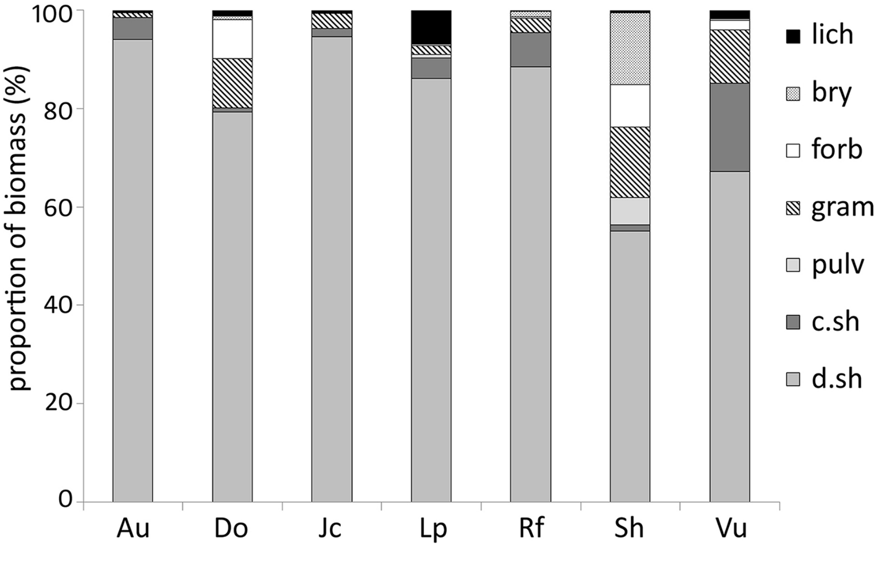

Fig. 1. Proportion of biomass of the different functional groups with respect to total biomass in the communities studied. lich, lichens; bry, bryophytes; forbs; gram, graminoids; pulv, pulvinular chamaephyte; c.sh, companion subshrubs; d.sh, dominant subshrub. Communities are identified by the initials of the dominant species: Au, *Arctostaphylos uva-ursi*; Do, *Dryas octopetala*; Jc, *Juniperus communis* subsp. *alpina*; Lp, *Loiseleuria procumbens*; Rf, *Rhododendron ferrugineum*; Sh, *Salix herbacea*; Vu, *Vaccinium uliginosum* subsp. *microphyllum*

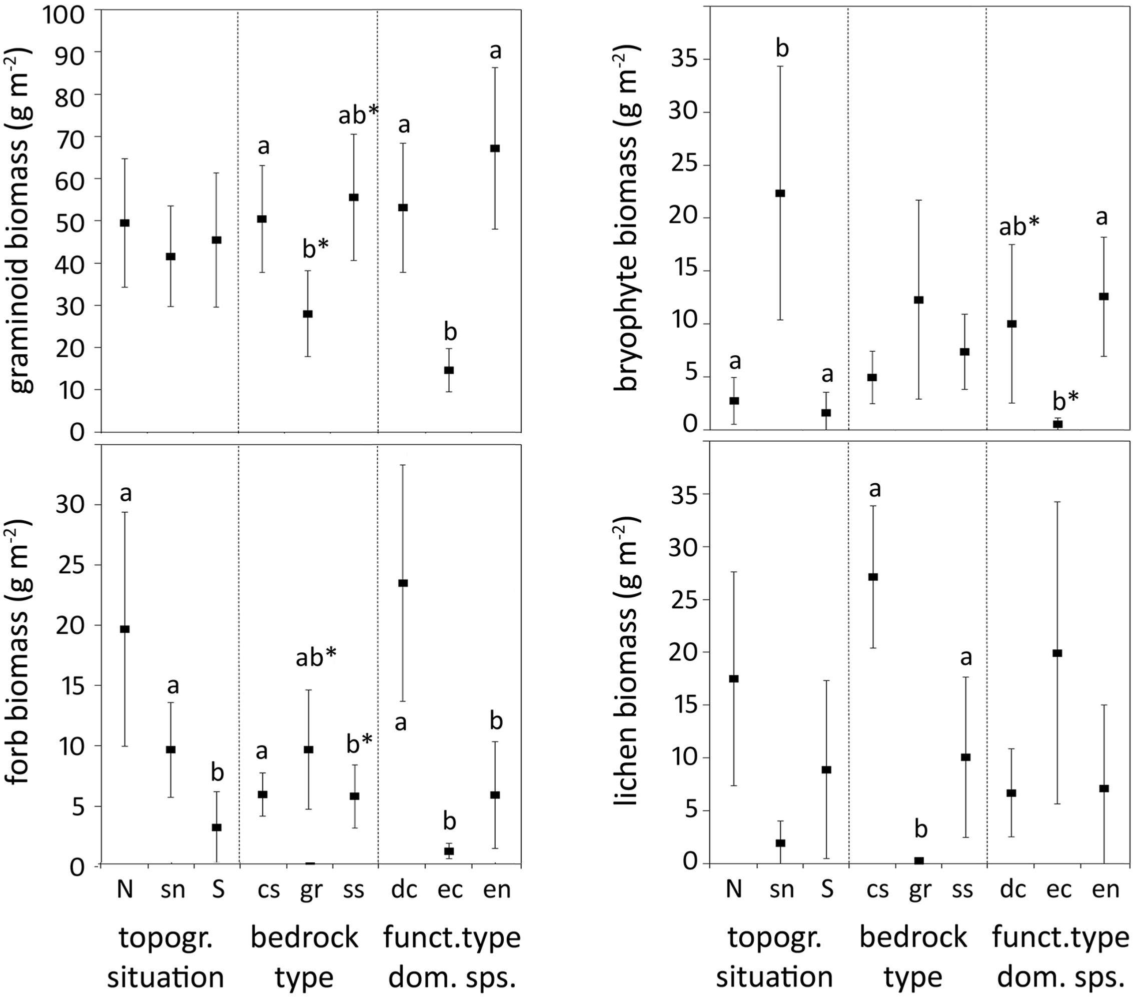

Fig. 2. Biomass distribution of the different non-dominant functional groups (graminoids, forbs, bryophytes and lichens) in relation to the topographical situation (N, northern slope not permanently covered by snow in winter; sn, northern slope permanently snow-covered in winter; S, southern slope), the bedrock type (cs, calcareous schist; gr, granite; ss, siliceous schist), and the functional type of the dominant species (dc, deciduous chamaephyte; ec, evergreen chamaephyte; en, evergreen nanophanerophyte). Error bars represent the 95% confidence interval. Different lowercase letters in the same section mean significant differences at $p < 0.05$ obtained from PERMANOVA pair-wise comparisons of fourth-root transformed data; when followed by an asterisk (*) mean $0.05 \leq p < 0.1$

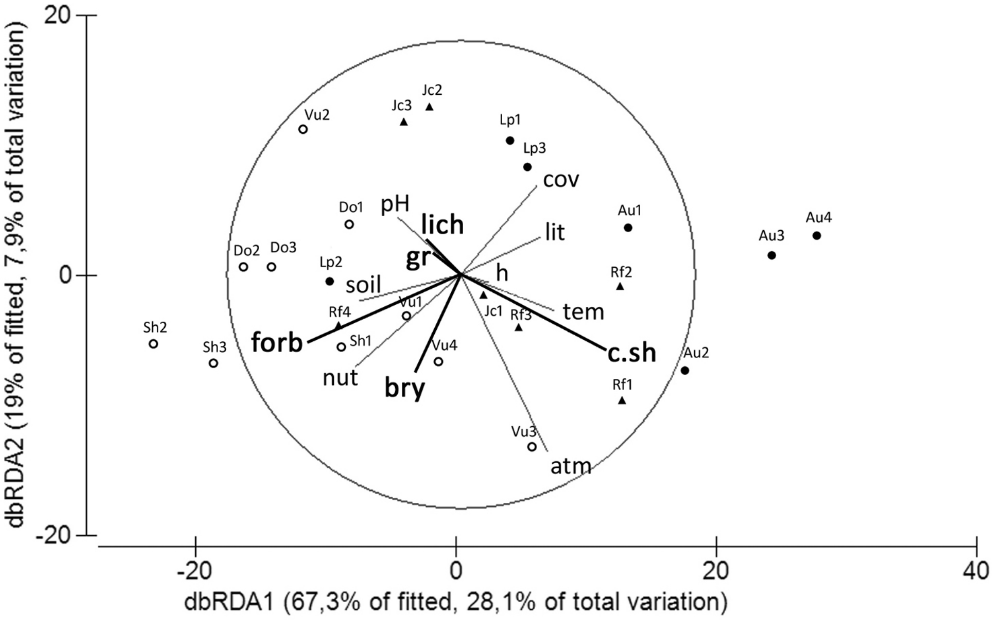

Fig. 3. Ordination of the sampling sites based on distance-based Redundancy Analysis (dbRDA). Environmental variables (atm, atmospheric moisture; nut, soil nutrients; pH, soil pH; soil, soil moisture; tem, temperature) and biotic variables (cov, cover of the dominant species; h, height of the dominant species; lit, total litter) are represented by thin arrows, community non-dominant functional groups (bry, bryophytes; c.sh, companion subshrubs; forb, forbs; gr, graminoids; lich, lichens) are represented by thick arrows. Sampling sites are classified through the functional type of the dominant species (▲ evergreen nanophanerophyte; ● evergreen chamaephyte; ○ deciduous chamaephyte), and identified by the initials of the dominant species: Au, *Arctostaphylos uva-ursi*; Do, *Dryas octopetala*; Jc, *Juniperus communis* subsp. *alpina*; Lp, *Loiseleuria procumbens*; Rf, *Rhododendron ferrugineum*; Sh, *Salix herbacea*; Vu, *Vaccinium uliginosum* subsp. *microphyllum*

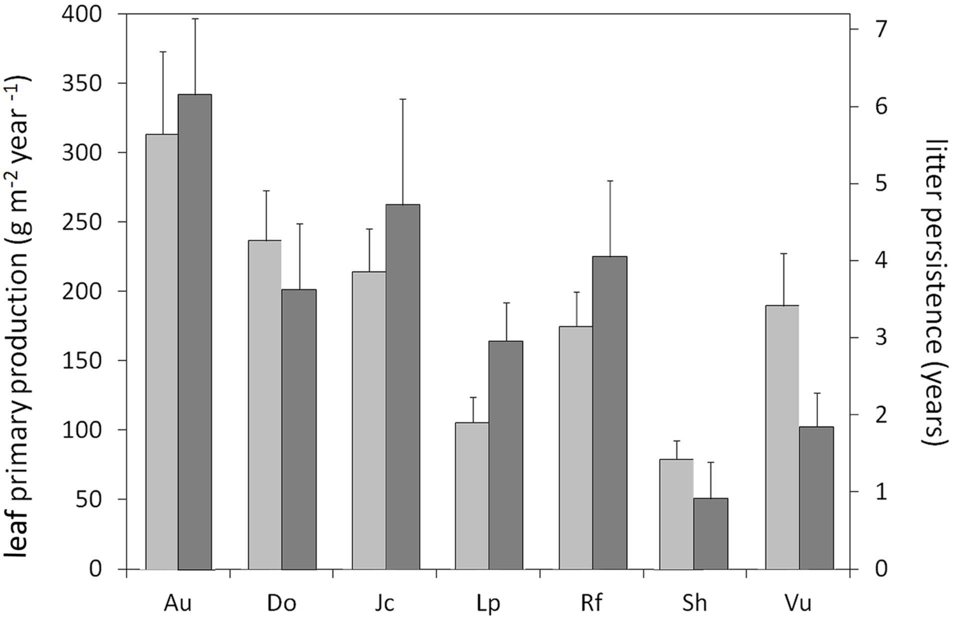

Fig. 4. Mean leaf primary production (light grey) and litter persistence (dark grey) in the communities studied. Communities are identified by the initials of the dominant species: Au, *Arctostaphylos uva-ursi*; Do, *Dryas octopetala*; Jc, *Juniperus communis* subsp. *alpina*; Lp, *Loiseleuria procumbens*; Rf, *Rhododendron ferrugineum*; Sh, *Salix herbacea*; Vu, *Vaccinium uliginosum* subsp. *microphyllum*

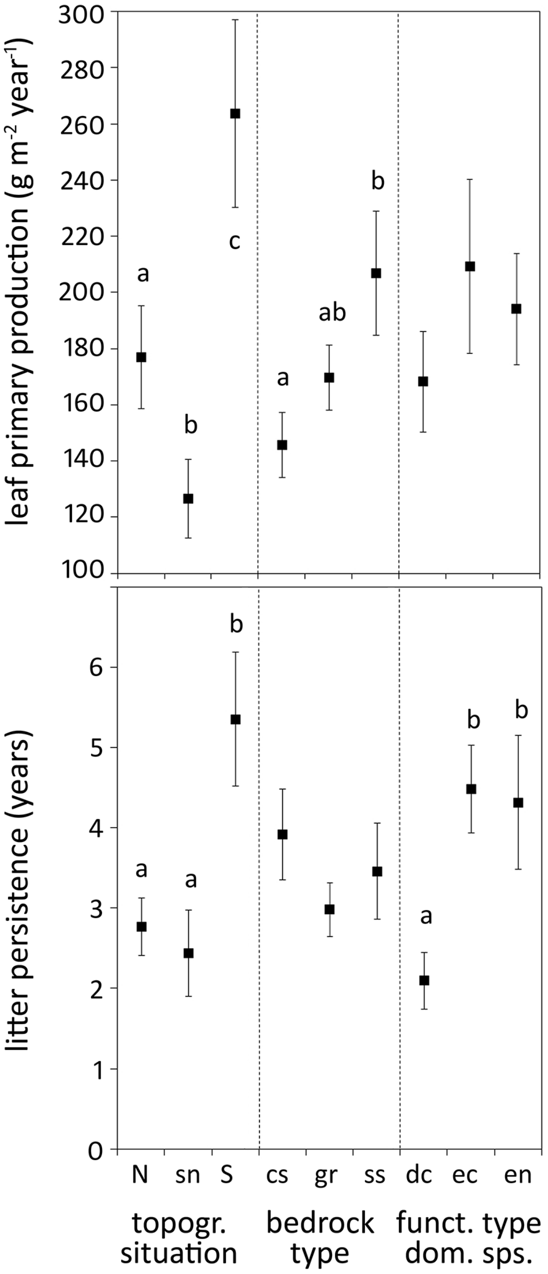

Fig. 5. Basic ecosystem processes in relation to topographical situation (N, northern slope not permanently covered by snow in winter; sn, northern slope permanently snow-covered in winter; S, southern slope), bedrock type (cs, calcareous schist; gr, granite; ss, siliceous schist), and functional type of the dominant species (dc, deciduous chamaephyte; ec, evergreen chamaephyte; en, evergreen nanophanerophyte). Error bars represent the 95% confidence interval. Different lowercase letters in the same section mean significant differences at $p < 0.05$ obtained from GLM pair-wise comparisons of fourth-root (leaf primary production) and square-root (litter persistence) transformed data

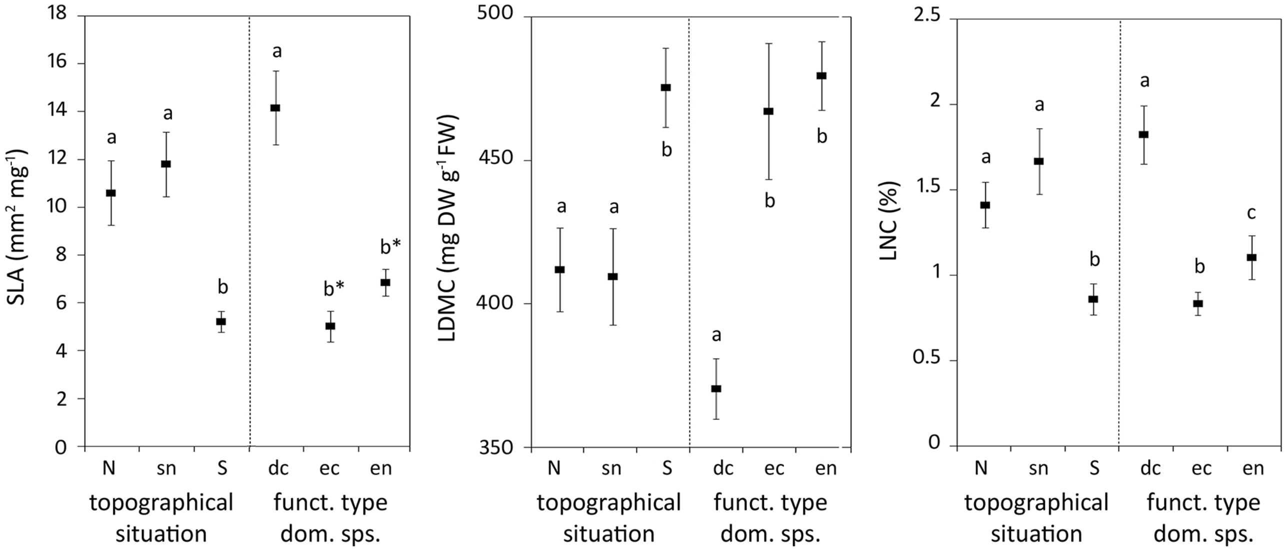

Fig. 6. Main community-weighted leaf traits according to topographical situation (N, northern slope not permanently covered by snow in winter; sn, northern slope permanently snow-covered in winter; S, southern slope) and functional type of the dominant species (dc, deciduous chamaephyte; ec, evergreen chamaephyte; en, evergreen nanophanerophyte). Bedrock type is not represented since significant differences were not found. Error bars represent the 95% confidence interval. Different lowercase letters in the same section mean significant differences at $p < 0.05$ obtained from ANOVA pair-wise comparisons; when followed by an asterisk (*) mean $0.05 \leq p < 0.1$

SUPPLEMENTARY MATERIAL

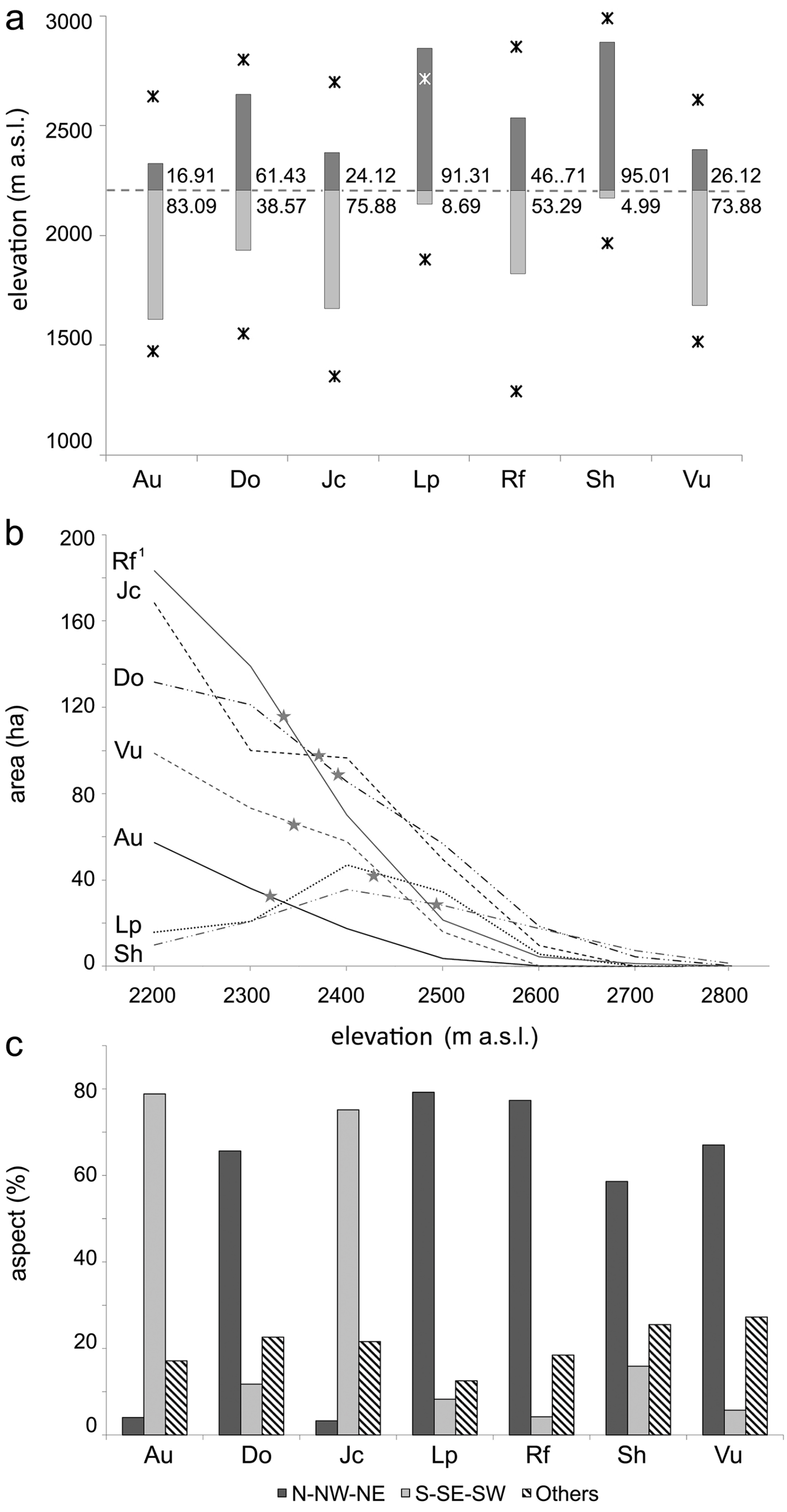

Fig. S1. Ecological characterization of the communities studied in the south-eastern Pyrenees: **a**, minimum and maximum elevation (asterisks) and percent area occupied below (grey bar) and above (dark grey bar) 2,200 m a.s.l. (the lower limit of the alpine belt); **b**, area occupied at each 100 m-elevational interval above 2,200 m a.s.l., with the mean elevation at the alpine belt labelled with a star (superscript 1 after Rf means a 10-fold reduced representation of the real area); **c**, percent area occupied at each aspect type. Communities are identified by the initials of the dominant species: Au, *Arctostaphylos uva-ursi*; Do, *Dryas octopetala*; Jc, *Juniperus communis* subsp. *alpina*; Lp, *Loiseleuria procumbens*; Rf, *Rhododendron ferrugineum*; Sh, *Salix herbacea*; Vu, *Vaccinium uliginosum* subsp. *microphyllum*

Table S1. Characterization of the sites sampled

	site	elevation (m a.s.l.)	aspect	slope (º)	bedrock*	species richness
Arctostaphylos uva-ursi	Au1	2220	S	40	calc sch	9
	Au2	2360	E	20	sil sch	10
	Au3	2400	SE	35	sil sch	5
	Au4	2500	ESE	15	granite	7
Dryas octopetala	Do1	2350	NE	40	calc sch	21
	Do2	2450	NE	25	calc sch	15
	Do3	2220	N	28	calc sch	--
Juniperus communis subsp. *alpina*	Jc1	2400	S	17	granite	8
	Jc2	2510	ESE	15	sil sch	12
	Jc3	2220	S	17	calc sch	5
Loiseleuria procumbens	Lp1	2400	NW	25	sil sch	9
	Lp2	2450	NE	17	calc sch	19
	Lp3	2400	N	15	granite	9
Rhododendron ferrugineum	Rf1	2400	NW	25	sil sch	8
	Rf2	2300	NE	35	calc sch	9
	Rf3	2360	ENE	30	sil sch	11
	Rf4	2400	NE	27	granite	13
Salix herbacea	Sh1	2400	-	0	granite	11
	Sh2	2600	-	0	sil sch	15
	Sh3	2425	-	0	calc sch	15
Vaccinium uliginosum subsp. *microphyllum*	Vu1	2400	NW	25	calc sch	13
	Vu2	2580	ENE	25	sil sch	13
	Vu3	2280	N	15	granite	--
	Vu4	2430	ENE	5	granite	15

*abbreviations of bedrock types: calc sch, calcareous schist; sil sch, siliceous schist

Table S2. Ellenberg ecological indicator values, modified by Julve (2014), for the communities studied. In bold, minimum and maximum values for each variable. Communities are identified by the initials of the dominant species: Au, *Arctostaphylos uva-ursi*; Do, *Dryas octopetala*; Jc, *Juniperus communis* subsp. *alpina*; Lp, *Loiseleuria procumbens*; Rf, *Rhododendron ferrugineum*; Sh, *Salix herbacea*; Vu, *Vaccinium uliginosum* subsp. *microphyllum*

	Au	Do	Jc	Lp	Rf	Sh	Vu
temperature[a]	**3.10**	2.25	2.56	**1.75**	2.51	1.93	2.37
atmospheric moisture[b]	4.99	5.06	**4.47**	4.72	5.38	**5.65**	5.40
soil moisture[c]	**4.43**	4.71	4.44	4.69	4.82	**5.45**	5.08
soil nutrients[d]	2.15	2.60	1.84	**1.68**	2.13	**2.74**	2.10
soil pH[e]	3.32	**6.18**	3.12	**2.87**	3.06	3.56	3.27

[a] Temperature: 1, alpine to nival; 2, subalpine; 3, montane; 4,colline

[b] Atmospheric moisture: 3, mesoxerophilous; 4, intermediate; 5, mesohydrophilous; 6, intermediate; 7, mesohygrophilous

[c] Soil moisture: 4, mesoxerophilous; 5, mesohydrophilous; 6, mesohygrophilous

[d] Soil nutrients: 1, hiperoligotrophic; 2, oligotrophic; 3, intermediate; 4, mesooligotrophic

[e] Soil pH: 2, acidophile; 3, intermediate; 4, acidocline (pH < 5.5); 5, intermediate; 6, neutrocline (pH > 5.5); 7, neutrophile

Table S3. Estimates of components of variation in functional structure of the communities studied, between- and within-sites (in percentage), obtained from the PERMANOVA test. In bold, the most unbalanced values. Communities are identified by the initials of the dominant species: Au, *Arctostaphylos uva-ursi*; Do, *Dryas octopetala*; Jc, *Juniperus communis* subsp. *alpina*; Lp, *Loiseleuria procumbens*; Rf, *Rhododendron ferrugineum*; Sh, *Salix herbacea*; Vu, *Vaccinium uliginosum* subsp. *microphyllum*

	between-sites	within-sites
Au	48.18	51.82
Do	44.63	55.37
Jc	50.17	49.83
Lp	**73.06**	**26.94**
Rf	59.12	40.88
Sh	51.15	48.85
Vu	**86.22**	**13.78**

Capítol V

Shrub encroachment above the Pyrenean treeline: identifying the main factors and the potential effects on ecosystem processes

Emmatament per sobre el límit del bosc als Pirineus: identificació dels factors principals que l’incentiven i dels efectes potencials en el funcionament de l’ecosistema

Estela Illa, Oriol Grau, Albert Ferré & Josep M. Ninot

Emmatament per sobre el límit del bosc als Pirineus: identificació dels principals factors que l'incentiven i dels efectes potencials en el funcionament de l'ecosistema

Resum

L'emmatament és un procés que afecta els ecosistemes pradencs a escala mundial. Als ambients alpins de les muntanyes temperades ha estat molt poc estudiat, tot i que hi ha diversos treballs centrats en l'estatge subalpí. En aquest treball vam quantificar l'emmatament de *Juniperus communis* subsp. *alpina* i de *Rhododendron ferrugineum* en un període de 17 anys. Vam relacionar aquest procés amb l'estructura de la població del matollar i el tipus de prat, i vam incloure com a covariables als anàlisis factors abiòtics (altitud, coordenada X, pendent) i biòtics (recobriment de l'arbust el 1997, incidència del bestiar) locals. També vam analitzar a grans trets els efectes de l'emmatament a nivell d'ecosistema. Els nostres resultats mostren que *J. alpina* presenta taxes de creixement superiors a *R. ferrugineum*, tant a través del creixement de taques grans de matollar com a través de l'establiment de nous individus. El tipus de prat no té efectes en les taxes d'emmatament, mentre que l'estructura de la població de l'arbust hi té una gran influència. També el recobriment inicial de l'arbust i la pressió del bestiar influeixen en l'emmatament. A nivell d'ecosistema, comporta increments en la biomassa i l'acumulació de virosta i reduccions en la taxa de descomposició de la virosta i la producció primària.

