Universitat de Lleida

Cartografia de les congestes i ecologia de les comunitats vegetals de les congesteres d’Andorra (Pirineus)

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CARTOGRAFIA DE LES CONGESTES I ECOLOGIA DE LES COMUNITATS VEGETALS DE LES CONGESTERES D'ANDORRA (PIRINEUS)

Marta Domènech Ferrés

Andorra, maig 2012

Cartografia de les congestes i ecología de les comunitats vegetals de les congesteres d'Andorra (Pirineus)

Cartography of Andorran snowdrifts and plant ecology of Andorran snowbeds (Pyrenees)

Ph.D. Thesis

Memòria presentada per:

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per a optar al grau de Doctora

Amb el vist-i-plau de:

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Als meus pares

Taula de continguts

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Resum

El canvi climàtic està afectant a la reducció de la coberta de neu, al retrocés de glaciars i a la desaparició de congestes en zones de muntanya. En aquest sentit, la congestera és un dels hàbitats més amenaçats als Pirineus.

En aquesta Tesi Doctoral s'ha realitzat la primera cartografia de congestes d'Andorra (Pirineus) estudiant-ne les variables físiques que afecten a la seva formació i conservació i se n'ha obtingut un mapa que permetrà avaluar la dinàmica futura de les mateixes. El període climàtic d'acumulació de la neu (gener-abril) ha resultat ser determinant en el nombre i extensió de les congestes, quan aquest és fred i humit. Per tant un augment de temperatura o una disminució de la precipitació, en els mesos d'acumulació de neu, suposarien una disminució important en l'extensió i el nombre de congestes. Aquesta cartografia, que ha permès inventariar fins a 2.520 congestes, ha assentat les bases per estudiar la vegetació de les congesteres (composició, diversitat, fenologia i trets funcionals) a fi de relacionar-la amb les variables ambientals i poder preveure les principals conseqüències del canvi climàtic.

En l'estudi de la vegetació, s'han inventariat fins a 85 plantes vasculars, 31 de les quals són típiques de la vegetació de pastures d'alta muntanya, i 21 són típiques de les congesteres (classe *Salicetea herbaceae*). S'han identificat fins 16 briòfits, 2 dels quals han estat descoberts per primera vegada al Pirineu andorrà. S'ha demostrat, que les espècies vegetals considerades típiques de congesta no viuen ni a les congesteres més innivades ni tampoc a les de més altitud. Això pot permetre, en el cas de desaparèixer progressivament les congestes de menys altitud per un hipotètic canvi climàtic -les situades per sota dels 2540 m-, que les plantes típiques de congestera puguin disposar d'altres congesteres a més altitud per poder-les colonitzar. La colonització, però, dependrà de la quantitat d'hàbitat disponible (sobretot de la presència de matèria orgànica en el sòl) i de les relacions inter-específiques. L'estudi fenològic ha demostrat que determinades espècies adapten la seva fenologia als factors físics locals (com la data de la fosa de la neu o la temperatura acumulada), a fi de permetre maximitzar les probabilitats d'èxit reproductiu. Contràriament, altres espècies no han mostrat cap tipus d'adaptació fenològica.

Finalment s’ha avaluat la diversitat funcional a fi de conèixer l’estabilitat de l’hàbitat de congestera i la seva resposta als canvis ambientals (com per ex. respostes en la productivitat o en la resiliència després de canvis sobtats o pertorbacions). Les espècies que dominen en les congesteres situades a menys altitud, amb presència de sòls orgànics i amb menys durada de la coberta de neu, i que d'altra banda són típiques de les pastures d’alta muntanya, s’han trobat relacionades amb valors alts de divergència funcional i amb valors elevats de biomassa aèria. Això s’explicaria per la existència de competència entre espècies. En canvi les espècies de la classe *Salicetea herbaceae* (considerades com típiques de congesta) s’ha trobat relacionades amb valors alts d’uniformitat funcional, fet que és atribuïble a les condicions físiques més rigoroses (congesteres de més altitud, amb més sòl orgànic i més durada de la coberta de neu) i amb poca competència entre espècies. També s’han mesurat i estudiat els trets biològics funcionals de les espècies més freqüents a fi de caracteritzar la vegetació. L’estudi de la relació entre els trets funcionals i els factors físics a petita escala (ex. data de la fosa de la neu) ha permès avaluar la plasticitat intraespecífica i demostrar que algunes de les espècies més comunes responen significativament als canvis ambientals, en augmentar el nombre d’inflorescències en els indrets de més durada de la coberta de neu.

Paraules clau: congesta, congestera, canvi climàtic, vegetació, Pirineus.

Resumen

El cambio climático está afectando a la reducción de la cubierta de nieve, al retroceso de los glaciares y a la desaparición de los neveros en zonas de montaña.

En esta Tesis Doctoral se ha realizado la primera cartografía de neveros de Andorra (Pirineos) estudiando las variables físicas que más afectan a su formación y conservación, habiéndose obtenido un mapa que permitirá evaluar la dinámica futura de los mismos. El periodo climático de acumulación de la nieve (enero-abril) se ha identificado como determinante en el número y extensión de los neveros, cuando éste es frío y húmedo. Por lo tanto un aumento de la temperatura o una disminución de la precipitación, en los meses de enero a abril, supondrían una mengua importante en el número y extensión de los neveros. Esta cartografía, que ha permitido incluir hasta 2.540 neveros, debe asentar las bases para el estudio de su vegetación (composición,

diversidad biológica, fenología y características funcionales) con el objetivo de relacionarla con los factores ambientales y poder predecir las principales consecuencias del cambio climático.

El estudio de la vegetación ha permitido catalogar hasta 85 especies de plantas vasculares, 31 de las cuales son típicas de la vegetación de pastos de alta montaña, y 21 son consideradas típicas de la vegetación de neveros (clase *Salicetea herbaceae*). Se han identificado 16 briófitos, 2 de los cuales constituyen la primera referencia en el Pirineo andorrano. También se ha evidenciado que las especies consideradas típicas de los neveros no viven en aquellos situados a más altitud ni tampoco en los más innivados. Esta circunstancia permite hipotizar que si progresivamente desaparecen los neveros por un hipotético cambio climático, las plantas de los neveros situados a menor altitud dispondrán todavía de otros neveros a mayor altitud para colonizar. Naturalmente, esa colonización dependerá en gran medida de la cantidad de hábitat disponible (sobre todo por la presencia de suelos orgánicos) y de las relaciones sujetas entre las especies. El estudio fenológico indica que algunas de las especies más comunes adaptan su fenología a las variables físicas locales (como fecha de fusión de la nieve o temperatura acumulada), permitiendo maximizar las probabilidades de éxito reproductor. Otras especies no han demostrado ninguna adaptación fenológica.

Finalmente se ha evaluado la diversidad funcional para conocer el nivel de estabilidad del hábitat de nevero y su respuesta a los cambios ambientales (como respuestas en la productividad o en la resiliencia después de los cambios o perturbaciones). Las especies identificadas en los neveros, y que son las consideradas típicas de los pastos de alta montaña, se han visto relacionadas con valores elevados de divergencia funcional y con valores altos de biomasa aérea, hecho que se explicaría por la competencia entre especies en los neveros que presentan menos altitud, mas temperatura, presencia de suelos orgánicos y menor duración de la cubierta de nieve. En cambio las especies de la clase *Salicetea herbacea*, se han visto relacionadas con altos valores de uniformidad funcional, hecho atribuible a las condiciones físicas más severas y a la baja competencia entre especies. También se han medido y estudiado las características funcionales de las especies mas comunes para caracterizar la vegetación. Finalmente el estudio de la relación entre las características funcionales y los factores físicos locales (como la fecha de la fusión de la nieve) han permitido detectar plasticidad intraespecífica de algunas especies, demostrando que responden significativamente a los cambios ambientales,

aumentando el número de inflorescencias en los lugares de mayor duración de la cubierta de nieve.

Palabras clave: nevero, ventisquero, cambio climático, vegetación, Pirineos.

Abstract

Climate change is contributing to a reduction in snow cover, the rate at which glaciers are receding, and the disappearance of snowbeds in mountains.

In this Doctoral Thesis, the snowbeds of Andorra (Pyrenees) were mapped for the first time, which was used to identify the physical factors that have had the greatest affect on the formation and persistance of the snowbeds. That information was used to produce a map that will facilitate assessments of the dynamics of snowbeds in the future. The climatic conditions of the period of snow accumulation (January-April) has a significant effect on the number and extent of snowbeds in the Andorran Pyrenees, but only when the period was cold and wet. An increase in temperature or a reduction in rainfall between January and April, reduces the number and extent of snowbeds. The map, which identified 2.540 snowbeds, has provided a basis from which to study the composition, diversity, phenology, and functional traits of the vegetation in the snowbeds and the influences of environmental factors, and for predicting the most important effects of climate change.

In the study, 85 species of vascular plants were documented, 31 of which are typical of mountain pastures and 21 are typical of the vegetation of snowbeds (Class *Salicetea herbaceae*). In addition, the study identified 16 bryophytes, two of which were documented for the first time in the Andorran Pyrenees. The plant species typical of snowbeds were not present in the snowbeds at the highest elevations or in those that had the longest snow cover; however, if the snowbeds at the lowest elevations disappear progressively, there will be snowbeds at higher elevations that the typical snowbed species can colonize. Colonization will depend largely on the amount of habitat available (especially, the availability of organic soils) and the nature of the relationships between species that become established. Some of the most common species have adapted their phenologies to local physical conditions (such as date of snowmelt), which favors their reproductive success. Other species did not exhibit any phenological adaptations.

To assess the stability of the snowbeds and the responses to environmental changes (such as changes in productivity or resilience following changes or disturbances), the functional diversity of the snowbeds was evaluated. The species identified in the snowbeds, which are typical of high mountain pastures, were associated with high functional divergence and high biomass, which probably was the result of the competition between species in the snowbeds at low elevations, those exposed to high temperatures that have organic soils, and a relatively short period of snow cover. In contrast, the species of the *Salicetea herbaceae* class were associated with a high degree of functional uniformity, which suggest severe physical conditions and low competition between species. To characterize the vegetation of the snowbeds, the functional traits of the most common species were assessed. To evaluate intraspecific plasticity, the relationships between the functional and local physical factors (such as date of snowmelt) were evaluated, which demonstrated that the most common species responded significantly to changes in the environment by increasing the number of inflorescences at the sites where snow cover persisted the longest.

Keywords: snowdrifts, snowbed, climate change, plant communities, Pyrenees.

CAPÍTOL 1: Introducció general, discussió general i conclusions

INTRODUCCIÓ GENERAL

Les congestes i les congesteres

Es considera congesta (*snowdrift* en anglès), tota aquella acumulació de neu que roman en una clotada o terreny de muntanya, i que recobreix el sòl tot o part del període estival. Aquesta neu és aportada habitualment per l'acció del vent, per una allau o per un canvi de pendent del vessant. La neu roman sense fondre's, bé perquè es troba situada en una zona obaga, bé per l'orografia del lloc, o perquè sovint es dóna més d'una d'aquestes condicions (VVAA 2002). Aquestes congestes acostumen sempre a fer-se en els mateixos indrets (Körner 2003), ja que les causes d'acumulació de neu són força estables (orografia, vents dominants, etc.). L'estabilitat en el temps d'aquesta coberta de neu fa que s'hi creï un ambient ecològicament particular anomenat congestera (*snowbed* en anglès). Per tant es considera congestera l'indret on es localitza una congesta, essent aquesta la definició que s'ha seguit al llarg de tot aquest treball. Certament, s'ha considerat vegetació de congestera, tots els agrupaments vegetals que trobem en el sí de la congestera independentment de la classe sintaxonòmica a la qual pertanyen.

Figura 1. Detall de l'espècie *Mucizonia sedoides*, planta considerada de *Salicetea herbaceae*.

A les congesteres se solen desenvolupar plantes molt diverses (vasculars i no vasculars), dites quionòfiles, moltes de les quals pertanyen sintaxonòmicament a la classe *Salicetea herbaceae* Br.-Bl. 1947. Però, tot sovint també hi conviuen altres espècies vegetals que no pertanyen a aquell conjunt, i que solen ser especialment pradenques (*Juncetea trifidi* Hadac 1944, *Elyno-Seslerietea* Br.-Bl. 1948), o bé de pedrusques i tarteres (*Thlaspietea rotundifolii* Br.-Bl. 1947). Les congesteres, degut a la seva ubicació, presenten una combinació exclusiva de variables ambientals: coberta de neu, orientació, altitud, data de la fosa de la neu, temperatura, contingut de matèria orgànica del sòl, etc. Les diferents relacions que s'estableixen entre variables poden ser molt significatives en la resposta de la vegetació. Per exemple: no es donen les mateixes condicions ecològiques entre una congestera que fon al juny i es troba a 2.800 m d'altitud a la solana que una altra que malgrat fondre també al juny es troba a 2.200 m d'altitud a l'obaga. Tota la combinació de condicions ecològiques possibles fa pensar que les espècies que s'hi puguin trobar siguin variades i no necessàriament totes pertanyents a *Salicetea herbaceae.* Per aquesta raó el concepte de congestera que s'adapta en aquest estudi es extensiu a la presència d'altres agrupaments vegetals, malgrat que no pertanyin a aquella classe fitocenològica. Conseqüentment s'ha cregut convenient prendre com a unitat experimental denominada "congestera", totes les superfícies de congesta d'Andorra sense tenir en compte a priori la vegetació que s'hi pugui fer, a fi de, posteriorment, estudiar-ne la vegetació.

Figura 2. Detall de la congesta del Port de l'Arbella (Andorra).

De totes maneres, de tot el reguitzell de variables ambientals que condicionen la vida en una congestera, està clar que la neu té una influència preferent i un efecte determinant en la composició florística i en l'establiment de la vegetació que hi viu. Això es tradueix en l'establiment de plantes predominantment quionòfiles o quiontolerants. La neu protegeix les plantes de les baixes temperatures, les conserva prop dels zero graus durant el període d'hivern, manté la humitat edàfica i assegura l'aportació d'aigua en el moment de màxim creixement (Conesa 1997, Björk and Molau 2007, Vigo 2008). Les espècies de congestera també estan adaptades a les condicions rigoroses d'aquests hàbitats i això els dóna un avantatge competitiu. La majoria de les espècies de les congesteres toleren millor l'efecte ombreig que no pas altres espècies alpines (Björk and Molau 2007) i totes sobreviuen any rera any amb un període vegetatiu molt curt. A més, aquestes plantes, són capaces d'obtenir una taxa fotosintètica positiva durant la fosa de la neu (Mullen and Schmidt 1993, Galen i Stanton 1995). Les herbes, no gramínies, són les que predominen a les congesteres, essent tant més freqüents com més llarga sigui la durada de neu. Però quan es tracta de congesteres on el període sense neu és molt i molt curt (menor de 15 dies) hi predominaran quasi exclusivament els briòfits (Björk and Molau 2007). En general, quan més llarg és el període lliure de neu major és la possibilitat de trobar sòls més desenvolupats (Bliss 1960) i taxes més elevades de biomassa aèria (Björk and Molau 2007).

La majoria d'espècies vegetals que es troben a les congesteres són exclusives d'aquest tipus d'hàbitat, el qual esdevé un reservori de biodiversitat únic al Pirineu. Tot i això la riquesa de plantes que s'hi troba és moderada en comparació a la d'altres hàbitats de l'alta muntanya pirinenca (*Festuco-Brometea* Br.-Bl. 1948) (Conesa 1997). La raó és que els Pirineus, tot i ser una serralada europea amb cims que superen els 3.000 m d'altitud, les espècies de la classe *Salicetea herbaceae*, de distribució bòreo-alpina, s'hi troben actualment d'una manera residual, malgrat haver estat més extenses durant el pleistocè. Els efectes del canvi climàtic poden provocar que espècies de l'hàbitat de congestera es vegin reemplaçades per espècies pròpies d'altres hàbitats adjacents (prats, pedrusques, etc.) (Schöb et al. 2009, Grabherr 2003). Primer de tot, però, cal conèixer quines són les espècies actualment pròpies de les congesteres silicícoles d'Andorra i quines són les classes sintaxonòmiques implicades (no només la classe *Salicetea herbaceae*).

Les congesteres i el canvi climàtic

Els Pirineus són rics pel que fa a la diversitat de plantes. Dels 2.554 tàxons que s'han catalogat al Pirineu navarrès i aragonès, uns 81 són rars o es troben en alguna situació d'amenaça (Villar et al. 1997). A Andorra trobem 1.537 tàxons, dels quals 298 es troben amenaçades (Carrillo et al. 2008). Segons diversos autors, la vegetació alpina és especialment sensible als canvis ambientals i respon a l'escalfament global

(Muñoz et al. 2007; Pauli et al. 2007, Thuiller et al. 2005, Theurillat et Guisan 2001). Entre les comunitats de vegetació alpines, les congestes són amb diferència les més sensibles al canvi climàtic, ja que les condicions ambientals que s'hi donen són particulars (tal com abans s'ha explicat). Així, la frágil diversitat florística de les congesteres contribueix de forma exclusiva a la biodiversitat global de les muntanyes pirinenques.

Actualment aquests hàbitats d'alta muntanya estan sotmesos a l'amenaça de l'escalfament global. Segons les prediccions de l'IPCC (IPCC 2007), s'espera que la temperatura mitjana del planeta augmenti entre 1,4ºC i 5,8ºC durant el període 1990 a 2100. A la zona pirinenca, i segons la *Agencia Estatal de Meteorología a* (AEMET 2008), es preveu, per l'any 2100, que la temperatura mitjana augmenti entre 4,5ºC i 5 ºC, especialment a l'hivern. Pel que fa a les congesteres, alguns autors exposen la idea que són probablement l'hàbitat alpí on les condicions mesoclimàtiques canviaran més depressa (Grabherr 2003, Heergaard et Valdvik 2004). L'escenari de l'escalfament propicia la fosa de la neu a dates cada cop més primerenques i exposa la vegetació quionòfila a sofrir canvis bruscs de la temperatura atmosfèrica. La fosa de la neu i l'augment de la temperatura del sòl obren un espai ecològic que pot ser ocupat per altres espècies menys especialistes, per bé que més oportunistes. Alguns autors (Grabherr et al. 1995, Grabherr 2003, Schöb et al. 2009, Lluent 2007, Illa et al. 2011) apunten la possibilitat que aquests hàbitats siguin envaïts per espècies pradenques, sobretot gramínies, o bé per espècies adaptades a ambients menys innivats, menys humits i més exposats als canvis de temperatura (Muñoz et al. 2007). No obstant això, no hi ha una predicció clara de quin és el futur de l'hàbitat de congestera. L'estudi de les preferències ecològiques de les espècies, la seva interrelació, l'estudi de la relació amb el medi i el coneixement actual de les unitats sintaxonòmiques que es troben a les congesteres són aspectes necessaris per preveure el futur d'aquest hàbitat. D'altra banda, les congesteres poden ser considerades com un model de comunitat vegetal per estudiar i predir les conseqüències del canvi climàtic sobre la vegetació alpina (Bjork et Molau 2007, Schöb et al. 2009).