Mots clau: estructura de la població de l'arbust, pastura, recobriment de l'arbust, camins de bestiar, acumulació de virosta, producció primària

Shrub encroachment above the Pyrenean treeline: identifying the main factors and the potential effects on ecosystem processes

Estela Illa[1 4], Oriol Grau[2 3], Albert Ferré[1] & Josep M. Ninot[1]

[1] Institute for Research on Biodiversity (IRBio) & Department of Evolutionary Biology, Ecology and Environmental Sciences, University of Barcelona, Av. Diagonal 643, E-08028, Catalonia, Spain.
[2] CSIC, Unitat d'Ecologia Global, CREAF-CSIC-UAB, 08193 Cerdanyola del Vallès. Catalonia. Spain.
[3] CREAF (Centre de Recerca d'Ecologia i Aplicacions Forestals), 08193 Cerdanyola del Vallès. Catalonia. Spain.
[4] Corresponding autor: Estela Illa
Telephone number: +34 93 402 14 76. E-mail address: estelailla@ub.edu

Abstract

Shrub encroachment is a process affecting grassland areas worldwide. It has been rarely analysed in European temperate environments above the treeline, although there are frequent studies referring to the subalpine belt. In this study we quantified the encroachment of *Juniperus communis* subsp. *alpina* and *Rhododendron ferrugineum* in a period of 17 years. We looked for the relation between this process and shrub population structure and grassland type, and we included local abiotic (elevation, x-coordinate, slope) and biotic (shrub cover, livestock incidence) covariates in the analyses. We also analysed the gross effects of shrub encroachment at ecosystem level. Our results showed that *J. alpina* performed higher increase rates than *R. ferrugineum*, both through expansion of large clumps and establishment of new individuals. Grassland type did not result into different encroaching rates, whereas former shrub population structure strongly influenced shrub expansion. Also, former shrub cover and changes in livestock pressure influenced encroachment. At ecosystem level, encroachment implied higher community biomass and litter accumulation, together with lower litter decay rates and productivity.

Keywords: shrub population structure, grassland, shrub cover, livestock paths, litter accumulation, primary production

Introduction

Shrub encroachment is a natural process occurring worldwide, affecting both semiarid areas (Knapp et al. 2008), Alpine (Dirnböck et al. 2003; Anthelme et al. 2007; Brandt et al. 2013) and Arctic regions (Tape et al. 2006; Forbes et al. 2010; Hallinger et al. 2010; Dumais et al. 2014). The causes of this process are mainly attributed to global change, understood as the combination of the effects of climate change and changes in land use. In European mountain areas climate change is promoting an upwards shift of a certain number of vascular plants (Klanderud and Birks 2003; Pauli et al. 2003; Parolo and Rossi 2008), some of which are woody species. Simultaneously, traditional land use (e.g. livestock grazing, tree logging) has been gradually abandoned during the second half of the twentieth century (Garcia-Ruiz et al. 1996; MacDonald et al. 2000; Tasser and Tappeiner 2002), causing the reforestation of the ancient subalpine pastures (Gellrich et al. 2007).

As a result of global change, in European mountains the upper limit of the tree, or the *treeline*, is densifying and rising up (Kullman 2002; Gehrig-Fasel et al. 2007), and the same trend has been confirmed for shrub communities (Tasser and Tappeiner 2002; Sanz-Elorza et al. 2003; Hallinger et al. 2010). Shrub cover is increasing at the expense of grassland at quite high rates, for instance expanding 5.6% per decade in the alpine belt of the Alps (Cannone et al. 2007).

Some manipulative experiments on Arctic and Alpine shrubs have confirmed the positive correlation between temperature and shrub biomass (Kudo and Suzuki 2003; Kaarlejärvi et al. 2012), and long-term modeling points towards a high increase in shrub biomass related to increases in temperature (Epstein et al. 2004). Shrub expansion occurs through three simultaneous processes, namely an increase in shrub density, an increase in shrub size, and the colonization of new areas (Myers-Smith 2011). Among these processes, in alpine landscapes most of the increase in shrub cover is due to vegetative growth, and only a minor proportion is due to new patch formation through colonization by seed (Formica et al. 2014).

Shrub encroachment have major effects on environmental conditions and on ecosystem functioning. In winter, where snow do not form a protective blanket, shrub canopies insulate soil from low temperatures, whereas in summer they reduce soil temperature due to its shading effect (Myers-Smith and Hik 2013). Changes in soil properties have been also reported after shrub encroachment (Doche et al. 2005; Montané et al. 2007; Caviezel et al. 2014). At ecosystem level, higher biomass of shrub communities results into an increase of the amount of carbon (C) stored into recalcitrant biomass (Formica et al. 2014), which have consequences in C cycle (Myers-Smith et al. 2011). Compared to grassland ecosystems, litter may accumulate under shrub canopies due to their less decomposable leaves and woody structures, resulting into increased soil C (Montané et al. 2010b).

In our study we focused on the treeless area (e.g. subalpine or alpine grassland) above the present treeline in the Pyrenean range. In the Pyrenees, the predictions for the near future point towards increased meteorological irregularity (López-Moreno et al. 2009), rising temperatures and decreasing precipitation (Diaz and Bradley 1997; Engler et al. 2011). In fact, temperatures have already increased over recent decades (Morán-Tejeda et al. 2013). Land-use changes have also promoted the reforestation of pastures (Roura-Pascual et al. 2005; Améztegui et al. 2016), and at the treeline ecotone seedlings and saplings of forest trees have become denser (Camarero and Gutiérrez 2004; Batllori et al. 2009), together with shrubs.

Some authors have already studied or modelled shrub encroachment in the Pyrenees (Pasche et al. 2004; Montané et al. 2010a; Komac et al. 2013), although they have focused on the forest level. Above the treeline, despite the harsher environmental conditions, current climate and land use changes are expected to promote shrub growth. Within this context, our aims were to answer the following questions: i) are shrubs encroaching into grasslands above the Pyrenean treeline?, ii) which are the main factors favouring shrub encroachment?, and iii) do contrasted shrub species show different behaviour in their rates and strategies of encroachment? We also discuss the potential consequences on ecosystem functioning after shrub encroachment in the Pyrenees.

Methods

Area and communities studied

The study area comprised the higher subalpine and lower alpine belts of the south-eastern Pyrenees in Catalonia and Andorra, from 2200 m a.s.l. to 2500 m a.s.l. The border between the subalpine and alpine belts in this area is about 2200 m on northern slopes and about 2400 on southern slopes (Ninot et al. 2007). Substrates are mainly acidic, comprising slate and granite, with calcareous outcrops occurring in small areas along the axial range or restricted to pre-Pyrenean summits. At the elevational interval considered, mean annual temperatures are between 2 and 5.5 ºC, and mean annual precipitation is between 1100 and 1500 mm (data generated by the authors, obtained from Institut Meteorològic de Catalunya, www.meteo.cat). The alpine vegetation there consists on a mosaic of grassland and rocky habitats, covering together more than 85% of the surface in the area studied (Illa et al. 2006). Shrub communities are a minor vegetation type at high elevations, and most of them arise from the subalpine belt and find at the lower alpine belt their upper limit of distribution (Ninot et al. 2007; Illa et al. submitted). Within the study area evergreen shrub communities occupy 7 to 9-fold more surface than deciduous shrubs (unpubl. data). In this study we focused on heaths growing on acidic substrata dominated by the evergreen nanophanerophytes *Rhododendron ferrugineum* (*Saxifrago-Rhododendretum* Br.-Bl., Sissingh et Vlieger 1939) and *Juniperus communis* subsp. *alpina* (*Cytiso-Arctostaphyletum uva-ursi* Br.-Bl. 1948). These shrub species represent more than 90% of total biomass in their respective communities, and their ecological requirements are opposed: whereas *R. ferrugineum* heaths are found on north-facing aspects and remain protected by a permanent snowpack during winter that prevents from frost damage, *J. alpina* heaths grow on south aspects, where it experiences warmer temperatures and a longer growing season length but may face frost events during winter and spring due to the non-permanent snowpack on southern slopes (Braun-Blanquet 1948; Illa et al. submitted). Besides, these two species make large enough clumps to be observed in aerial photographs. Plant nomenclature follows Bolòs et al. (2005).

Determination of coexisting grasslands

To evaluate which grasslands share more area with *R. ferrugineum* and *J. alpina* heaths, and thus are more prone to be encroached, we used the existing digital cartographies of vegetation at a scale of 1:50,000 for Catalonia (Carreras and Vendrell 2012) and 1:25,000 for Andorra (Carreras et al. 2012), where polygons include up to three different vegetation units with their respective percentage cover. After combining the cartography of habitats with a topographic map, we selected all the polygons with shrub presence ranging from 2200 to 2500 m a.s.l., and obtained the area occupied by all the vegetation units found in these polygons (Table S1). The shrub communities studied coexisted with three acidic grassland types dominated by the same few graminoid species, concretely *Festuca airoides*, *Festuca eskia* and *Nardus stricta*. These coexisting grassland types have different ecological requirements and physiognomic characteristics. *Festuca airoides* grassland community (*Hieracio-Festucetum supinae* Br.-Bl. 1948) is low in height and host quite high species diversity. It grows on ridges and culminant northern slopes, except in the eastern part of the range, where it finds its optimum and grow at high altitudes irrespectively of the aspect. The *Festuca eskia* dominated communities are two contrasting types, namely a mid- to low-cover garland-grassland found on southern slopes coexisting with *J. alpina* heaths (*Festucetum eskiae* Br.-Bl. 1948, occasionally *Carici-Festucetum eskiae* Rivas-Mart. 1974) and a dense, mesophilic grassland mostly found on lower northern slopes or flat areas mainly in contact with

R. ferrugineum heaths (*Selino-Festucetum eskiae* Nègre 1968). *Nardus stricta* grassland (*Alchemillo-Nardetum* Gruber 1975) includes low species richness pastures growing on northern aspects or on flat areas.

Evaluation of shrub encroachment by means of aerial photographs

Once we had identified the grassland types with higher percentage of coexistence with the studied shrub communities, we proceeded to confirm and evaluate the change of shrub cover on them. For that purpose, in the cartography of habitats we selected five polygons distributed along the study area for each combination of grassland and heath units, i.e. a total of 30 polygons (Fig. 1). In each of these polygons, in the contact area between shrubland and grassland, we projected a grid of 225 5 x 5 m cells, each grid covering an area of 5,625 m^2.

To detect and evaluate shrub encroachment, we performed a diachronic analysis through the comparison of 1997 grey-scale aerial photographs (50 cm pixel side) and 2014 infrared-colour aerial photographs (25 cm pixel side), obtained from Institut Cartogràfic de Catalunya (www.icc.es). In each grid we first visually discarded cells containing habitats not related to our aims (mainly scree or rock, but also other pasture types) and cells where we were not able to identify correctly vegetation units. For the remaining cells we noted relevant information concerning shrub cover, structure and grazing pressure (see detailed information in Table 1). Specifically, we estimated shrub cover (when present) in 1997 and in 2014, using cover categories of 1-25%; 25-50%: 50-75% and 75-100%. We also noted in these cells if we identified or not changes in shrub cover over the 17 years considered, considering that ‘change’ included cells where, although increase was clear, remained in the same cover category. Cells with shrub presence in 1997 were classified depending on the shrub population structure, which was divided into four categories. One category included cells with already 100% shrub cover in 1997 (thus, with no invasive ability in the same cell). The three other categories included cells with simultaneous presence of grassland and shrub, and corresponded to isolated shrub elements (i.e. well individualised shrub element surrounded by grassland), small shrub clusters (i.e. different shrub elements contacting and forming small patches occupying a maximum of 4 cells), and large shrub clusters (i.e. a medium to large shrub patches occupying more than 4 cells). Cells without apparent shrubs in 1997 were classified as empty cells. Finally, we also noted the presence of livestock paths in the cells for the two years studied, to incorporate the difference in their proportion between 2014 and 1997 as a potential influencing factor on shrub encroachment. We also noted the elevation, x-coordinate (which corresponds to a climatic gradient from oceanic at east to continental at west) and slope of the central cell of the grids studied. All procedures implying GIS techniques were carried with the software ArcGIs 10.1 (ESRI).

Grid calculations

From the total 6,750 cells (3,375 for each shrub species), we retained those cells that could be sensitive to encroachment, that is 2,691 in the case of *J. alpina* and 2,371 in the case of *R. ferrugineum*. The remaining cells, including those with full cover of shrub in 1997 (155 in *J. alpina* grids and 705 in *R. ferrugineum* grids), were discarded.

Once the different grids (sites) were fully analysed through the comparison of images, we calculated for each one the proportion of cells of a given type of shrub population structure experiencing increase in shrub cover. In order to quantify encroachment, for each grid we also estimated the global increase in shrub cover, from which we derived the global increase in shrub area in 17 years. To estimate the increase in cover we assigned to each cell the mean value of its percent cover category (i.e. 12.5, 37.5, 62.5 or 87.5), and computed the mean for each grid. To estimate the increase in the area occupied by each shrub species on each grassland type, we multiplied the increase in cover by the potential encroaching area in each grid.

Changes in ecosystems

To infer changes in ecosystem structure and processes we used data describing functional compartmentalization of the most frequent Pyrenean alpine pasture and shrub communities found in Illa and Ninot (2005) and Illa et al. (submitted), together with own unpublished data (Table S2). In these studies, we recorded the biomass of different functional groups and structural compartments of the most abundant grassland and subshrub communities above the treeline in the Pyrenees. Then, with these data and with the values of the total area encroached in 17 years per grid, we computed the changes in carbon storage (total community aboveground biomass), aboveground leaf primary production (the amount of leaves that are renewed yearly), litter accumulation (the total amount of litter on the ground) and litter persistence (the relation between leaf biomass that is renewed yearly and the total amount of litter).

Statistical analyses

To identify the key variables with the strongest influence on shrub encroachment we employed multiple linear mixed effects models fitted with the maximum likelihood method (ML). Our response variable was in all cases the proportion of cells experiencing encroachment. In the individualised analyses for each shrub species, the fixed factors included in the models were grassland type (with three levels: *F. airoides*, *F. eskia* and *N. stricta*) and shrub population structure (with three levels: isolated elements, small clusters and large clusters). In the global analyses we excluded the non shared *F. eskia* grassland types, and the fixed factors included in the models were shrub species (with two levels: *J. alpina* and *R. ferrugineum*), grassland (with two levels: *F. airoides* and *N. stricta*) and shrub population structure (with the same three levels than in individualised models). The grid (site) was considered in all models as a random effect. We included in the models mean grid elevation, mean grid x-coordinate, mean grid slope, shrub cover in 1997, number of livestock paths in 2014 and changes in the proportion of livestock paths between 1997 and 2014 as covariates. In all cases we began the analyses with the full models with interaction terms, and performed a manual backward stepwise selection based on the Akaike's information criterion (AIC) to select the best model. To obtain F values and significance when fixed factors showed signification in the models we conducted two-way ANOVAs, and when they showed significant effects we performed post-hoc Tukey HSD tests to look for differences between the different levels of the factor. Finally, to obtain approximate adjusted R^2 and significance of the relationships found in the models we also performed ordinary least square (OLS) regressions.

To assess if *J. alpina* and *R. ferrugineum* performed different colonisation strategies, we computed for each grid the proportion of encroached cells where we detected new individuals in 2014. After that, we performed two-way ANOVAs with shrub and grassland community as fixed effects factors. When significant effects were found, we ran post-hoc Tukey HSD tests.

We square root- or log-transformed response variables when necessary, to reach the assumptions of normality and homoscedasticity of residuals. Effects were considered significant at $p < 0.05$ and marginally significant at $0.05 < p < 0.10$.

All the analyses were performed with the R software (R Development Core Team 2016), using the nlme package (Pinheiro et al. 2016) for mixed effects models.

Results

General trends for J. alpina and R. ferrugineum

The comparison of images and posterior analyses showed different encroachment rates in 17 years between *J. alpina* and *R. ferrugineum* (Table 2). The proportion of cells experiencing increase in shrub cover was significantly higher in *J. alpina*, both when considering all grassland types ($F_{1,25}$ = 15.024, $p < 0.001$) and when considering only the shared *F. airoides* and *N. stricta* grassland communities ($F_{1,17}$ = 9.60, $p = 0.0065$). Although we did not find significant differences between grassland types, *F. eskia* garland-grasslands had the maximum proportion of cells experiencing increase (31.57%), and for both shrubs we observed the lowest proportion of encroached cells in *N. stricta* grasslands (Table 2).

Our approximations to quantify the increase in shrub area showed that *J. alpina* increased between 2 and 3% per decade and hectare, depending on the grassland type, whereas *R. ferrugineum* increased about 1.5% in any case (Table 2). Changes of shrub cover between 1997 and 2014 were significantly higher in *J. alpina* when considering all grassland types ($F_{1,25}$ = 5.511, $p = 0.0271$), but they had non-significant effects when we only considered the shared communities ($F_{1,17}$ = 1.749, $p = 0.204$). The same results were observed for the total area encroached ($F_{1,25}$ = 5.519, $p = 0.027$ and $F_{1,17}$ = 1.751, $p = 0.203$), due to the high correlation between the estimations of increases in shrub cover and area.

Factors determining shrub encroachment

The model selection for *J. alpina* revealed strong support for retaining both fixed factors (grassland type and shrub population structure), and shrub cover in 1997 and changes of proportion in livestock paths among the covariates. The model selection for *R. ferrugineum* retained the same variables except shrub cover in 1997 (Table 3). In *J. alpina*, the subsequent analysis of variance revealed that none of the fixed factors had significant effects, whereas in *R. ferrugineum* we found values near the signification level for grassland type ($F_{2,40}$ = 2.546, $p = 0.091$) and significant effects for shrub population structure ($F_{2,40}$ = 13.853, $p < 0.001$). Proportion of encroachment related to shrub population structure increased from isolated elements to large shrub clusters (Fig. 2), and post-hoc comparisons showed significant differences between all levels, except between isolated elements and small clusters, where *p*-values were near the signification level ($p = 0.0732$).

Shrub cover in 1997 influenced significantly *J. alpina* encroachment (Fig. S1). Individualised OLS regressions showed that the occurrence of *F. airoides* grasslands, small shrub clusters and large shrub clusters were significantly correlated with encroachment. Changes in the proportion of livestock paths correlated positively with the proportion of cells experiencing increase in shrub cover for both *J. alpina* (Fig. S2) and *R. ferrugineum* (Fig. S3). In both cases, isolated elements showed significant positive correlations with changes in the proportion of livestock paths, and also large clusters of shrub in *R. ferrugineum* model. *Nardus stricta* grassland was the only pasture type that appeared to have positive correlation with changes in the proportion of livestock paths, and showed a significant correlation in *R. ferrugineum* and *p*-values near the signification level in *J. alpina*.

The general model with the shared grassland types between *J. alpina* and *R. ferrugineum* showed similar results than those obtained in the individualised models. The model selection retained the three fixed factors, and as in the individualised models, also retained the covariates shrub cover in 1997 and the proportion of change of livestock paths (Table 4). The subsequent analysis of variance revealed that shrub species ($F_{1,52}$ = 8.316, $p = 0.0057$), shrub population structure ($F_{2,52}$ = 4.023, $p = 0.0237$) and the interaction between shrub and shrub structure ($F_{2,40} = 4.631$, $p = 0.0141$) had significant effects. *Juniperus communis alpina* had, in all cases except for large clusters, higher proportion of cells with increase in shrub cover than *R. ferrugineum* (Fig. 3, Fig. S4). The OLS regressions for shrub cover in 1997 resulted in non-significant effects ($R^2adj = -0.01131$, $p = 0.554$), although when we performed OLS separately for each level of shrub population structure we found a significant negative correlation between isolated individuals and shrub cover in 1997 ($R^2adj = 0.4356$, $p < 0.001$). Finally, OLS regressions showed that changes in the proportion of livestock paths were positively correlated to isolated elements and small shrub clusters, and to *F. airoides* and *N. stricta* grassland types (Fig. S5).

Colonisation by seed

ANOVAs did not show significant differences of the proportion of newly encroached cells detected in 2014, neither between shrub species ($F_{1,25} = 0.204$, $p = 0.655$) nor grassland communities ($F_{3,25} = 0.469$, $p = 0.706$). However, *F. eskia* garland-grasslands, followed by *N. stricta* grasslands encroached by *J. alpina*, showed a tendency towards a higher proportion of new shrub colonisation (Fig. S6). Mean values for each shrub species were similar, concretely 12.7 for *J. alpina* and 11.1 for *R. ferrugineum* (data not shown).

Changes in community biomass and processes

The total area encroached in the sampled grids after 17 years was variable between shrub species and grassland types (Table 5). *Festuca eskia* garland-grassland experienced the highest encroachment (1,318.75 m^2), which corresponded to an increase of *ca*. 3 tones in aboveground biomass in the grids analysed. The lowest values of area encroached were those of *R. ferrugineum* in the *F. airoides* grassland (368.77 m^2), which corresponded to an increase of 630 kg in the grids sampled. In 17 years, *J. alpina* colonised 2,954.28 m^2 in the grids analysed and *R. ferrugineum* 1,481.36 m^2. These encroached areas involved an increase in aboveground biomass of 6,361.7 kg and 2,282.5 kg, respectively. They also corresponded to an increase of 2,551.5 kg in litter accumulation in the case of *J. alpina* and of 904.9 kg in that of *R. ferrugineum*, and to a 4- to 6-fold increase of litter persistence, compared to grassland (Table S2). On the contrary, encroachment reduced the rates of leaf primary production, more strikingly in the case of *R. ferrugineum*, which implied a reduction of 20 kg m^{-2} year^{-1} in the grids analysed, compared to the reduction of 10.88 kg m^{-2} year^{-1} in *J. alpina*.

Discussion

Rates of shrub encroachment

We confirmed that shrub encroachment is occurring at high elevations above the treeline in the Pyrenees. The two shrub species studied, which belong to very distant families and have contrasted environmental requirements, showed contrasted growth rates. In *J. alpina*, a higher proportion of cells experienced shrub increase than *R. ferrugineum*. It could be related not only to the particular characteristics of each species (e.g. Pornon and Doche (1996) documented the expansion of *R. ferrugineum* as a very slow process), but also to the contrasted environmental conditions they experience, with the sunny slopes where *J. alpina* grows being more favourable to growth due to the higher energy budget they receive during the growing season (Tasser and Tappeiner 2002; Illa et al. submitted).

The relevance of shrub expansion in increasing shrub cover was probably mainly due to clonal expansion. The proportion of shrub increase related to vegetative growth vs. that resulting from seed colonization was about 88% vs. 12%, similarly than the values found in other studies (Formica et al. 2014), and confirming that at high elevations vegetative growth (via layering or simply by growth of the individuals) is the most important contributor to the increase in shrub cover. Despite we did not find significant differences in the proportion of cells with new individuals between the two shrub species, the reproductive strategy of *J. alpina* may lead to a higher number of saplings (Thomas et al. 2007), which were not detected in the aerial images, whereas *R. ferrugineum* is known to have very low seedling recruitment (Pornon and Doche 1995) and to expand mainly through clonal growth (Pornon et al. 1997).

The role of shrub population structure and grassland type

Shrub population structure appeared to be a key factor determining the increase in shrub cover in *R. ferrugineum*. These results relate primarily to community structure, since *R. ferrugineum* usually forms large patches and basically expands through clonal growth by layering (Pornon et al. 1997). Then, it is not surprising to find that major contributors to increase in community cover are large clusters of shrub. Moreover, Pornon et al. (1997) reported that layering steadily increases with increasing population closure and maturity. On the other hand, in *J. alpina* the different typologies of shrub community structure seemed to result in similar expanding dynamics, although there was a trend towards higher relevance of isolated individuals and small clusters of shrub. Again, this is related to community structure. *Juniperus communis alpina* usually reproduces by seed (Thomas et al. 2007), which implies an irregular, scattered distribution of individuals, but also can experience a fair clonal growth by layering (cf. Sullivan 2001), and thus forming shrub clusters. These highly heterogeneous patches of *J. alpina* translate into similar proportions of cells with increase in shrub cover between the different typologies of shrub population structure.

Grassland type appeared to have reduced effects on encroachment in our study, contrarily to the findings of Dullinger et al. (2003) and Montané et al. (2010a), who observed differential encroachment suitability between different grassland types. The low competitive ability for soil nutrients of shrubs (Pornon et al. 2007), which decreases as elevation increases (Callaway 1998), could explain the similar invasion rates between grassland communities in our study sites, placed at higher elevations than the studies reported before.

In the study of Dullinger et al. (2003), soil erosion potential was the only relevant environmental predictor of grassland invasion. Among the grassland communities we studied, those of *F. eskia* forming garlands, which are subjected to periodical soil movement and erosion (Braun-Blanquet 1948), showed a non-significant trend towards higher proportion of encroached cells. Thus, it contradicts the results of Dullinger et al. (2003) about improved shrub growth in less eroded grassland types.

Local abiotic vs. biotic conditions

Abiotic factors related to site location did not have any influence on the proportion of cells experiencing increase in shrub cover in our studied sites. We did not find any influence of elevation, as was also found by Dullinger et al. (2003), whereas other studies observed elevation effects on shrub growth rates (Ortiz et al. 2002; Tasser and Tappeiner 2002; Hallinger et al. 2010).

We found positive correlations between changes in the proportion of livestock paths and the proportion of cells with increase in shrub cover for both *J. alpina* and *R. ferrugineum*, which translate in these cases into increased local soil erosion. Moreover, seedling germination of alpine conifers is constrained by large amounts of grass litter (Talavera and Ninot, unpubl. data), and the presence of livestock paths implies not only the absence of litter, but also the absence of graminoid biomass. These open paths, together with moderate grazing pressure, have been suggested to favor *J. alpina* germination (Thomas et al. 2007). However, in order to better understand the benefits and disadvantages of livestock pressure in encroachment processes, more accurate studies focused on grazing pressure should be conducted.

Consequences at ecosystem level

At ecosystem level, there are several potential consequences derived from the encroachment of both *J. alpina* and *R. ferrugineum*. First, there is a high increase in aboveground biomass, which translates into higher amounts of C stored not only aboveground, but also belowground due to the coarser and deeper root system of shrubs when compared with graminoid species (Caviezel et al. 2014; Pornaro et al. 2016).

Second, litter accumulation and persistence also experience an increase after shrub encroachment, which result into changes on soil structure and composition. Soil organic carbon (SOC) has been reported to increase after shrub encroachment (Montané et al. 2007; Dirnböck et al. 2008; Pornaro et al. 2016) as a consequence of higher C content in shrub structures (Formica et al. 2014) and of lower decomposition rates of shrub litter (Pornon and Lamaze 2007; Montané et al. 2010b) compared with grasses. Not only litter, but also humus accumulates after shrub encroachment, in this case as a consequence of the simultaneous effect of increased litter input and decreased organic matter mineralization due to cooler conditions under shrub canopy (Dirnböck et al. 2008). In addition, the composition of soil microorganism communities may change under different community types, and implies a higher fungal:bacterial ratio under shrub canopies (Sundqvist et al. 2011) that translates into a reduction of litter decomposition rates (Eskelinen et al. 2009). Moreover, mycorrhizal fungi favored with shrub encroachment are better competitors for N than are saprotrophs and other microbial decomposers, and thus this vegetation shift would limit the N available for litter decomposition and contribute to C sequestration (Clemmensen et al. 2013). All these processes reinforce the capacity of shrubs to monopolize nutrients (Pornon and Lamaze 2007), which may difficult the establishment fast-growing species such as grasses and thus may favor the maintenance of shrub patches.

Finally, leaf primary production decreased after shrub encroachment. Evergreen shrubs take up nutrients slowly (Pornon et al. 2007), and the consequence are low growth rates. The lower productivity of evergreen is also a consequence of the longer retention of nutrients in their leaves, compared to herbaceous species (Pornon et al. 2007), contributing again to nutrient monopolisation. These reduced primary production rates are also related to the cycle of nutrients in shrub communities, thus closing a circle and impeding the establishment of other vegetation types without the occurrence of any perturbation.

Concluding remarks

Juniperus communis alpina showed higher encroachment rates than *Rhododendron ferrugineum* above the treeline, presumably responding to more productive bioclimate in its south-facing locations. In both species, encroachment seemed to be driven by similar factors, mainly related to shrub population structure. Simultaneously, also shrub cover and the increase in the proportion of livestock paths seemed to influence positively shrub encroachment. At ecosystem level the consequences of shrub encroachment are noticeable, irrespectively of the shrub species. On one hand higher biomass and litter accumulation in shrub communities translates into higher amounts of C sequestration. On the other hand, poorer litter quality under shrubs, promoting lower decay rates and nutrient release, contributes not only to increase of soil organic C, but also to reduce soil fertility. At a regional scale, the speed at which encroachment can occur determines the impact of these processes.

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Table 1. Information noted in each cell of the 30 grids (sites) studied

Changes in shrub cover	
no change (no apparent change)	
change	Increase in cover- Through increase in shrub / shrubland size
	Increase in cover- Through apparition of new shrub individuals
	Reduction in cover
not identifiable or not analysed habitat types	
Type of shrub population structure in 1997	
element	Cell with isolated shrub elements
small cluster	Cell with shrub presence as part of a small cluster (thin structure reaching a maximum length of 4 cells)
large cluster	Cell with shrub presence as part of a big cluster of shrubland
shrubland	Cell with 100% shrub cover, thus without possibility of grassland encroachment in the same cell
Shrub cover (for 1997 and 2014 separately)	
0	
< 25%	
between 25 and 50%	
between 50 and 75%	
> 75%	
Livestock paths (for 1997 and 2014 separately)	
0 (absent)	
1 (present)	

Table 2. Mean values and standard deviation (in parenthesis) of the different variables describing changes of *R. ferrugineum* and *J. alpina* cover in the pastures studied. Values are given as percentages with respect to the total number of cells with shrub presence in 2014. Grassland communities are identified with the initials of the dominant species: fa, *Festuca airoides*; feg, *Festuca eskia* garland; fem, *Festuca eskia* mesophile; ns, *Nardus stricta*

	Juniperus communis alpina			*Rhododendron ferrugineum*		
	fa	feg	ns	fa	fem	ns
cells with increase in shrub cover (%)	30.49 (0.72)	31.41 (1.31)	24.98 (3.13)	18.16 (9.15)	21.63 (8.50)	12.44 (11.57)
change in shrub cover (%)	3.69 (1.54)	5.38 (1.38)	3.69 (2.38)	2.59 (2.01)	2.88 (1.58)	2.26 (2.70)
increase in shrub area (m^2 ha^{-1} $year^{-1}$)	21.70 (9.06)	31.64 (8.13)	21.73 (13.99)	15.24 (11.84)	16.96 (9.32)	13.32 (15.88)

Table 3. Fixed effects and covariates of the individualised mixed linear effects models with the best fits. *Festuca eskia* grassland (either forming garlands in the case of *J.alpina* or mesophile in the case of *R.ferrugineum*) and isolated elements of shrub were used as baseline levels

	Juniperus communis alpina				*Rhododendron ferrugineum*			
	df	coeff ± SE	*t*-value	*p*-value	df	coeff ± SE	*t*-value	*p*-value
Festuca airoides grassland	12	-0.387 ± 0.27	-1.407	0.1848	12	-0.382 ± 0.26	-1.464	0.1689
Nardus stricta grassland	12	-0.579 ± 0.27	-2.137	**0.0539 .**	12	-0.531 ± 0.26	-2.056	**0.0622 .**
small shrub clusters	23	-0.421 ± 0.26	-1.610	0.1210	27	0.683 ± 0.21	3.273	**0.0029** **
large shrub clusters	23	1.328 ± 0.30	-4.483	**< 0.001** ***	27	1.194 ± 0.20	5.828	**< 0.001** ***
shrub cover in 1997	23	0.161 ± 0.03	5.832	**< 0.001** ***				
changes in livestock paths	23	0.046 ± 0.01	3.568	**0.0016** **	27	0.058 ± 0.02	2.756	**0.0103** *

Table 4. Fixed effects and covariates of the general linear mixed effects model with the best fit. *Festuca airoides* grassland, isolated elements of shrub and *Juniperus communis alpina* were used as baseline levels

	df	coeff ± SE	*t*-value	*p*-value	
N. stricta grassland	17	-2.205 ± 1.12	-1.964	**0.0661**	**.**
small shrub clusters	35	-2.972 ± 1.24	-2.404	**0.0216**	*
large shrub clusters	35	-4.759 ± 1.70	-2.802	**0.0082**	**
R. ferrugineum	17	-14.314 ± 2.04	-7.031	**< 0.001**	***
shrub cover in 1997	35	0.523 ± 0.08	6.489	**< 0.001**	***
changes in livestock paths	35	0.250 ± 0.06	3.906	**< 0.001**	***

Table 5. Changes in the area encroached, aboveground biomass, litter accumulation, and primary production in the sampled grids for each shrub community in the different grassland communities, expressed as mean values and standard deviation (in parenthesis)

	average area encroached in 17 years (m^2)	total area encroached (m^2)	average changes in aboveground biomass (kg)	total changes in aboveground biomass (kg)	average changes in litter accumulation (kg)	total changes in litter accum (kg)	average changes in primary production (kg m^{-2})	total changes in primary production (kg m^{-2})
J. alpina								
F. airoides	165.10 (80.20)	825.03	356.60 (173.32)	1783.02	137.18 (66.67)	685.91	-1.41 (0.68)	-7.04
F. eskia garland	263.75 (66.59)	1318.75	582.68 (146.91)	2913.42	230.42 (58.09)	1152.09	-5.01 (1.26)	-25.04
N. stricta	162.10 (102.13)	810.5	333.06 (209.84)	1665.30	142.71 (89.91)	713.54	-30.58 (19.27)	-152.92
R. ferrugineum								
F. airoides	73.75 (39.87)	368.77	126.34 (68.30)	631.70	49.80 (26.92)	248.98	-3.37 (1.82)	-16.86
F. eskia mesophile	116.89 (72.01)	584.46	162.47 (100.08)	812.35	54.70 (33.69)	273.50	-40.88 (25.18)	-204.40
N. stricta	105.63 (138.65)	528.16	169.69 (222.75)	848.44	76.49 (100.41)	382.45	-23.86 (31.32)	-119.29

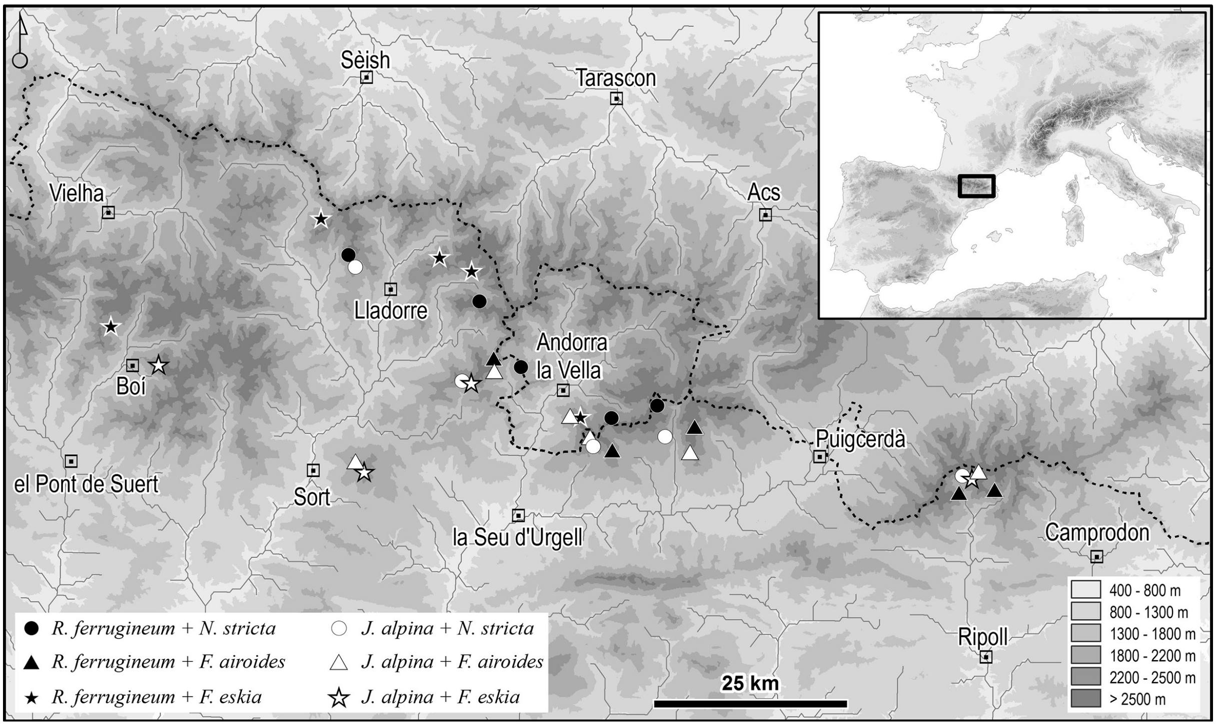

Fig. 1. Study area and distribution of the sites analysed, referred to the six vegetation combinations considered

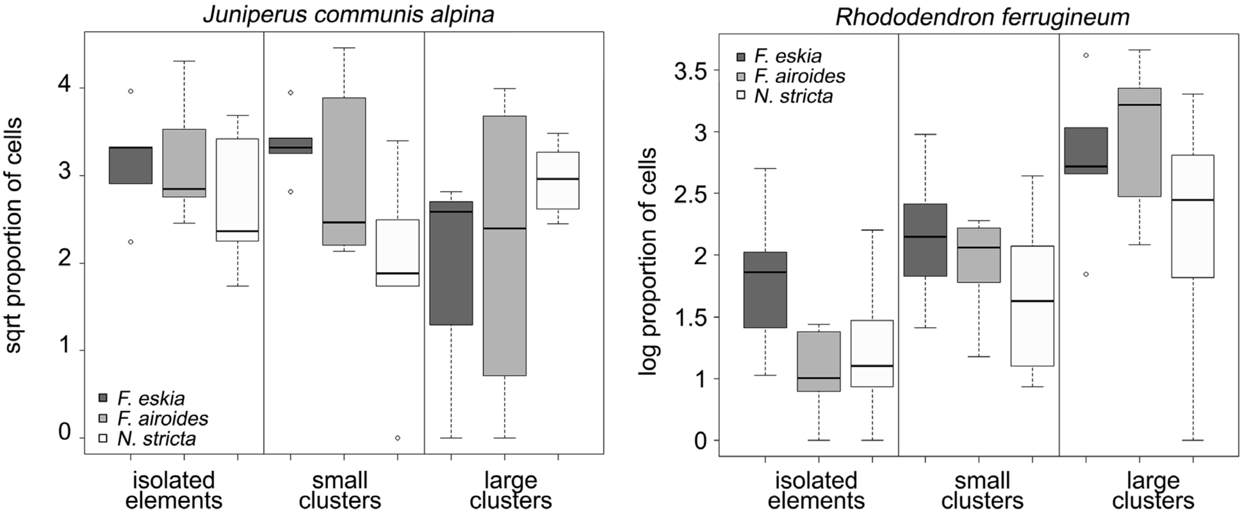

Fig. 2. Contribution of the different shrub population structure and grassland community type on *J. alpina* and *R. ferrugineum* encroachment

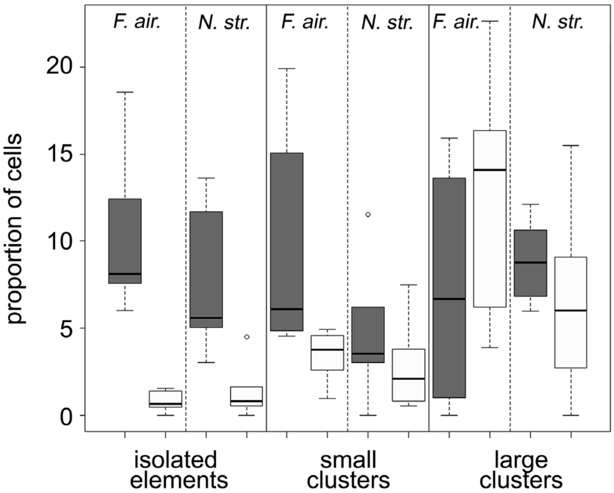

Fig. 3. Contribution of the different shrub population structure, shrub species and grassland community type on *J. alpina* (grey) and *R. ferrugineum* (white) encroachment. Grassland communities are abbreviated as follows: *F.air*, *Festuca airoides*; *N. str, Nardus stricta*

SUPPLEMENTARY MATERIAL

Table S1. Percentage of area occupied by *Rhododendron ferrugineum* and *Juniperus communis alpina* heaths and the coexisting vegetation units in polygons with shrub presence between 2200 and 2500 m a.s.l. in southern Pyrenees

	cover (%)	area (ha)
***Rhododendron ferrugineum* heaths**	**67.77**	**3.582.40**
Pinus mugo uncinata forests	9.14	483.40
Acidic rocks	6.37	336.96
Acidic screes	6. 07	354.25
Festuca eskia mesophilous grasslands	2.87	151.94
Nardus stricta grasslands	2.49	131.85
Empetrum nigrum hermaphroditum heaths	1.91	100.88
Festuca airoides grasslands	0.69	36.34
Acidic snowbeds	0.43	22.92
Vaccinium uliginosum microphyllum heaths	0.38	20.33
Other vegetation units	1.23	65.01
***Juniperus communis alpina* heaths**	**46.02**	**273.99**
Acidic rocks	14.45	86.06
Festuca eskia garland-grasslands	9.95	59.25
Pinus mugo uncinata forests	6.62	39.44
Festuca airoides grasslands	5.39	32.07
Nardus stricta grasslands	4.84	28.82
Acidic screes	3.46	20.61
Genista balansae europaea heaths	2.17	12.92
Arctostaphylos uva-ursi carpets	1.25	7.43
Festuca gautieri calcareous grasslands	0.97	5.80
Calcareous screes	0.97	5.79
Calcareous rocks	0.50	2.99
Other vegetation units	3.95	23.50

Table S2. Community functional descriptors for the two shrub communities studied and the main neighbouring pastures

	total biomass (g m^{-2})	productivity (g m^{-2} year^{-1})	litter accumulation (g m^{-2})	litter persistence (year)
heaths				
J. alpina	2483.13^{1}	212.43^{1}	922.97^{1}	4.60^{1}
R. ferrugineum	2034.96^{1}	175.23^{1}	766.75^{1}	4.46^{1}
grassland				
Festuca airoides	312.97^{2}	220.96^{3}	91.58^{2}	1.07^{3}
Festuca eskia garland	273.90^{2}	231.42^{3}	49.39^{2}	0.82^{3}
Festuca eskia mesophile	645.04^{2}	524.96^{3}	298.79^{2}	1.24^{3}
Nardus stricta	428.48^{2}	401.10^{3}	42.58^{2}	0.77^{3}

Data obtained from: ^{1} Illa et al. (submitted); ^{2} Illa & Ninot (2005); ^{3} unpublished data

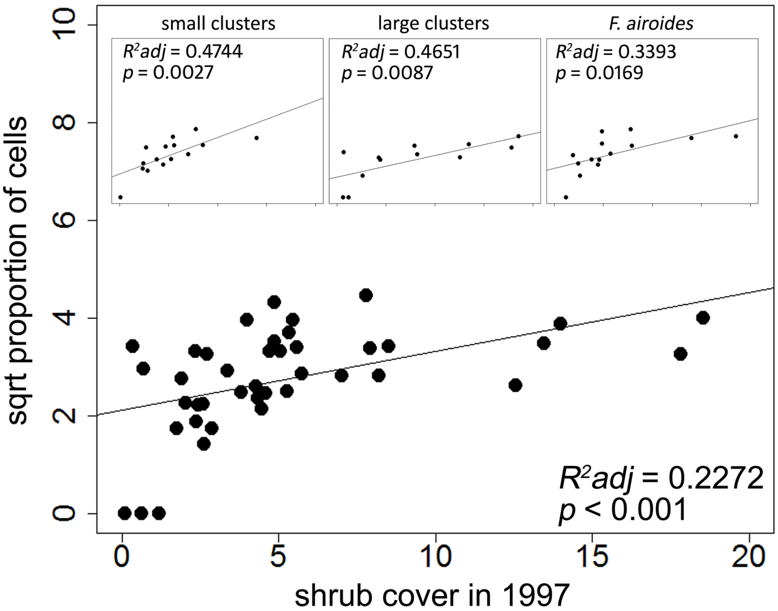

Fig.S1. Correlations between the proportion of cells experiencing increase in *J. alpina* cover (square-root transformed) and *J. alpina* cover in 1997. In small boxes, individualised correlations for grassland type or shrub population structure which were significant

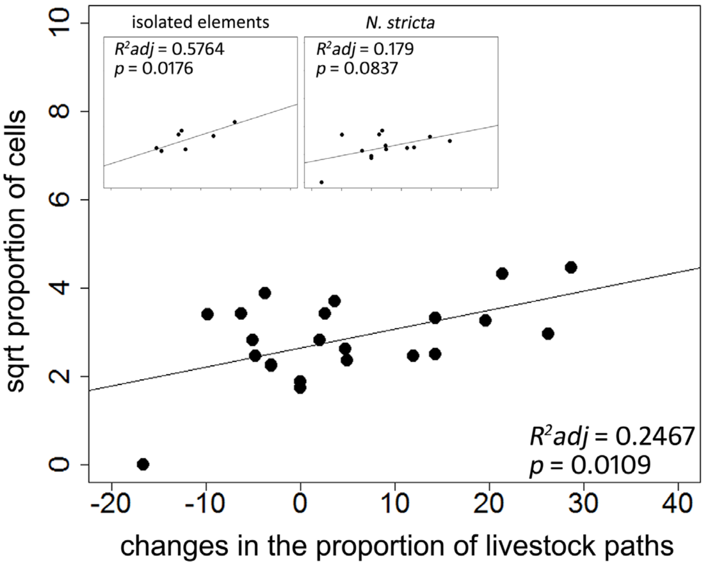

Fig.S2. Correlations between the proportion of cells experiencing increase in *J. alpina* cover (square-root transformed) and the changes in the proportion of livestock paths. In small boxes, individualised correlations for grassland type or shrub population structure which were significant

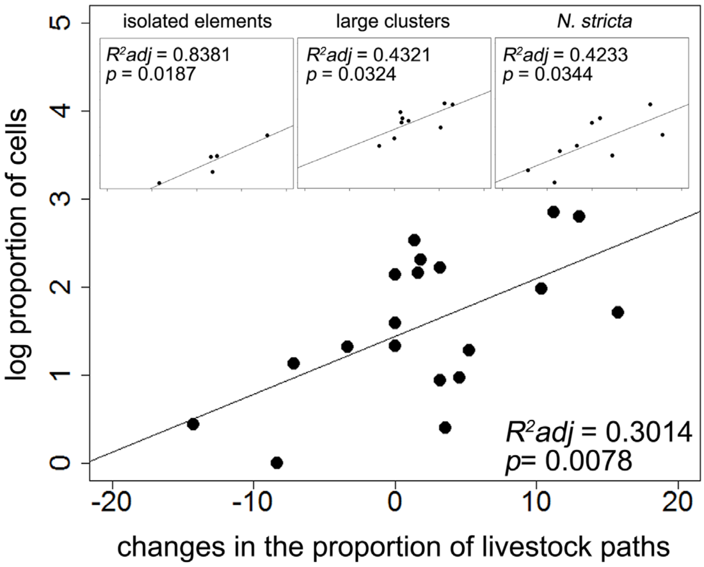

Fig.S3. Correlations between the proportion of cells experiencing increase in *R. ferrugineum* cover (log-transformed) and changes in the proportion of livestock paths. In small boxes, individualised correlations for grassland type or shrub population structure when significant