Les congestes i congesteres al Pirineu: antecedents

En l'actualitat no existeix cap estudi ni cartografia sobre les congestes del Pirineu. No obstant hi ha alguns estudis als Alps (Durand et al. 2004, Lehning et al. 2002) que han analitzat la dinàmica de la distribució i acumulació de la neu. Considerant que la formació de la congesta és la base per mantenir l'hàbitat de la congestera al Pirineu, la presència de congestes és quelcom que caldria quantificar i descriure; primer de tot per entendre la disposició i la composició de la vegetació que hi viu, i segon per valorar la dinàmica futura d'aquests hàbitats.

Contràriament, les congesteres estan més estudiades florísticament, ja que al llarg dels anys s'ha reunit un nombre considerable d'inventaris florístics realitzats al Pirineu (Braun-Blanquet 1948, Rivas Martínez 1969, Rivas Martínez et al. 1991, Corriol 2009, Lluent et al. 2006, Lluent 2007, Illa et al. 2011).

Malgrat tot, continuen essent escassos els treballs en els que s'hagi estudiat la relació existent entre les variables ambientals de les congesteres i les plantes que s'hi fan. Braun-Blanquet (1948), Rivas Martínez (1969), Rivas Martínez et al. (1991) i Corriol (2009) han publicat extensos inventaris florístics i han desenvolupat anàlisis fitosociològiques de les congesteres del Pirineu occidental, central i oriental, tant de la part Ibèrica com de la part més atlàntica. L'estudi de la relació de les plantes de congesta amb el seu medi físic, no ha estat, però, un dels seus objectius. En canvi, Muñoz et al. (2007) han centrat el seu estudi en una sola congestera de dimensions grans a la Sierra de Guadarrama (encara que fora del Pirineu), i han descrit detalladament la composició i la distribució de la vegetació relacionant-la amb la coberta de neu i el règim tèrmic i han pogut mostrar el grau de dependència de la coberta de neu de les espècies més importants. Lluent (2007) estudia l'efecte de la temperatura i la humitat sobre la fenologia d'algunes de les plantes de congestera. Fa a més una descripció acurada dels perfils de vegetació que es troben dels indrets més a menys innivats de sis congesteres del Pirineu. Lluent et al. (2006) i Illa et al. (2011) també estudien l'efecte tèrmic sobre la vegetació de congestera a través de transsectes de més a menys innivació, demostrant l'augment de la presència de les espècies menys quionòfiles cap a l'exterior de les congesteres i la possible invasió d'espècies pradenques en el context de canvi climàtic. De totes maneres l'aproximació d'aquests valuosos treballs a l'hàbitat de congesta (Lluent et al. 2006, Lluent 2007, Illa et al. 2011) és estrictament florístic, havent detectat i identificat la congestera com l'indret on apareixen les espècies de la classe *Salicetea herbacea*, diferenciant-se per tant de la definició de congestera i de la metodologia emprada en el present treball.

Hi ha un grup de plantes que malgrat no ser tant estudiades, també són força abundants en l'hàbitat de congestera: es tracta del briòfits. S'ha de tenir en compte, com bé s'ha exposat en l'anterior punt, que en les congestes més innivades, conseqüentment congesteres en les que les plantes disposaran d'un període vegetatiu més curt, els briòfits poden arribar a predominar sobre les plantes vasculars. Malgrat que en la majoria dels anteriors estudis, es descriu l'aparició d'alguns dels briòfits més abundants, aquests encara són força desconeguts en el sí de les congesteres pirinenques. En el cas d'Andorra no existeix cap estudi que inclogui les espècies de briòfits que viuen a les congesteres andorranes.

Objectius i estructura de la tesi

Aquest és el primer estudi que publica una cartografia de congestes d'Andorra (Pirineu central). Es considera que aquest és un pas obligat per poder avaluar els efectes del canvi climàtic en les congestes a mig i llarg termini. Per l'avaluació dels efectes del canvi climàtic, cal conèixer amb detall quina és la situació actual de les congestes andorranes. En aquest cas, cal avaluar el nombre de congestes que es troben a Andorra, on es troben i quins són els principals factors que expliquen la seva formació i conservació. Alguns d'aquests factors formadors de congestes no són pas modificables per la mà de l'ésser humà, com l'altitud o l'exposició, però d'altres en el context de canvi climàtic, com la temperatura o la precipitació, sí. Per tant, l'estudi de la relació entre el nombre de congestes i la seva extensió, i els factors físics que hi imperen ens apunten a inferir quins podrien ser els efectes del canvi climàtic en les congestes andorranes.

D'altra banda, la cartografia de les congestes ens permet detectar de manera totalment objectiva quin és l'habitat potencial de les congesteres i per tant serveix de base pels estudis florístics posteriors a aquesta cartografia. Si a més a més cada congesta cartografiada s'associa a una determinada combinació de variables físiques, ens permetrà conèixer la possible relació existent entre la congestera i la vegetació que s'hi fa.

Existeixen, però, certes hipòtesis que es plantegen en el present treball que no són fàcils d'abastar amb l'escala de treball d'una cartografia de congestes. Aquest és per exemple el cas de l'estudi fenològic, o de l'estudi de la variació intra-específica dels trets biològics d'algunes les espècies de les congesteres. En aquest cas s'ha treballat amb una escala de més detall triant unes determinades congestes i estudiant els efectes de la innivació i la temperatura.

Així, el principal objetiu ha estat poder quantificar i tipificar totes les congestes d'Andorra, així com la vegetació que hi viu tot relacionant-la amb les variables ambientals més importants. El segon gran objectiu ha estat poder avaluar els efectes dels factors físics que afecten la vegetació de congestera a escala més local. Amb tot plegat es pretén disposar d'un estat de la qüestió de les congestes i congesteres andorranes que permeti respondre a les preguntes ecològiques més importants de cara a avaluar impactes i possibles adaptacions de les congesteres al canvi climàtic als Pirineus.

Els objectius específics de cadascun dels capítols que formen part de la tesi es detallen a continuació:

I. Realitzar la cartografia de congestes d'Andorra i avaluar les variables físiques que de forma significativa contribueixen a la seva formació i conservació (**Capítol 2**).

II. Inventariar les espècies vegetals que es troben a les congesteres silicícoles andorranes, incloent'hi els briòfits (**Capítol 3**).

III. Identificar els grups de vegetació (segons les unitats sintaxonòmiques) que es troben a la congesteres andorranes, a fi d'avaluar-ne la diversitat i relacionar-los amb les variables ambientals (**Capítol 3**).

IV. Avaluar la diversitat funcional de les congesteres i relacionar-la amb les variables ambientals i amb els trets biològics de les plantes que hi viuen (**Capítol 4**).

V. Estudiar els efectes de la temperatura i del règim nival a escala local i relacionar-los amb la fenologia i variació intra-específica dels trets biològics de les plantes de congestera a fi d'avaluar les possibles adaptacions al canvi climàtic (**Capítol 5**).

VI. Disposar de la informació necessària per preveure quins podrien ser els efectes del canvi climàtic a les congestes i congesteres del Pirineu central (tots els capítols).

En el **capítol 2**, s'ha dut a terme la cartografia de congestes d'Andorra i l'anàlisi geogràfica per determinar les variables físiques que tenen un efecte en el nombre i l'extensió de les congestes andorranes. Mitjançant la digitalització de totes les ortofotografies d'estiu (juliol i agost) que es disposen d'Andorra (1948, 1972, 1995 i 2003), i de l'anàlisi SIG, s'ha pogut assolir la cartografia vectorial (www.sigma.ad). En aquest capítol també s'ha analitzat l'efecte de les situacions sinòptiques en la formació i conservació de les congestes, posteriorment validada amb dades climàtiques regionals.

El **capítol 3** es centra en l’estudi de la vegetació de congesteres des d’un punt de vista ecològic. S’ha deixat de banda l’aproximació al concepte de congestera des del punt de vista estrictament botànic, per avaluar florísticament aquelles congesteres prèviament detectades per la cartografia de congestes i que per tant, garanteixen com a mínim de disposar de nou mesos de coberta de neu. Aquest capítol ha permès poder disposar d’un catàleg o llistat de la majoria d’espècies de congestera andorranes de substrat silíci (que és el més abundant a Andorra), havent'hi inclòs els briòfits. A més, s’ha descrit i avaluat la relació de les espècies i els agrupaments vegetals amb les variables ambientals. Això ha permès respondre a les preguntes següents: quins són els agrupaments vegetals que predominen a les congesteres andorranes? L'agrupament vegetal que caracteriza la classe *Salicetea herbaceae* es troba en les congesteres més innivades? Com es relaciona la temperatura i la coberta de neu amb els agrupaments vegetals? Quins podrien ser els efectes d’un augment de temperatura i d’una reducció de la coberta de neu sobre la riquesa i la presencia de les espècies típiques de congestera?

En el **capítol 4**, s’ha fet una recopilació dels trets biològics de les plantes més freqüents i abundants a les congesteres andorranes a fi d’avaluar quins són els que hi predominen. A més, aquests trets s’han relacionat amb les variables ambientals per veure com aquestes condicionen les estratègies de les plantes. Un dels altres objectius destacats d’aquest capítol és la determinació de la diversitat funcional de les congesteres. La diversitat funcional és defineix com la diversitat dels trets biològics de les plantes en tant que influencia l’estructura de la comunitat vegetal i les funcions de l’ecosistema (Schleuter et al. 2010). Ens permet entendre i preveure l’estabilitat d’una comunitat i les respostes dels hàbitats als canvis ambientals, com respostes en la productivitat (Petchey and Gaston 2006) o en la resiliència de l’hàbitat després del canvis o pertorbacions (Bellwood and Hoey 2004). Recentment diversos autors plantegen la utilització de tres índexs complementaris de diversitat funcional (Mason et al. 2005, Mouchet et al. 2010, Villéger 2008) els quals han de permetre obtenir una molt bona aproximació als efectes de la diversitat de trets biològics als processos i a les respostes dels ecosistemes. Aquest índexs són la riquesa funcional, l’equitat funcional i la divergència funcional. La utilització d’aquests índexs juntament amb el benefici de mètodes complementaris (com l’avaluació de la diversitat filogenètica) han de permetre entendre com la biodiversitat interacciona amb els factors ambientals de l’hàbitat de congestera. A més obren la possibilitat de ser utilitzats com a indicadors de la dinàmica funcional de les comunitats i dels hàbitats. Però atès que són índexs definits recentment, i per tant no sempre testats amb dades reals extretes del camp, cal que siguin avaluats en diversos hàbitats. Per tant això dóna un valor afegit a l'anàlisi realitzada a fi de contribuir a testar aquests índexs indicadors. Finalment, en aquest capítol també s'han mesurat i estudiat alguns trets de les espècies més freqüents per avaluar els efectes dels factors a petita escala (lloc i data de la fosa de la neu) a la plasticitat intraespecífica. La plasticitat intraespecífica pot garantir l'adaptació a les noves condicions ambientals com a resposta al canvi climàtic.

En el **capítol 5**, s'ha avaluat l'efecte de la data de la fosa de la neu i de la temperatura, i també dels factors locals de petita escala, com la microtopografia i l'origen de la neu respecte la fenologia i la riquesa de les espècies. Concretament s'ha avaluat la durada de les diferents fenofases en funció dels factors ambientals locals. S'ha volgut respondre a preguntes com ara: poden els factors locals, com la microtopografia, afectar la data de la fosa de la neu i les condicions microclimàtiques? Els factors locals afecten la fenologia de les plantes? Afecten diferent a les diferents fenofases (finalització del creixement vegetatiu i floració)? La fenologia de les diferents espècies respon de la mateixa manera a la data de la fosa de la neu?

Els capítols centrals (2, 3 4 i 5) es presenten en format d'article científic, fet que comporta algunes redundàncies en les introduccions dels diferents capítols. Aquests capítols centrals han estat íntegrament escrits en anglès. El capítol 1 (corresponent a la introducció general, i a la discussió i les conclusions generals) però, es presenta en català. Abans del capítol 1 es mostren resums de la memòria de la tesi doctoral en català, castellà i anglès.

DISCUSSIÓ GENERAL I CONCLUSIONS

La cartografia de congestes d’Andorra

Aquest capítol contribueix a millorar el coneixement de les congestes pirinenques i representa l’estat de la qüestió de l’actual distribució de les congestes d’Andorra presentant una cartografia l’accés lliure (Sistema d’Informació Geogràfica i Medioambinetal d’Andorra a www.sigma.ad). L’interès de realitzar una primera cartografia de les congestes d’Andorra (Pirineu central) és doble. Primer de tot posa les bases per tal d’utilitzar les congestes com a indicadors de canvi climàtic a mig i llarg termini. En segon lloc serveix per localitzar i descriure uns espais indispensables per l’assentament i desenvolupament d’un tipus de vegetació exclusiu: les comunitats vegetals de congestera.

En la present Tesi Doctoral s’han identificat 2.520 congestes que ocupen una extensió de 169 ha dels Pirineus andorrans. La presencia de congestes a Andorra està determinada significativament per factors estructurals, com l’exposició i l’altitud, i per factors temporals (climatologia). L’origen de la neu, considerat un factor mixte entre l’estructural i el temporal, també s’ha detectat com a determinant en la formació de les congestes. Així els factors que han estat interpretats com els que afavoreixen millor la formació i conservació de les congestes han estat:

- Exposició: vessant d’obaga.
- Origen de la neu: acumulació per les allaus.
- Altitud: congestes localitzades entre els 2.500 i 2.600 m.
- Climatologia: anys en els quals el període d’acumulació (gener-abril) ha estat fred i humit en comparació amb el període climàtic de referència.

Els factors temporals, i no pas els estructurals, són els que tindran un efecte futur sobre el nombre, extensió i distribució de les congestes d’Andorra i per tant, els que es veuran afectats pel canvi climàtic. En aquest sentit, la precipitació i la temperatura del primer trimestre de l’any seran factors determinants pel futur de les congestes.

La vegetació de les congesteres d'Andorra

La composició florística i el recobriment de les espècies són variables que ens caracteritzen la vegetació d'un indret. Aquest és un primer pas ineludible per conèixer la vegetació de les congesteres d'Andorra: la realització d'inventaris florístics en una mostra representativa de les congesteres andorranes. Com bé s'ha esmentat en el capítol introductori, en la present Tesi Doctoral, s'ha emprat la definició de congestera com l'hàbitat format per l'efecte de la congesta, independentment de les unitats sintaxonòmiques que s'hi puguin veure representades. Aquesta aproximació permet la possibilitat de trobar altres unitats sintaxonòmiques diferents a la típica de les congesteres: la classe *Salicetea herbaceae*. Deixant de banda la descripció *sensu stricto* de la vegetació, l'estudi de la relació que s'estableix entre aquesta i les variables ambientals de les congesteres, permet tenir una visió general de quin espai ocupen els agrupaments vegetals de les congesteres en l'espai multidimensional de condicions ambientals.

Les principals conclusions d'aquest **capítol 2** es detallen a continuació.

- S'han inventariat fins a 85 plantes vasculars; 31 característiques de les pastures d'alta muntanya i 21 característiques de la classe *Salicetea herbaceae*. Per tant pel que fa a la riquesa total, les espècies més representades a les congesteres d'Andorra no pertanyen a la vegetació considerada com a característica o típica de la flora de congestera (pertanyent a la clase *Salicetea herbaceae*). Tot i això les espècies més frequents (*Gnaphalium supinum*, *Poa alpina*, *Carex pyrenaica*, *Mucizonia sedoides*, *Murbeckiella pinnafitica* i *Nardus stricta*) a excepció de *M. pinnafitida* i de *N. stricta*, pertanyen totes a la classe *Salicetea herbaceae*. Les espècies més abundants (*N. stricta*, *Gnaphallium supinum* i *Agrostis rupestris*), a excepció de *G. supinum*, pertanyen a les pastures d'alta muntanya.

- S'han identificat 16 briòfits, 3 són hepàtiques i 13 són molses. D'aquests, *Bryum elegans* i *Sciuro-hypnum glaciale* són noves espècies detectades per primera vegada a Andorra. *Polytrichum sexangulare* coindideix en ser el briòfit més freqüent i abundant. Aquestes dades contribueixen a millorar l'estat del coneixement dels briòfits alpins d'Andorra.

- Les congesteres situades a l'exposició de solana i que presenten unes condicions mitjanes de coberta de neu, règim tèrmic i altitud són les que presenten valors més alts de riquesa. En aquestes condicions és on predominen les espècies típiques de congestera (classe *Salicetea herbaceae*).

- Les congesteres que presenten les temperatures mitjanes més elevades, que es troben a baixa altitud, i a més a més estan situades damunt dels sòls amb més contingut de matèria orgànica, presenten una elevada proporció d'espècies del grup de vegetació de les pastures i dels matollars d'alta muntanya.

- Les congesteres situades en les condicions més rigoroses (elevada altitud, elevada durada de la coberta de neu i sòls amb nul·la o poca matèria orgànica, hi predominen les espècies de roquissars de l'estatge alpí i de prats humits.

- No s'ha detectat correlació entre l'altitud i la riquesa, a diferència del que succeeix en altres hàbitats alpins del Pirineu (Grau et al. 2011, Villar and Benito 2003, Gómez et al. 2003). Es creu que les condicions físiques especials de les congesteres, com l'efecte de la durada coberta de neu, fa que la dinàmica de la davallada del nombre d'espècies en altitud que es dóna en hàbitats adjacents, quedi esmorteïda.

- Si s'esdevenen les condicions de canvi climàtic esperades al Pirineu, i per tant la neu es retira abans, les congesteres més afectades seran les d'altitud baixa i mitjana (concretament per sota dels 2.454 m, que correspon a l'altitud mitjana de les congestes d'Andorra). Les plantes de la classe *Salicetea herbaceae* tindran un espai potencial a més altitud per poder-se refugiar. Tot i això, la colonització i adaptació de les espècies en aquestes congesteres dependrà de la disponibilitat de l'hàbitat, en particular de la presència de sòl orgànic i de les relacions competitives entre les espècies. Així mateix les espècies del grup de vegetació de les pastures i dels matollars d'alta muntanya podran colonitzar congestes més elevades, partint de la base que ara predominen en les congesteres de menys altitud.

Els trets biològics i la diversitat funcional de les plantes de congestera d'Andorra

La majoria de comunitats vegetals segueixen gradients ambientals, de la mateixa manera que ocorre en hábitats de congesta (Lluent 2007). Això determina que els trets funcionals de les comunitats estiguin determinats per la interacció entre espècies i per la relació d'aquests amb el medi. Aquest tipus de relació (comunitat-medi) és molt més senzill d'estudiar si es tenen en compte els gradients ambientals (McGill et al. 2006) i per tant els factors ambientals específics o locals de la congestera. La resposta de les plantes al gradient ambiental ens pot servir per preveure els canvis i les possibles adaptacions de les comunitats de congestera. En aquest sentit, la caracterització dels trets funcionals de les plantes de congestera ens ha permès estudiar les relacions entre aquests i el medi físic, i conèixer la diversitat funcional. Tant l'estudi de la diversitat funcional, com la dels trets de les plantes lligats als factors ambientals ens han servit, en aquest **capítol 4,** per preveure l'estructura funcional de l'hàbitat de congestera i per poder detectar les respostes als factors locals o específics d'algunes de les espècies més comunes de les congesteres andorranes.