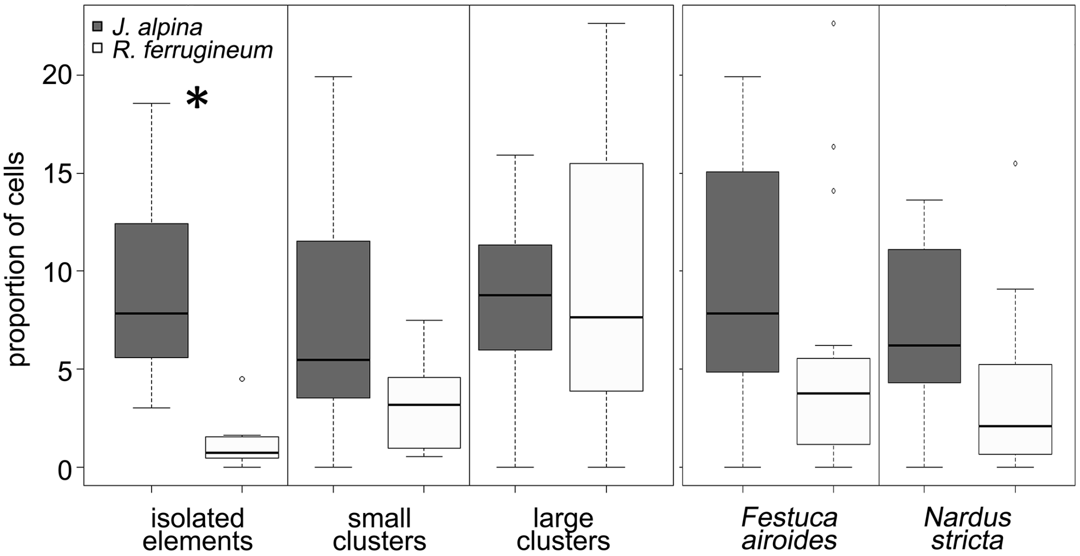

Fig.S4. Contribution of the different shrub population structure and grassland communities to *J. alpina* and *R. ferrugineum* encroachment separately. An asterisk means significant differences ($p < 0.05$) between shrub species

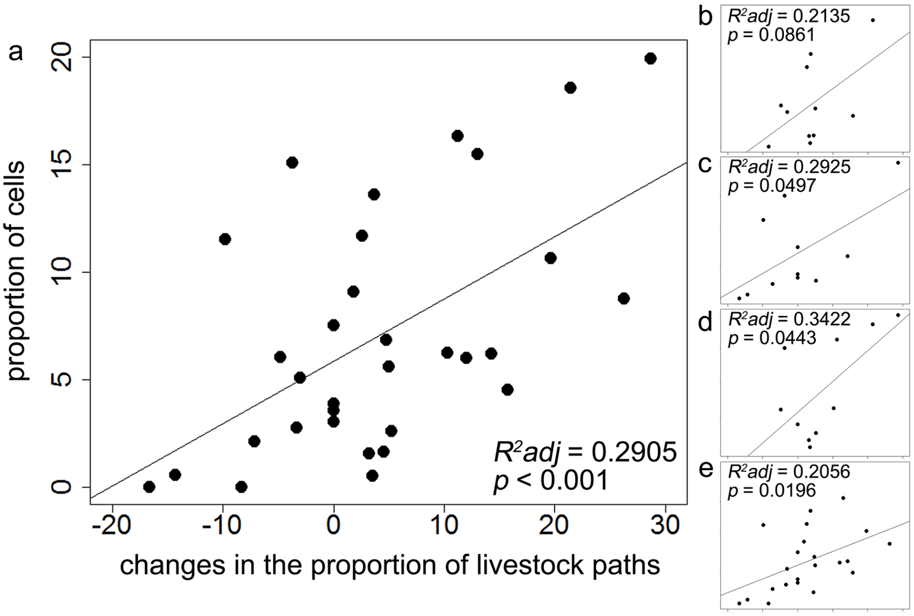

Fig.S5. Correlations between the proportion of cells experiencing increase in shrub cover and the changes in the proportion of livestock paths obtained in the general linear mixed effects model (a). In small boxes, individualised significant correlations for *F. airoides* grassland (b), *N. stricta* grassland (c), isolated elements (d) and small shrub clusters (e)

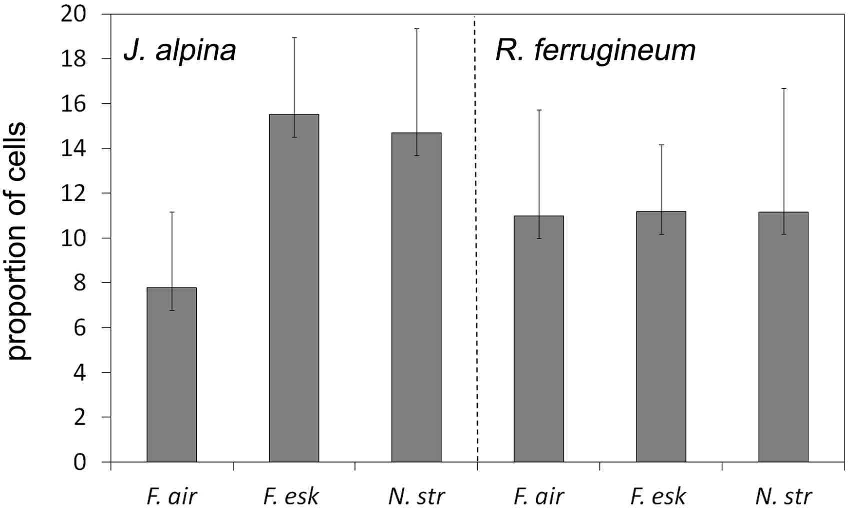

Fig.S6. Mean values and standard error of the proportion of newly encroached cells found in each combination of grassland community and shrub species. Grassland types are abbreviated as follows: *F. air*, *Festuca airoides* grassland; *F. esk, Festuca eskia* garland-grassland in *J. alpina* and mesophile grassland in *R. ferrugineum*; *N. str.*, *Nardus stricta* grassland

Capítol VI

Changes in snowbed vegetation as a response of climatic variability: a case study

Canvis en la vegetació de congestera com a resposta a la variabilitat climàtica: un cas d'estudi

Estela Illa, Artur Lluent & Empar Carrillo

Bull. Societé Histoire Naturelle Toulouse (en premsa)

Canvis en la vegetació de congestera com a resposta a la variabilitat climàtica: un cas d'estudi

Resum

El seguiment d'un transsecte de vegetació de congestera al cap de nou anys mostra petits canvis en la seva composició específica. El conjunt de les comunitats vegetals segueix essent el mateix, però observem alguns canvis en les zones de transició entre les comunitats. Les espècies especialistes de congestera mostren una tendència a reduir la seva freqüència, i a situar-se cap a la part més interna de la congestera on la neu roman més temps, mentre que algunes espècies pradenques incrementen la seva freqüència cap a la part més interior de la congestera. Aquests canvis podrien estar relacionats amb les notables irregularitats pluviomètriques que s'han produït durant aquest període.

Mots clau: Pirineus, seguiment de comunitats vegetals, canvi climàtic

Changes in snowbed vegetation as a response of climatic variability: a case study

Estela ILLA, Artur LLUENT & Empar CARRILLO

IRBio (Institut de Recerca de Biodiversitat) & Departament de Biologia Evolutiva,
Ecologia i Ciències Ambientals
Universitat de Barcelona. Av. Diagonal, 643. Barcelona 08028.
mcarrillo@ub.edu, estelailla@ub.edu

Abstract

Monitoring a snowbed vegetation transect after nine years revealed small changes in species composition. The set of plant communities remained the same, but we observed some shifts in the boundaries between communities. Snowbed specialists showed a trend to reduce their space occupancy and moved towards the area of thickest snowpack, whereas some grassland species settled on the spaces left. Such changes could be related to the noticeable irregularities in the rainfall regimes occurred during this period.
Key words: Pyrenees, monitoring, plant communities, climate change

Résumé

Le suivi d’un transect de végétation de combe à neige après neuf ans révèle des légers changements en la composition des espèces. L’ensemble des communautés végétales reste le même, mais nous avons observé certains changements dans les frontières entre les communautés. Les espèces spécialistes des combes à neige montrent une tendance à réduire leur occupation de l’espace et à se localiser vers la zone centrale de la combe à neige, tandis que certaines espèces des pelouses s’installent dans les espaces libérés. Tels changements pourraient être liés à des irrégularités notables de précipitation pendant cette période.
Mots-clés: Pyrénées, suivi des communautés végétales, changement climatique

Resumen

El seguimiento de un transecto de vegetación de ventisquero revela pequeños cambios en la composición de las especies después de nueve años. El conjunto de las comunidades vegetales sigue siendo el mismo, pero observamos algunos cambios en los límites entre las comunidades. Los taxones especialistas de ventisqueros mostraron una tendencia a reducir la ocupación del espacio situándose hacia la zona más interior del nevero donde la nieve permanece más tiempo, mientras que algunas especies pratenses avanzaron también más hacia el centro. Tales cambios podrían estar relacionados con las notables irregularidades pluviométricas ocurridas durante este período.

Palabras clave: Pirineos, monitoreo de comunidades vegetales, cambio climático

Introduction

In alpine environments the highly pronounced microrelief results into sharp floristic and ecological gradients (Johnson and Billings 1962), which in snowbeds are mainly caused by the duration and thickness of snow cover (Galen and Stanton 1995) and, to a lesser extent, by the distribution of melting water and by the soil organic matter content (Stanton et al. 1994). Snowbed specialists (or chionophilous species) benefit from thermal insulation by snow during winter and spring (Lluent 2007), and from water and nutrient supply during the growing season (Bowman 1992; Lluent 2007). However, these favourable conditions for growth are constrained by a short growing season due to a long-lasting snowpack. Snowbed species are adapted to complete their life cycle in a short period of time and to receive a limited amount of energy during the growing season (Lluent 2007; Illa et al. 2011).

Snowbeds occupy fragmented and reduced areas in alpine ranges, and many of their characteristic species have in the Pyrenees their southern distribution limits. In the context of climate change, evidences show that glaciers are experiencing a clear retreat in mountain areas (Haeberli and Beniston 1998) and all models suggest that during the current century winter snow will significantly diminish (Beniston et al. 2003; López-Moreno et al. 2009). It is expected that climate change will affect the Pyrenees with an important climatic irregularity (López-Moreno et al. 2009; Engler et al. 2011), which can change environmental conditions in snowbeds. In a context of reduced snowpack and increased growing season, low-competitive chionophilous specialists may be excluded from snowbeds by surrounding grassland species, more abundant and competitive (Heegaard and Vandvik 2004; Björk and Molau 2007; Schöb et al. 2008). Thus, snowbed species and communities are very vulnerable and threatened in all alpine areas, and even more in the Pyrenees due to their geographic situation.

Nowadays, few studies are aimed to investigate if changes are occurring in snowbed vegetation, and at which speed they can occur. With the aim to survey vegetation changes and assess their magnitude in snowbeds, during the period 2003-2007 we established some permanent transects along the snowmelt gradient in the National Park of Aigüestortes i Estany de Sant Maurici (Lluent et al. 2006).

The main objective of this work was to check whether the distribution of species and communities had changed in a snowbed transect first studied in 2003. We hypothesize that climatic irregularity affecting the Pyrenees may have promoted the colonisation of the snowbed by grassland species and pushed chionophilous species to the snowiest areas in the snowmelt gradient.

Methods

Study area and sampling design

The snowbed studied is situated on the northern slope of port de Ratera, at 2540 m a.s.l. in the peripheral area of Aigüestortes i Estany de Sant Maurici National Park (Fig. 1). Climatic conditions in the nearest alpine meteorological station (la Bonaigua, 2266 m a.s.l.) are characterized by relatively low temperatures (mean annual temperature 3.1 ºC) and high precipitation (mean annual rainfall of 1146 mm; Fig. 2 left). Data obtained from the last ten years (2003 and period 2008-2012) show rainfall irregularities mainly during summer, which has on average decreased (Fig. 2 right; Table 1). The critical period for snowbed vegetation regarding rainfall is mid- to late-summer, concretely July and especially August, when snow is gone and snowbed plants do not benefit from snowmelt water.

The transect studied follows the snowmelt gradient: it begins in the grassland outside the snowbed (which experiences usual conditions of alpine snowpack) and finishes in the snowbed core (where vegetation experiences increased snowpack conditions). The transect is 14 meters long and has a total of 70 subsamples. The methodology used is the same followed by Lluent et al. (2006). Concretely, at every 20 cm length we recorded a vegetation subsample setting a frame of 10 x 50 cm perpendicular to the direction of the transect. In each subsample we recorded all vascular plant and bryophyte species found and their cover, divided into 3 classes: 1 <10%, 2 between 10 and 50%, 3> 50%. Sampling was performed during the optimal vegetation period (late July to mid-August). Plant nomenclature follows Bolòs et al. (2005).

Statistical analyses

To look for differences in the distribution of subsamples into groups and in the structure of transitions between groups, we performed the same analyses that Lluent (2007) employed. Concretely, we classified subsamples into groups with the non-hierarchical clustering technique Fuzzy C-means (Bezdek 1987). This method classifies subsamples according to their floristic composition and gives them a membership value between 0 and 1. Low membership values in one subsample mean that it belongs simultaneously to two or more groups, and is then considered as a transition between groups. We first created a rectangular matrix for each year, where columns were species and rows were subsamples. Data were transformed with the Hellinger distance (Rao 1995), which uses the cover values to compute the distance between objects. Then we performed the fuzzy analysis with a *fuzziness* value of 1.2 (it is the highest value with which membership values of 1 can be obtained, but it is also useful in detecting transitional samples). We performed different partitions, and retained the best according to the Dunn coefficient partition (Dunn 1976). Once we obtained the total number of groups, we checked whether the different species discriminate between them by computing the ϕ-fidelity of each species to each group (Chytrý et al. 2002). We considered a threshold value of $\phi=0.3$, whose statistical significance is $p < 0.05$ for datasets with more than 46 samples and $p < 0.01$ for datasets with more than 61 samples (de Cáceres 2005). All analyses were performed with the program Ginkgo in the package VegAna (Bouxin 2005; de Cáceres 2005).

To look for trends in the frequency of species along the transect, we computed a frequency index for each species. We substracted the total number of subsamples where a species was present in a given group in 2003 to the total number of subsamples where it was present in the same section of the transect in 2012. Positive values meant an increase and negative values a decrease of the frequency of species along the section of the transect included in the group analysed. To know if there were differences between the different vegetation groups and between habitat specificity of species (grassland species and snowbed specialists), we performed a general two-way ANOVA. Afterwards, we also performed individualised one-way ANOVAs for each vegetation group in order to look for differences in habitat specificity of species at group level. These analyses were conducted with R (R Development Core Team 2016).

Results

Vegetation groups resulting from the Fuzzy-C-means analyses were four, the same that were evidenced in 2003, and corresponded to the same plant communities identified by Lluent (2007). Concretely, following the snowmelt gradient from the earliest snow-melting end to the latest snow-melting end, the first group identified corresponded to the *Carex curvula* subsp. *curvula* grassland (*Gentiano-Caricetum curvulae* Nègre 1969), the second group to the chionophilous *Salix herbacea* carpet (*Anthelio-Salicetum herbaceae* Br.-Bl. 1948), the third group to the chionophilous community of small snowbed hemicryptophytes (*Gnaphalio-Sedetum candollei* Br.-Bl. 1948) and the last group to the bryophyte community dominated by *Brachythecium glaciale* (Fig. 3).

The distribution of these different communities on the snowmelt gradient was similar between years, although some minor variations were detected in subsamples corresponding to the transition area between communities (Fig. 4). The most noticeable differences were that the boundary area between *Gentiano-Caricetum* and *Anthelio-Salicetum* increased at expenses of the second community, that the transition between *Anthelio-Salicetum* and *Gnaphalio-Sedetum* became more defined, and that the border between *Gnaphalio-Sedetum* and bryophyte community moved slightly towards the end of the snowmelt gradient.

The fidelity of species to each vegetation group also showed some differences (Table 2). In *Gentiano-Caricetum curvulae* faithful species were characteristic taxa of this grassland in both years, except *Anthelia juratzkana*, a snowbed specialist liverwort which had been associated with this group in 2003, but belonged to *Anthelio-Salicetum herbaceae* in 2012, as it would be expected. *Gnaphalio-Sedetum candollei* and bryophyte community showed the most apparent changes. In 2003 the only species that showed fidelity to the bryophyte communtiy was the moss *Brachythecium glaciale*, while in 2012 also *Cerastium cerastoides* and *Cardamine bellidifolia* subsp. *alpina* had fidelity for this vegetation group. The case of this last species proves that snowbed vegetation is experiencing important changes: in 2003 it was the species with the highest fidelity for *Gnaphalio-Sedetum candollei*, whereas in 2012 it appeared as significantly faithful (although it had lower fidelity values) to both *Gnaphalio-Sedetum* and the bryophyte community.

The set of species found along the transect for 2003 was 36, and it was almost the same in 2012 (38 taxa). The new species found in 2012 were generalists (*Festuca eskia*, *Murbeckiella pinnatifida* and *Vaccinium uliginosum* subsp. *microphyllum*) and occurred only in one subsample. On the other hand, *Campanula scheuchzeri*, which in 2003 appeared only in one subsample, was not detected in 2012.

ANOVA analyses of changes in the frequency of species showed contrasted results. On one hand, vegetation groups did not show significant differences between them ($F_{3,85} = 1.16$, $p = 0.329$; Fig. 5a), whereas species habitat specificities were significantly different ($F_{1,85} = 5.77$, $p = 0.0185$), with grassland species showing an increase of frequency along the transect and snowbed specialists a decrease (Fig. 5b). In the analyses of habitat specificity of species in each group separately we observed the same trends as in the general test, i.e. an increase in the frequency of grassland species and a decrease of snowbed specialists (Fig. 5c). We found significant differences between habitat specificity of species in the communities situated in the central part of the snowbed, concretely *Anthelio-Salicetum* ($F_{1,22} = 6.891$, $p = 0.0155$) and *Gnaphalio-Sedetum* ($F_{1,26} = 4.956$, $p = 0.0349$). Although in the *Gentiano-Caricetum* grassland community we also observed a decrease of snowbed species, differences with grassland species were not significant. On the other hand, at the snowiest end of the transect snowbed specialists showed a non significant trend towards an increased frequency.

At species level, the distribution and abundance of most species along the transect remained more or less constant after 9 years (Appendices 1, 2), although some of them showed clear trends. Species that were faithful to *Gentiano-Caricetum* did not show any trend in their group, but *Agrostis rupestris* and *Poa alpina* experienced a considerable increase in their frequency in *Gnaphalio-Sedetum* (Fig. 6a, Appendix 1). *Euphrasia* gr. *minima*, *Nardus stricta* and *Salix herbacea*, all of them faithful to *Anthelio-Salicetum*, also experienced a considerable increase in *Gnaphalio-Sedetum* (Fig. 6b). Finally, snowbed specialists with high fidelity values for *Gnaphalio-Sedetum*, not only decreased in frequency in *Gentiano-Caricetum* and *Anthelio-Salicetum* when they were present, but also experienced an enormous decrease in their own group, mainly *Cardamine bellidifolia* subsp. *alpina*, *Cerastium cerastoides* and *Mucizonia sedoides*. However, the frequency of *Cardamine bellidifolia* subsp. *alpina* and *Gnaphalium supinum* showed a slight tendency to increase in the bryophyte community, at the snowiest end of the transect (Fig. 6c).

Discussion

After nine years, the snowbed studied had the same vegetation communities along the snowmelt gradient, and the species were mostly the same. However, there were changes in the distribution and frequency of these species. On one hand we found a generalised decrease of chionophilous plants except in the snowiest part of the snowbed, where they seemed to experience a slight increase. On the other hand, grassland species colonised the internal sectors of the transect and became more frequent in the different snowbed groups except in the bryophyte community. Thus, our findings confirm what some authors had already predicted about the vulnerability of chionophilous species to the neighbouring grassland species (Heegaard and Vandvik 2004; Björk and Molau 2007; Schöb et al. 2008).

Climatic variability, mainly a decrease in summer precipitation, has been observed during the last ten years in a meteorological station near our study site. In addition, a three-year monitoring-period of environmental conditions in this site showed a high irregularity on the date of snowmelt (Lluent 2007), and the monitoring of other snowbeds in the Pyrenees confirms this situation (Lluent 2007; Illa et al. 2011; unpub. data). Regarding snowfall, although López-Moreno (2005) observed a reduction of snow depth due to a reduction in winter precipitation during the second half of the 20th century in the Pyrenees, in the study area winter precipitation has remained similar than the reference values during the 2003-2012 period (data not shown).

The high reduction of summer rainfall could be the main factor explaining the observed decrease in the frequency of snowbed specialists along the transect, as they need a fair water supply, which comes from the melting snow in early to mid summer and from summer rainfall.

Species with high moisture requirements such as *Cerastium cerastoides* or *Epilobium anagadillifolium* (Matthews 1992; Bolòs et al. 2005) could have suffered from summer drought, exemplified by a reduction of their frequency in the snowbed communities of the central part of the transect, only remaining more or less constant in the snowiest end of the snowmelt gradient.

Other climate-related events can also have negative effects on snowbed vegetation. A reduction of snowpack persistence can expose plants to frost events, and differences in the growing season length affect the phenological cycle of some snowbed species (Lluent et al. 2013) and thus, their reproductive success. Not only the negative effects of frost damage or summer drought on snowbed species, but also their low competitive ability, can allow grassland species to colonize gaps within snowbed plants, especially when the total cover of the vegetation is low. In our study site, *Gnaphalio-Sedetum* illustrates this situation. Small hemicriptophytes dominate in this community, where vegetation cover is not as high as in the neighbouring *Anthelio-Salicetum* (where the creeping subshrub *Salix herbacea* largely covers the surface), and bare ground is abundant. Certainly, this community experienced the largest changes in the frequency of both snowbed and grassland species, with the latter becoming relatively abundant. Grassland species colonising snowbed patches were mainly graminoids, which in alpine meadows were found to increase with increasing growing season (Ostler et al. 1982). Their higher frequency in 2012 could then suggest a trend towards an earlier snowmelt or towards an increased amount of energy during the growing season in the snowbed studied.

A relevant aspect when assessing changes in vegetation is the ability of species to colonize new favourable areas. As mentioned above, snowbed vegetation is subjected to a short growing season (Körner 2003; Illa et al. 2011), but also to a certain development of soil (Braun-Blanquet 1948). Usually, the snowiest end of a snowbed has a rocky, very immature soil, so the retreat of snowbed communities to this area may be unfeasible. In addition, permanent or almost permanent snowfields are usually rocky places which do not hold any vegetation, or just typical species of rocky habitats. Then, even if snow melts, these are not suitable places for the establishment of snowbed vegetation.

Conclusions

The period between 2003 and 2012 was long enough to evidence changes in snowbed vegetation. Meteorological data for this period showed strong inter-annual irregularity, with a tendency to reduced summer precipitation, which affects water availability in summer. Although the shifts found in the snowbed vegetation were small, they drew a rather clear directionality, concretely a retraction of the area occupied by chionophilous species and an increase of the area occupied by grassland species, mainly grasses.

Aknowledgements

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Table 1. Summer rainfall (mm) in the meteorological station of la Bonaigua (2266 m a.s.l.) based on the reference ombrothermal diagram (Fig. 2 left) and on data for years 2003 and the period 2008-2012 (Fig. 2 right)

	Reference diagram	2003	2008	2009	2010	2011	2012
June	105	50	110	75	184	90	107
July	78	35	45	35	75	95	73
August	92	115	37	100	27	48	73
July-August rainfall	**170**	**150**	**82**	**135**	**102**	**143**	**146**

Data generated by the authors from raw data obtained from Institut Meteorològic de Catalunya

Data from period 2004-2007 were not available

Table 2. Fidelity values of species to the different groups of vegetation in years 2003 and 2012. Dashed lines separate faithful species belonging to the different vegetation groups in 2003. In bold, significant fidelity values ($\phi \geq 0.3$, $p < 0.05$)

	Gentiano-Caricetum		*Anthelio-Salicetum*		*Gnaphalio-Sedetum*		*bryophyte community*	
	2003	2012	2003	2012	2003	2012	2003	2012
Carex curvula curvula	**0.95**	**0.82**	-0.21	-0.09	-0.38	-0.45	-0.22	-0.20
Primula integrifolia	**0.63**	**0.71**	**0.30**	0.21	-0.51	-0.56	-0.33	-0.26
Polytrichum piliferum	**0.61**	0.13	-0.17	0.12	-0.22	-0.15	-0.13	-0.07
Gentiana acaulis alpina	**0.59**	**0.66**	**0.35**	**0.32**	-0.54	-0.60	-0.31	-0.28
Phyteuma hemisphaericum	**0.59**	**0.58**	**0.35**	**0.39**	-0.54	-0.57	-0.31	-0.31
Agrostis rupestris	**0.57**	**0.49**	0.24	-0.12	-0.39	-0.04	-0.36	-0.36
Leontodon pyrenaicus pyrenaicus	**0.54**	**0.45**	-0.05	0.27	-0.24	-0.40	-0.17	-0.27
Anthelia juratzkana	**0.50**	0.10	0.23	**0.31**	-0.41	-0.16	-0.24	-0.25
Poa alpina alpina	**0.42**	-0.03	-0.11	-0.27	-0.37	**0.32**	0.19	-0.11
Luzula spicata montsignatica	0.26	**0.34**	-0.07	-0.09	-0.10	-0.15	-0.05	-0.07
Pedicularis kerneri	0.09	**0.34**	0.03	-0.09	-0.02	-0.15	-0.10	-0.07
Plantago maritima alpina	-0.02	0.08	**0.78**	**0.67**	-0.48	-0.44	-0.28	-0.26
Sibbaldia procumbens	-0.15	-0.17	**0.62**	**0.32**	-0.27	0.03	-0.24	-0.21
Euphrasia gr. minima	0.36	0.25	**0.59**	0.19	-0.55	0.08	-0.35	-0.62
Salix herbacea	0.23	0.22	**0.55**	**0.39**	-0.32	-0.12	-0.45	-0.55
Nardus stricta	-0.09	-0.18	**0.53**	**0.62**	-0.26	-0.17	-0.20	-0.28
Cardamine bellidifolia alpina	-0.42	-0.36	-0.60	-0.45	**0.73**	**0.33**	0.19	**0.47**
Mucizonia sedoides	-0.38	-0.24	-0.45	-0.25	**0.70**	**0.39**	0.00	0.01
Veronica alpina	-0.37	-0.37	-0.24	-0.32	**0.61**	**0.72**	-0.14	-0.22
Carex pyrenaica	-0.49	-0.45	0.36	0.09	**0.55**	**0.63**	-0.65	-0.49
Polytrichum sexangulare	-0.39	-0.40	0.19	0.30	**0.44**	**0.30**	-0.39	-0.32
Gnaphalium supinum	0.21	-0.20	0.28	0.17	**0.36**	**0.37**	-1.00	-0.51
Taraxacum alpinum	-0.16	-0.17	-0.22	-0.17	**0.36**	0.09	-0.04	0.27
Sagina saginoides	-0.29	-0.40	-0.24	-0.27	**0.34**	**0.48**	0.13	0.10
Cerastium cerastoides	-0.41	-0.23	-0.16	-0.15	**0.30**	0.05	0.20	**0.36**
Oreochloa disticha blanka	-0.16	-0.15	-0.02	-0.16	0.27	**0.34**	-0.16	-0.12
Arenaria biflora	-0.16	-0.02	0.05	-0.23	0.27	**0.33**	-0.25	-0.18
Brachythecium glaciale	-0.20	-0.20	-0.26	-0.21	-0.34	-0.36	**0.95**	**1.00**

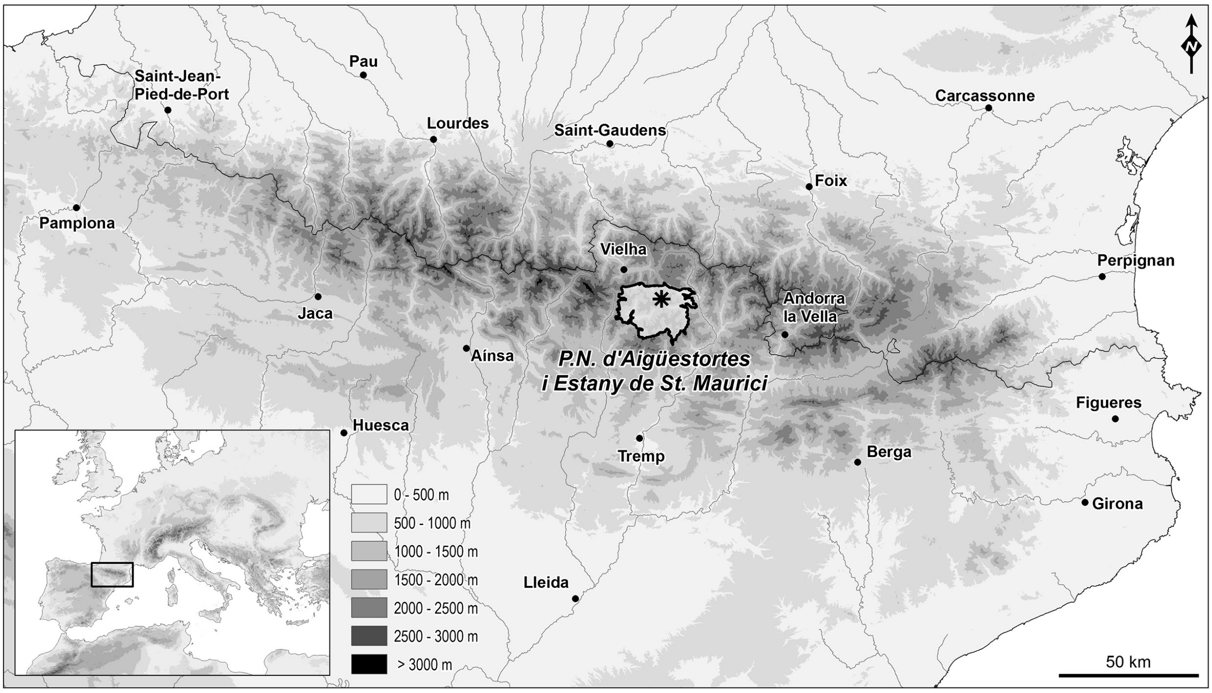


Fig. 1. Situation of Aigüestortes i Estany de Sant Maurici national park (delimited with a dark line) and the snowbed studied (asterisk)

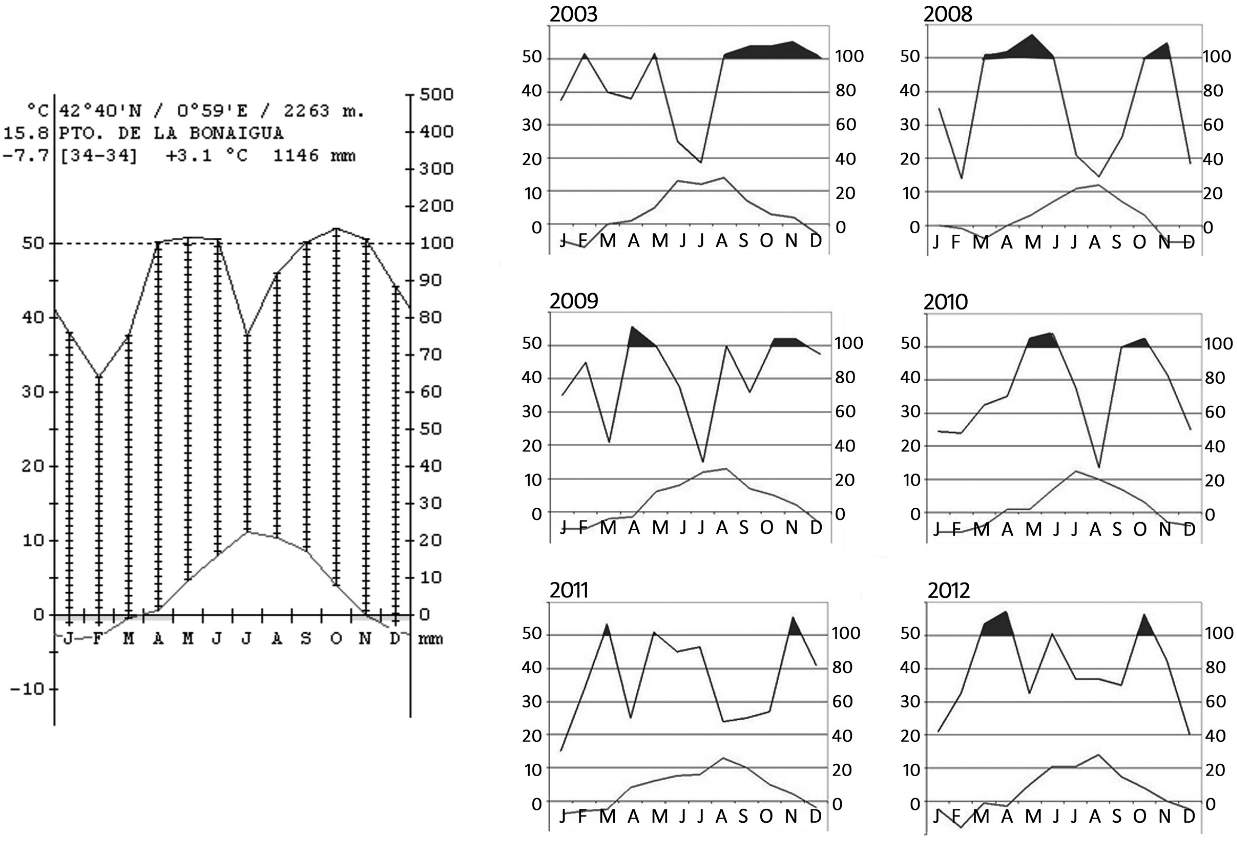


Fig. 2. Ombrothermal diagrams from la Bonaigua station, near the transect studied; reference diagram (left) and annual diagrams for years 2003, 2008, 2009, 2010, 2011 and 2012 (right)

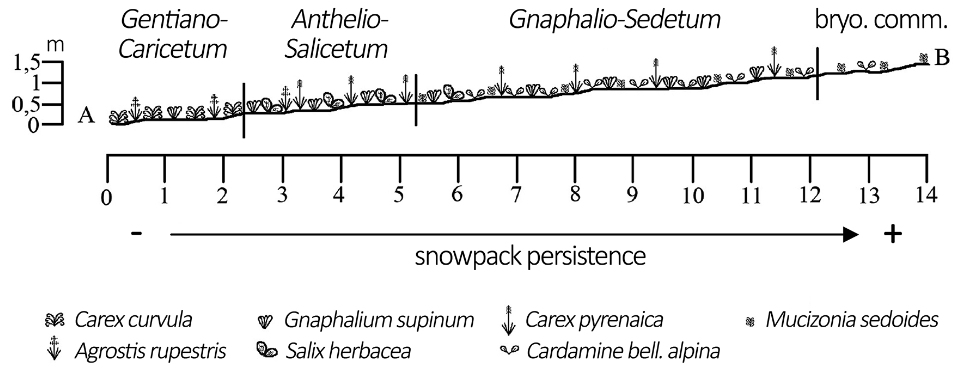


Fig. 3. Situation of the different plant communities (with the most abundant species) along the transect, following the snowmelt gradient. A- starting point of the transect; B- endpoint of the transect; scale in meters (figure obtained from Lluent 2007)

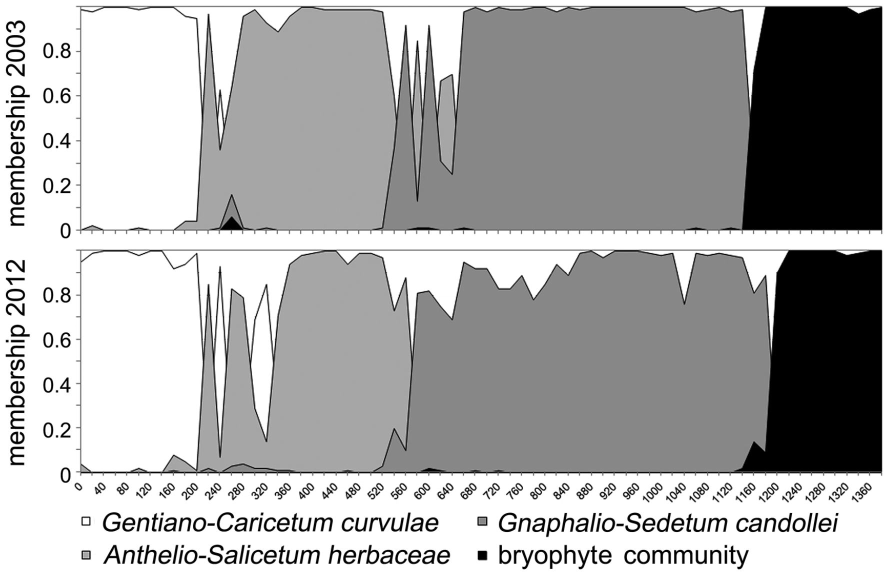


Fig. 4. Distribution of subsamples into the vegetation groups for years 2003 and 2012

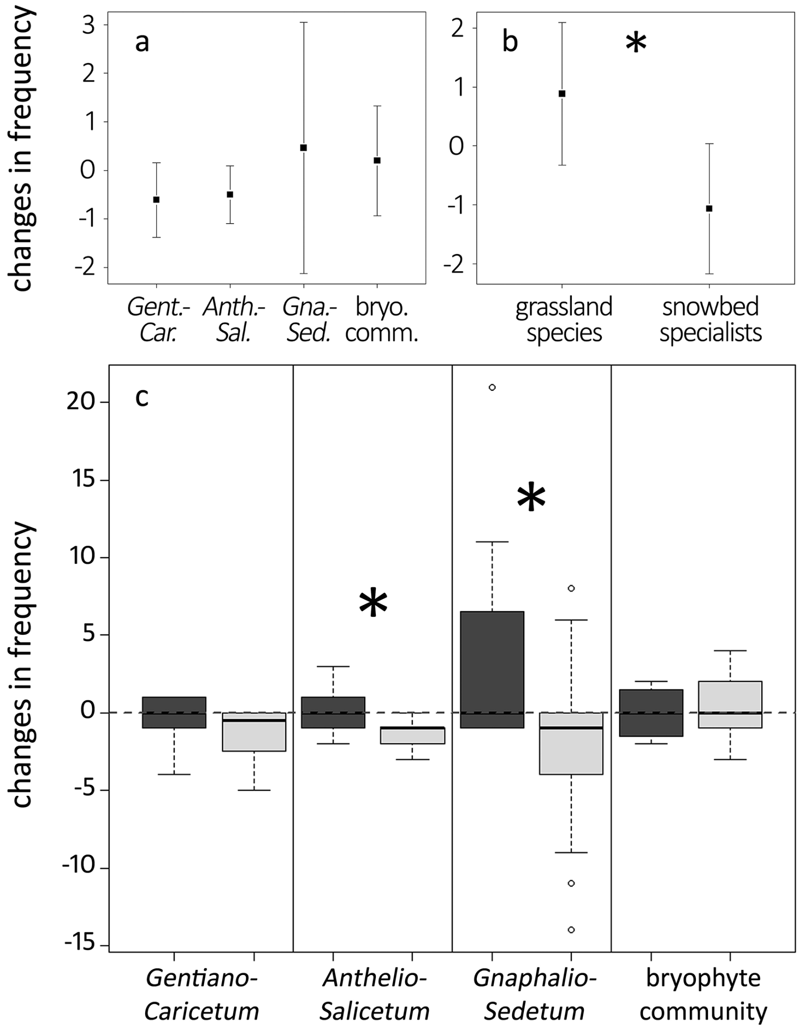
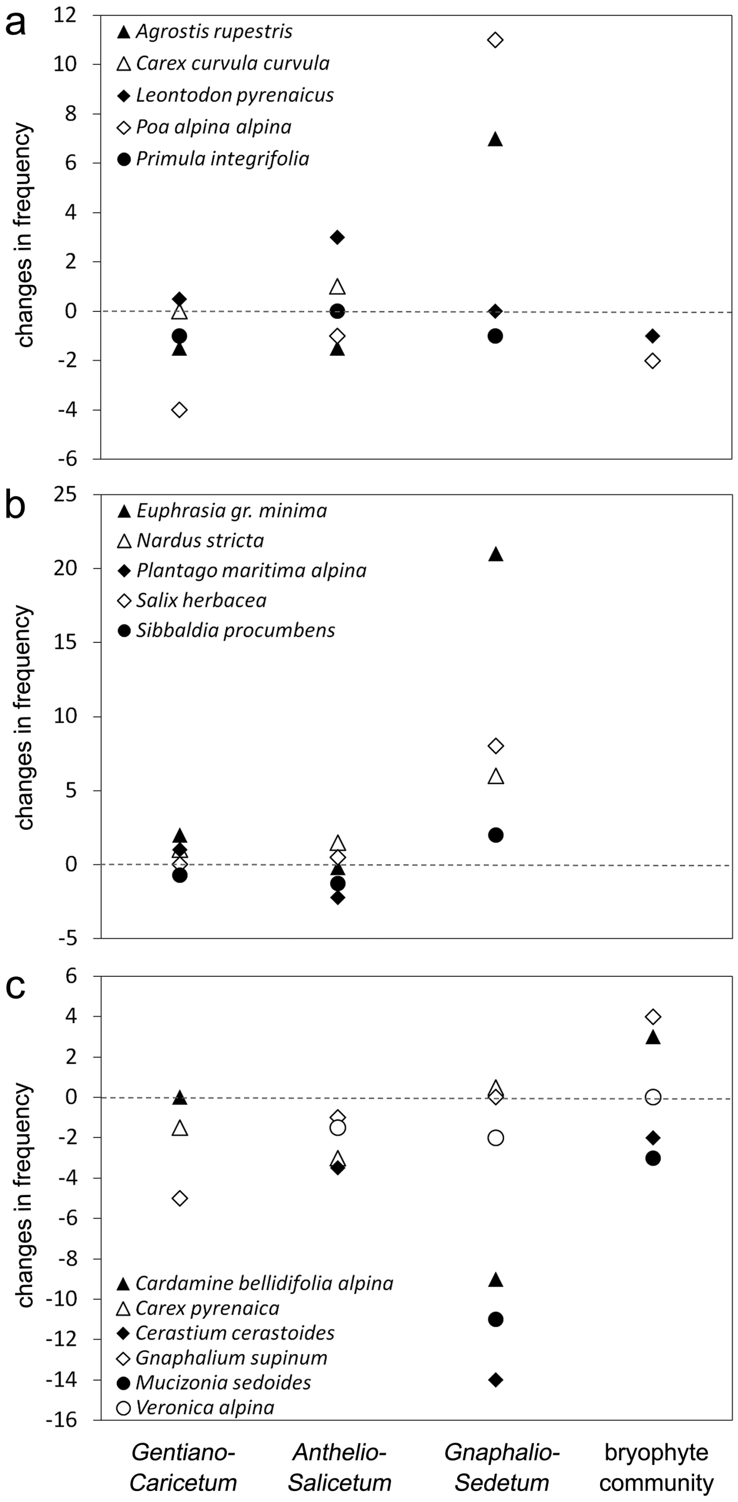


Fig. 5. Changes in the frequency of species between groups and habitat specificity of species: **a**, mean and 95% confidence interval between vegetation groups; **b**, mean and 95% confidence interval between habitat specificity of species; **c**, distribution of values for the combination of vegetation groups and habitat specificity of species (dark grey, grassland species; light grey, snowbed specialists). Asterisks in a plot or in a section of a plot mean significant differences ($p < 0.05$) between habitat specificity of species


a
b
c
changes in frequency
▲ Agrostis rupestris
△ Carex curvula curvula
◆ Leontodon pyrenaicus
◇ Poa alpina alpina
● Primula integrifolia
▲ Euphrasia gr. minima
△ Nardus stricta
◆ Plantago maritima alpina
◇ Salix herbacea
● Sibbaldia procumbens
▲ Cardamine bellidifolia alpina
△ Carex pyrenaica
◆ Cerastium cerastoides
◇ Gnaphalium supinum
● Mucizonia sedoides
○ Veronica alpina
12
10
8
6
4
2
0
-2
-4
-6
25
20
15
10
5
0
-5
6
4
2
0
-2
-4
-6
-8
-10
-12
-14
-16
Gentiano-Caricetum
Anthelio-Salicetum
Gnaphalio-Sedetum
bryophyte community

APPENDIX 1. Changes in the frequency of all species present along the transect in the different vegetation groups where they are present

	Gentiano-Caricetum	*Anthelio-Salicetum*	*Gnaphalio-Sedetum*	bryophtye community
grassland species				
Agrostis rupestris	-1.00	-1.00	7.00	
Armeria maritima alpina	1.00		0.00	2.00
Campanula gr. *scheuchzeri*			-1.00	
Carex curvula curvula	0.00	1.00		
Euphrasia gr. *minima*	1.00	0.00	21.00	
Festuca eskia				
Gentiana acaulis alpina	-1.00	-1.00		
Leontodon pyrenaicus pyrenaicus	0.00	3.00	0.00	-1.00
Luzula spicata monsignatica	1.00			
Murbeckiella pinnatifida				1.00
Nardus stricta	1.00	1.00	6.00	
Pedicularis kerneri	1.00	-1.00	-1.00	
Phyteuma hemisphaericum	1.00	2.00		
Plantago maritima alpina	1.00	-2.00		
Poa alpina alpina	-4.00	-1.00	11.00	-2.00
Polytrichum alpinum	0.00			
Polytrichum piliferum	-3.00			
Primula integrifolia	-1.00	0.00	-1.00	
Ranunculus pyrenaeus pyrenaeus		0.00	0.00	
Selinum pyrenaeum		-1.00	-1.00	
Vaccinium uliginosum microphyllum		1.00		
snowbed species				
Anthelia juratzkana	-4.00	-1.00	6.00	
Arenaria biflora	0.00		-2.00	
Brachythecium glaciale				-1.00
Cardamine bellidifolia alpina	0.00		-9.00	3.00
Carex pyrenaica	-1.00	-3.00	0.00	
Cerastium cerastoides		-3.00	-14.00	-2.00
Epilobium anagallidifolium			-4.00	0.00
Gnaphalium supinum	-5.00	-1.00	0.00	4.00
Luzula alpinopilosa			0.00	
Mucizonia sedoides			-11.00	-3.00
Oreochloa disticha blanka		-2.00	0.00	
Polytrichum sexangulare		0.00	-1.00	
Sagina saginoides		-1.00	4.00	2.00
Salix herbacea	0.00	0.00	8.00	
Sedum alpestre	-1.00			-1.00
Sibbaldia procumbens	0.00	-1.00	2.00	
Taraxacum alpinum			-1.00	2.00
Veronica alpina		-1.00	-2.00	0.00

Annexos

ANNEX 1: Atributs dels diferents trets adaptatius estudiats en les espècies alpines pirinenques (capítol I)

La forma de creixement, llenyositat, suculència i sempervirència s'han avaluat per a totes les espècies. Per a l'expansió lateral i el tipus de disseminació s'han tingut en compte només les espècies amb recobriments superiors al 3% en les comunitats respectives, marcades amb un asterisc (*)

Forma de creixement:

CH	camèfit difús
CP	camèfit pulviniforme
CR	camèfit reptant
CS	camèfit sufruticós
G	geòfit
HG	hemicriptòfit graminoide
HNG	hemicriptòfit no-graminoide
NP	nanofaneròfit
T	teròfit

Llenyositat:

LL	llenyosa
SL	semi-llenyosa

Suculència:

CR	crassa
SC	semi-crassa

Sempervirència:

V	sempreverda
SV	semi-sempreverda

Expansió lateral:

A	gens clonal
B	pocs rebrots, curta distància (< 2,5 cm)
C	pocs rebrots, llarga distància (> 2,5 cm)
D	molts rebrots, gespa densa

Tipus de disseminació:

A	llarga distància: espores o similar
B	llarga distància: vilà o similar
C	mitjana distància: ales, membranes...
D	in situ
E	endozoocòria

		forma de creixement	llenyositat	suculència	sempervirència	expansió lateral	tipus de disseminació
Apiaceae							
	Bupleurum angulosum	HNG					
	Bupleurum ranunculoides	HNG					
	Chaerophyllum hirsutum	HNG					
	Conopodium majus	G					
	Endressia pyrenaica	HNG					
*	*Meum athamanticum*	HNG				B	D
*	*Peucedanum ostruthium*	HNG				C	C
	Pimpinella major	HNG					
*	*Selinum pyrenaeum*	HNG				B	C
	Seseli montanum subsp. *nanum*	HNG					
	Trinia glauca	HNG					
	Xatardia scabra	HNG					
Asteraceae							
	Achillea millefolium	HNG					
	Achillea ptarmica subsp. *pyrenaica*	HNG					
*	*Adenostyles alliariae*	HNG				C	B
	Antennaria carpatica	HNG					
	Antennaria dioica	HNG					
	Anthemis cretica subsp. *saxatilis*	CS					
	Arnica montana	HNG					
	Artemisia umbelliformis	CP					
	Aster alpinus	HNG					
	Astrantia major	HNG					
	Astrantia minor	HNG					
*	*Carduus carlinoides*	HNG				C	B
*	*Carduus defloratus* subsp. *carlinifolius*	HNG				C	B
	Carlina acaulis	HNG					
	Centaurea montana	HNG					
	Cicerbita plumieri	HNG					
	Cirsium acaule	HNG					
	Crepis mollis	HNG					
*	*Crepis pygmaea*	G				C	B
*	*Doronicum grandiflorum*	HNG				C	B
	Doronicum pardalianches	HNG					
	Doronicum pyrenaicum	HNG					
	Erigeron alpinus	HNG					
	Erigeron glabratus	HNG					
*	*Erigeron uniflorus* subsp. *aragonensis*	HNG				B	B
	Erigeron uniflorus subsp. *uniflorus*	HNG					
	Eryngium bourgatii	HNG					
	Erysimum grandiflorum	CS					
	Gnaphalium hoppeanum	HNG					

		forma de creixement	llenyositat	suculència	sempervirència	expansió lateral	tipus de disseminació
	Gnaphalium norvegicum	HNG					
*	*Gnaphalium supinum*	HNG				B	B
	Gnaphalium sylvaticum	HNG					
	Hieracium amplexicaule	HNG					
*	*Hieracium breviscapum*	HNG				B	B
	Hieracium hypeuryum	HNG					
*	*Hieracium lactucella*	HNG				C	B
	Hieracium lawsonii	HNG					
	Hieracium olivaceum	HNG					
	Hieracium piliferum	HNG					
	Hieracium piliferum subsp. *piliferum*	HNG					
	Hieracium pilosella	HNG					
	Hieracium ramondii	HNG					
	Hypochoeris maculata	HNG					
	Jurinea humilis	HNG					
	Leontodon autumnalis	HNG					
*	*Leontodon duboisii*	HNG				B	B
	Leontodon hispidus	HNG					
*	*Leontodon pyrenaicus*	HNG				B	B
*	*Leucanthemopsis alpina*	HNG				B	D
	Leucanthemum vulgare	HNG					
*	*Saussurea alpina*	HNG				B	B
	Senecio adonidifolius	HNG					
	Senecio doronicum	HNG					
*	*Senecio leucophyllus*	CS			S	C	B
*	*Senecio pyrenaicus*	HNG				D	B
	Senecio viscosus	T					
	Solidago virgaurea	HNG					
	Taraxacum alpinum	HNG					
	Taraxacum dissectum	HNG					
Boraginaceae							
	Erinus alpinus	HNG					
	Myosotis sylvatica	HNG					
	Myosotis sylvatica subsp. *alpestris*	HNG					
	Onosma tricerosperma subsp. *alpicola*	HNG					
Brassicaceae							
	Alyssum alpestre subsp. *serpyllifolium*	CS					
*	*Alyssum cuneifolium*	CS				A	D
	Alyssum lapeyrousianum	CS					
	Alyssum montanum	CS					
	Arabis alpina	HNG					
	Arabis ciliata	HNG					
	Arabis hirsuta	HNG					
	Arabis serpillifolia	HNG					
	Biscutella laevigata	CH					
	Brassica repanda subsp. *saxatilis*	HNG					
*	*Cardamine amara*	HNG		SC		B	D
*	*Cardamine bellidifolia* subsp. *alpina*	HNG				B	D
	Cardamine pratensis var. *hayneana*	HNG					
*	*Cardamine resedifolia*	HNG				B	D
	Coincya cheiranthos	HNG					
	Draba aizoides	CP					
*	*Draba dubia*	CP				B	D
	Draba dubia subsp. *laevipes*	CP					
	Draba fladnizensis	CP					
	Draba siliquosa	CP					
	Draba siliquosa subsp. *carinthiaca*	CP					
	Draba tomentosa subsp. *ciliigera*	CP					
*	*Draba tomentosa* subsp. *subnivalis*	CP				B	D
	Erysimum sylvestre subsp. *pyrenaicum*	HNG					
*	*Iberis saxatilis*	CS				A	D