Les principals conclusions han estat:

- La majoria de les plantes de les congesteres d'Andorra són camèfits, presenten fulles basals o semi basals i formen clons damunt del nivell del sòl La pol·linització per insectes és la més extensa, seguida per la pol·linització anemòfila.

- Els camèfits i les espècies amb major àrea específica de fulla (SLA) es troben fortament associats amb les congesteres de temperatures més elevades, de menor duració de coberta de neu i amb presència de sòls orgànics; mentre que els hemicriptofits no graminoids i les plantes amb clonació damunt del nivell del sòl predominen en els ambients contraris (baixes temperatures, durada de la coberta de neu superior i sòls amb poca o sense presència de matèria orgànica).

- Els factors locals de les congestes (especialment la data de la fusió de la neu) afecten significativament a la variació intra-específica dels trets funcionals de *Sibbaldia procumbens*, *Poa alpina* i *Gnaphalium supinum*; mentre que *Cardamine alpina* i *Mucizonia sedoides* no presenten plasticitat adaptativa a la data de la fusió de la neu. Per tant, es demostra que només algunes espècies responen canviant els seus trets funcionals dependent de la data de la fosa de la neu.

- En general les espècies que presenten plasticitat en els seus trets funcionals, coincideixen en presentar valors més alts en el nombre d'inflorescències i de ramets florits en els llocs on la data de la fosa de la neu és més tardana respecte els llocs on la fosa de neu és més primerenca. Per contra, l'alçada de les plantes, és menor en els llocs on la fosa de la neu és més tardana

- Els canvis intra-específics en els trets de les plantes poden afectar a la diversitat funcional. Certament, depenent del lloc on viuen les espècies, algunes disposen de la capacitat d'adaptar els seus trets funcionals o bé respondre canviant-los.. En un futur seria d'interès quantificar la diversitat en la plasticitat de les espècies i incloure-la en les anàlisis de la diversitat funcional

- Els valors elevats de divergència funcional (FDiv), que indiquen una forta dissimilaritat entre els trets funcionals de les espècies, s'han trobat associats amb les congesteres de condicions abiòtiques menys estressants. Elevats valors d'área foliar específica i d'alçada de les plantes es troben positivament correlacionats amb elevats valors de FDiv, indicant possiblement una resposta de les plantes per competir per la llum. Les plantes característiques de les pastures d'alta muntanya són les predominants en aquestes congesteres.

- Els valors elevats d'equitat funcional (FEve), que representen la regularitat en la representació de l'abundància dels trets funcionals, presenten els valors més alts en les congesteres on s'hi donen les condicions abiòtiques més estressants (període vegetatiu més curt degut a la durada de la neu, temperatures més baixes, i sòls esquelètics sense pràcticament matèria orgànica). En aquestes congesteres, la correlació inversa entre FDiv i FEve ens indica que possiblement s'hi dòna un filtratge de la FDiv que es tradueix en una disminució de la biomassa aèria. Les plantes de la classe *Salicetea herbacea* dominen en aquestes condicions.

- Els resultat de l'aplicació dels tres índex (FRic, FEve i FDiv), és similar a la d'altres estudis (Mason et al. 2007, 2008), coincidint a destacar que FEve revela una pressió elevada dels factors ambientals, i que la FDiv apunta a un creixement de les interaccions competitives entre espècies.

- La diversitat de factors ambientals presents a les congesteres andorranes incrementa la diversitat funcional de les comunitats de plantes de congestera i crea un ús diferent de l'espai funcional.

- L'ús dels tres índexs, ha resultat ser una bona eina per poder comprendre les relacions existents entre la biodiversitat, l'efecte dels factors ambientals i les respostes de l'hàbitat de congestera.

L'efecte dels factors locals sobre la riquesa i la fenologia de les plantes de congestera d'Andorra

La data de la fosa de la neu és un dels factors més importants que controla la fenologia de les plantes (Galen and Stanon 1995, Körner 2003, Hüelber et al. 2006, Totland and Alatalo 2002). Però la temperatura també té una influència cabdal durant el període de creixement (Kudo and Hirao 2006, Molau et al. 2005, Hüelber et al. 2006, Körner 2003), que resulta ser molt curt en el cas de les congesteres. De totes maneres hi ha una conjunt d'altres factors, difícils de mesurar, que depenen estrictament de l'ambient microtopogràfic, i que també poden incidir (augmentant o disminuint) l'efecte de la data de la fosa de la neu i la temperatura del període de creixement.

Les principals conclusions d'aquest **capítol 5** han estat:

- La durada del període lliure de neu és de mitjana de 77,5 dies als llocs de fosa primerenca i de 47,7 dies en els llocs de fosa tardana dins el gradient de fusió de cada congestera. La temperatura acumulada en els llocs de fosa primerenca és significativament inferior als llocs on la fosa és tardana, arribant a ser de fins 744 ºC.

- Els valors més alts, tant de riquesa florística com de recobriment herbaci, s'assoleixen a les isoclines de la congesta on la neu es fon abans. Aquests llocs presenten una dominància de gramínies (*Poa alpina*, *Agrostis rupestris* i *Nardus stricta)* respecte a les altres famílies botàniques. En canvi en les isoclines de fosa tardana hi dominen els briòfits i les espècies de *Salicetea herbaceae*. Per tant el gradient de fosa de la neu, afavoreix una divergència en els patrons de diversitat que contribueix a l'augment de la diversitat total de la congestera.

- La data de la fosa de la neu afecta significativament la fenologia (floració i creixement vegetatiu) de les plantes de congestera. Encara que la temperatura acumulada sigui més elevada en les isoclines de fosa primerenca, tal com s'ha demostrat en altres estudis (Wipf 2010, Hüelber 2006 et al., Galen and Stanton 1995), la velocitat de creixement vegetatiu és superior en les isoclines de fosa tardana. Per contra el nombre de dies transcorreguts des la fosa de la neu fins assolir la floració no presenta diferències significatives entre les isoclines en el gradient de fosa de la neu. En canvi el temps entre la finalització del creixement vegetatiu i la floració s'allarga en les isoclines de fosa tardana de la neu, segurament perquè les temperatures acumulades són molt baixes. És en aquestes isoclines on només en el 50% de les parcel·les s'assoleix la floració i on el nombre d'espècies florides és menor. En aquest sentit, si tal com es preveu, el canvi climàtic allarga el període lliure de neu a les congestes (Schöb et al. 2009, Nagy 2006), l'èxit reproductiu de les plantes es pot veure afectat positivament en les congesteres on la neu es retira més tard.

- La variació climàtica interanual té influència significativa sobre la fenologia de les plantes. Però cal afegir que els factors locals (microtopogràfics) afecten la data de la fosa de la neu i per tant també tenen una importància destacada en la fenologia de les comunitats de congestera.

- La fenologia de les plantes es veu afectada de forma diferent en funció de l'espècie, allargant o escurçant les diferents fenofases, possiblement degut a les adaptacions fenològiques. *Poa alpina* no ha demostrat cap resposta fenològica a les diferents dates de fosa de la neu, contràriament a *Mucizonia sedoides* i *Sedum alpestre*. Aquestes dues espècies tenen capacitat d'escurçar el temps per assolir la floració, fet que significa que tenen més probabilitats d'aconseguir llavors madures i disposar d'un avantatge competitiu en els llocs on la neu es fon més tard. Això significa que l'avantatge competitiu que tenen algunes espècies depèn estretament dels factors locals, com la data de la fosa de la neu, i no només de les variables climàtiques globals.

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CAPÍTOL 2: First cartography and shifts of the Andorran Pyrenean snowdrifts

First cartography and shifts of the Andorran Pyrenean snowdrifts

ABSTRACT

Global warming is affecting the Pyrenees as glaciers recede, snowdrifts disappear, and the extent of snow cover decreases. In the Northern Hemisphere, snow cover is expected to decrease further in this century. If the number of and area covered by snowdrifts diminishes in the near future, ecological conditions in these environments will change, which will have an impact on exclusive and endemic species. This study sought to determine the status of snowdrifts and the physical factors that influence their formation and persistence as a means of identifying the changes that might occur in response to global warming. Maps created and the snowdrifts in the Andorran Pyrenees in 1948, 1972, 1995, and 2003 were characterized based on aerial photographs, which were used to examine the effects of the annual climatology and the orography (exposure and elevation) on the number, size, and accumulation of snow in the snowdrifts in Andorra. Most of the 2.520 snowdrifts that were identified had been formed by snow avalanches and were located in sheltered spots or on level terrain. Snowdrifts were most common and extensive in the coldest and most humid years. Temperature and precipitation in the first third of the year appeared to be the most important factors influencing the formation of snowdrifts in the Andorran Pyrenees.

KEYWORDS: snowdrifts, snow cover, climate change, global warming, Andorra, Pyrenees

INTRODUCTION

High mountain habitats and their vegetation are highly influenced by temperature, wind, light, snow cover and soil (Bliss 1960). All these factors are affected directly by topography (relief, exposure, elevation) and climate (Nagy and Grabherr 2009, Körner 2003), and generate a great number of different environments and particular communities. Snowdrift communities, composed by species of *Salicetea herbacea* Class, constitute one of them (Schöb et al. 2008, Hassol 2004, Huelber et al. 2006, Grabherr et al. 1995, Grabherr 2003).

A snowdrift is an accumulation of snow that remains in a depression or other areas of the mountain and covers the ground for all or part of the year (VVAA, 2002). At landscape scales, the action of wind, an avalanche, or variations in slope gradient contribute to the formation of snowdrifts in lee-side of ridges or in concavities (Venn and Morgan 2007). The snow does not melt readily because it is located in a sheltered area and tends to occur in the same places, annually, because the causes of snow accumulation, typically, are consistent (e.g., orography, prevailing winds) (Billings and Bliss 1960; Williams 1987; Körner 1999; Hiemstra et al. 2002).

Snowdrift vegetation depends strongly on snow cover so plants living there are adapted to conclude their lifespan in two or three months, sometimes in weeks (Björk and Molau 2007; Bliss 1960). Snow cover provides a protection against low temperatures and frost (Bell and Bliss 1979; Mark and Dickinson 1997; Inouye et al. 2002). Therefore snow cover is a very determinant factor for the ecology of snowdrifts. These strong conditionings lead to the evolution of highly specialized species and tend to present endemism (Kudo 1991; Körner 2003; Dullinger et al. 2000). As a consequence, snowdrift habitats are endangered by the effects of increased global warming, which include reductions in the duration and the spatial extent of snow cover (Dye 2002, Beniston et al. 2003, Paul et al. 2004, Pauli et al. 2007). Global warming is expected to influence significantly snowdrift habitats, and changes in composition and phenology are expected (Schöb et al. 2008, Hassol 2004, Huelber et al. 2006, Nagy 2006). Some studies have observed the invasion of snowdrifts by species, mainly grasses, from neighbouring communities as a consequence of the reduction of the snow cover (Grabherr et al. 1995, Grabherr 2003, Schöb et al. 2009) affecting the current flora composition and deriving in a decline of snowdrift typical species.

The presence of snowdrifts depends on the snowiness and therefore on the latitude and atmospheric circulation. Atmospheric circulation contributes narrowly to the relationship between air temperature and precipitation. If the increase in temperatures forecasted by the AEMET (Agencia Estatal Española de Meteorología 2008) and the IPCC (2007) occur, it might lead to a reduction or to disappearance of snowdrifts. Between 1990 and 2100, the average global temperature is expected to rise between 1.4 ºC and 5.8 ºC (IPCC 2007). In the Pyrenees, one of the southern snowed mountains in Europe, the average annual temperature is expected to rise by 2.5 to 5 ºC by 2100 (AEMET 2008). In many regions of the world, glaciers are receding (Oerlemans, 2005, Dyurgerov 2003, Meier et al. 2003) and snowdrifts are disappearing (Muñoz et al. 2007). In the Northern Hemisphere, the extent of snow cover is expected to decrease further in this century (EEA 2004), which poses a threat to habitats and the species that occur there (Theurillat and Guisan 2001, Grabherr 2003, Huelber et al. 2006, Schöb et al. 2009, Björk and Molau 2007). In Andorra, average air temperatures have increased significantly (Esteban et al. 2009), which might affect the persistence of the snow cover. This study aimed to conduct an inventory-cartography and to quantify the state of snowdrifts in the Andorran Pyrenees and the changes that have occurred in the last half-Century, and to identify the main physical variables influencing their formation and attributes. The study addressed the following questions: 1) How many snowdrifts there are and which is their extension in Andorra? 2) What are the topographical patterns of the snowdrifts in the Andorran Pyrenees? 3) Would climate change impact more on snowdrift located in south-facing slopes? 4) Are there any demonstrable relationships between climate and the number and extension of snowdrifts? If yes, what are the relations?

METHODS

Study area

The study focused on the region above 2.000 m in Andorra, a small country (area = 468 km^2) in the center of the Pyrenees massif, between France and Spain, where the elevation ranges between 837 m and 2.942 m (Figure 1). The country is within a region that has a Mediterranean mountain climate, but continentality, elevation, and a south-facing aspect within the Pyrenees contribute to significant variation in temperature and precipitation spatially and temporally. The most abundant geological materials are slate, clay, and conglomerates from the Cambro-Ordovician period. Siliceous bedrock is predominant in Andorran mountains. Above 2.000 m, the most common habitats are pastures, marshes, snowdrifts, and boulder fields.

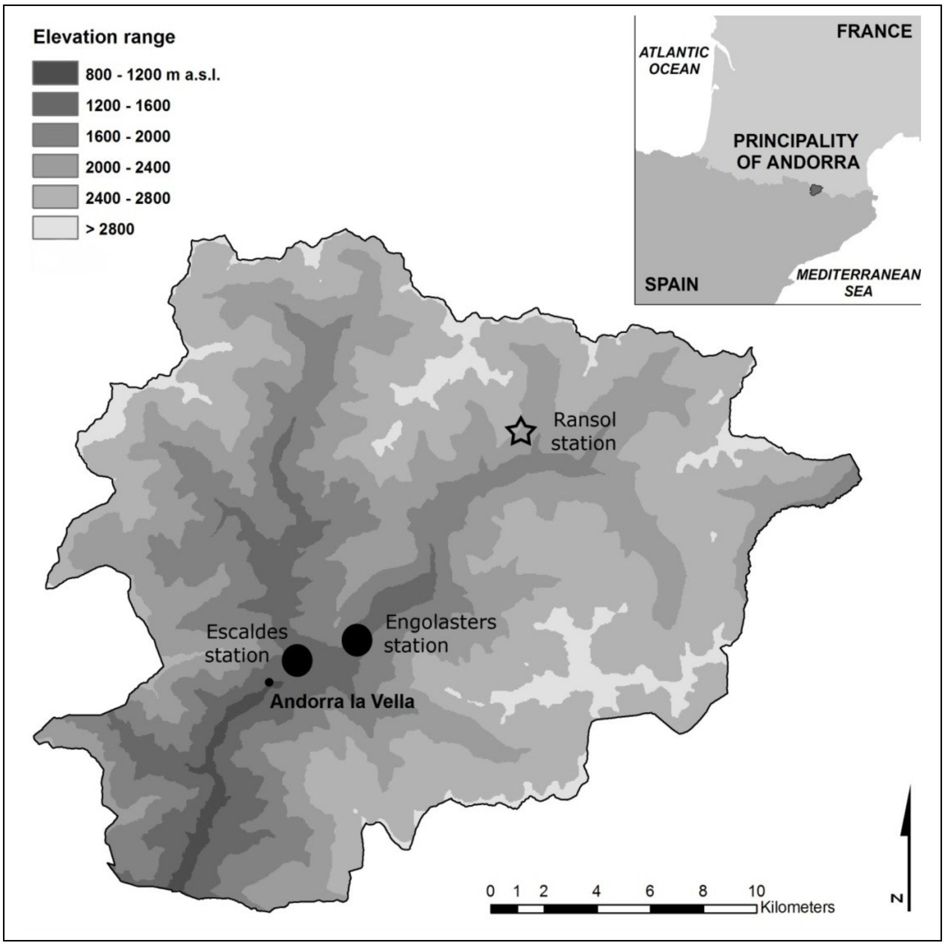

Figure 1. Location of Andorra in the Pyrenees. Star symbol indicates the meteorological station used in the analysis (Ransol station). Black dots indicate the two other historical meteorological stations of Andorra.

Inventory and cartography of snowdrifts

Snowdrifts were identified in aerial photographs taken in the summers of 1948, 1972, 1995, and 2003 (in 1948 and 1995, in late August; in 1972 and 2003 in July). The quality of the photographs differed among years; therefore, the aerial photographs were analyzed and digitalized using several methods. The snowdrifts in the aerial photographs taken in 1948 (black and white colour) were quantified using the traditional stereoscopic technique; initially, using the printed version of the photographs, which were later digitalized at a 1:5.000 scale. Aerial photographs were used to produce the map of snowdrifts in 1972. Orthophotographs were used to produce the maps for 1995 and 2003, which were digitalized at a scale of 1:2.000.

To quantify the number, size, and distribution of the snowdrifts in Andorra, all of the digitalized maps of the years included in the study were combined into a single map. This also allowed to compare the number and distribution of snowdrifts among years.

The origin of the snow was identified using aerial photographs and orthophotographs with expert criteria classifying snowdrifts in six categories (table 1). The criterion was based on the position of the snow patches on the relieve visualizing the aerial photographs and orthophotographs with stereoscopy techniques. Stereoscopy techniques, with 3D perspective, allow detecting exactly the place where snow patch is in the relief (runout zone of an avalanche, concave form, near ridges, etc.) according to the definition and criteria used in table 1. Elevation was obtained from a 30-m resolution DEM and exposure was derived from it. The Arcgis 9.3 software was used for all if the digitalization and analysis (ESRI, Redland 2006).

Table 1. Categories for the origin of the snow in snowdrifts in the Andorran Pyrenees. Definition and criteria used.

Categories	Definition and criteria used
Avalanche	Snow accumulated in the runout zone of an avalanche. Identified by avalanche paths on the ground and in the runout zones. In the first case, the accumulations tend to be elongate and in the second, the form often is conical.
Wind	Snow accumulated mainly from snow transported by the wind. They are located in high areas, near ridges, leeward of dominating winds, although this is not always strictly the case because it depends on the wind episodes in each season. Snow accumulates when an obstacle (ridge or rocky massif) reduces wind velocity and, consequently, the capacity to transport snow.
Orography	Snow that accumulates because the terrain is favourable to accumulation. In most cases, the most receptive relief forms are concave or slightly flat.
Purge	Snow of small magnitude accumulated in the track zone. Ii is an avalanche of very small dimensions (less than half of the maximum length of an avalanche).
Wind-purge	Snow accumulated through the transport of snow and avalanche accumulation.
Shade	Snow that accumulates in shade-dominated location and where melting is slower than in adjacent zone. Individualized according to orientation of sheltered slope.

Climatological and geospatial data

To describe the main climate properties and analyse their influence over the snowdrifts in each of the four years studied, we used the NCEP-NCAR gridded reanalysis (2,5*2,5º) data provided by the National Oceanic & Atmospheric Administration Research (Kalnay et al. 1996). For the purposes of the analyses, the period considered of snow accumulation was from January through April and the snow-melting period was determined for May and June (Figure 2). The following maps of the synoptic sector over the European continent were obtained:

- Sea level pressure anomalies in the months of January through April (accumulation period)
- Air temperature anomalies at 700 mb in the months of January through April (accumulation period)
- The air temperature anomaly at 700 mb in May and June (snow-melting period)

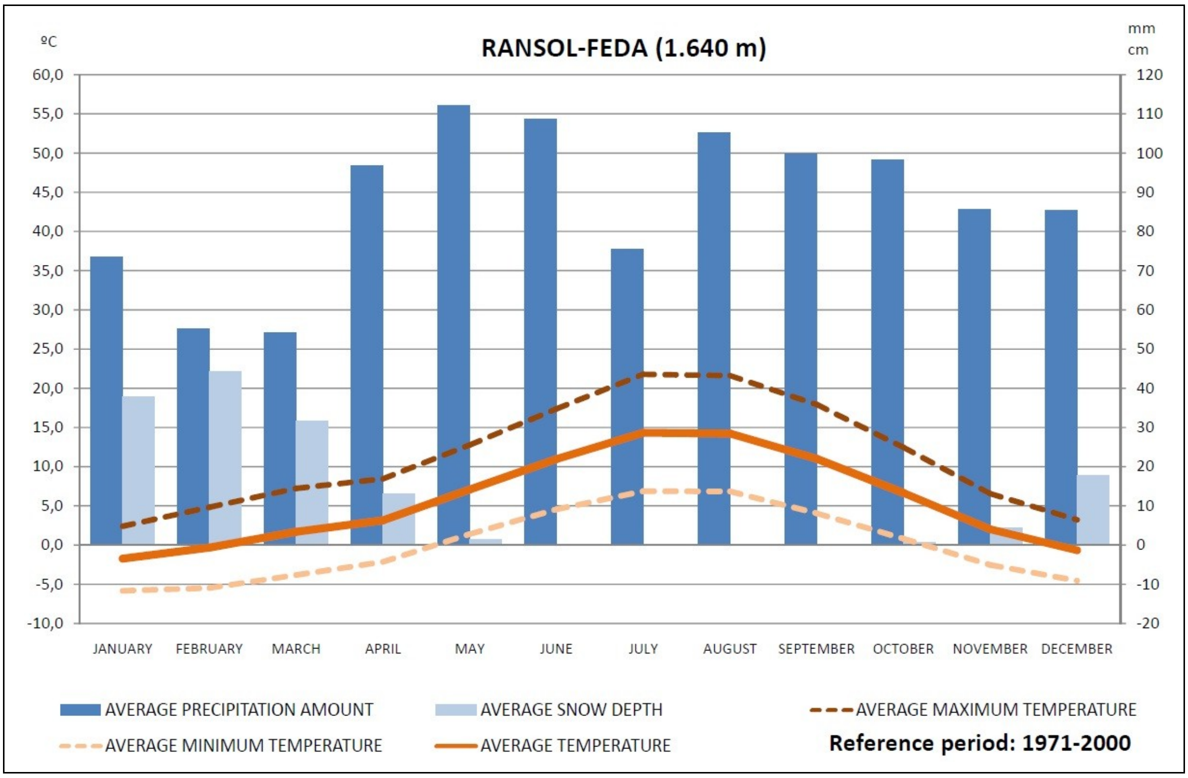

Figure 2. Climograph for Meteorological station of Ransol-FEDA calculated for the 1971-2000 reference period.

Note that NCEP-NCAR reanalysis data used do not include precipitation information. This is because the data derived from this reanalysis, the availability of data over the mountain regions, and the influence of orography can vary substantially the accuracy of the fields obtained over areas as the Pyrenees. To solve this limitation, we also used instrumental weather observations in Andorra provided by FEDA (Andorran Electricity Suppliers) at www.feda.ad and revised by Esteban et al (2009). The average temperature and precipitation values used were calculated using the Ransol meteorological station data, one of the three long term observatories existing in Andorra that have recorded weather data since 1934 (Ransol, Engolasters and Escaldes). The precipitation measures include snow melt. The data from Ransol station was used because it is the one situated on the most similar physical conditions to high mountain Andorran areas (where snowdrifts occurred), and also the anomalies were calculated using 1971-90 as reference period. However, the annual average temperature and precipitation of the two others meteorological stations of Andorra (Escaldes and Engolasters) were used to compare with the data from Ransol station. Escaldes is situated at 1.140 m (42º 31’; 1º 32’), Engolasters at an elevation of 1.635 m (42º 31º; 1º34’) and Ransol of an elevation of 1.640 m (42º 34’; 1º 39’).

Data analysis

The effects of explanatory variables (elevation, snow origin, exposure and year) of the size (area) of the snowdrifts were evaluated using a Generalized Linear Mixed Model (GLMM) procedure. Snow origin, exposure and year were considered fixed effects. To test significant differences of area values between the explanatory variables, various Tukey-HSD tests were performed. To test for normality, the data were subjected to a Kolmogorov-Smirnov Test and plotted thoughts the normal probability and the histogram plot. To test for homocedasticity and in order to validate the Model (GLMM) the data were analyzed with the stundentized residuals and the predicted values of the GLMM. In order to reach the normality of the data, these were transformed using a logarithmic distribution. All analysis reported here were conducted with the SAS statistical package (SAS 9.0, SAS Institute, 2003).

RESULTS

Geophysical attributes

Number and size

In the four years included in the study, we identified 2.520 snowdrifts, which covered 169 ha (Map available at www.sigma.ad). In the digitized dataset, 1972 had the highest number of snowdrifts (1.373), which covered the largest area (107 ha) (Table 2). In 2003 there were 963 snowdrifts, which covered 55 Ha. In 1995 and 1948, only 4,1 ha and 3,3 ha were covered by snowdrifts.

Table 2. Number and size of the snowdrifts in the Andorran Pyrenees in the years studied.

Year	Number	Size (ha)
1948	38	3,34
1972	1373	107,3
1995	146	4,12
2003	963	54,56

Exposure (F=15,51; p<0,001) had a highly significant effect on the size of snowdrifts. The largest snowdrifts (mean = 735 m^2) occurred on north-facing slopes. On flat terrain and southerly exposures, the average sizes of snowdrifts were 406 m^2 and 452 m^2 respectively. The extent of the snow cover differed significantly between northerly exposures to flat areas and from north to south, but it was not significantly different between flat areas and southerly exposures. Year (F=29,97; p<0,001) had a significant effect. The smallest area covered by snow was measured in 1995 (282 m^2) and the highest in 2003 (879 m^2). Snow origin (F=2,82; p<0,009) also have a significant effect on the variation in the size of snowdrifts in Andorra. The highest snowdrift areas were found in the purge snow origin category (941 m^2) and the smallest in the wind category (272 m^2). Significant differences in the area of the snowdrifts were only between avalanche and orography snow origin. Elevation (F=0,69; p<0,15) did not have a significant effect on the variation in the size of snowdrifts in Andorra.

Exposure

In each year included in the study, the highest number of snowdrifts occurred on north-facing slopes and in flat areas (Figure 3a). In 1972 and 1995, the greatest number of snowdrifts occurred in areas without significant relief and, therefore, without a defined exposure. In 1972, 553 out of 1.366 and, in 1995, 172 out of 335 snowdrifts were found in flat areas. In 1948 and 2003, however, snowdrifts were concentrated in areas that had northerly exposures. In addition, in all years, areas that had southerly exposures had the fewest snowdrifts.

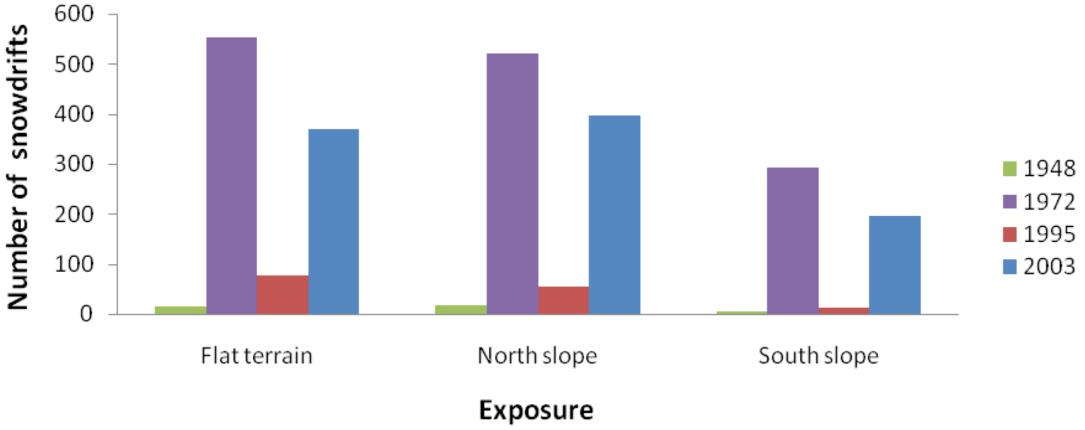

Figure 3a: Comparison of number of snowdrifts for the years 1948, 1995, 1972 and 2003 depending on the exposure.

Elevation

In the four years included in the study, the average elevation of the snowdrifts in Andorra was 2.454 m, the highest snowdrift occurred at 2.650 m (the Estany Negre Snowdrift), and the lowest occurred at 2.280 m (the Juglar Snowdrift). The largest numbers of snowdrifts occurred between 2.500 m and 2.600 m (Figure 3b).

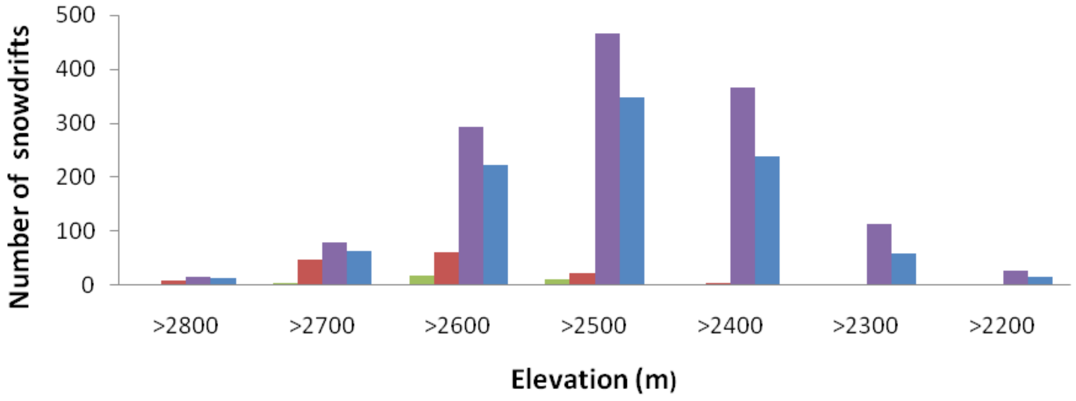

Figure 3b. Comparison of number of snowdrifts in 1948, 1995, 1972 and 2003 according to elevation (m).

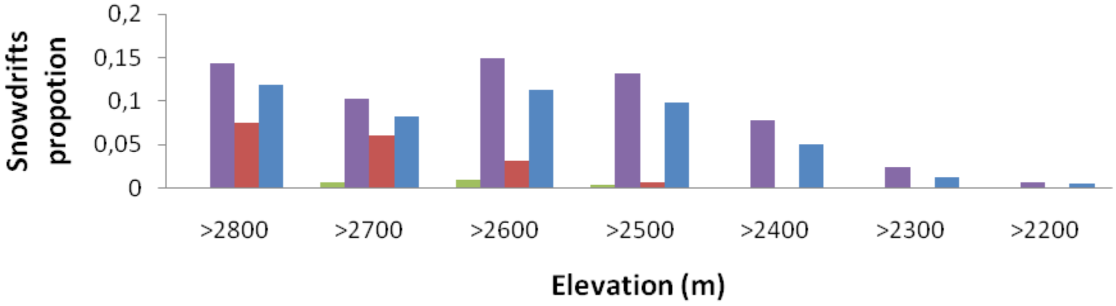

Figure 3c. comparison of the proportion of snowdrifts in 1948, 1995, 1972 and 2003 according to elevation (m) corrected by projected area of different elevation interval.

Origin of the snow in snowdrifts

Avalanches produced 62% of the snow cover and, thus, they were the main factor in the accumulation of snow in snowdrifts in Andorra (Figure 7 and Table 3). Orography, purge, and wind explained 20%, 8%, and 5% of the snowdrifts, respectively. Other potential factors (wind-purge and shade) were not so important in the formation of snowdrifts.

Table 3. Number and percentage (%) of the snowdrifts in the Andorran Pyrenees classified in the snow origin categories.

Snow origin categories	Number	%
Wind-purge	105	4,2
Avalanche	1550	61,8
Wind	129	5,1
Orography	507	20,2
Purge	186	7,6
Shade	33	1,3

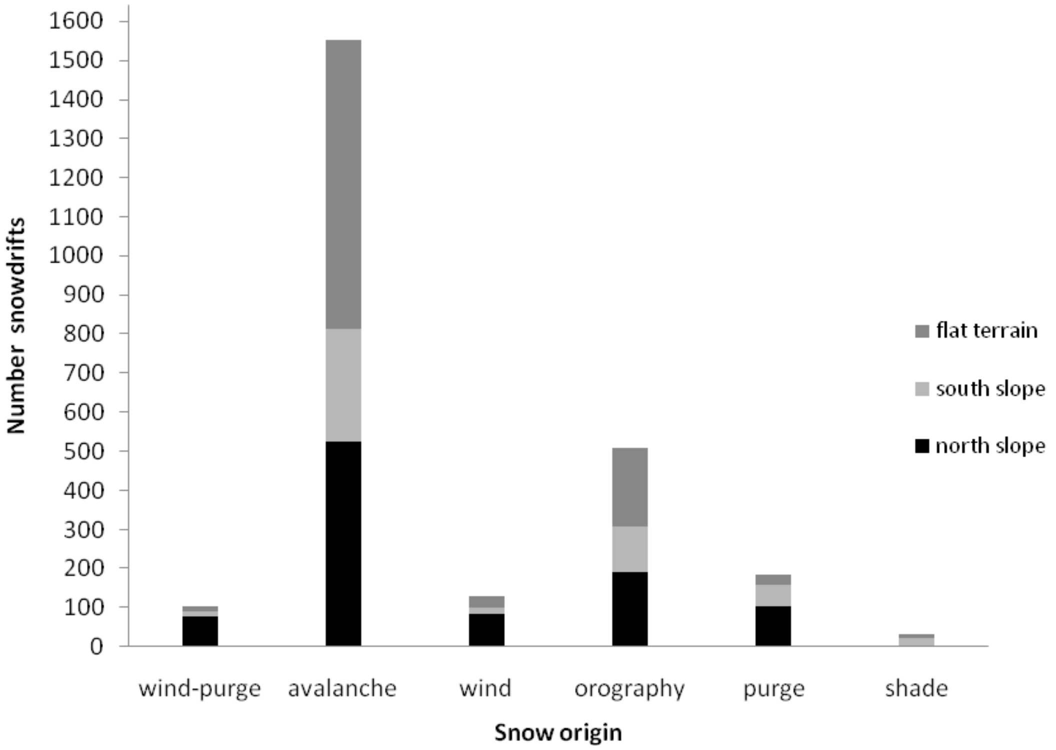

Figure 7. Origin of the snowdrifts snow in relation to exposure.

Climate, snow accumulation and snowmelt variability

The comparison of the annual average temperature and precipitation of the three meteorological stations of Andorra indicated a higher mountain climate in Ransol than in the other two stations. Ransol temperature data was lower and precipitation data was higher than the others (Raso 1999).

Based on the data obtained from the NCEP-NCAR reanalysis (Figure 4) and from the Ransol weather station (Figure 5), the year 1948 was especially warm and with dominance of anticyclonic conditions (atmospheric stability), which lead to low precipitations amounts and temperatures above the climatological average. For 1972, conditions were much colder, with temperatures significantly lower than average and with clear domain of conditions tending to atmospheric instability. Relevant amounts of precipitation were also registered. For 1995, temperatures were above average and stability conditions associated to the domain of the westerly winds predominated. This is not true for January, when temperatures were colder than normal. In addition, average monthly precipitation values showed amounts lower that the climatological reference values.

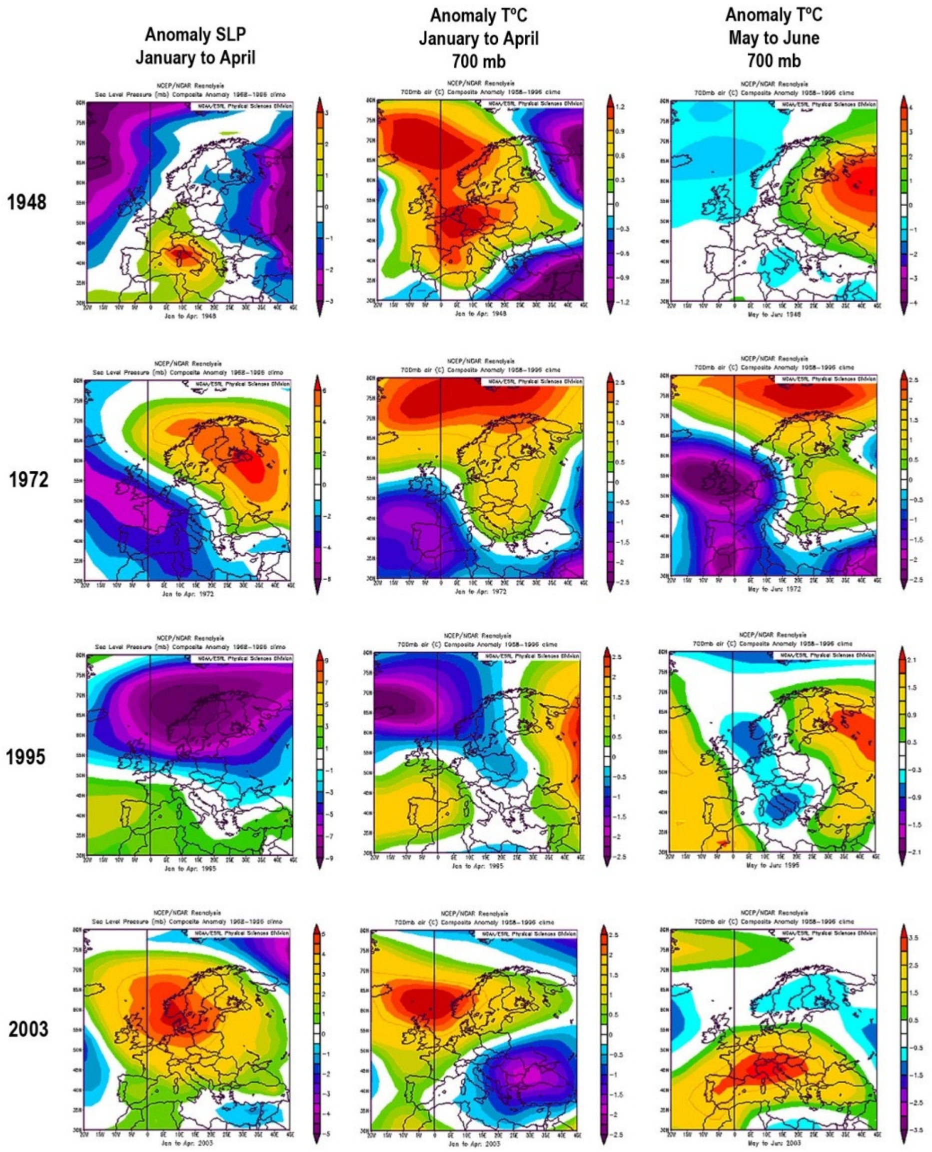

Figure. 4. Synoptic situation of the years studied (1948, 1972, 1995 and 2003). SLP =Sea Level Pressure. Cold colors indicate low values; warm colors indicate high values.