	forma de creixement	llenyositat	suculència	sempervirència	expansió lateral	tipus de disseminació
Iberis sempervirens	CS		SC	S		
* *Iberis spathulata*	T				A	D
Kernera saxatilis	HNG					
Lychnis alpina	HNG					
Murbeckiella pinnatifida	HNG					
* *Petrocallis pyrenaica*	CP				B	D
* *Pritzelago alpina*	CH				B	D
Campanulaceae						
Campanula cochlearifolia	HNG					
Campanula glomerata	HNG					
Campanula rotundifolia	HNG					
* *Campanula scheuchzeri*	HNG				C	D
Campanula scheuchzeri subsp. *ficarioides*	HNG					
Campanula scheuchzeri subsp. *scheuchzeri*	HNG					
Campanula speciosa	HNG					
Jasione crispa subsp. *crispa*	CP					
Jasione laevis	CS					
Phyteuma charmelii	HNG					
* *Phyteuma globulariifolium* subsp. *pedemontanum*	HNG				B	D
* *Phyteuma hemisphaericum*	HNG				B	D
Phyteuma orbiculare	HNG					
Phyteuma spicatum	HNG					
Caprifoliaceae						
Lonicera pyrenaica	NF	LL				
Caryophyllaceae						
Arenaria biflora	CR					
Arenaria ciliata	CR					
* *Arenaria grandiflora*	CP				B	D
Arenaria purpurascens	CR					
Arenaria tetraquetra subsp. *condensata*	CP					
Cerastium alpinum	CH					
Cerastium alpinum subsp. *lanatum*	CH					
Cerastium alpinum subsp. *squalidum*	CH					
Cerastium arvense	CH					
* *Cerastium cerastoides*	CH				B	D
Cerastium fontanum subsp. *vulgare*	CH					
* *Cerastium latifolium* subsp. *pyrenaicum*	CH				C	D
Dianthus hyssopifolius	CH					
Gypsophila repens	CP		SC			
Herniaria alpina	CR					
* *Minuartia recurva*	CP			S	B	D
Minuartia rubra subsp. *rostrata*	CP					
* *Minuartia sedoides*	CP		SC		D	D
Minuartia verna	CP					
Paronychia kapela subsp. *serpyllifolia*	CR					
* *Paronychia polygonifolia*	CR				C	D
Sagina saginoides	CP					
* *Silene acaulis*	CP		SC		D	D
* *Silene borderei*	CP				B	D
Silene ciliata	HNG					
* *Silene rupestris*	HNG				A	D
Silene vulgaris	HNG					
Chenopodiaceae						
Chenopodium bonus-henricus	HNG					
Cistaceae						
Helianthemum canum	CS	SL				
Helianthemum nummularium	CS	SL				
* *Helianthemum oelandicum* subsp. *italicum*	CS	SL			A	D
Clusiaceae						
Hypericum maculatum	HNG					
Hypericum richeri	HNG					

	forma de creixement	llenyositat	suculència	sempervirència	expansió lateral	tipus de disseminació
Crassulaceae						
* *Mucizonia sedoides*	T		CR		A	D
Sedum alpestre	CH		CR	V		
Sedum annuum	T		CR			
Sedum atratum	T		CR	V		
* *Sedum brevifolium*	CH		CR	V	B	D
Sedum hirsutum	CP		CR	V		
Sedum villosum	T		CR			
Sempervivum arachnoideum	CP		CR	V		
Sempervivum montanum	CP		CR	V		
Cupressaceae						
* *Juniperus communis* subsp. *nana*	NF	LL		V	C	E
Cyperaceae						
Carex atrata	HG					
Carex atrata subsp. *atrata*	HG					
Carex atrata subsp. *nigra*	HG					
Carex capillaris	HG					
Carex caryophyllea	HG					
Carex curta	HG					
* *Carex curvula* subsp. *curvula*	HG				D	C
Carex curvula subsp. *rosae*	HG					
Carex davalliana	HG					
Carex depressa	HG					
* *Carex echinata*	HG				D	C
* *Carex ericetorum*	HG				C	C
Carex flava	HG					
Carex flava subsp. *alpina*	HG					
* *Carex flava* subsp. *lepidocarpa*	HG				D	C
Carex frigida	HG					
Carex halleriana	HG					
* *Carex humilis*	HG				D	C
Carex macrostylon	HG					
Carex montana	HG					
* *Carex nigra*	HG				D	C
Carex ornithopoda	HG					
Carex ornithopoda subsp. *ornithopoda*	HG					
Carex ornithopoda subsp. *ornithopodioides*	HG					
Carex ovalis	HG					
Carex panicea	HG					
* *Carex pyrenaica*	HG				D	C
Carex rostrata	HG					
Carex rupestris	HG					
Carex sempervirens	HG					
* *Carex sempervirens* subsp. *pseudotristis*	HG				D	C
* *Carex sempervirens* subsp. *sempervirens*	HG				D	C
Carex umbrosa subsp. *huetiana*	HG					
Eleocharis palustris	HG					
Eleocharis quinqueflora	HG					
Eriophorum angustifolium	HG					
Eriophorum latifolium	HG					
Eriophorum vaginatum	HG					
* *Kobresia myosuroides*	HG				D	D
* *Scirpus cespitosus*	HG				D	D
Dipsacaceae						
Knautia dipsacifolia subsp. *arvernensis*	HNG					
Scabiosa columbaria	HNG					
Succisa pratensis	HNG					
Droseraceae						
Drosera rotundifolia	HNG					
Empetraceae						
* *Empetrum nigrum* subsp. *hermaphroditum*	CS	LL		V	C	E

		forma de creixement	llenyositat	suculència	sempervirència	expansió lateral	tipus de disseminació
	Ericaceae						
	Arctostaphylos alpinus	CR	LL				
*	*Arctostaphylos uva-ursi*	CR	LL		V	C	E
*	*Calluna vulgaris*	CS	LL		S	C	D
	Erica tetralix	CS	LL				
*	*Loiseleuria procumbens*	CR	LL		V	C	D
*	*Rhododendron ferrugineum*	NF	LL		V	C	D
*	*Vaccinium myrtillus*	CS	LL		S	C	E
*	*Vaccinium uliginosum* subsp. *microphyllum*	CH	SL			C	E
	Euphorbiaceae						
	Euphorbia cyparissias	HNG					
	Fabaceae						
	Anthyllis montana	HNG					
	Anthyllis vulneraria subsp. *boscii*	HNG					
*	*Anthyllis vulneraria* subsp. *vulnerarioides*	HNG				B	C
	Astragalus alpinus	HNG					
	Astragalus australis	HNG					
	Astragalus depressus	HNG					
	Astragalus monspessulanus var. *alpinus*	HNG					
	Astragalus sempervirens subsp. *catalaunicus*	CP	SL				
	Coronilla minima	CS					
*	*Genista balansae* subsp. *europaea*	NF	LL		V	C	D
	Genista pilosa	CS	LL				
	Hippocrepis comosa subsp. *comosa*	HNG					
	Lotus corniculatus	HNG					
*	*Lotus corniculatus* subsp. *alpinus*	HNG				B	D
	Lotus corniculatus subsp. *corniculatus*	HNG					
	Medicago suffruticosa	CH					
	Ononis cristata	CR					
*	*Oxytropis campestris* subsp. *campestris*	HNG				B	D
	Oxytropis halleri	HNG					
	Oxytropis lapponica	HNG					
	Oxytropis neglecta	HNG					
*	*Oxytropis neglecta* subsp. *occidentalis*	HNG				B	D
	Oxytropis neglecta subsp. *pyrenaica*	HNG					
*	*Trifolium alpinum*	HNG				B	C
	Trifolium badium	HNG					
	Trifolium montanum	HNG					
	Trifolium pratense	HNG					
	Trifolium repens	HNG					
*	*Trifolium thalii*	HNG				B	C
	Vicia pyrenaica	HNG					
	Gentianaceae						
	Gentiana acaulis	HNG					
	Gentiana acaulis subsp. *acaulis*	HNG					
*	*Gentiana acaulis* subsp. *alpina*	HNG				B	D
	Gentiana burseri	HNG					
	Gentiana campestris	HNG					
	Gentiana lutea	HNG					
	Gentiana nivalis	T					
	Gentiana pyrenaica	HNG					
	Gentiana tenella	T					
	Gentiana verna	HNG					
*	*Swertia perennis*	HNG				C	D
	Geraniaceae						
	Erodium foetidum subsp. *glandulosum*	CP					
	Geranium sylvaticum	HNG					
	Gesneriaceae						
	Ramonda myconi	HNG					
	Globulariaceae						
	Globularia cordifolia	CR	SL		S		

	forma de creixement	llenyositat	suculència	sempervirència	expansió lateral	tipus de disseminació
* *Globularia cordifolia* subsp. *repens*	CR	SL		S	C	C
Iridaceae						
Crocus vernus	G		SC			
Juncaceae						
Juncus alpinus	HG					
Juncus articulatus	HG					
Juncus balticus subsp. *pyrenaeus*	G					
* *Juncus filiformis*	G				C	D
* *Juncus trifidus*	HG				D	D
Juncus triglumis	HG					
Luzula alpinopilosa	HG					
Luzula campestris	HG					
* *Luzula glabrata* subsp. *desvauxii*	HG				D	D
* *Luzula lutea*	HG				B	D
Luzula multiflora	HG					
* *Luzula nutans*	HG				D	D
Luzula spicata subsp. *monsignatica*	HG					
Luzula sudetica	HG					
Juncaginaceae						
Triglochin palustre	HNG					
Lamiaceae						
Ajuga pyramidalis	HNG					
* *Galeopsis ladanum* subsp. *pyrenaica*	T				A	D
Mentha longifolia	HNG					
Prunella vulgaris	HNG					
Satureja alpina	CH					
Scutellaria alpina	HNG					
Sideritis hyssopifolia	CS					
Teucrium pyrenaicum	CR					
Thymus serpyllum	CR	SL				
Thymus serpyllum subsp. *chamaedrys*	CR	SL				
* *Thymus serpyllum* subsp. *nervosus*	CR	SL			C	D
Thymus serpyllum subsp. *polytrichus*	CR	SL				
Lentibulariaceae						
Pinguicula alpina	HNG					
Pinguicula grandiflora	HNG		SC			
* *Pinguicula vulgaris*	HNG		SC		B	D
Liliaceae						
Allium schoenoprasum	G		SC			
Allium senescens	G		SC			
Allium victorialis	G		SC			
Bulbocodium vernum	G		SC			
Erythronium dens-canis	G		SC			
Fritillaria pyrenaica	G		SC			
Narthecium ossifragum	G					
Streptopus amplexifolius	G					
Tofieldia calyculata	HNG					
Veratrum album	G					
Linaceae						
Linum perenne subsp. *alpinum*	CH					
Lycopodiaceae						
Lycopodium selago	CH			V		
Onagraceae						
* *Epilobium alsinifolium*	HNG				B	B
Epilobium anagallidifolium	HNG					
Epilobium angustifolium	HNG					
Epilobium collinum	HNG					
Epilobium nutans	HNG					
Epilobium palustre	HNG					
Ophyoglossaceae						
Botrychium lunaria	G					

	forma de creixement	llenyositat	suculència	sempervirència	expansió lateral	tipus de disseminació
Orchidaceae						
Coeloglossum viride	G					
Nigritella nigra	G		SC			
Orchis maculata	G		SC			
Orchis majalis	G		SC			
Oxalidaceae						
Oxalis acetosella	HNG					
Papaveraceae						
Papaver alpinum subsp. *rhaeticum*	HNG					
* *Papaver alpinum* subsp. *suaveolens*	HNG				B	D
Pinaceae						
Pinus mugo subsp. *uncinata*	NF	LL		V		
Plantaginaceae						
Plantago lanceolata	HNG					
Plantago maritima subsp. *alpina*	HNG		SC		B	D
Plantago maritima subsp. *serpentina*	HNG		SC			
Plantago media	HNG					
Plantago monosperma	HNG					
Plumbaginaceae						
* *Armeria maritima* subsp. *alpina*	HNG		SC		B	D
Armeria maritima subsp. *muelleri*	HNG		SC			
Poaceae						
Agrostis agrostiflora	HG					
Agrostis alpina	HG					
Agrostis canina	HG					
Agrostis capillaris	HG					
* *Agrostis rupestris*	HG				D	C
* *Agrostis stolonifera*	HG				C	C
Alopecurus gerardii	HG					
Anthoxanthum odoratum	HG					
Avenula pratensis subsp. *iberica* var. *pilosa*	HG					
Avenula versicolor	HG					
Bellardiochloa variegata	HG					
Briza media	HG					
Bromus erectus	HG					
Deschampsia cespitosa	HG					
Deschampsia flexuosa	HG					
* *Festuca airoides*	HG				D	C
* *Festuca borderi*	HG				D	C
* *Festuca eskia*	HG				D	C
* *Festuca gautieri*	HG				D	C
* *Festuca glacialis*	HG				D	C
* *Festuca indigesta*	HG				D	C
Festuca indigesta subsp. *aragonensis*	HG					
* *Festuca indigesta* subsp. *durissima*	HG				D	C
Festuca liviensis	HG					
Festuca ovina	HG					
* *Festuca paniculata*	HG				D	C
* *Festuca paniculata* subsp. *paniculata*	HG				D	C
* *Festuca pyrenaica*	HG				C	C
* *Festuca rubra*	HG				D	C
* *Festuca rubra* subsp. *commutata*	HG				D	C
Festuca rubra subsp. *rivularis*	HG					
Festuca rubra subsp. *rubra*	HG					
Festuca rubra subsp. *trichophylla*	HG					
* *Helictotrichon sedenense*	HG				D	C
Koeleria macrantha	HG					
* *Koeleria vallesiana*	HG				D	C
Molinia coerulea	HG					
* *Nardus stricta*	HG				D	C
* *Oreochloa disticha* subsp. *blanka*	HG				D	C

	forma de creixement	llenyositat	suculència	sempervirència	expansió lateral	tipus de disseminació
Phleum alpinum	HG					
Phleum alpinum subsp. *alpinum*	HG					
Phleum phleoides	HG					
* *Poa alpina*	HG				D	C
* *Poa annua* subsp. *supina*	HG				B	C
* *Poa cenisia* subsp. *sardoa*	HG				C	C
Poa chaixii	HG					
* *Poa laxa*	HG				B	C
Poa minor	HG					
* *Poa nemoralis* var. *glaucantha*	HG				D	C
Polypogon viridis	HNG					
* *Sesleria coerulea* subsp. *coerulea*	HG				C	C
Polygalaceae						
Polygala alpina	HNG					
Polygala calcarea	CH					
Polygala vulgaris subsp. *alpestris*	HNG					
Polygonaceae						
* *Oxyria digyna*	HNG				B	C
Polygonum alpinum	HNG					
Polygonum bistorta	HNG					
* *Polygonum viviparum*	HNG				B	D
Rumex acetosa subsp. *amplexicaulis*	HNG					
Rumex acetosella	HNG					
Rumex scutatus	CS					
Polypodiceae						
Asplenium ruta-muraria	HNG					
Asplenium seelosii subsp. *glabrum*	HNG					
* *Asplenium septentrionale*	HNG				B	A
* *Asplenium trichomanes*	HNG				B	A
Asplenium viride	HNG					
* *Athyrium distentifolium*	HNG				C	A
Athyrium filix-femina	HNG					
* *Cryptogramma crispa*	G				C	A
* *Cystopteris fragilis*	HNG				C	A
Cystopteris fragilis subsp. *alpina*	HNG					
Dryopteris carthusiana	HNG					
Dryopteris filix-mas	HNG					
* *Dryopteris filix-mas* subsp. *oreades*	HNG				C	A
* *Gymnocarpium dryopteris*	G				C	A
Gymnocarpium robertianum	G					
Polypodium vulgare subsp. *vulgare*	G					
Polystichum aculeatum	HNG					
* *Polystichum lonchitis*	HNG			S	C	A
Portulacaceae						
* *Montia fontana*	HNG				B	D
Primulaceae						
Androsace carnea	HNG			S		
Androsace ciliata	CP					
* *Androsace vandellii*	CP			S	D	D
Androsace villosa	HNG					
Primula elatior subsp. *intricata*	HNG					
* *Primula integrifolia*	HNG				B	D
* *Primula latifolia*	HNG				B	D
Soldanella alpina	HNG			S		
* *Vitaliana primuliflora*	CP				D	D
Pyrolaceae						
Pyrola minor	HNG					
Ranunculaceae						
Aconitum napellus subsp. *vulgare*	HNG					
* *Aconitum vulparia*	HNG				C	D
Adonis pyrenaica	HNG					

	forma de creixement	llenyositat	suculència	sempervirència	expansió lateral	tipus de disseminació
Anemone alpina	HNG					
Anemone alpina subsp. *apiifolia*	HNG					
Anemone alpina subsp. *font-queri*	HNG					
Anemone hepatica	HNG					
Anemone narcissiflora	HNG					
Anemone vernalis	HNG					
Aquilegia viscosa subsp. *montsicciana*	HNG					
* *Caltha palustris*	HNG				B	D
Delphinium elatum subsp. *montanum*	HNG					
Ranunculus aconitifolius	HNG					
Ranunculus aconitifolius subsp. *platanifolius*	HNG					
Ranunculus acris	HNG					
Ranunculus alpestris	HNG					
Ranunculus auricomus	HNG					
Ranunculus bulbosus	HNG					
* *Ranunculus glacialis*	HNG				B	D
Ranunculus montanus	HNG					
Ranunculus montanus subsp. *carinthiacus*	HNG					
Ranunculus montanus subsp. *gouanii*	HNG					
Ranunculus montanus subsp. *ruscinonensis*	HNG					
* *Ranunculus parnassifolius*	HNG				B	D
* *Ranunculus parnassifolius* subsp. *heterocarpus*	HNG				B	D
* *Ranunculus pyrenaeus*	HNG				B	D
Ranunculus serpens	HNG					
Ranunculus thora	HNG					
* *Thalictrum alpinum*	HNG				B	D
Thalictrum minus	HNG					
Resedaceae						
Reseda glauca	CS					
Sesamoides clusii	CH					
Rhamnaceae						
Rhamnus alpina	NF	LL				
Rhamnus pumila	CR	LL				
Rosaceae						
Alchemilla alpina	HNG					
Alchemilla alpina subsp. *asterophylla*	HNG					
Alchemilla alpina subsp. *saxatilis*	HNG					
Alchemilla alpina subsp. *transiens*	HNG					
Alchemilla fissa	HNG					
Alchemilla hybrida	HNG					
Alchemilla hybrida subsp. *colorata*	HNG					
* *Alchemilla hybrida* subsp. *flabellata*	HNG				B	D
Alchemilla hybrida subsp. *lapeyrousii*	HNG					
Alchemilla vulgaris	HNG					
Alchemilla vulgaris subsp. *coriacea*	HNG					
Alchemilla vulgaris subsp. *glabra*	HNG					
Alchemilla vulgaris subsp. *xanthochlora*	HNG					
Cotoneaster integerrimus	NF	LL				
* *Dryas octopetala*	CR	SL		S	C	B
Geum montanum	HNG					
Geum rivale	HNG					
Homogyne alpina	HNG					
Potentilla alchemilloides	HNG					
Potentilla brauneana	HNG					
* *Potentilla crantzii* subsp. *latestipula*	CH				B	D
Potentilla erecta	HNG					
* *Potentilla frigida*	HNG				B	D
Potentilla neumanniana	HNG					
* *Potentilla nivalis*	HNG				D	D
Potentilla pyrenaica	HNG					
Potentilla rupestris	HNG					

		forma de creixement	llenyositat	suculència	sempervirència	expansió lateral	tipus de disseminació
	Rosa pendulina	NF	LL				
	Rubus idaeus	NF	LL				
	Sibbaldia procumbens	HNG					
	Sorbus aucuparia	NF	LL				
	Sorbus chamaemespilus	NF	LL				
Rubiaceae							
	Asperula cynanchica subsp. *pyrenaica*	HNG					
	Cruciata glabra	HNG			S		
*	*Galium cometerhizon*	CR				C	D
	Galium pumilum	HNG					
	Galium pumilum subsp. *marchandii*	HNG					
*	*Galium pyrenaicum*	CP				D	D
	Galium verum	HNG					
Salicaceae							
*	*Salix herbacea*	CR	SL			B	B
*	*Salix pyrenaica*	CS	LL			C	B
*	*Salix reticulata*	CR	LL			C	B
*	*Salix retusa*	CR	LL			C	B
Santalaceae							
	Thesium alpinum	HNG					
	Thesium pyrenaicum	HNG					
Saxifragaceae							
*	*Parnassia palustris*	HNG				B	D
	Saxifraga aizoides	CP		CR	S		
	Saxifraga androsacea	HNG					
*	*Saxifraga aquatica*	CR		SC		D	D
*	*Saxifraga bryoides*	CP			S	D	D
	Saxifraga caesia	CP					
	Saxifraga clusii	HNG		SC			
	Saxifraga geranioides	CP					
	Saxifraga longifolia	HNG		SC	V		
*	*Saxifraga media*	CP		SC	V	B	D
*	*Saxifraga moschata*	CP			S	D	D
*	*Saxifraga nervosa*	CP			S	D	D
*	*Saxifraga oppositifolia* subsp. *oppositifolia*	CR			S	C	D
*	*Saxifraga paniculata*	CP		SC	V	B	D
	Saxifraga pentadactylis	CP			S		
*	*Saxifraga praetermissa*	CR		SC		C	D
*	*Saxifraga pubescens*	CP			S	B	D
*	*Saxifraga pubescens* subsp. *iratiana*	CP			S	B	D
	Saxifraga retusa	CP					
*	*Saxifraga stellaris*	CR		SC		C	D
Scrophulariaceae							
	Antirrhinum asarina	HNG					
	Bartsia alpina	HNG					
	Euphrasia alpina	T					
	Euphrasia hirtella	T					
	Euphrasia minima	T					
	Euphrasia minima subsp. *sicardii*	T					
	Euphrasia salisburgensis	T					
*	*Linaria alpina*	CR		SC		C	D
	Linaria origanifolia	CP					
	Linaria supina	CR		SC			
	Melampyrum pratense	T					
	Pedicularis comosa	HNG					
	Pedicularis kerneri	HNG					
	Pedicularis pyrenaica	HNG					
	Pedicularis pyrenaica subsp. *lasiocalyx*	HNG					
	Pedicularis rosea subsp. *allionii*	HNG					
	Pedicularis sylvatica	HNG					
	Pedicularis tuberosa	HNG					

	forma de creixement	llenyositat	suculència	sempervirència	expansió lateral	tipus de disseminació
Rhinanthus mediterraneus	T					
* *Veronica alpina*	HNG				B	D
Veronica aphylla	HNG					
Veronica beccabunga	HNG					
Veronica bellidioides	HNG					
* *Veronica fruticulosa*	CS	SL			C	D
* *Veronica fruticulosa* subsp. *saxatilis*	CS	SL			C	D
* *Veronica nummularia*	CR				C	D
Veronica ponae	HNG					
Veronica serpyllifolia	HNG					
Selaginellaceae						
Selaginella selaginoides	CH					
Thymelaeaceae						
Daphne cneorum	CS	SL				
Thymelaea dioica	CR	SL		S		
Urticaceae						
Urtica dioica	HNG					
Valerianaceae						
* *Valeriana apula*	HNG				B	B
Valeriana montana	HNG					
Violaceae						
* *Viola biflora*	HNG				B	D
* *Viola cenisia* subsp. *lapeyrousiana*	HNG				C	D
* *Viola palustris*	HNG				B	D
Viola rupestris	HNG					
Viola sylvestris	HNG					