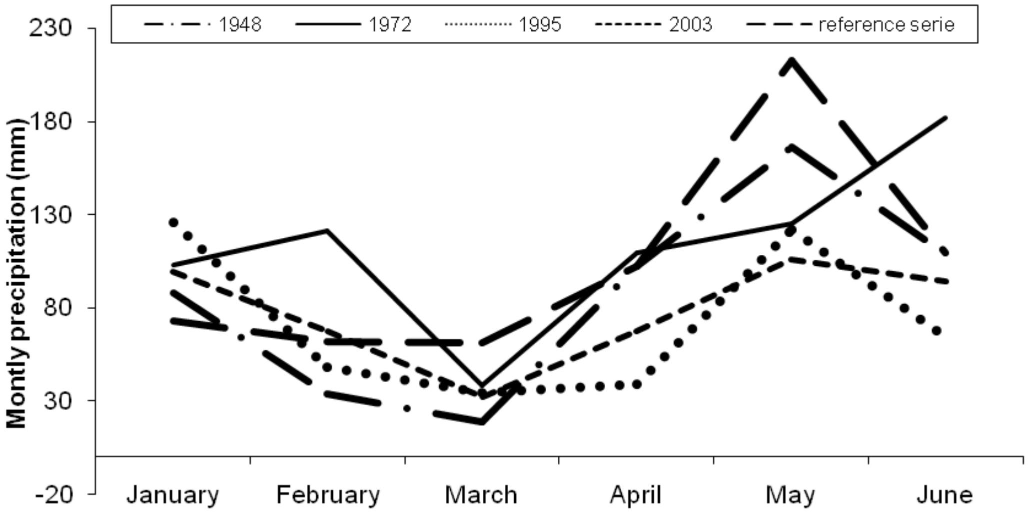

Figure 5a. Monthly precipitation (mm) registered in the FEDA meteorological station in Ransol in 1948, 1972, 1995, and 2003 and for each month. The precipitation for the reference period for each month in the period between 1961 and 1990 is also depicted.

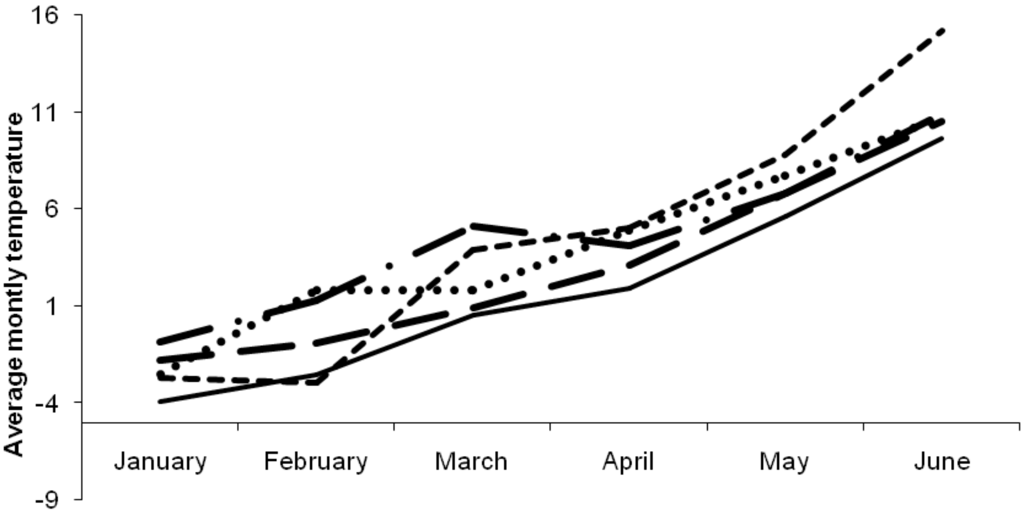

Figure 5b. Average monthly temperature (ºC) registered in the FEDA meteorological station in Ransol for 1948, 1972, 1995, and 2003. The average monthly temperature for the reference period in the period between 1961 and 1990 is also depicted.

In 2003, the period from January to March presented anomaly values of precipitation and temperature, higher and lower respectively than the 1961-1990 average, i.e., it was a very cold and snowy beginning of the year over the study area. Despite of this, year 2003 is mainly remembered because of the hot wave that affected Europe during spring and summer (Beniston, 2004; Schär et al., 2004) (Figure 6). A blocking pattern, in terms of atmospheric circulation, facilitated low precipitation amounts and very high positive temperature anomalies centred over the Alps and the Pyrenees area (see the temperature anomaly map at 700 hPa for May and June, Figure 4). Then, very dry and warm conditions characterize the climate from April to June. Nevertheless, 2003, as 1972, were the two years that had the highest number of snowdrifts and most extensive snow cover.

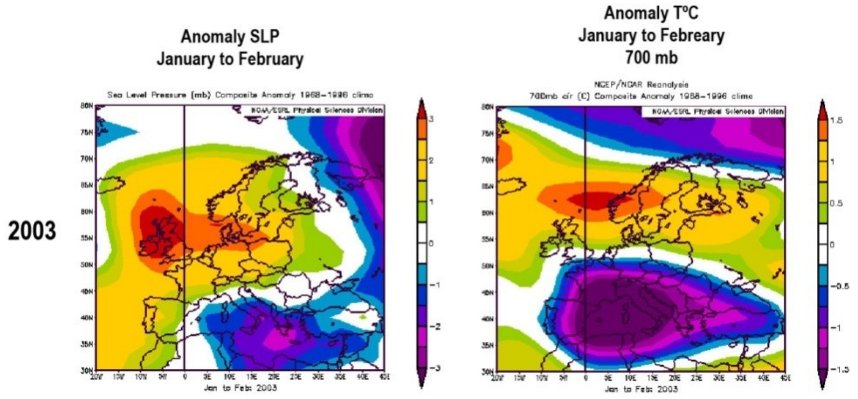

Figure 6. Synoptic situation in January and February of the year 2003. SLP: Sea Level Pressure. Cold colors indicate low values; warm colors indicate high values.

DISCUSSION

In the Andorran Pyrenees, the northerly exposed areas and the flat areas had the highest number of snowdrifts (in Andorra, above 2.000 m, 132 km^2 correspond to northerly slopes; 131 km^2 to southerly slopes and 10,5 km^2 to flat areas). The microtopography of snowdrifts was a major factor in the significant accumulation of snow in flat areas. Those areas are prone to accumulating snow because they are placed where avalanches often end. In addition, sunrays, especially in winter, can have less of an effect on flat terrain than they have on the surfaces of slopes, which might contribute to the slower rate at which snow melts compared to the rates on southerly and northerly slopes. It seems obvious that there should be more snowdrifts on north-facing slopes that on south-facing slopes because the rate at which snow melts is much slower on the former than it is on the latter.

In 2003 and 1972, the major number of snowdrifts occurred at 2.500 m (figure 3b), and not at higher elevations where there was still a lot of snow left to melt, as a result of the low temperatures and the significant amounts of precipitation that occurred in these years. In 1995 and 1948, the greatest number of snowdrifts occurred at 2.600 m (figure 3b), which might have been because of the climatology and the time of year in which the aerial photographs were taken. In those years, the temperatures in January, February, March, and April were higher, and the amounts of snowfall were lower than the averages in the reference period.

As shown in figure 3c, in 1972 and 2003, snowdrifts were most extensive at 2.600 m and, in 1948, at 2.700 m, which was not surprising because the amount of area at the highest elevations was less that the amounts at lower elevations and, therefore, the proportion of the area covered by snowdrifts increased with an increase in elevation. Unlike in other years, in 1995, snowdrifts were most extensive at elevations above 2.800 m. In any case, at the higher elevations (> 2.600 m), small changes in the number of snowdrifts had a more significant effect on the amount of area covered by snowdrifts than they did at lower elevations because the amount of area covered by an elevational interval differed substantially; i.e., between 2.500 m and 2.600 m there were 3.541 ha, between 2.600 m and 2.700 m there were 1976 ha, and >2.800 m there were 119 ha).

In general, avalanches were the main factor responsible for the accumulation and preservation of snowdrifts in Andorra and were most important in flat areas (Figure 7). Changes in the dynamics of avalanches might result in significant variation in the number of snowdrifts created in any given year. Drifted snow created by wind action was most important in the formation of snowdrifts on north slopes (Figure 7). The prevailing winds in Andorra, located in the southern fringe of the temperate zone of the northern hemisphere, come from west (Raso 1999). The westerly winds and the lesser effect of sunlight exposure on north slopes, explain the higher accumulation of snow by the wind in these exposures. Snowdrifts that originated from snow that was retained in sheltered areas did not occur on north-facing slopes, which indicated that the shelter effect was the result of variation in microtopography.

The snowdrifts that resulted from the wind-driven accumulation of snow mainly occurred above 2.800 m. Purges created most of the snowdrifts found between 2.300 m and 2.400 m and orography created most of the snowdrifts that occurred at lower elevations, mainly between 2.200 m and 2.300 m.

The month in which the aerial photographs were taken had some influence on the results because melting was more advanced in the photographs that were taken later in the year. In 1972 and 2003, the photographs were taken in July but, in 1948 and 1995, most of the photographs were taken in late August. Nevertheless, the climatology data explained a significant amount of the variation in the number, distribution, and extent of snowdrifts in the Andorran Pyrenees, which were greatest in the coldest and most humid years. The close relationship between climate and snowdrifts indicated that inter-annual variation in climate will have an influence on snowdrifts in the future.

Thus, in the Andorran Pyrenees, the precipitation and temperature in the months of the snow accumulation period (January, February and March) appeared to be highly influential on the formation of snowdrifts, which was especially evident in 2003, the year that had the second largest number of snowdrifts and, at the same time, had an exceptionally warm melting period (an anomaly that was three times higher than the standard deviation; Schaär et al. (2004) and Beniston (2004). Therefore, if the projected scenarios for climate change in the Pyrenees become real (AEMET 2008), increasing air temperatures will affect snowpack (see López-Moreno et al 2008; López-Moreno et al 2009). The increasing temperatures forecasted for the Pyrenees will also modify climatic conditions in the snow accumulation period in Andorra (a crucial period of snow accumulation) and this apparently will also have a significant impact reducing the number and extent of snowdrifts in the region.

In conclusion here we find two kinds of factors affecting the distribution and extend of Andorran snowdrifts: (1) a fixed inter annual pattern depending on the elevation and (2), variable factors related to inter annual climatology, especially the climatology occurred in the snow accumulation period. However studies in order to cope with other important aspects of snowdrifts such as the relation between snow depth and snow distribution patches are still lacking in the Pyrenean snowdrifts. These potential studies could add important information in order to detail the relation between the melting rates and the climatology and therefore a useful tool to forecast the impacts of global warming in the Pyrenean snowdrifts.

This study contributes to improve the knowledge of Pyrenean snowdrifts traits and represents the state of the art of the current and recent distribution of Andorran snowdrifts by presenting detailed open and free cartographies. These cartographies will allow further evaluation of the trends in snowdrifts when new ortophothographies become available for Andorra.

CONCLUSIONS

We identified 2.520 snowdrifts covering 1.69 ha of the Andorran Pyrenees. The area of the snowdrifts was significantly determined by exposure, year and snow origin. The main factors influencing the accumulation and the conservation of snowdrifts were: (1) areas situated in north-facing slopes, (2) areas were snow origin were attributed to avalanches, (3) areas located between 2.500 and 2.600, (4) and years were the period of snow accumulation in the Pyrenees was in comparison to reference period, significantly cold and humid. Therefore two kinds of factors influenced the extension and the number of snowdrifts: structural factors (exposure, elevation) and temporary factors (climatology). We consider snow origin a mixed factor (structural and temporary).

Moreover, this study showed that, although the year were the aerial photographs were taken is a crucial factor in the number of snowdrifts, the inter-annual climate variation have also an effect in the formation of the snowdrifts, concretely the accumulation period (January to April), whereas snow-melting period (May and June) did not have so much significance. Therefore changes in temperatures and precipitation between January to April will have a strong effect over the future of the Pyrenean snowbeds.

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CAPÍTOL 3: Plant diversity and physical factors in Andorran snowbeds: potential responses to global warming

Plant diversity and physical factors in Andorran snowbeds: potential responses to global warming

ABSTRACT

In mountain alpine ranges, the effects of global warming threaten snowbed habitats. This study examined the floral communities and physical factors of 32 snowbeds in the Pyrenees, Andorra. Elevation, exposure, temperature, snowbed size, snow cover, and soil type characterized the sites. Of the 101 species (16 bryophytes and 85 vascular plants), 31 vascular plants were characteristic of high-mountain vegetation group and 21 were characteristic of snowbed vegetation group (*Salicetea herbaceae* class). The average richness per snowbed was 16 species and the average Shannon Index was 2.01. Redundancy analyses indicated that the richness of vascular plants was highest in south-facing snowbeds that had intermediate snow cover at intermediate elevations. In Andorra, species in the *Salicetea herbaceae* Class were not present in the snowbeds that had the highest snow cover. Thus, if the projections for global warming come to pass, the plants in the *Salicetea herbaceae* Class will have the potential to colonize snowbeds that have high snow cover at high elevations; however, the amount of habitat available to each of these species at the highest elevations and inter-specific competition will influence the likelihood of successful colonization.

KEYWORDS: snowbeds, global warming, Andorra, plant diversity, Pyrenees, climate change.

INTRODUCTION

Global climate change is expected to have a significant impact on plant diversity in alpine areas (Thuiller et al. 2005, Nogués-Bravo et al. 2006), particularly among highly specialized species, e.g., those that have a narrow niche (Nagy and Grabherr 2009). The severe conditions in snowbeds, which develop in areas that accumulate large amounts of snow in winter, have contributed to the evolution of highly specialized species (Körner 2003). Typically, snowbeds have low plant species richness and are characterized by the predominance of endemic species (Dullinger et al. 2000), which contributes significantly to the overall biodiversity of the alpine landscape.

In the Alps and in Arctic regions, ice and snowfields are receding (Dye 2002, Beniston et al. 2003, Paul et al. 2004), which affects alpine and nival habitats, particularly (Pauli et al. 2007). In addition, temperatures in Europe are expected to increase in this century (IPCC 2007). In the Pyrenees, a meridionally snow-covered mountain range in Europe, snowpack has decreased (López-Moreno et al. 2009) and the average annual temperature is expected to increase by 2,5-5,0 ºC by 2100 (AEMET 2008). In Andorra, for example, average temperatures have increased significantly since 1937 (Esteban et al. 2009), which can affect the duration of snow cover. Furthermore, snowbeds are disappearing in the Iberian Peninsula (Munoz et al. 2007). All of those changes can affect the phenologies of the biota and many other biological and physical phenomena.

Increases in global temperatures are likely to have a significant influence on snowbed communities because plants will be exposed to new climatic conditions and community composition and plant phenologies are expected to change (Schöb et al. 2008, Hassol 2004, Huelber et al. 2006). Although little is known about the dynamics of snowbed communities (Nagy 2006.), studies have shown that plant species (mainly, grasses) from neighbouring communities have invaded snowbeds in Europe (Grabherr et al. 1995, Grabherr 2003, Schöb et al. 2009).

Snowbed vegetation, which is included in the *Salicetea herbaceae* class defined by Rivas Martínez el al. (2002), comprises small (20-30 cm high) herbs, mostly hemicryptophytes. The vascular plants and bryophytes of snowbeds are adapted for growing and reproducing within a few weeks or months during the period in which they are not covered by snow (Björk and Molau 2007, Bliss 1960). In winter, snow cover keeps ground-level temperatures above –2 ºC, even though temperatures can be as low as – 15 ºC in nearby habitats that have limited snow cover. Typically, many snowbed plants begin growing when air and soil temperatures are near 0 ºC (Billings and Bliss 1959), and snow provides a good supply of water during the growing season

(Bliss 1960). In snowbeds, asexual reproduction is more common than is sexual reproduction (Conesa 1997) because of the limited presence of pollinators (Bingham and Orthner 1998, Cruden 1972, Arroyo et al 1982, Heinrich 1993) and because the short active period often does not allow fruit to mature and seeds to be dispersed before the next period of snow cover, which favors selfing, apomixes, polyploidy, and vegetative reproduction (Mosquin 1966, Molau 1993).

In the last 50 yr, several surveys have provided very good inventories of snowbed vegetation in the Pyrenees (Braun-Blanquet 1948, Rivas-Martínez 1969, Corriol 2009, Lluent 2007, Lluent et al. 2006, Illa et al. 2011), where *Carex pyrenaica*, *Epilobium anagallidifolium*, *Gnaphalium supinum*, *Plantago atrata*, *Salix herbacea*, *Salix reticulata*, *Sedum alpestre*, *Sibbaldia procumbens*, and *Veronica alpina* are the most common species; however, the ecology and floristic composition of snowbeds in the Pyrenees have not been well studied. Physical factors of the habitat such as snow conditions, shade, and soil type influence the floristic composition of snowbeds and the abundance of some species (Björk and Molau 2007). In the Alps, Schöb et al. (2009) found that temperature and the timing of snowmelt were the most important factors influencing the ecology of snowbed species. In addition, snow cover is considered the most important factor in explaining differences in species distributions among snowbeds because it can affect soil depth, soil organic matter content, and the amount of rock cover (Oster et al 1982, Stanon et al. 1982). Some of those factors such as shade and soil type remain relatively stable over time, but snow cover, which is strongly influenced by the length of the snowmelt period, varies considerably among years (Billings and Bliss 1959, Johnson and Billings 1962, Oster el al. 1982, Wijk 1986, Shimono and Kudo 2003 and Watson and Haeberli 2004) and is strongly affected by climate change (Lopez-Moreno et al 2009).

Although the ecology of snowbeds has been studied in several regions of Europe (Bjork and Molau 2007, Huelber et al. 2006, Schöb et al. 2009), to our knowledge, only few studies have been conducted in the Pyrenees (Lluent 2007, Lluent et al. 2006). Those studies found a strong relationship between air temperature and the phenologies of some snowbed species, but it did not examine the relationships between the physical factors attributes of the different numbers of Pyrenean snowbeds and the species within them. Some plant species living at low elevations in the Western Mediterranean region have responded to climate change through phenotypic responses such as phenological shifts (Peñuelas et al. 2002), genotypic responses (Jump et al. 2006), and elevational shifts (Peñuelas and Boada 2003, Peñuelas et al.

2007); therefore, global warming is expected to have a significant affect on the snowbeds on the Iberian side of the Pyrenees, and snowbeds in southern Europe are are shrinking and disappearing as Mediterranean climate traits reach them (Tomaselli 1991).

An understanding of the relationships between plant communities and their physical environment is essential in forecasting the impacts of environmental changes on the vulnerable high-mountain habitats in the Pyrenees, which is needed to protect species and habitats, and for the development of management programs.

The objective of this study was to evaluate the vegetation in snowbeds in the Andorran Pyrenees to (i) characterize the vegetation and to provide a current knowledge of the state of the plant diversity and composition, (ii) identify correlations between environmental factors and the vegetation, and (iii) assess the responses to current and projected global warming. Specifically, the study addressed the following questions:

1. Which vegetation groups occur in Andorran snowbeds? Vegetation groups were defined as the sum of the syntaxonomical classes that characterize the habitats. Does an increase in vascular plant diversity imply a reduction in typical snowbed species *(Salicetea herbacea* Class)?
2. What are the relationships between the vegetation and the environmental attributes of snowbeds?
3. Which vegetation groups are likely to be displaced by others in response to climate change?

MATERIALS AND METHODS

Study site

We used aerial photographs to locate all of the snowbeds in Andorra (Domènech et al. submitted;http://www.iea.ad/index.php?option=com_content&view=article&id=493&catid=55&Itemid=153.). Snowdrifts were defined as patches of accumulated snow that persisted for more than nine months a year (VVAA 2002), and a snowbed is the habitat that is created under a snowdrift because of the long period of snow cover (Gjaerevoll 1956, Björk and Molau 2007). The scales of the photographs differed; therefore, several methods were used to digitalize the snowbeds in the photographs. The snowdrifts in the (black and white) aerial photographs taken in 1948 were quantified using the traditional stereoscopic technique, which were later digitalized at a 1:5.000 scale. Aerial photographs were used to produce a map of snowbeds in 1972. Orthophotographs were used to produce the maps for 1995 and 2003, which were digitalized at a scale of 1:2.000. Snowbeds were identified in the aerial photographs based on the presence of a snowdrift (white) in the summer, when snow occurs in snowdrifts, only. Under the snowdrifts lies snowbed habitat (independent of the vegetation that was present).

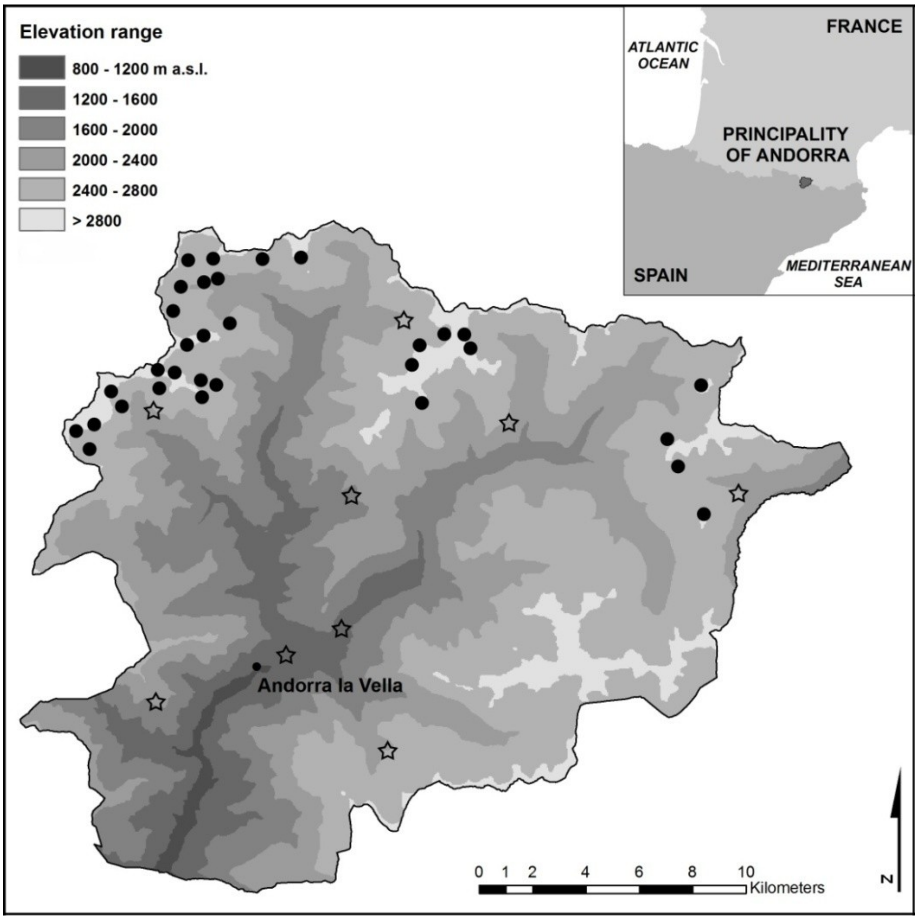

Figure 1. Location of the snowbeds evaluated (black dots) in the study area in the Andorran Pyrenees. The locations of six meteorological stations are indicated (Ninyerola and Julià 2009) (star symbols).

We selected randomly 40 snowbeds identified in the photographs in a previous study (Domènech et al. submitted); however, eight of the snowbeds were excluded from the study because of inaccessibility. Thus, 32 snowbeds (above 2.280 m) were surveyed in the Central Pyrenees in northern Andorra (Figure 1). The snowbeds were within an ~16 km^2 area, and the maximum distance between snowbeds was 30 km. The average elevation of the snowbeds was 2.454 (Table 1), and most were between 2.500 m and 2.600 m (Domènech et al. submitted). We documented the form (concave, convex, or flat) of each snowbed. All of the snowbeds had similar microtopography, viz., on undisturbed concave surfaces (no frost upheaval or livestock grazing).

Table 1. Plant species diversity and physical factors of 32 snowbeds in the Andorran Pyrenees. Soil types: IOM=inexistent organic matter; ANEOM=almost non existent organic matter (depth less than 1 cm) and OM=organic matter depth at least 1 cm.

Snowbed	UTM Coordinates		Elevation (m)	Snow cover duration	Exposure	Temp (ºC)	Soil type	Area (m^2)	Shannon Index	Richness
	X	Y								
1	537813,73	34466,26	2400	intermediate	north	14,73	IOM	275	1,81	15
2	537603,43	34405,83	2410	low	north	14,76	IOM	658	1,87	14
3	530265,88	38343,28	2300	intermediate	flat	15,1	OM	2481	1,88	19
4	530466,63	38953,53	2350	intermediate	flat	14,69	IOM	1054	1,62	8
5	530336,24	35583,75	2600	intermediate	north	12,99	IOM	6534	2,20	13
6	530336,24	33583,75	2350	intermediate	north	12,99	ANEOM	1401	1,81	15
7	532380,1	38313,98	2325	intermediate	south	15,05	OM	13133	1,89	13
8	534262,03	38826,92	2500	high	south	12,17	ANEOM	5643	2,07	14
9	527631,36	33702,19	2500	intermediate	south	13,51	ANEOM	9810	2,19	13
10	527266,6	33746,11	2650	high	south	12,56	ANEOM	6373	2,19	13
11	528977,76	33688,82	2500	intermediate	flat	14,18	ANEOM	2382	2,15	23
12	530386	34348,67	2300	intermediate	south	15,09	ANEOM	1550	2,51	15
13	547967,24	31648,84	2400	low	north	13,6	IOM	1090	1,56	18
14	548587,44	31878,01	2410	low	north	13,88	IOM	959	2,21	15
15	529820,09	35569,38	2400	intermediate	north	13,45	IOM	3203	1,90	10
16	537776,23	33147,13	2450	low	south	14,65	IOM	2161	1,65	11
17	540239,06	35633,24	2550	low	south	13,2	ANEOM	116	2,74	17
18	540418,28	35559,11	2480	intermediate	south	13,51	ANEOM	446	2,59	19
19	540196,65	35595,97	2550	intermediate	south	13,2	IOM	5098	2,27	15
20	539713,86	35829,85	2450	intermediate	flat	13,24	OM	1141	2,34	19
21	526096,2	32228,85	2625	high	south	12,59	IOM	3979	1,80	7

22	526234,66	32410,28	2650	high	flat	12,27	IOM	2935	1,68	10
23	525777,12	31704,45	2500	low	south	13,79	2	312	2,39	20
24	549261,7	27614,4	2570	low	north	13,36	OM	107	1,95	14
25	530870,21	38620,3	2460	intermediate	north	13,75	ANEOM	845	2,43	14
26	531101,07	38952,63	2500	intermediate	flat	13,37	IOM	14567	1,64	22
27	530682,48	38574,64	2410	low	flat	14,28	OM	1496	1,92	20
28	548816,71	33806,89	2280	intermediate	north	14,75	ANEOM	1413	2,44	13
29	529227,01	36080,41	2540	low	south	13,36	ANEOM	455	1,42	23
30	530246,14	34442,05	2350	intermediate	south	14,8	ANEOM	631	2,56	18
31	529518,98	34482,49	2460	low	north	13,74	IOM	4377	2,10	16
32	530571,63	34540,82	2300	low	south	15,28	OM	858	1,85	15

In the period 1971-2000, the average annual rainfall in the area of the snowbed sites was 1.275 mm (summer = 332 mm, autumn = 342 mm, winter = 270 mm, spring = 331 mm) (Batalla et al. 2011) and the average annual summer air temperature was 3.8ºC (Batalla et al. 2011). Most of the soils are acidic, and on gneiss, granodiorite, or granite rocks. For about 9 month of the year, the vegetation is covered by snow.

Previous studies of snowbeds in the Pyrenees, which used a phytosociological approach to identify snowbeds, documented the presence of species of the *Salicetea herbaceae* Class (Braun-Blanquet 1948, Rivas-Martínez 1969, Lluent 2007) independent of the detection of a real snowdrift. Nevertheless, the correlation between the presence of the *Salicetea herbaceae* class and snowbed areas appears to be strongest in the highest mountains in Central Europe, and weaker in Oroarctic and Arctic areas (Dierssen 1984). Tomaselli (1991) noted that the association between *Salicetea herbacea* species and snowbeds in Apennines Mountains is strong; however, the strength of the association between this class and snowbeds in the Pyrenees is unknown. By using the snowdrifts identified in aerial photographs, we were able to identify the groups of vegetation that were present in snowbed habitats thus considering that species of the *Salicetea herbaceae* Class were not the only species in the snowbeds.

Field sampling

The floristic inventories were documented using transects between 10 Jul and 15 Aug 2009. Snowbeds were between 107 m^2 to 1,567 m^2 in size (Table 1). Given the wide range in the sizes of the snowbeds, and to avoid any border effects, we established a 10-m-long transect at the approximate centre of each snowbed, extended along the east-west contour line, 5 m in each direction. All of the plant species found within a 20 x 50-cm rectangle placed on the ground every 40 cm along each transect were recorded. A cover-abundance scale was used to quantify the area covered by each species.

Characterization of the vegetation

In each snowbed, the vegetation was characterized using cover-abundance (Braun-Blanquet 1979), which was used to calculate the proportions (%) of vascular plants, bryophytes, lichens, and bare ground cover. We calculated the frequency (number of snowbeds in which the species occurred) and the amount of cover (sum of the cover-abundances in all snowbeds) of each species. In addition, the vegetation was characterized using species richness, Shannon Index, and by classifying the species as functional groups (grass, forbs, scrubs, bryophytes, or pterydophytes). The number of species in each of those vegetation groups (Table 2) was used to quantify the contribution of each group to each snowbed. Those vegetation groups were described for the Iberian Mountains Peninsula by Rivas Martínez et al. (2002), which included all of the characteristic syntaxonomical classes (Table 2). Bryophytes were excluded from the analyses. The names of the higher plants follow the nomenclature of de Bolòs et al. (2005).

Table 2. Vegetation groups including characteristic syntaxonomical classes (Rivas-Martínez et al. 2002).

Vegetation Group	Syntaxonomical Class
Snowbed vegetation	*Salicetea herbaceae*
	Caricetea curvulae
High mountain meadows	*Carici rupestris-Kobresietea bellardi*
	Nardetea strictae

Pastureland and mesophitic meadows of perennial plants	*Festuco-Brometea* *Festuco hystricis-Ononidetea striatae* *Festucetea indigestae* *Sedo-Scleranthetea*
Rock vegetation	*Thlaspietea rotundifolii* *Asplenietea trichomanis*
Above treeline scrublands	*Vaccinio-Piceetea* *Loiseleurio-Vaccinietea* *Calluno-Ulicetea*
Humid meadows and grasslands	*Molinio-Arrhenatheretea* *Montio-Cardaminetea* *Mulgedio-Aconitetea*

Physiographic and climatic variables

The environmental variables that were quantified included elevation (m), exposure (south slope, flat terrain, or north slope), temperature (ºC), type of soil (poor, immature, or developed) (Table 1), and snow cover (low, intermediate, high). The elevation, exposure, and snow cover of each snowbed have been documented elsewhere (Domènech et al. submitted; cartography in http://www.iea.ad/index.php?option=com_content&view=article&id=493&catid=55&Itemid=153). The elevation of each snowbed was measured using a 30-m resolution DEM and the exposure was derived. Digitalization and analyses were preformed using Arcgis 9.3 software (2008, ESRI, Redland, USA). Exposure was classified on north-facing slopes, flat areas, and south-facing slopes.

Snowbeds were identified in aerial photographs taken between mid-July and August of 1948, 1972, 1995 and 2003, which indicated that all of the snowbeds in Andorran were covered by snow for at least 8-9 months of the year (Raso 1999) and typically, the new snowfall occurs in October (Batalla et al. 2011). In the years that the photographs were taken, the numbers and sizes of the snowdrifts varied because, although the distribution of snow remains fairly stable, the timing of snowmelt varies annually (Friedel 1961, Körner 2003), which is influenced by precipitation and temperature (López-Moreno 2005). To approximate the duration of snow cover at each site, sites were categorized as having low (LSC), intermediate (ISC), or high snow cover (HSC) if snowdrifts were present in one, two, or three or four of the years studied (1948, 1972, 1995 and 2003), respectively.

Organic soil depth defined three types of soil: inexistent organic matter (IOM: poor soils), almost non-existent organic matter (ANEOM: depth <1 cm, immature soils), and organic matter depth ≥1 cm (OM: developed soils). The average air temperature above each snowbed in the summer (June, July, and August) of 2009 was estimated by applying multivariate interpolation regression (Ninyerola and Julià 2009) to the data from six automatic high-mountain meteorological stations that were established by the Snow and Mountain Research Center in Andorra (CENMA) (Figure 1) and three from FEDA (www.feda.ad) (Figure 1). The interpolated data, standard deviations, and the methods for the calculation of the temperatures were publicly available and described in the Digital Climatic Atlas of Andorra (2011) (Batalla et al. 2011 in http://opengis.uab.es).

Data analysis

To characterize the snowbeds and their floristic composition, functional groups, species diversity, and the environmental factors in the snowbeds in Andorra, the data were subjected to a redundancy analysis (RDA). The factors included soil type, snow cover, area (snowbed size), exposure, temperature, species richness, Shannon Index, functional groups, and vegetation group (snowbeds, high-mountain meadows, pastureland and mesophitic meadows, rock vegetation, above tree-line scrub, and humid meadows and grassland). Categorical factors were converted into dummy variables. The species composition data were transformed using a logarithmic transformation. To test the significance, the species data were permuted using a global permutation test (Monte Carlo Test), computing reduce model under 999 permutations. The multivariate analyses were performed using the CANOCO 4.5 software program.

RESULTS

Flora of Andorran snowbeds

In the 32 snowbeds in the Andorran Pyrenees, average vegetation cover was 51,5% and the remainder was covered by bare ground, rocks, dead organic material and, to a limited extent (<0,1%), lichens. The average species richness in the snowbeds was 16 species (range = 7-23; SE = 4.22) and the average Shannon Index was 2,01 (range = 1,56-2,74; SE = 0.32). The snowbeds comprised 85 vascular plant and 16 bryophyte species. The bryophytes included three liverworts (*Anthelia Juratzkana*, *Cephalozia ambigua*, *Marsupella emarginata*) and 13 mosses (*Bryum elegans*, *Ceratodon purpureus*, *Dicranoweisia cirriata*, *Kiaeria starkei*, *Lescuraea saxicola*, *Sciuro-hypnum glaciale*, *Oligotrichum hercynicum*, *Pohlia drumondi*, *Polytrichum piliferum*, *Polytrichium sexangulare*, *Racomitrium macounii*, *Syntrichia norvegica*, *Tortula hoppeana*). *Bryum elegans* and *Sciuro-hypnum glaciale* are new additions to the Andorran bryoflora (Casas et al. 2003a, Casas et al. 2003b). *Polytrichum sexangulare*, *Polytrichium piliferum*, and *Pohlia drumondi* were the most common (by frequency) mosses, and *Polytrichum sexangulare* was the most widespread (by abundance).

Of the 85 species of vascular plants, 31 are characteristic of the high-mountain meadows vegetation group, 21 are in the snowbed vegetation group, 14 are in the rock vegetation group, 7 are in the mesophitic meadows, 6 are in the above-treeline scrub, and 6 are in the humid meadows and grasslands group. *Gnaphalium supinum*, *Poa alpina*, *Carex pyrenaica*, *Mucizonia sedoides*, *Murbeckiella pinnafitica*, and *Nardus stricta* were the most frequently occurring vascular plants and, with the exception of *N. stricta* and *M. pinnafitida*, all are in the *Salicetea herbaceae* Class (Table 4). *Nardus stricta* had the greatest coverage*,* and *Agrostis rupestris*, *Oreochloa disticha*, and *Trifolium alpinum* were the most widespread. *Gnaphalium supinum* was the most frequently occurring and the second-most widespread species.

Based on abundance, the most common species in the snowbeds were present in the adjacent habitats, particularly, species in the high-mountain meadows vegetation group; e.g., hygrophilous pastures of *Nardus stricta*, silicicolous meadows of *Agrostis rupestris*, *Festuca eskia* grasslands, and acidophilous meadows of *Carex curvula*. Based on frequency, however, species in the *Salicetea herbaceae* class (typical snowbed vegetation group) predominated (Table 3). Those species are better adapted to protracted snow cover than are the pasture species, which predominate in the habitats adjacent to the snowfields.

Table 3. The 30 most frequent species, their frequency (number of snowbeds where present), plant cover (sum of cover-abundance in all snowbeds), syntaxonomical class, and vegetation group (Rivas Martínez et al. 2002).