ANNEX 2: Recobriment de les diferents famílies de plantes vasculars en les comunitats alpines pirinenques (capítol I)

	matollars caducifolis			matollars perennifolis				tarteres terofítiques				tarteres amb vegetació perenne			
família	*Carici-Salicetum*	*Dryado-Salicetum*	*Salici-Anthelietum*	*Cetrario-Loiseleurietum*	*Empetro-Vaccinietum*	*Genisto-Arctostaphyletum*	*Saxifrago-Rhododendretum*	*Galeopsido-Poetum*	*Gnaphalio-Sedetum*	*Iberidetum spathulatae*	*Violetum diversifoliae*	*Crepidetum pygmaeae*	*Cryptogramo-Dryopteridetum*	*Festucetum glaciali-pyrenaicae*	*Senecietum leucophylli*
Apiaceae	0,3	1,0	0,4	0,1			0,7		0,1	0,1		0,2	1,0	0,2	0,5
Asteraceae	4,0	1,3	8,5	4,7	4,3	7,0	5,4	28,0	24,3	3,3	0,9	9,8	1,9	7,4	25,3
Boraginaceae	0,2	0,6					0,4			0,6	0,2	0,7			
Brassicaceae	1,2	1,6	0,6	0,1		0,8		2,3	6,7	16,0	0,7	4,4		3,9	1,4
Campanulaceae	0,3	2,3	0,8	2,7	1,4	6,8	1,7	0,5	0,2		0,4	1,5	0,3	0,7	0,3
Caprifoliaceae															
Caryophyllaceae	1,8	3,3	2,4	2,4	1,1	1,2		2,9	4,8	1,9	2,0	2,7		3,6	3,0
Chenopodiaceae															
Cistaceae	0,8	1,1		0,1											
Crassulaceae	0,4		1,6				0,2	0,9	19,4	0,3		0,3		0,2	1,5
Cupressaceae		0,7		0,2	1,5	31,4	4,4								
Cyperaceae	9,4	8,7	6,3	3,9	4,5	4,0	2,4		6,8	0,3		0,5	0,3		
Dipsacaceae															
Droseraceae															
Empetraceae				0,3	30,0										
Ericaceae	0,8	5,2	0,3	86,5	65,0	44,7	129,6		0,0				1,1		
Euphorbiaceae															
Fabaceae	4,0	5,3	7,8	0,8	0,5	20,9	2,1	1,3	0,7	0,3	0,2	0,9		0,6	
Gentianaceae	1,6	0,9	2,3	1,5	1,8	0,4	1,3		0,9						
Geraniaceae		1,7													
Gesneriaceae															
Globulariaceae						0,4									
Hypericaceae															
Iridaceae															
Juncaceae	0,5		2,4	9,2	1,8	1,2	0,8		1,8			0,2	2,9		0,3
Juncaginaceae															
Lamiaceae	0,3	1,3	0,1	0,4	0,2	1,2		23,3		1,6	7,0	0,9		1,1	1,1
Lentibulariaceae	0,5														
Liliaceae												0,3			
Linaceae															
Lycopodiaceae				0,6	2,5				0,0						
Onagraceae							0,4	2,6	0,4	0,4		0,2	0,3		0,5
Ophioglossaceae	0,2	0,4	0,3			1,0						0,2			
Orchidaceae		0,2													
Oxalidaceae							0,7								
Papaveraceae										2,4				2,2	
Pinaceae	0,1			0,1	0,2	1,0	1,0								
Plantaginaceae	1,9	0,8	1,7	0,7					1,3						
Plumbaginaceae	0,2		0,6	0,2					0,5						0,2
Poaceae	5,9	27,2	8,3	4,7	4,2	14,1	11,8	6,4	10,6	6,3	3,8	9,0	1,4	16,9	7,5
Polygalaceae	0,7														
Polygonaceae	5,3	8,1	4,8	1,2	0,5		0,4	0,5	0,0	0,3		0,8			
Polyopdiaceae	0,1						1,5	0,3	0,0			0,7	22,6		0,9
Portulacaceae															
Primulaceae	3,1	1,7	2,8	3,3	4,0		0,6		1,2	0,4	2,4				0,2
Pyrolaceae							0,5								
Ranunculaceae	3,6	1,4	5,1	0,4	0,3	1,0	0,9	0,9	0,1	5,1	0,9	2,4		5,4	0,8
Resedaceae															
Rhamnaceae															
Rosaceae	11,5	52,5	10,5	1,8	2,2	4,6	8,2		3,5	0,4		0,5		0,2	0,2
Rubiaceae	0,4	0,4					0,4			2,1	5,1	2,4		6,0	1,9
Salicaceae	56,5	20,7	60,9	0,7	0,3				1,0						
Santalaceae	0,1			0,1											
Saxifragaceae	1,8	1,9	1,1	0,1	0,2		3,7	0,3	0,3	2,3	0,4	1,9		4,6	0,8
Scrophulariaceae	3,5	4,1	2,8	2,2	1,2	0,8	0,2	3,3	4,0	1,6	0,7	4,3		1,3	0,8
Selaginellaceae	0,4	0,2	0,8	0,1	0,3										
Thymeleaceae	0,1	0,4		0,1	0,2	0,4	0,2								
Urticaceae													0,3		
Valerianaceae												0,3			
Violaceae	0,1	1,1			0,2	0,4		0,3	0,0	0,1	10,6		0,3		2,0
Total famílies	34	29	24	29	24	20	25	15	25	20	14	23	11	15	19

	vegetació rupícola							vegetació higròfila			prats densos						
família	*Oxyrio-Doronicetum*	*Saxifragetum iratianae*	*Saxifragetum mediae*	*Saxifragetum pubescentis*	*Saxifrago-Androsacetum*	*Saxifrago-Minuartietum*	*Sileno-Potentilletum*	*Montio-Bryetum*	*Saxifragetum aquaticae*	*Saxifragetum pratermissae*	*Alchemillo-Nardetum*	*Carici-Festucetum*	*Festuco-Trifolietum*	*Gentiano-Caricetum*	*Ranunculo-Festucetum*	*Selino-Nardetum*	*Trifolio-Phleetum*
Apiaceae			0,2					0,2	0,2	0,4	0,7	2,1	0,9	1,0	4,3	16,1	4,0
Asteraceae	3,2	0,2	2,2		0,4	8,3		0,5	0,2	10,2	16,8	6,9	14,2	15,3	4,2	9,4	10,7
Boraginaceae	0,4		0,5			0,2					0,4	0,4	0,7		0,1		0,1
Brassicaceae	6,2	2,7	2,9	2,8	0,8	0,8	2,4	3,2	4,1	15,1	0,2	1,4	0,3	0,5	1,3	0,0	0,5
Campanulaceae	0,1	0,2	1,6	1,3	3,2	5,8	1,2			0,4	1,3	7,0	1,1	4,9	7,0	2,5	1,4
Caprifoliaceae			0,3														
Caryophyllaceae	2,5	2,5	2,0	1,2	0,4	40,7	5,7	3,4	0,3	3,4	1,7	3,6	7,7	5,0	1,3	0,7	1,3
Chenopodiaceae													0,3		0,0		
Cistaceae			0,4										0,3				
Crassulaceae	1,0		0,9	4,2	2,0	0,3		0,2				0,3		0,6	0,1		0,2
Cupressaceae			0,4		0,4							0,3					
Cyperaceae	0,1	0,2	0,7		1,2	11,0	0,2	4,9	2,2	0,4	6,9	6,0	5,7	33,1	3,7	8,4	13,5
Dipsacaceae									0,2								
Droseraceae																	
Empetraceae																	
Ericaceae				0,7	1,2	1,4					0,4	2,2		1,6	0,7	0,3	0,3
Euphorbiaceae															0,2		
Fabaceae	0,1		0,3	0,3		0,2					31,1	9,9	35,6	15,7	33,4	7,0	26,6
Gentianaceae						4,2					13,9	1,4	3,0	11,3	3,0	2,0	3,4
Geraniaceae			0,1														
Gesneriaceae			0,8														
Globulariaceae			3,5		3,0		0,4										
Hypericaceae												0,1			0,0		
Iridaceae											0,2						
Juncaceae	1,4			0,3		4,6		0,2	3,6	1,0	1,7	9,1	1,7	4,8	1,3	0,3	0,3
Juncaginaceae																	
Lamiaceae	0,1		0,5		0,8	0,2	0,2		0,3		2,2	1,4	1,6	0,1	0,6		
Lentibulariaceae								0,8	0,8								
Liliaceae															0,1		
Linaceae																	
Lycopodiaceae														0,1			
Onagraceae	0,5							6,6	3,9	1,4							
Ophioglossaceae											0,2		0,6		0,2		0,1
Orchidaceae								0,2	0,2		0,2				0,0		
Oxalidaceae																	
Papaveraceae																	
Pinaceae																	
Plantaginaceae						0,1					4,4		4,4	0,1	2,0	2,8	9,8
Plumbaginaceae	2,5	1,2				6,1							0,7	1,4	0,2		0,1
Poaceae	7,4	2,6	3,8	1,0	6,0	22,8	5,0	4,6	6,1	5,2	77,8	88,7	81,8	30,9	82,2	83,8	58,7
Polygalaceae											0,2	1,6	0,3		0,1		
Polygonaceae	4,5					0,2			0,2	2,6			1,7	0,2	0,1	0,3	0,1
Polyopdiaceae	0,4		3,3	4,3	3,6		2,2			0,4							
Portulacaceae								4,5	0,2								
Primulaceae	1,0	0,2	0,1	4,2	3,4	5,5		0,8	0,8	1,8	1,7	0,3	3,6	12,4	1,8	0,3	3,9
Pyrolaceae																	
Ranunculaceae	4,8	0,2	0,3			0,1	0,2	5,3	1,2	1,0	8,6	3,3	3,9	3,7	8,2	2,0	9,4
Resedaceae			0,1									0,3			0,1		
Rhamnaceae			0,7		1,0												
Rosaceae	0,5	0,4	9,9	1,5	4,2	6,0	12,4		1,4	2,2	2,1	1,1	18,7	1,9	2,0	2,7	1,9
Rubiaceae	0,1		1,2		0,4		1,1				0,9	1,1	2,3		0,8	0,3	
Salicaceae													0,3	1,5			0,1
Santalaceae											0,2	0,1			0,2		
Saxifragaceae	8,8	13,9	7,8	3,7	4,6	26,3	4,8	12,4	73,9	67,1			1,0	0,7	0,1		
Scrophulariaceae	2,9		0,2	1,5		1,8		1,4	0,8	6,2	0,2	4,9	1,9	2,3	1,1	3,3	1,1
Selaginellaceae													0,6	0,3			0,2
Thymeleaceae			0,1		0,8							0,9	0,7	0,1	0,3		
Urticaceae																	
Valerianaceae			6,6				7,8										
Violaceae			1,6				1,4	0,8	0,2		0,2				0,1	0,3	0,2
Total famílies	21	11	29	13	18	21	14	17	20	16	25	25	28	25	34	18	24

	prats culminants						prats de vessant					molleres			megaf.
família	*Elyno-Oxytropidetum*	*Hieracio-Festucetum typicum*	*Hieracio-Festucetum caricetosum*	*Hieracio-Festucetum juncetosum*	*Hieracio-Festucetum kobresietosum*	*Leontodo-Caricetum*	*Arenario-Festucetum*	*Festucetum eskiae*	*Festucetum scopariae*	*Oxytropido-Caricetum typicum*	*Oxytropido-Caricetum helictotrichetosum*	*Caricetum fuscae*	*Narthecio-Tricophoretum*	*Swertio-Caricetum*	*Peucedano-Luzuletum*
Apiaceae	1,1	0,3				0,2	0,1	1,4	1,2	0,3		3,1	1,7	5,4	25,2
Asteraceae	7,0	17,2	17,6	27,9	12,2	13,4	1,6	9,9	9,6	4,5	1,3	5,4	6,0	3,2	43,5
Boraginaceae	0,4			0,3			0,1	0,4	0,7			0,1			1,2
Brassicaceae	1,7	1,0	0,2	1,5		0,2	1,3	5,2	4,7	3,5	10,4	0,1			
Campanulaceae	0,7	7,7	8,5	5,7	7,6	10,2	3,7	11,2	1,8	0,3	2,3		0,3		
Caprifoliaceae															
Caryophyllaceae	6,7	8,2	14,1	13,5	8,6	8,6	7,8	3,4	9,9	3,3	5,4	0,4	0,1		0,4
Chenopodiaceae															
Cistaceae	3,2	0,0					0,1	0,1	5,2	11,7	2,2				
Crassulaceae	0,9	0,9	1,5	0,7		1,0	0,4	0,8	1,1			0,2			
Cupressaceae	0,1	0,1					0,1	0,7	0,4	0,7	0,6	0,1	0,0		
Cyperaceae	41,2	15,1	41,8	8,7	56,1	29,1	1,8	0,8	7,1	29,8	2,5	79,2	90,2	69,7	
Dipsacaceae									0,1			0,3	0,3		0,4
Droseraceae												0,1	0,3		
Empetraceae															
Ericaceae	0,7	3,6	1,6	0,7	9,3	1,3		0,1	0,5			0,7	5,4	1,6	1,4
Euphorbiaceae		0,0					0,1		0,8		0,1				
Fabaceae	17,2	5,7	6,7	12,5	13,2	4,4	2,1	8,4	17,1	16,1	3,4	1,1	1,5	2,2	
Gentianaceae	2,2	9,4	16,7	10,5	4,4	24,6	0,2	2,5	1,7	0,7	0,6	0,3	0,9	28,5	0,8
Geraniaceae															3,4
Gesneriaceae															
Globulariaceae	0,4								1,8	0,7	0,1				
Hypericaceae								0,5							
Iridaceae															
Juncaceae	0,7	6,8	8,5	40,9	8,8	11,5	0,4	2,1	0,1			14,3	1,8	2,8	26,4
Juncaginaceae												0,1			
Lamiaceae	2,5	3,9	1,6	2,2	4,2	0,2	8,3	2,1	13,8	5,5	8,1	0,1	0,0	1,0	
Lentibulariaceae												2,4	7,4	6,4	
Liliaceae									0,5	0,3		0,1	3,4		3,4
Linaceae									0,1						
Lycopodiaceae													0,0		
Onagraceae												0,7	0,1		
Ophioglossaceae	0,5	0,2					0,1	0,2	0,1	0,7	0,4				
Orchidaceae	0,0							0,1				0,2	0,3		
Oxalidaceae															
Papaveraceae															
Pinaceae	0,0														
Plantaginaceae	2,0	3,9	0,6	1,5	4,4	0,2		0,1	1,3	0,7			0,2		
Plumbaginaceae	0,1	0,5	0,8	0,3	0,4	0,4							0,1		
Poaceae	23,1	53,5	32,7	36,3	31,0	18,9	42,6	60,3	69,4	30,8	37,5	11,2	6,4	6,4	9,7
Polygalaceae	0,5	0,0					0,1	0,3	1,3				0,0		
Polygonaceae	6,7	0,5		0,3	2,4			0,7		0,8		0,1	0,1	0,4	1,8
Polyopdiaceae	0,0														8,0
Portulacaceae															
Primulaceae	2,4	3,4	6,0	7,6	2,4	3,9	0,3	0,4	1,5		0,1	1,8	25,7	9,4	
Pyrolaceae															
Ranunculaceae	2,0	2,5	0,9	1,0	1,8		1,8	2,7	1,7	0,3	1,7	0,9	0,6	0,8	13,3
Resedaceae			0,1			0,2		0,2							
Rhamnaceae	0,0														
Rosaceae	23,9	4,5	0,5	1,7	1,6	0,4	0,9	0,7	2,1		1,6	4,0	3,7	0,4	2,2
Rubiaceae	1,2	0,1					1,2	0,5	4,9	3,8	6,0				
Salicaceae	0,9				1,4										
Santalaceae		0,0						0,2	0,1	0,3					
Saxifragaceae	2,0	1,3	1,2	4,3	3,4	2,2	1,0	0,1	2,0	1,2	2,5	8,5	5,2	8,4	0,4
Scrophulariaceae	2,7	5,5	7,7	4,0	2,8	1,1	1,1	10,6	1,9	2,8	2,3	1,8	3,4	1,6	
Selaginellaceae	0,2								0,1			0,5	0,8	1,8	
Thymeleaceae	0,6	0,4			0,4			0,3	0,8	1,5	0,1				
Urticaceae															
Valerianaceae	0,1								0,1						
Violaceae	0,4	0,1					1,8	0,1	0,7	1,7	1,2	6,8	1,0	1,0	3,0
Total famílies	37	30	20	21	20	20	25	32	35	24	22	29	30	18	17

ANNEX 3: Recobriment dels atributs dels diferents trets adaptatius estudiats en les comunitats alpines pirinenques (capítol I)

	matollars caducifolis			matollars perennifolis				tarteres terofítiques				tarteres amb vegetació perenne				vegetació rupícola							vegetació higròfila		
	Carici-Salicetum	*Dryado-Salicetum*	*Salici-Anthelietum*	*Cetrario-Loiseleurietum*	*Empetro-Vaccinietum*	*Genisto-Arctostaphyletum*	*Saxifrago-Rhododendretum*	*Galeopsido-Poetum*	*Gnaphalio-Sedetum*	*Iberidetum spathulatae*	*Violetum diversifoliae*	*Crepidetum pygmaeae*	*Cryptogramo-Dryopteridetum*	*Festucetum glaciali-pyrenaicae*	*Senecietum leucophylli*	*Oxyrio-Doronicetum*	*Saxifragetum iratianae*	*Saxifragetum mediae*	*Saxifragetum pubescentis*	*Saxifrago-Androsacetum*	*Saxifrago-Minuartietum*	*Sileno-Potentilletum nivalis*	*Montio-Bryetum*	*Saxifragetum aquaticae*	*Saxifragetum pratermissae*
formes biològiques																									
nanofaneròfits	0,1	0,6	0,0	0,6	7,5	38,1	43,8	0,0	0,0	0,0	0,0	0,0	3,5	0,0	0,0	0,0	0,0	1,4	2,5	3,2	0,0	0,0	0,0	0,0	0,0
camèfits difusos	1,3	0,1	5,6	0,5	2,0	0,3	0,0	1,4	3,9	9,1	3,1	6,0	0,0	4,4	6,1	13,2	6,5	0,4	13,0	3,2	2,8	2,0	2,1	0,3	13,0
camèfits sufruticosos	4,0	8,3	0,2	16,7	58,0	11,9	31,2	1,9	0,1	5,1	0,0	3,4	1,8	0,0	51,9	0,0	0,0	1,1	4,3	4,3	1,0	1,5	0,0	0,0	0,0
camèfits reptants	51,0	43,4	44,7	41,6	4,9	22,0	0,0	6,5	3,7	8,9	16,0	12,8	0,0	18,3	4,8	7,0	9,6	10,8	0,0	12,8	3,4	2,9	8,2	69,2	52,2
camèfits pulviniformes	1,7	4,3	1,5	2,5	1,1	1,7	2,1	1,0	0,4	11,1	13,5	10,8	0,0	8,7	3,7	18,3	43,0	26,8	29,6	25,7	39,5	26,0	1,5	0,7	0,7
hemicriptòfits graminoides	12,5	22,9	12,4	11,7	7,5	13,4	8,2	8,7	18,1	14,3	10,7	21,6	14,2	31,1	15,9	16,6	8,7	8,5	4,9	19,3	25,2	11,5	7,3	11,2	5,4
hemicriptòfits no-graminoides	24,6	18,2	30,0	10,8	11,0	11,1	12,3	45,5	41,6	28,0	37,4	24,5	39,8	20,4	12,3	34,5	7,4	50,7	45,7	30,5	23,5	56,0	18,4	13,6	23,6
geòfits	0,2	0,4	0,2	0,0	0,0	0,7	0,2	2,6	0,0	1,2	0,0	18,8	40,7	12,3	1,9	0,6	0,0	0,2	0,0	1,1	0,0	0,0	0,1	0,2	2,5
teròfits	0,6	1,8	2,3	0,9	0,6	0,6	0,1	32,5	16,3	22,3	19,2	2,1	0,0	4,8	3,0	0,0	0,0	0,2	0,0	0,0	1,0	0,0	0,1	0,0	0,0
briòfits	3,8	0,0	3,2	0,0	0,7	0,0	1,2	0,0	15,7	0,0	0,0	0,0	0,0	0,0	0,3	9,8	24,8	0,0	0,0	0,0	1,8	0,0	62,2	4,8	2,7
líquens	0,4	0,0	0,0	14,9	6,7	0,3	0,8	0,0	0,2	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	1,8	0,0	0,0	0,0	0,0
suculència																									
suculents	0,4	0,1	1,2	0,0	0,0	0,0	0,1	1,2	21,8	0,8	0,0	0,7	0,0	0,3	3,0	2,2	0,0	2,2	15,4	5,3	0,2	0,5	3,1	0,7	0,0
semi-suculents	1,3	0,6	2,0	1,1	0,5	0,0	0,0	3,2	2,5	2,2	1,9	7,2	0,0	3,0	1,4	12,4	13,6	10,1	3,7	3,7	27,2	0,0	29,2	77,7	53,3
sempervirència																									
sempreverds	0,4	0,9	0,9	48,7	38,4	56,7	43,6	0,0	2,6	0,5	0,0	0,7	3,5	0,3	1,9	2,2	0,0	10,9	21,6	11,2	0,2	0,0	0,0	0,0	0,0
semi-sempreverds	10,0	33,9	0,4	1,5	2,6	8,9	19,5	0,7	0,4	5,2	1,3	4,6	13,3	8,5	52,7	15,9	54,7	12,5	11,1	17,6	19,3	11,1	3,1	0,7	1,9
llenyositat																									
llenyoses	43,2	16,6	0,0	48,6	38,9	69,8	63,7	0,0	0,1	0,0	0,0	0,0	3,5	0,0	0,0	0,0	0,0	2,6	3,7	7,0	0,0	0,0	0,0	0,0	0,0
semi-llenyoses	13,3	34,4	46,2	20,5	37,1	2,4	12,7	2,2	1,1	0,8	1,3	0,7	0,0	1,0	1,6	0,2	0,0	8,4	3,1	13,4	1,1	1,5	0,0	0,0	0,0
expansió lateral																									
no-clonals	0,0	0,0	0,0	0,0	0,0	0,0	0,0	30,2	19,2	22,3	18,6	0,0	0,0	3,5	0,0	0,0	0,0	0,0	4,3	0,0	0,0	0,0	0,0	0,0	0,0
clonals dist. curtes (<2,5 cm)	7,9	5,2	61,7	3,8	3,0	0,0	0,0	0,0	35,9	19,6	0,0	3,1	3,1	12,6	0,0	45,6	42,0	20,8	60,5	18,7	14,4	32,1	47,9	7,8	15,4
clonals dist. llargues (>2,5 cm)	48,4	58,3	0,0	66,2	71,8	61,3	72,2	40,7	0,0	6,3	45,3	26,0	72,6	32,4	63,8	7,2	12,8	9,7	3,1	8,0	3,3	0,0	21,7	3,3	52,6
molts rebrots, gespes denses	3,2	3,6	0,0	0,0	0,0	5,9	0,0	0,0	10,7	11,5	6,9	22,6	13,7	25,3	3,1	10,1	25,1	23,3	9,9	38,5	46,9	43,4	6,4	73,8	4,0
disseminació llavors																									
llarga distància: espora o similar	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	69,0	0,0	0,0	0,0	0,0	3,1	13,6	7,5	0,0	0,0	0,0	0,0	0,0
llarga distància: vil·là o similar	51,9	45,3	50,5	0,0	0,0	0,0	0,0	32,4	25,2	3,0	0,0	17,5	4,9	12,3	50,9	0,0	0,0	12,3	0,0	0,0	0,0	17,3	9,9	3,7	0,0
mitjana dist.: ales, membranes…	0,0	16,5	0,0	0,0	0,0	5,9	0,0	5,1	10,7	8,2	0,0	17,3	0,0	27,9	3,1	16,6	9,1	11,8	0,0	18,7	12,8	7,9	13,8	3,3	4,0
in situ	7,5	5,2	11,2	51,2	14,7	18,4	45,0	33,4	30,0	48,5	70,8	17,0	15,5	33,8	13,0	46,3	70,8	26,5	64,2	39,0	51,8	50,2	52,3	77,9	68,0
endozoocòria	0,0	0,0	0,0	18,9	60,1	42,8	27,2	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0