Species	Frequency	Plant cover	Syntaxonomical class	Vegetation group

Species	Frequency	Plant cover	Syntaxonomical class	Vegetation group
Gnaphalium supinum	28	4395	*Salicetea herbaceae*	Snowbed
Poa alpina	25	2244	*Salicetea herbaceae*	Snowbed
Carex pyrenaica	21	1799	*Salicetea herbaceae*	Snowbed
Mucizonia sedoides	21	628	*Salicetea herbaceae*	Snowbed
Murbeckiella pinnatifida	21	1005	*Thlaspietea rotundifolii*	Rock vegetation
Nardus stricta	20	5604	*Nardetea strictae*	High-mountain meadows
Cardamine alpina	19	988	*Salicetea herbaceae*	Snowbed
Criptogama crispa	18	1351	*Thlaspietea rotundifolii*	Rock vegetation
Agrostis rupestris	15	4097	*Caricetea curvulae*	High-mountain meadows
Sibbaldia procumbens	14	1428	*Salicetea herbaceae*	Snowbed
Sedum alpestre	13	806	*Salicetea herbaceae*	Snowbed
Trifolium alpinum	13	2320	*Nardetea strictae*	High-mountain meadows
Armeria maritima subsp. alpina	12	640	*Caricetea curvulae*	High-mountain meadows
Leucantemopsis alpina	12	857	*Festucetea indigestae*	Pastureland-mesophitic meadows
Veronica alpina	12	1107	*Salicetea herbaceae*	Snowbed
Oreochloa disticha	11	2331	*Salicetea herbaceae*	Snowbed
Arabis alpina	10	68	*Thlaspietea rotundifolii*	Rock vegetation
Festuca eskia	10	2040	*Caricetea curvulae*	High-mountain meadows
Hieracium gr. pilosella	10	193	*Nardetea strictae*	High-mountain meadows
Jasione crispa	10	626	*Festucetea indigestae*	Pastureland-mesophitic meadows
Phyteuma hemisphaericum	9	172	*Caricetea curvulae*	High-mountain meadows
Cerastium cerastiodes	8	247	*Salicetea herbaceae*	Snowbed
Doronicum grandiflorum	7	435	*Thlaspietea rotundifolii*	Rock vegetation
Gentiana acaulis	7	618	*Nardetea strictae*	High-mountain meadows
Androsace carnea subsp. laggeri	6	321	*Caricetea curvulae*	High-mountain meadows
Calluna vulgaris	6	1133	*Calluno-Ulicetea*	Above-treeline scrubland
Epilobium anagallifolium	6	236	*Salicetea herbaceae*	Snowbed
Linaria apina	6	145	*Thlaspietea rotundifolii*	Rock vegetation
Phleum alpinum	6	404	*Nardetea strictae*	High-mountain meadows
Saxifraga stellaris	6	151	*Montio-Cardaminetea*	Humid meadows and grasslands

Most of the species were forbs (60,82%), grasses (15,45%), or bryophytes (14,43%), but scrubs (7,22%) and pteridophytes (2,06%) were present. Unlike the study by Björk and Molau (2007) in the Pyrenees, forbs were present in the Andorran snowbeds that had a very late snowmelt (Figure 2). In Andorra, forbs and grasses were occurred in all of the snowbeds, but scrubs occurred in the snowbeds that had the warmest conditions and organic soils, (where snow cover was less extensive), only, and they did not occur in the coldest areas that had high snow cover or were at the highest elevations.

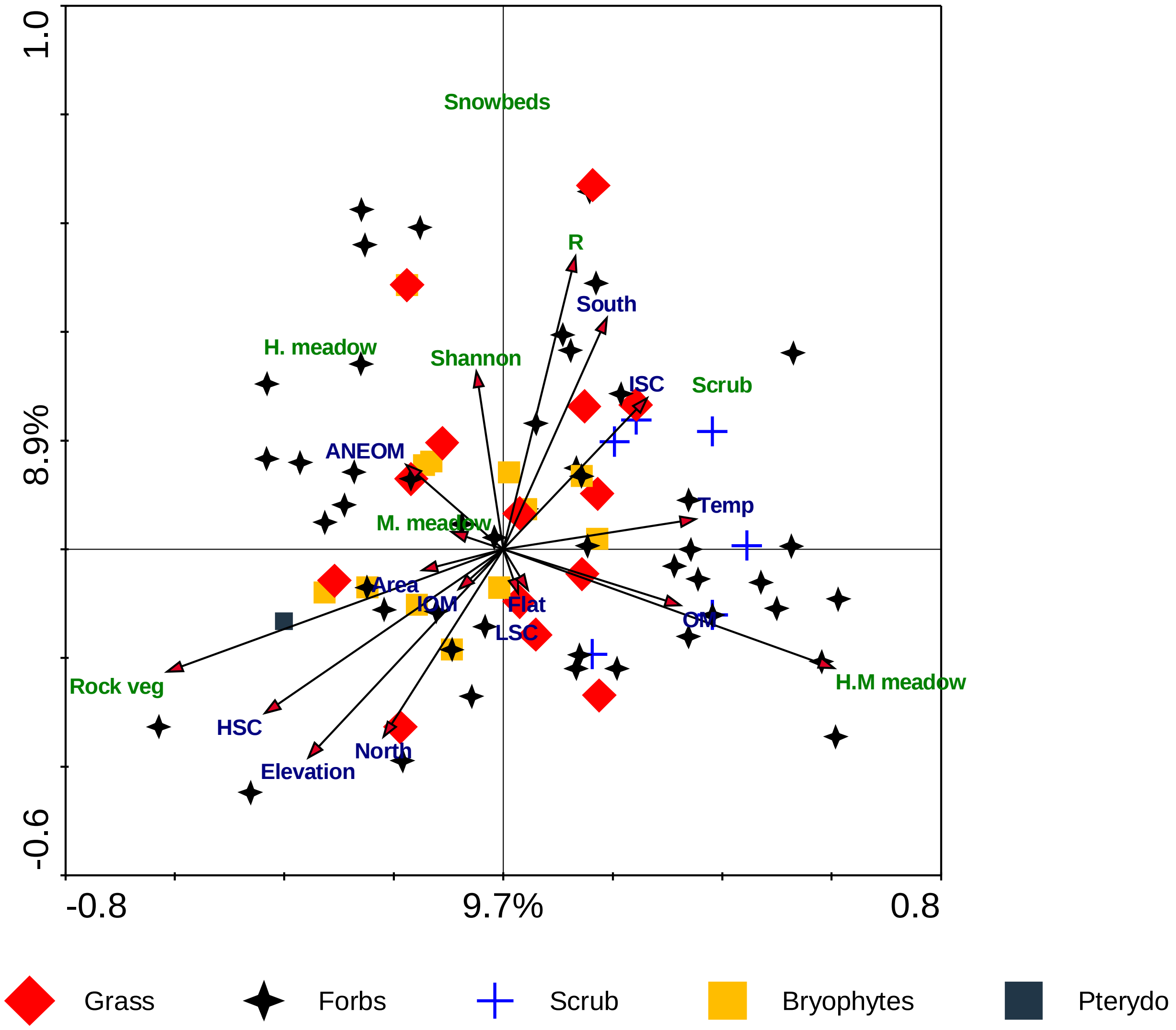

Figure 2. Redundancy Analysis (RDA) (constrained linear ordination method) of the environmental variables (Elevation, Snow cov, Exposure, Temp, Soil, Area), community variables (Shannon Index and Richness), and the vegetation group (snowbeds, high-mountain meadows (HM mead), pastureland and mesophitic meadows (M. meado), rock vegetation (Rock veg), above-treeline scrub (Scrub) and humid meadows and grassland (H. meado)) in snowbeds in the Andorran Pyrenees. The classifying groups of all the species are also depicted with symbols (Pterydo means pterydophytes).

Patterns in the species composition of snowbeds: diversity and physical factors

The first two components of the RDA explained 23,8% of the variation in the species data and environmental variables. The 32 snowbeds were distributed evenly between the two main components (Figure 3). The three main groups were snowbeds exposed to warm temperatures and low snow cover, at low elevations, and having organic matter soils (Group 1, Figure 3), snowbeds exposed to cold temperatures at high elevations, and having shallow soils (Group 2, Figure 3), and snowbeds that had intermediate snow cover, experienced intermediate temperatures, on south-facing slopes, and at intermediate elevations (where plant species diversity was highest) (Group 3, Figure 3).

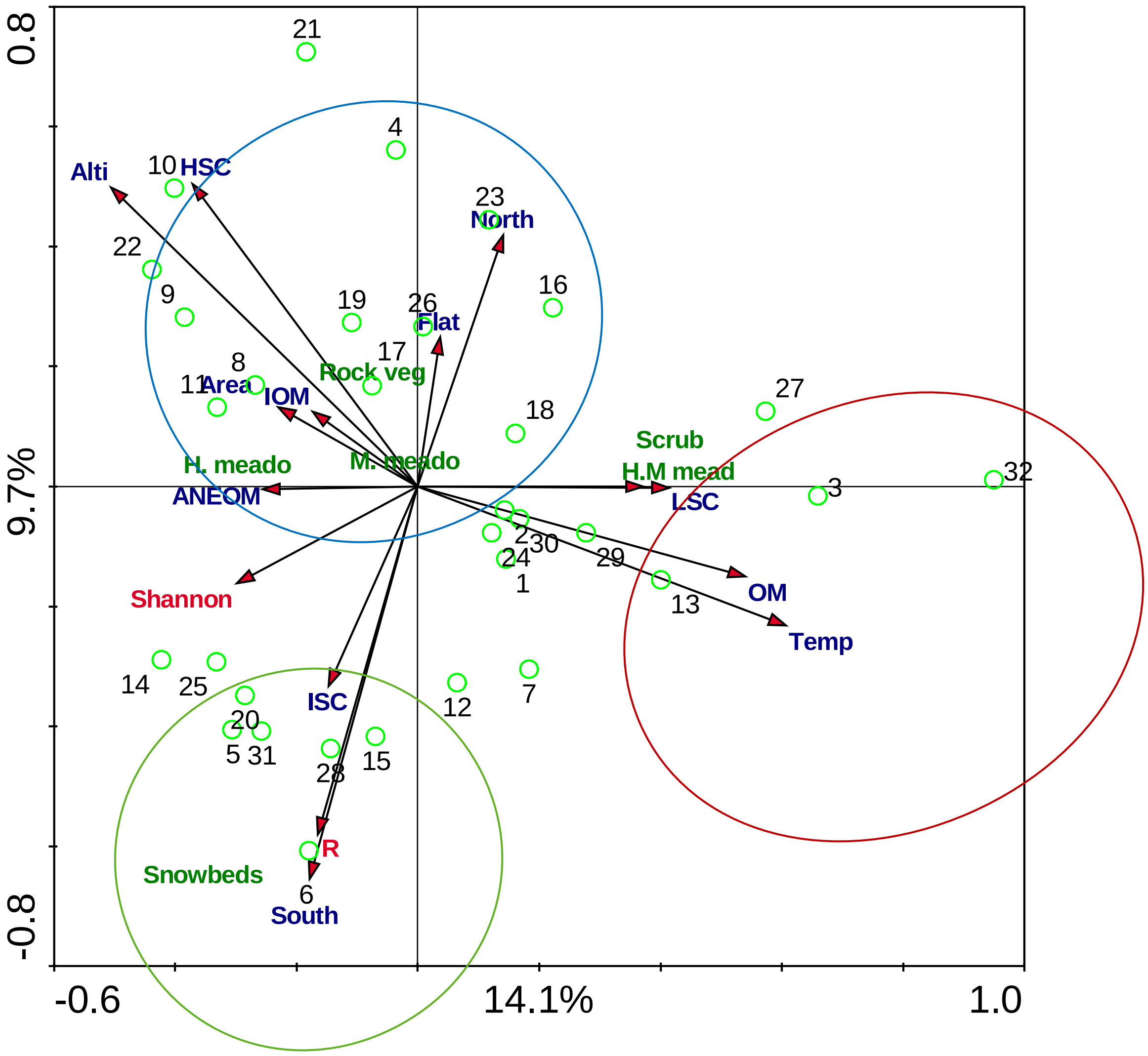

Figure 3. Redundancy Analysis (RDA) (constrained linear ordination method) of the environmental variables (elevation, snow cover (HSC, ISC and LSC), exposure, temperature (Temp), soil group (OM, ANEOM and IOM) and snowbed size (Area), community variables (Shannon index and richness (R)), and the vegetation groups (snowbeds, high-mountain meadows (H.M meadow), pastureland and mesophitic meadows (M. meadow), rock vegetation (rock veg), above-treeline scrub (scrub) and humid meadows and grassland (H. meadow)) in snowbeds studied. Red circle represents group 1 (warmer snowbeds); blue circle represents group 2 (colder snowbeds) and green circle represents group 3.

The rocky vegetation group had the lowest diversity and occurred at the highest elevations, where the snow cover and snowbed sizes were most extensive. The distributions of the species in the pastureland and mesophitic meadows group did not exhibit any trends.

Five members of the *Salicetea herbacea* class (snowbed vegetation group), *Armeria maritima*, *Carex pyrenaica*, *Gnaphallium supinum*, *Veronica alpina*, and *Mucizonia sedoides*, were strongly associated with snowbeds that had south-facing exposures (Group 3). *Oreoclhoa distica*, *Murbeckiella pinnatifida*, *Sedum alpestris,* and *Leucantemopsis alpina* were strongly associated with the snowbeds at the highest elevations (Group 2) and with the rock vegetation group. *Jasione crispa*, *Gentiana acaulis*, *Nardus stricta*, and *Trifolium alpinum*, members in the high-mountain meadow vegetation group were associated with the warmest sites (Group 1).

DISCUSSION

Patterns in the species composition of snowbeds

In the snowbeds of the Andorran Pyrenees, developed soils predominated in areas where the period of snow cover was relatively short and poor soils were associated with areas in which the period of snow cover was long. Ostler et al. (1982) and Stanon et al. (1994) found that the soil layer was thickest and the organic matter content highest at early snowmelt snowbeds sites in USA, which experienced higher than average temperatures. In Andorran snowbeds the plant species present at those sites are part of the high-mountain meadows group (e.g., *Trifolium alpinum*, *Nardus stricta*, *Jasione crispa*), which had the largest representation of species (31 of 85) in the snowbeds and has the potential to adapt to changes in conditions caused by global warming. Several alpine grassland species, which can invade snowbeds, will benefit from increases in air temperature and, probably, will be better able to compete with the current snowbed vegetation (Grabherr et al. 1995, Grabherr 2003, Nagy 2006, Bjork and Molau 2007, Lluent 2007, Schöb et al. 2009).

In the snowbeds of the Andorran Pyrenees, the *Salicetea herbacea* class (the snowbed vegetation group) exhibited the highest diversity and, generally, was associated with intermediate snow cover and intermediate elevations (2.280-2.650 m) (mean elevation = 2.454 m (n = 2.520) (Figure 4). The humid meadows vegetation group was associated with snowbeds that experienced low temperatures and had poor soils, possibly, because *Saxifraga stellaris* was the most abundant species in this group (Figure 4), which occurred mainly in humid and rocky soils that had little organic matter.

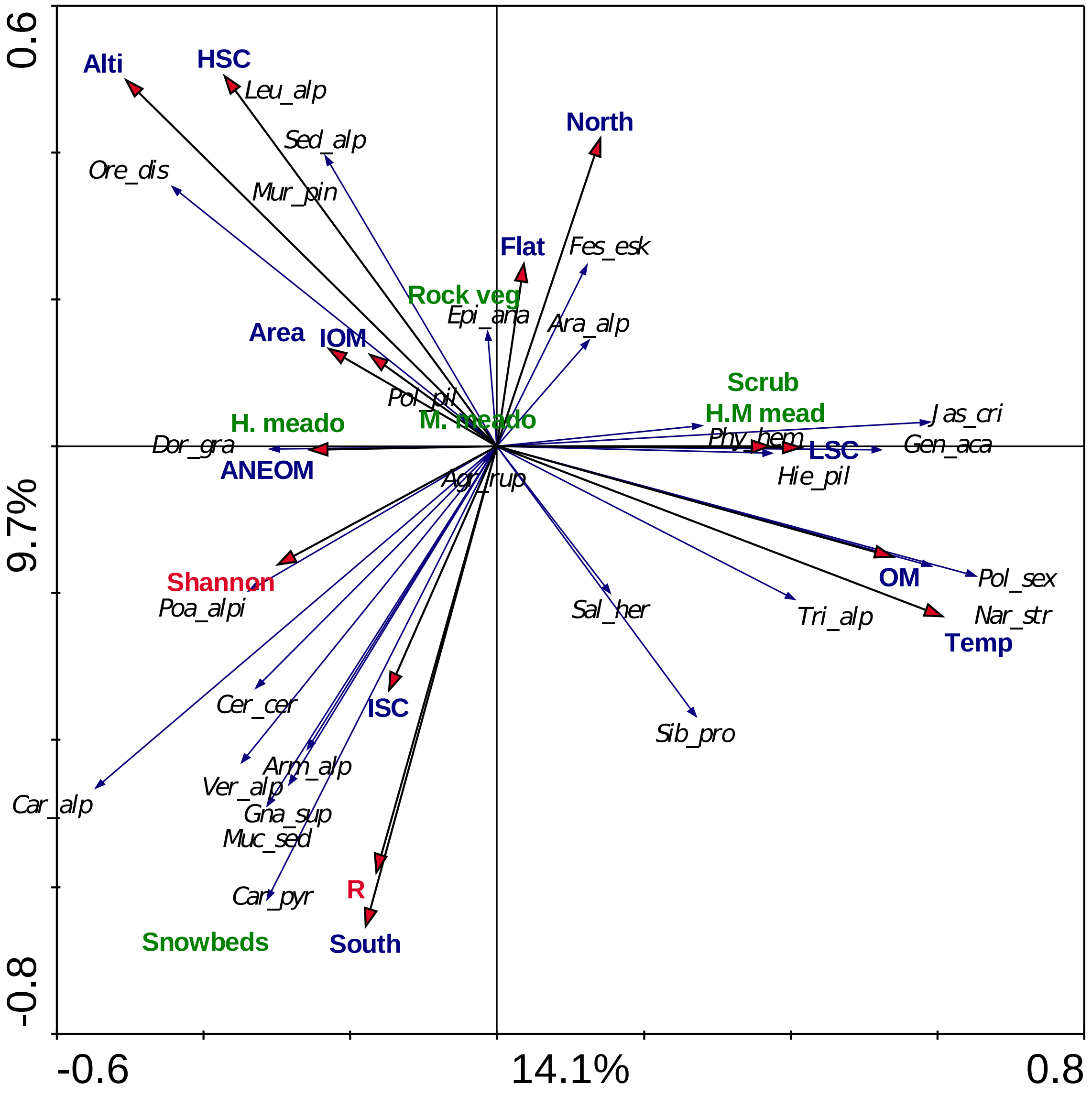

Figure 4. Redundancy Analysis (RDA) (constrained linear ordination method) of the environmental variables (elevation, snow cover (HSC, ISC and LSC), exposure, temperature (Temp), soil group (OM, ANEOM and IOM) and snowbed size (Area), community variables (Shannon index and richness (R)), and the vegetation groups (snowbeds, high-mountain meadows (H.M meadow), pastureland and mesophitic meadows (M. meadow), rock vegetation (rock veg), above-treeline scrub (scrub) and humid meadows and grassland (H. meadow)) and all the species of the samples (fit range from 15% to 100%): Agr_rup (*Agrostis rupestris*), Ara_alp (*Arabis alpina*), Arm_alp (*Armeria maritima alpina*) Car_bel (*Cardamine alpina*), Car_pyr (*Carex pyrenaica*), Cer_cer (*Cerastium cerastoides*), Dor_gra (*Doronicum grandiflorum*), Epi_ana (*Epilobium anagallifolium*), Fes_esk (*Festuca eskia*), Gen_aca

(*Gentiana acaulis*), Gna_sup (*Gnaphalium supinum*), Hie_pil (*Hieracium* gr. *pilosella*), Jas_cri (*Jasione crispa*), Leu_alp (*Leucantemopsis alpina*), Muc_sed (*Mucizonia sedoides*), Mur_pin (*Murbeckiella pinnatifida*), Nar_str (*Nardus stricta*), Ore_dis (*Oreochloa disticha*), Phy_hem (*Phyteuma hemisphaericum*), Poa_alp (*Poa alpina*), Sal_her (*Salix herbacea*), Sed_al (*Sedum alpestre*), Sib_pro (*Sibbaldia procumbens*), Tri_alp (*Trifolium alpinum*) and Ver_alp (*Veronica alpina*).