	prats densos							prats culminants						prats de vessant					molleres			megaf.
	Alchemillo-Nardetum	*Carici-Festucetum*	*Festuco-Trifolietum*	*Gentiano-Caricetum*	*Ranunculo-Festucetum*	*Selino-Nardetum*	*Trifolio-Phleetum*	*Elyno-Oxytropidetum*	*Hieracio-Festucetum typicum*	*Hieracio-Festucetum caricetosum*	*Hieracio-Festucetum juncetosum*	*Hieracio-Festucetum kobresietosum*	*Leontodo-Caricetum*	*Arenario-Festucetum*	*Festucetum eskiae*	*Festucetum scopariae*	*Oxytropido-Caricetum typicum*	*Oxytropido-Caricetum helictotrichetosum*	*Caricetum fuscae*	*Narthecio-Tricophoretum*	*Swertio-Caricetum*	*Peucedano-Luzuletum*
formes biològiques																						
nanofaneròfits	0,0	0,3	0,0	0,1	0,0	0,0	0,0	0,1	0,0	0,0	0,0	0,1	0,0	0,1	2,5	0,4	0,6	0,5	0,1	0,1	0,0	1,2
camèfits difusos	1,7	0,6	7,0	0,7	0,3	0,5	0,8	1,8	0,6	1,4	0,0	0,8	1,1	1,7	0,7	3,3	0,7	0,0	0,4	0,5	1,0	0,3
camèfits sufruticosos	0,3	4,0	0,7	1,0	2,7	0,5	0,3	3,1	0,9	0,3	4,9	2,3	0,5	0,8	9,7	6,6	10,3	14,1	0,3	3,0	0,9	0,0
camèfits reptants	1,4	0,7	0,8	1,1	0,4	0,0	0,4	16,8	1,0	1,4	4,0	2,7	0,6	9,5	2,6	9,6	13,2	5,1	1,3	0,1	0,0	0,3
camèfits pulviniformes	0,4	0,4	2,8	4,1	0,4	0,0	0,5	5,6	11,2	9,7	7,1	8,2	8,0	15,3	2,0	9,9	18,4	5,8	0,5	0,0	0,2	0,0
hemicriptòfits graminoides	49,5	67,3	45,5	45,8	54,2	64,9	49,0	40,4	48,9	43,7	51,0	46,1	41,0	56,6	49,2	46,1	44,2	49,1	51,7	55,9	45,0	25,0
hemicriptòfits no-graminoides	46,3	24,9	41,5	45,8	41,1	33,4	48,9	27,4	34,2	35,2	25,0	33,6	39,5	13,6	30,9	22,8	10,2	22,0	18,6	33,3	38,5	68,5
geòfits	0,4	0,7	0,3	0,0	0,6	0,2	0,1	0,4	0,0	0,0	0,0	0,1	0,0	0,1	0,7	0,4	0,8	0,8	5,0	2,2	0,0	4,7
teròfits	0,0	1,1	1,0	0,8	0,2	0,6	0,2	1,4	2,7	0,8	1,7	1,8	0,5	2,1	0,7	1,0	1,6	1,5	0,2	0,0	0,5	0,0
briòfits	0,0	0,0	0,1	0,1	0,0	0,0	0,0	0,7	0,3	0,9	0,0	0,5	3,9	0,0	1,0	0,0	0,0	0,0	21,9	4,5	14,0	0,0
líquens	0,1	0,0	0,1	0,5	0,0	0,0	0,0	2,4	0,1	6,4	6,3	3,8	5,0	0,1	0,0	0,0	0,0	1,1	0,0	0,4	0,0	0,0
suculència																						
suculents	0,0	0,2	0,0	0,4	0,0	0,0	0,1	0,6	0,6	0,9	0,4	0,0	0,8	0,5	0,6	0,7	0,0	0,0	0,6	0,0	0,3	0,0
semi-suculents	1,0	0,2	2,3	3,8	1,2	2,0	6,8	1,3	1,9	4,8	3,8	2,3	5,4	0,9	3,1	1,3	0,5	0,3	3,4	4,9	4,2	1,0
sempervirència																						
sempreverds	0,0	0,5	0,0	0,6	0,1	0,0	0,1	0,9	0,8	0,9	0,7	0,2	1,3	0,7	3,2	1,2	0,5	0,6	0,1	0,1	0,0	1,0
semi-sempreverds	0,8	1,3	1,2	2,8	1,4	0,5	1,2	14,8	4,8	5,8	4,5	9,5	4,8	6,3	3,2	2,9	1,5	3,1	0,9	2,6	1,7	0,3
llenyositat																						
llenyoses	0,0	1,3	0,1	0,2	0,3	0,2	0,1	0,9	0,1	0,2	4,5	1,6	0,5	0,1	2,7	0,5	0,6	0,5	0,5	2,6	0,8	1,2
semi-llenyoses	1,5	2,3	1,3	2,0	0,8	0,0	0,2	17,6	1,8	1,4	4,9	3,6	0,7	8,7	6,3	10,0	11,2	15,0	0,0	0,6	0,3	0,0
expansió lateral																						
no-clonals	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	7,2	9,6	0,0	0,0	0,0	0,0
clonals dist. curtes (<2,5 cm)	25,4	5,7	25,9	30,6	25,1	18,2	32,9	4,3	26,5	24,1	11,8	8,4	34,3	9,1	3,6	0,0	8,8	12,4	12,2	22,4	18,7	8,7
clonals dist. llargues (>2,5 cm)	0,0	0,0	3,1	0,0	0,0	0,0	0,0	16,8	0,0	0,0	4,3	4,5	0,0	8,6	8,8	7,0	15,2	8,1	6,2	0,0	18,9	44,6
molts rebrots, gespes denses	38,5	60,4	36,7	34,4	45,7	54,6	43,3	24,4	40,2	35,5	40,2	27,5	41,4	50,0	44,7	33,5	38,4	39,3	47,3	47,6	42,3	23,7
disseminació llavors																						
llarga distància: espora o similar	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
llarga distància: vil·là o similar	0,0	0,0	3,1	5,8	0,0	5,2	3,3	13,1	7,0	12,5	4,0	3,5	5,8	0,0	0,0	0,0	0,0	0,0	3,7	0,0	0,0	28,7
mitjana dist.: ales, membranes…	52,9	60,8	48,7	44,9	65,9	67,6	61,2	9,1	40,2	20,0	11,3	32,1	35,4	50,0	48,3	36,9	38,7	47,9	47,3	6,5	45,9	21,4
in situ	11,1	5,3	13,9	14,2	5,0	0,0	11,7	23,3	19,5	27,0	40,9	5,0	34,5	17,7	8,8	3,6	30,9	21,4	14,7	63,4	34,0	26,9
endozoocòria	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0

ANNEX 4: Pes dels compartiments funcionals en prats alpins (capítol III)

	troncs	bases	fulles	pulvínuls	flors	molses i líquens	biomassa total	necrom.	virosta
Alchemillo-Nardetum									
Alnar 1	0,00	40,13	405,14	0,00	1,19	0,00	446,47	270,09	48,98
Alnar2	0,00	14,63	393,61	0,00	2,26	0,00	410,50	262,40	36,17
Arenario-Festucetum									
Arfest1	0,14	21,84	36,44	4,93	0,05	0,00	63,40	24,29	4,50
Arfest2	2,66	8,57	59,81	76,63	1,68	17,56	166,90	39,87	20,74
Carici-Festucetum									
Carfest1	9,52	21,08	265,01	0,00	0,26	0,00	295,87	176,68	71,19
Carfes2	8,22	7,99	181,03	0,00	1,46	0,07	198,78	120,69	31,31
Elyno-Oxytropidetum									
Elynox1	2,72	10,92	199,47	5,64	6,39	33,56	258,70	132,98	66,43
Elynox1*	15,95	19,53	197,69	0,00	2,04	19,33	254,54	131,79	--
Elynox2	1,90	6,14	127,12	1,78	7,33	4,95	149,22	84,74	12,45
Elynox3	0,00	21,04	126,58	12,79	0,36	0,25	161,03	84,39	16,27
Elynox4	61,87	22,44	198,36	9,65	1,65	11,70	305,66	132,24	215,16
Festucetum eskiae									
Festesk1	0,00	12,13	170,79	0,00	0,09	0,00	183,01	113,86	39,66
Festesk1*	0,00	5,97	146,41	0,00	0,35	0,00	152,73	97,61	--
Festesk2	8,03	59,71	131,54	4,66	1,87	0,00	205,80	87,69	24,79
Festesk3	0,00	102,93	258,23	0,00	0,96	0,00	362,13	172,15	88,73
Festesk4	11,74	11,92	280,45	0,00	3,12	0,00	307,24	186,97	36,94
Festuco-Trifolietum									
Festrif1	2,76	36,55	139,24	0,14	2,99	21,48	203,16	92,83	9,50
Festrif2	1,99	27,97	157,05	0,00	12,94	2,30	202,25	104,70	23,67
Festucetum scopariae									
Festscop1	12,40	20,81	133,57	0,00	7,75	0,29	174,82	89,05	37,52
Festscop1*	28,24	10,39	213,17	0,00	6,41	0,00	258,21	142,11	--
Festscop2	1,75	9,67	318,62	0,00	4,75	0,00	334,79	212,41	48,22
Festscop3	0,44	69,25	171,64	0,97	2,62	0,00	244,93	114,43	11,63
Festscop4	3,40	121,44	257,73	76,59	1,53	0,01	460,70	171,82	59,91
Hieracio-Festucetum									
Festsup1	0,00	20,37	378,56	1,73	13,77	13,32	427,76	252,37	129,54
Festsup1*	0,32	19,59	263,22	0,00	0,90	6,82	290,86	175,48	--
Festsup2	0,81	9,31	248,57	6,37	5,23	2,40	272,70	165,71	110,93
Festsup2*	6,79	36,48	391,68	8,13	2,52	0,00	445,60	261,12	--
Festsup3	1,06	51,74	163,12	11,25	1,04	51,80	280,02	108,75	103,46
Festsup4	0,33	129,77	141,23	25,48	0,94	11,10	308,84	94,15	15,39
Festsup5	6,85	54,16	176,72	23,44	0,46	7,68	269,32	117,81	99,29
Festsup6	21,36	23,71	188,28	1,70	0,59	48,47	284,11	125,52	90,86
Leontodo-Caricetum									
Leocar1	0,00	14,23	95,99	0,00	1,12	4,86	116,20	64,00	66,54
Leocar2	28,51	16,38	131,85	12,04	2,60	0,63	192,01	87,90	41,31
Leocar3	22,05	19,80	126,67	0,00	0,49	0,03	169,04	84,45	94,78
Selino-Festucetum									
Selfest1	0,00	216,73	795,82	0,00	0,03	0,00	1012,58	530,55	314,82
Selfest2	0,00	78,81	312,43	0,00	0,56	0,00	391,80	208,29	99,38
Selfest3	0,00	49,48	478,50	0,00	0,44	0,06	528,48	319,00	146,22
Selfest4	0,00	133,80	512,04	0,00	0,00	1,46	647,29	341,36	634,75

El pes dels compartiments funcionals, i de la biomassa, necromassa i virosta totals, està expressat en g/m^2

* Mostres repetides a la mateixa localitat en anys consecutius

ANNEX 5: Pes dels compartiments funcionals, i valors de producció primària i persistència de la virosta, en matollars alpins (capítol IV)

	arbust dominant		altres arbustos		pulvínuls	gramínies		herbes		briòfits	líquens	biomassa total	virosta	producció primària (g/m^2/any)	persist. virosta (anys)
	troncs	fulles	troncs	fulles		bases	fulles	bases	fulles						
Arctostaphylos uva-ursi															
Au1	946,83	460,23	5,20	0,42	0,00	11,58	24,11	0,00	2,46	0,00	0,00	1450,82	1664,99	196,96	8,88
Au2	700,57	606,63	84,94	27,29	0,00	6,11	21,49	0,00	0,00	2,24	26,66	1475,94	1450,20	266,42	5,49
Au3	1413,57	1355,44	105,74	56,41	0,00	0,00	0,17	0,00	0,00	0,00	0,05	2931,38	2719,93	515,78	5,27
Au4	459,75	686,13	12,65	17,55	0,00	0,33	8,99	0,00	0,87	0,00	0,00	1186,28	1260,78	274,70	4,61
Dryas octopetala															
Do1	312,65	148,87	2,16	0,71	0,00	33,15	78,61	0,00	2,78	9,27	0,70	588,91	965,55	230,97	4,30
Do2	313,98	162,07	0,55	0,81	0,00	14,29	33,39	0,00	71,44	0,90	2,98	600,41	876,60	267,71	3,28
Do3	258,48	136,56	5,61	2,81	0,00	4,24	6,14	0,00	58,33	1,84	15,46	489,47	490,04	239,59	2,86
Juniperus communis alpina															
Jc1	1510,75	570,86	70,00	18,38	0,00	6,17	40,48	1,70	10,41	5,13	0,16	2234,04	594,10	211,98	2,83
Jc2	2304,95	649,02	26,73	2,87	0,00	14,29	69,13	0,00	0,00	0,00	15,98	3082,96	1169,57	234,25	5,35
Jc3	1549,33	468,87	4,91	1,38	0,00	24,26	68,31	0,00	4,80	3,11	7,40	2132,38	1079,69	191,06	6,06
Loiseleuria procumbens															
Lp1	265,77	181,75	0,24	0,05	12,27	5,48	11,62	0,00	1,61	0,42	13,63	492,83	217,46	78,71	2,62
Lp2	256,29	236,44	1,91	0,80	1,68	2,89	10,14	0,00	3,05	1,19	106,44	620,82	342,67	102,90	3,70
Lp3	328,77	280,24	35,91	36,54	0,00	0,14	1,87	0,00	0,94	0,04	0,20	684,65	377,69	140,23	2,69
Rhododendron ferrugineum															
Rf1	1228,77	230,66	132,99	12,88	0,00	20,92	90,84	0,00	6,94	29,08	9,78	1762,86	507,90	210,49	2,45
Rf2	1675,49	242,25	333,81	36,75	0,00	32,72	37,77	0,00	3,32	17,27	1,43	2380,80	515,13	186,86	2,81
Rf3	2297,56	387,14	0,02	0,29	0,00	0,00	14,66	0,00	0,58	38,96	1,02	2740,23	1506,59	189,74	7,58
Rf4	969,79	171,17	45,07	9,34	0,00	14,14	25,80	9,86	2,87	7,89	0,00	1255,94	537,41	113,84	4,56
Salix herbacea															
Sh1	44,40	62,38	0,00	0,00	0,17	6,17	21,98	0,00	19,97	57,32	0,00	212,38	190,39	104,32	1,92
Sh2	15,58	28,27	0,00	0,00	11,24	1,91	14,52	0,00	26,48	1,10	1,45	100,53	41,47	55,15	0,45
Sh3	42,34	44,85	0,00	0,00	24,34	3,21	5,60	0,00	4,71	9,18	2,21	136,42	22,07	77,56	0,33
Vaccinium uliginosum microphyllum															
Vu1	183,58	49,44	39,95	35,48	0,00	17,32	45,56	0,00	6,56	7,69	45,28	430,86	205,56	120,00	1,75
Vu2	563,40	130,48	0,00	0,00	0,00	15,11	126,85	0,00	24,54	0,00	0,30	860,68	704,62	281,87	2,61
Vu3	507,68	119,68	290,78	45,49	0,00	12,71	39,79	0,00	9,13	0,00	0,00	1025,25	456,44	214,09	2,19
Vu4	204,00	66,72	36,52	39,63	0,00	8,30	26,63	1,11	12,50	1,41	0,25	395,96	92,58	143,06	0,65

El pes dels compartiments funcionals, i de la biomassa i virosta totals, està expressat en g/m^2

ANNEX 6: Paràmetres foliars de les espècies dominants en prats i matollars alpins (capítols III i IV)

	SLA (mm^2/mg)	àrea foliar (mm^2)	comunitats vegetals*
Hemicriptòfits graminoides			
Carex curvula curvula	14,133 (5,26)	97,189 (10,30)	L.Car
Carex ericetorum	9,033 (2,82)	90,625 (25,76)	H.Fes
Carex sempervirens pseudotristis	9,716 (0,75)	447,388 (86,53)	C.Fes
Festuca airoides	14,180 (2,73)	70,485 (50,70)	H.Fes
Festuca eskia	7,808 (2,15)	293,716 (82,65)	C.Fes, F.esk, S.Fes
Festuca gautieri	18,730 (6,57)	79,445 (71,67)	F.sco
Festuca indigesta durissima	10,657 (1,32)	184,030 (70,88)	A.Fes, F.sco
Festuca rubra commutata	17,938 (5,19)	56,547 (23,76)	F.Tri
Helictotrichon sedenense	13,844 (1,17)	211,980 (83,59)	F.sco, E.Oxy
Juncus trifidus	20,210 (0,19)	84,670 (3,53)	H.Fes
Kobresia myosuroides	18,002 (2,06)	129,263 (21,18)	E.Oxy
Nardus stricta	10,734 (1,18)	101,266 (55,53)	A.Nar, L.Car, S.Fes
Hemicriptòfits no-graminoides			
Anemone vernalis	8,268 (0,38)	227,702 (51,20)	E.Oxy, H.Fes, L.Car
Campanula gr. *scheuzcheri*	20,489 (5,78)	79,762 (6,95)	F.esk, F.sco, S.Fes
Gentiana acaulis alpina	7,041 (0,06)	51,424 (21,34)	H.Fes, L.Car
Gentiana verna	8,474 (1,45)	79,913 (51,93)	E.Oxy
Hieracium lactucella	9,690 (0,77)	48,138 (3,31)	F.esk, H.Fes
Leontodon pyrenaicus pyrenaicus	13,639 (--)	82,321 (--)	L.Car
Primula integrifolia	11,626 (4,48)	90,646 (28,69)	L.Car
Trifolium alpinum	14,720 (1,77)	253,321 (194,53)	A.Nar, C.Fes, L.Car, S.Fes
Trifolium thalii	11,295 (0,52)	54,345 (22,47)	F.Tri
Camèfits difusos			
Vaccinium uliginosum microphyllum	14,566 (0,62)	57,358 (23,41)	A.uva, E.Oxy, H.Fes, L.Car, J.com, L.pro, R.fer, V.uli
Camèfits pulviniformes			
Minuartia recurva recurva	10,915 (--)	1,275 (--)	A.Fes
Minuartia sedoides (dades inèdites)	18,166 (6,34)	2,296 (0,21)	A.Fes
Silene acaulis	17,129 (--)	2,221 (--)	A.Fes
Vitaliana primuliflora	8,691 (--)	4,167 (--)	F.sco
Camèfits reptants			
Arctostaphylos uva-ursi	4,276 (0,42)	109,858 (18,53)	A.uva, J.com
Dryas octopetala	12,261 (2,67)	184,199 (96,54)	D.oct, E.Oxy
Loiseleuria procumbens	5,138 (0,65)	11,554 (1,45)	L.pro, R.fer, V.uli
Salix herbacea	16,107 (2,19)	88,923 (14,76)	L.Car, L.pro, R.fer, S.her, V.uli
Salix reticulata	11,632 (1,86)	108,063 (38,82)	D.oct, S.her, V.uli
Thymus serpyllum chamaedrys	15,910 (--)	9,321 (--)	F.sco
Thymus serpyllum nervosus	11,583 (2,33)	3,621 (1,55)	A.Fes, E.oxy, F.esk, F.sco, H.fes
Camèfits sufruticosos			
Calluna vulgaris	14,584 (0,41)	1,100 (0,35)	A.uva, J.com, R.fer, V.uli
Empetrum nigrum hermaphroditum	7,361 (--)	5,150 (--)	A.uva
Helianthemum nummularium	9,877 (2,83)	53,373 (25,54)	F.sco
Jasione laevis laevis	11,224 (3,32)	23,771 (9,46)	F.esk, F.sco
Vaccinium myrtillus	24,094 (2,87)	136,25 (31,31)	A.uva, J.com, R.fer, V.uli
Veronica fruticulosa saxatilis	9,708 (2,41)	14,852 (5,22)	F.esk
Nanofaneròfits			
Cotoneaster integerrimus	11,739 (--)	90,810 (--)	J.com
Juniperus communis alpina	5,850 (0,58)	8,807 (0,67)	A.uva, J.com, R.fer
Rhododendron ferrugineum	6,778 (0,72)	160,563 (41,50)	R.fer, V.uli

Valors mitjans, desviació estàndard entre parèntesi

La nomeclatura segueix Bolòs et al. (2005)

***Prats:** A.Fes, *Arenario-Festucetum*; A.Nar, *Alchemillo-Nardetum;* C.Fes, *Carici-Festucetum*; E.Oxy, *Elyno-Oxytropidetum*; F.esk, *Festucetum eskiae*; F.sco, *Festucetum scopariae*; F.Tri, *Festuco-Trifolietum*;H.Fes, *Hieracio-Festucetum*; L.Car, *Leontodo-Caricetum*; S.Fes, *Selino-Festucetum*. **Matollars:** A.uva, *Arctostaphylos uva-ursi*; D.oct, *Dryas octopetala*; J.com, *Juniperus communis alpina*; L.pro, *Loiseleuria procumbens*; R.fer, *Rhododendron ferrugineum*; S.her, *Salix herbacea*; V.uli, *Vaccinium uliginosum microphyllum*

ANNEX 7: Valors mitjans dels paràmetres foliars de les espècies subarbustives presents als matollars alpins (capítol IV)

	superfície foliar (mm^2)	LDMC (mg g^{-1})	SLA (mm^2 mg^{-1})	LNC (%)	LCC (%)	C/N
espècies dominants						
Arctostaphylos uva-ursi	109,86 (18,53)	449,28 (23,27)	4,28 (0,42)	0,78 (0,07)	50,84 (1,94)	65,54 (7,44)
Dryas octopetala	184,20 (96,54)	356,93 (6,83)	12,26 (2,67)	1,54 (0,20)	48,28 (1,74)	31,86 (4,86)
Juniperus communis alpina	8,81 (0,67)	504,32 (14,12)	5,85 (0,58)	0,91 (0,15)	49,75 (1,96)	55,6 (10,34)
Loiseleuria procumbens	11,55 (1,45)	502,03 (9,35)	5,14 (0,65)	0,82 (0,11)	53,87 (0,48)	66,71 (8,16)
Rhododendron ferrugineum	160,56 (41,50)	462,4 (11,64)	6,78 (0,72)	1,25 (0,18)	52,43 (0,52)	42,35 (5,38)
Salix herbacea	88,92 (14,76)	364,21 (27,19)	16,11 (2,19)	2,07 (0,29)	46,09 (0,38)	22,56 (3,08)
Vaccinium uliginosum microphyllum	57,36 (23,41)	381,77 (7,55)	14,57 (0,62)	1,95 (0,56)	50,17 (1,53)	27,77 (9,96)
espècies acompanyants						
Calluna vulgaris	1,1 (0,35)	471,85 (60,01)	14,58 (0,41)	1,50 (--)	45,00 (--)	30 (--)
Cotoneaster integerrimus	90,81 (--)	413,83 (--)	11,74 (--)	(--) (--)	(--) (--)	(--) (--)
Empetrum nigrum hermaphroditum	5,15 (--)	491,23 (--)	7,36 (--)	1,02 (--)	52,93 (--)	51,67 (--)
Salix reticulata	108,06 (38,82)	328,34 (26,24)	11,63 (1,86)	2,06 (0,39)	42,42 (0,54)	20,96 (3,70)
Vaccinium myrtillus	136,25 (31,31)	339,04 (37,66)	24,09 (2,87)	1,81 (0,15)	48,1 (0,29)	26,79 (2,06)

ANNEX 8: Mitjanes ponderades dels paràmetres foliars per a cada localitat d'estudi en matollars alpins (capítol IV)

	SLA (mm^2/mg)	LDMC (mgPS/gPF)	LNC (%)	LCC (%)	C/N
Arctostaphylos uva-ursi					
Au1	4,47	415,40	0,84	50,93	60,57
Au2	4,04	451,74	0,81	48,17	61,22
Au3	4,63	465,50	0,70	52,03	75,41
Au4	4,64	460,09	0,83	51,65	61,86
Dryas octopetala					
Do1	12,98	348,89	1,43	47,99	33,59
Do2	14,48	359,70	1,77	46,66	26,33
Do3	9,36	361,14	1,42	49,98	35,27
Juniperus communis alpina					
Jc1	6,51	505,92	0,89	51,42	58,86
Jc2	6,30	487,69	0,80	50,06	62,98
Jc3	5,19	514,57	1,09	47,62	43,83
Loiseleuria procumbens					
Lp1	4,39	506,77	0,94	54,27	57,44
Lp2	5,51	507,62	0,74	53,98	72,73
Lp3	6,55	444,75	0,88	52,58	64,56
Rhododendron ferrugineum					
Rf1	6,80	451,38	1,23	52,51	42,92
Rf2	8,67	433,81	1,55	52,19	34,00
Rf3	7,49	473,91	1,10	52,75	47,99
Rf4	7,40	467,13	1,20	51,56	43,59
Salix herbacea					
Sh1	14,33	366,00	1,94	45,85	23,60
Sh2	18,55	336,17	1,86	46,53	24,99
Sh3	15,13	385,15	2,40	45,63	19,03
Vaccinium uliginosum microphyllum					
Vu1	11,12	408,87	1,90	51,28	35,99
Vu2	14,21	388,59	2,18	50,45	23,12
Vu3	16,90	383,10	1,84	47,92	26,24
Vu4	13,93	389,52	1,43	49,74	36,93

ANNEX 9: Valors d’emmatament i dades descriptives de les malles estudiades (capítol V)

	prop. cel·les amb incr. de recobriment (%)	incr. de recobriment (%)	incr. de superfície (m^2)	altitud (m)	coordenada x (UTM ED50, 31N)	pendent (°)	recobriment arbust 1997 (%)	canvis prop. camins de bestiar (%)
J. alpina								
F. airoides								
1	23,12	2,64	15,52	2285	395221	16,91	19,79	-3,52
2	31,82	3,69	21,72	2512	369797	38,73	24,91	
3	36,76	6,22	36,57	2350	431933	23,96	15,27	
4	16,89	2,28	13,41	2345	382593	11,31	12,16	
5	43,89	3,62	21,29	2245	352276	16,07	12,67	28,05
F. eskia								
1	30,16	6,08	35,79	2295	379679	29,16	18,58	0,00
2	33,03	4,13	24,28	2395	366557	26,57	11,12	
3	30,17	6,28	36,97	2225	431607	29,25	15,43	-2,23
4	31,25	6,73	39,59	2290	326427	31,63	5,05	3,37
5	32,46	3,66	21,56	2215	352563	21,80	8,70	
N. stricta								
1	23,36	0,12	0,73	2205	365767	17,70	1,15	7,30
2	27,19	3,57	21,01	2287	351916	12,77	12,04	-0,46
3	21,12	3,88	22,84	2190	382696	21,18	22,20	6,21
4	28,99	6,80	40,03	2345	391690	19,12	25,52	9,47
5	24,24	4,09	24,06	2235	430640	30,28	18,11	-1,82
R. ferrugineum								
F. airoides								
1	6,80	0,55	3,21	2410	385069	22,59	17,29	1,94
2	28,30	5,42	31,91	2220	434761	28,00	34,20	
3	23,53	1,88	11,05	2235	429943	24,27	33,09	7,84
4	21,83	3,87	22,78	2435	369665	27,81	23,59	
5	10,36	1,23	7,24	2515	395770	22,96	19,56	5,70
F. eskia								
1	16,42	2,33	13,72	2210	320105	25,56	25,93	1,49
2	22,46	2,45	14,39	2270	362621	36,43	26,63	0,72
3	33,53	5,61	33,02	2355	380911	25,38	19,99	
4	24,64	2,55	14,98	2380	347183	30,45	21,50	
5	11,11	1,48	8,68	2295	367028	32,62	27,43	-0,69
N. stricta								
1	32,00	7,00	41,18	2185	351109	17,48	11,94	14,00
2	5,46	0,89	5,22	2330	391022	13,10	18,65	0,00
3	11,89	1,49	8,74	2255	373373	27,76	20,37	-2,80
4	2,48	0,31	1,82	2330	368013	31,07	22,83	
5	10,38	1,64	9,64	2440	385111	10,08	18,78	