Salix herbacea, was as strongly associated with the high mountain meadow vegetation group as it was associated with snowbed vegetation group, particularly, at sites on organic soils, on south-facing slopes, and that experienced high temperatures. *S. herbacea* grows in a wide variety of environments including areas that have extreme wind exposure, rocky habitats that have a thin snow cover, and areas that experience significant snow cover (Beerling 1998). In Nordic countries, S. *herbacea* occurs at lower elevations than it does in the Alps and the Pyrenees. In alpine areas, *S. herbacea* occurs where there is significant snow cover but, in eastern Scandinavia and Scotland, the species is most common in exposed and snow-free areas (Beerling 1998). The ecology of the species in the Pyrenees has not been well studied.

Species diversity

In Andorra, snowbeds on south-facing and north-facing slopes had the highest and the lowest species richness, respectively. In addition, diversity was highest in the snowbeds that had intermediate snow cover (ISC), possibly because species that also occurred in adjacent habitats were present in these snowbeds. Schöb (2009) found that species richness was highest at early snowmelt sites and suggested that plant species from high-mountain meadows avoid late snowmelt snowbeds.

Unlike other studies of alpine flora in the Pyrenees (Grau et al. 2011, Villar and Benito 2003; Gómez et al. 2003), in Andorra, species richness and elevation were not correlated (r=0,02), perhaps, because the strong effect of snow cover on snowbeds suppresses the effects of elevation. These studies indicated that species richness and elevation were negatively correlated. Snow cover provides protection against low temperatures and frost (Björk and Molau 2007), and we hypothesize that the protection against low temperatures in winter and spring is more important than is elevation, per se. Snow cover provides conditions that are suitable to more conservative and specialized species and, thus, diversity remains constant, independent of elevation. In that way, the snowbeds at the highest elevations might act as biodiversity reservoirs. Exposure did not have a significant effect on species diversity and, probably, microtopographic factors had a significant effect on the variation in species richness among snowbeds.

The average species richness of the snowbeds (16 species, range = 7-23) in Andorra were similar to the richness observed in snowbeds in other Iberian mountain ranges e.g., Spanish Pyrenees (range = 25-48 spp.) (Lluent 2007), Sierra Central (range = 9-17 spp.) (Rivas-Martínez 1969), Sierra Cantábrica (28 spp.) (Muñoz et al. 2007), (range = 7-21 spp.) (Díaz et al. 1991)], with the exception of Sierra Nevada (range = 6-8 spp.) (Martínez-Parras et al. 1987). Among snowbeds in other high-mountain regions of the world, plant species richness varies widely e.g., Atlantic Pyrenees (19 spp.) (Corriol 2006), Alps (70 spp.) (Schöb 2009) and 12 spp. (Béguin et al 2006), Apennines (17 spp.) (Tomaselli 1991), Tatra Mountains, Poland (27 spp.) (Kozlowska and Raczkowsa 2006), Caucasus (range = 5-18 spp.) (Onipchenko and Semenova 1995), Scandinavia (range = 5-18 spp.) (Gjærevoll 1956) and Svalbard Archipelago (18 spp.) (Elvebakk 1984). Probably, site-specific environmental factors explain a significant amount of the variation in the species richness of snowbeds worldwide; however, the relationships between the species that occur in snowbeds and specific environmental factors need to be evaluated in a variety of regions.

Global warming and shifts in snowbed vegetation

Global warming is expected to reduce the amount of accumulated snow and advance the timing of snowmelt (IPCC 2007, Dye 2002, Beniston et al. 2003); consequently, plants in the snowbeds at the low snow cover sites and at the lowest elevations (< 2.454 m) will be the ones that are most affected. In the Andorran Pyrenees, most of the species in the *Salicetea herbaceae* Class were not present in the snowbeds that had the most protracted snow cover. Thus, if the projections for global warming come to pass, species of the *Salicetea herbaceae* Class that area growing in intermediate or low snow cover snowbeds will have the potential to colonize snowbeds that have high snow cover at high elevations, where the amount of habitat available to these species at these sites and inter-specific competition will influence the likelihood of successful colonization. In snowbed habitats that have high snow cover, however, soil organic matter content will have a significant effect on colonization by plants. In Andorra, most of the snowbeds that had the greatest snow cover were on poor organic soils, which might have limited the capacity of some species to expand to higher elevations; however, in the context of global warming, a long-term reduction in snow cover will reduce albedo effects, and lead to the warming of soils in high-mountain areas where soil processes might be accelerated (Betts 2000), which might favour snowbed plant communities.

Some plants possess traits that allow them to adapt to new climatic conditions. In the snowbeds at the highest elevations, latency seeds (e.g., *Veronica alpina*) can be essential for successful colonization (Onipchenko et al. 1998, Cavieres 1999) and can contribute to a permanent seed bank (Thompson et al. 1998). Chionophilous species, e.g., *Salix herbacea* and *Gnaphalium supinum*, which have anemochorous seed dispersal, will have an advantage in colonizing snowbeds at high elevations. To better understand the processes of colonization in those habitats, the nature of snowbed seed banks, germination, and plant traits needs to be studied further.

Global warming is expected to raise the freezing line, (which will have a particularly strong affect on the snowdrifts at the lowest elevations), which might lead to species expanding into high snow cover snowbeds at high elevations. In the Andorran Pyrenees, plants in the rock vegetation group (14 of the 85 species) were the best adapted to rocky, undeveloped, and poor soils (a common condition at the high snow cover snowbeds) and, probably, they are the species that are nest prepared to adapt to the effects of global warming in that environment. As temperatures increase, it is likely that species from high mountain grasslands will invade low snow cover snowbeds. Currently, those species predominate in the areas adjacent to the snowbeds surroundings, and some occurred within snowbeds (31 of 85 species).

Global warming is expected to have a significant effect on the species composition of Pyrenean snowbed habitats, which probably will affect inter-species interactions, lead to some extinctions, and alter the biodiversity of the alpine communities in the Pyrenees.

CONCLUSIONS

This study examined the plant communities and their relationships to the physical factors of 32 snowbeds in the Andorran Pyrenees. Of the 85 species of vascular plants found in the snowbeds, 31 are characteristic of the high-mountain vegetation group and 21 are characteristic of the snowbed vegetation group. Average richness per snowbed was 16 species, which was similar to the values in snowbeds in other Iberian mountain ranges. Species diversity was highest in snowbeds on south-facing slopes, where species of the *Salicetea herbaceae* class predominated. Those species occurred at intermediate snow cover sites at intermediate elevations and they have the potential to colonize snowbeds at higher elevations, but habitat availability and the dynamics of inter-specific competition will influence their success (particularly, on well-developed soils).

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CAPÍTOL 4: Habitat specific factors increase functional diversity in snowbed plants communities

Habitat-specific factors increase functional diversity in snowbed plant communities

ABSTRACT

Functional diversity, the diversity in species traits that influences community structure and ecosystem function, is helpful in understanding the effects of environmental constraints on ecosystem functioning; however, very few studies have established the relationships between functional diversity indices and environmental constraints.

In this study, we measured environmental variables and plant traits within 32 snowbeds in the Pyrenees Andorra. In addition, we measured the traits of plant species along a snowmelt gradient in 72 plots that included early- snowmelt isoclines and late-snowmelt isoclines. Snowbeds on late snowmelt isoclines and on early snowmelt isoclines differed significantly in mean plant traits.

To identify the community assembly rules, we used three independent functional diversity indices: functional richness, functional evenness, and functional divergence, which coupled with complementary measures (phylogenetic and taxonomic diversity), provided insights into how habitat environmental constraints influence biodiversity. Habitat-specific factors enhanced the functional diversity of the snowbed plant communities in the Pyrenees because a variety of environmental factors and stressful conditions of the habitat provide for multiple uses of the functional space.

KEYWORDS: snowbeds, functional diversity, functional traits, Pyrenees, climate change.

INTRODUCTION

Functional diversity, which is the diversity in species traits that influences community structure and ecosystem function (Schleuter et al. 2010), provides insights into the composition and stability of plant communities and the effects of environmental factors on ecosystem functions such as productivity (Petchey et al 2004, Hooper et al 2005) and resilience after perturbation (Bellwood et al 2004). In addition, Villérger et al. (2008) suggested that functional diversity provides a means of quantifying the distribution of functional units within a multidimensional space. Recently, functional diversity has become an important descriptor of species assemblages in the study of ecosystem functioning (Pakeman 2011); however Mason et al. (2005) argued that functional diversity cannot be expressed as a single number and they recommended dividing functional diversity into three complementary components: functional richness (FRic), functional evenness (FEve), and functional divergence (FDiv). Mouchet et al. (2010) and Villéger et al. (2008) demonstrated that the combination of those indices provides a robust means of assessing the effects of trait diversity on ecosystem processes. Furthermore, those indices meet the following important criteria: (1) can assess multiple traits, simultaneously, (2) takes into account species abundances, and (3) measures all of the facets of functional diversity (Villérger 2008). Those indices coupled with complementary measures (phylogenetic and taxonomic diversities) help to understand how environmental factors influence biodiversity and ecosystem processes, and they might be suitable indicators of the dynamics that drive community assemblages. Few studies have evaluated functional diversity across environmental gradients (Pakeman 2011).

Functional traits, environmental factors (Cornwell & Ackerly 2010, Pakeman et al. 2011, Katovai et al. 2012), and ecosystem functioning (Hooper et al. 2005, McGill et al. 2006, Laliberté et al. 2010) can be correlated; however, the relationships have not been evaluated at length on a local scale (i.e., comparing local site-specific factors within a given habitat). Wright et al. (2004) identified intraspecific variation caused by plastic differentiation in functional traits at a local scale which was influenced by environmental factors. The functional trait responses of plants] to site-specific factors, which are influenced by species plasticity, can lead to changes in biodiversity and species phenologies (Kudo and Hirao, 2006, Domènech et al. submitted). In this study, we evaluated the plasticity of some of the species in the snowbeds in Andorra.

The distribution of snow, which tends to be highly conservative, has a significant effect on alpine vegetation; however, the timing of annual snowmelt is highly variable (Körner 2003), which leads to high variation in the site-specific factors that can influence snowbeds. For that reason, in the *Arctic Climate Change Impact Assessment* (ACIA 2005), snowbed habitats were regarded as particularly vulnerable because the plant species in those habitats cannot persist in other alpine habitats. Snowbed species are unable to invade other plant communities such as fellfields, but fellfield species can survive in snowbed environments (Shimono and Kudo 2003). In snowbed habitats, the plants are under snow for most of the year and the growing season is very short, and the timing of snowmelt has a significant effect on the ecology of snowbeds. In alpine regions, within a few meters of the snowbeds, the vegetation differs dramatically because of the absence of snow cover and the species there have to be adapted to freezing temperatures. In those areas, in the face of increasing global temperatures, the species in fellfields have the potential outcompete snowbed species (Lluent 2007, Schöb et al. 2009). In the Alps and in the Scandes, the vegetation in snowbeds has changed (Schöb et al. 2009, Grabherr 2003, Virtanen 2000) and, in most cases, the coverage of grass species has increased (Nagy 2006).

The Iberian side of the Pyrenees is the southern limit of the ranges of several arctic, alpine, and orophytic plant species, which occur in isolated populations within a narrow strip of land] (Tomaselli 1994, Bolòs et al. 2005). Although the strip is within a mountain range, the climate has a strong Mediterranean influence. In the Mediterranean region in general (Kuglitsch et al. 2010), and in the Andorran Pyrenees (Esteban et al. 2009), specifically, surface temperatures have increased significantly over the last 50 years. An increase in temperature is likely to have significant effect on the species diversity and functional diversity of the snowbed habitats in the Andorran Pyrenees (Esteban et al. 2009) and, in particular, the effects might be greatest in species that are adapted to alpine conditions. The future of snowbed habitats in the Pyrenees will depend on the capacity of the species in the snowbed community to persist in the face of a changing environment. To be able to predict the future of snowbed habitats, it is necessary to understand better the relationships between environmental constraints, functional diversity, and species traits.

In this study, we addressed the following questions: (1) which traits best define the plant species that predominate in snowbeds in Andorra? (2) Do site-specific factors affect the intraspecific plasticity of snowbed species? (3) Which environmental factors are significantly correlated with the traits of species in Andorran snowbeds? (4) Can functional diversity explain the similarities or dissimilarities between the traits of coexisting species, (5) Do three functional indices identify the relationships among environmental factors, plant traits, species abundances, and ecosystem functioning?, and (6) Do site-specific factors enhance functional diversity in Pyrenean snowbed habitats?

METHODS

Study site

In an earlier study, 32 snowbeds (mean elevation = 2.454 m a.s.l.) (Table 1) in northern Andorra (on the Iberian side of the Pyrenees) were surveyed and characterized (Figure 1) (Domènech et al. submitted).

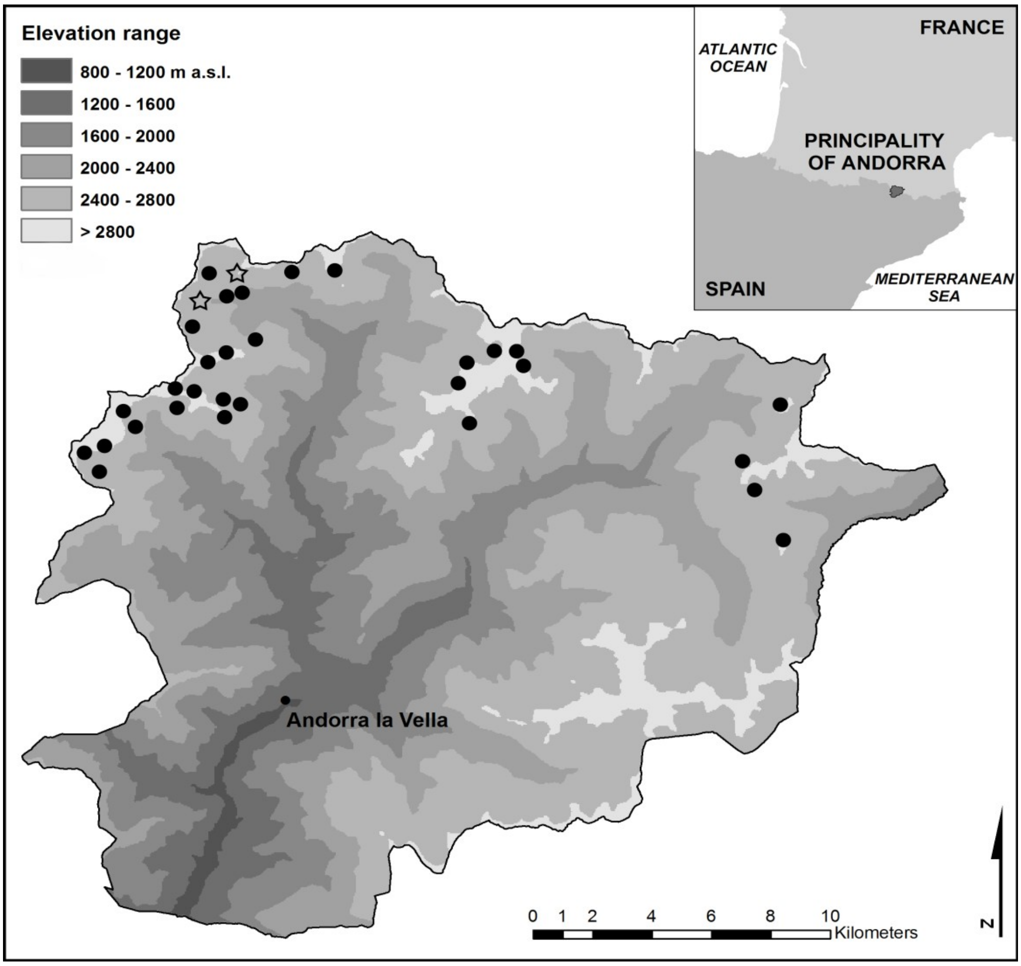

Figure 1. Locations of 32 snowbeds (black dots) in the Andorran Pyrenees. Open stars indicate the two snowbeds (snowbeds 6 and 9) from which plants were collected for the measurement of some functional traits.

The snowbeds were exposed to the same microtopographic conditions; specifically, all were on undisturbed (neither frost upheaval nor livestock grazing), concave surfaces. Slate, clay, and conglomerates from the Cambro-Ordovician periods were the most abundant geological materials.Domènech et al. (submitted) provided the criteria upon which each snowbed was assigned to one of three groups based on the duration of snow cover: low snow cover (LSC), intermediate snow cover (ISC), or high snow cover (HSC). The criteria were derived from a detailed map of the Andorran snowbeds detected in aerial photographs that were taken in the summers of 1948, 1972, 1995, and 2003 (www.sigma.ad). High snow cover (HSC), intermediate snow cover (ISC), and low snow cover (LSC) snowbeds were those that occurred in the aerial photographs in three or four of the years (34,4%), in two of the years (53,1%), and in one of the years (12,5%), respectively. Most of the snowbeds were on southern (43,7%) or northern (34,4%) slopes. In 1971-2000, the average annual air temperature in summer among the snowbeds was 3,8ºC (http://opengis.uab.es). In 2011, the average vegetation cover was ~ 52%, and the snowbeds contained 85 vascular plants and 16 bryophytes (Domènech et al. submitted).

Environmental conditions

In an earlier study (Domènech et al. submitted), the snowbeds were characterized based on elevation, temperature, snow cover (low, intermediate, or high), exposure (southern, flat, or northern), and soil type [inexistent organic matter (IOM), almost non-existent organic matter (ANEOM) (depth <1 cm), and organic matter depth $\geq$1 cm (OM)] (Table 1).

Vegetation surveys

The vegetation in each of the snowbeds was surveyed once (Domènech et al. submitted), and the surveys included the number of species and the abundance of each species in each snowbed. Plants species identification and nomenclature followed Bolòs et al. (2005).

Table 1. Physiographic and climatic conditions and plant diversity in 32 snowbeds in the Andorran Pyrenees. Soil types: IOM=inexistent organic matter, ANOM=almost non-existent organic matter (depth <1 cm), and OM=organic matter (depth ≥ 1 cm).

Snowbed	UTM Coordinates **X**	**Y**	Elevation (m)	Timing of snowmelt	Exposure	Temperature (ºC)	Soil type	Shannon Index	Species Richness	FRic	FEve	FDiv
Snowbed 1	537813,73	34466,26	2400	intermediate	north	14,73	IOM	1,81	15	0,19	0,58	0,81
Snowbed 2	537603,43	34405,83	2410	low	north	14,76	IOM	1,87	14	0,30	0,02	0,72
Snowbed 3	530265,88	38343,28	2300	intermediate	flat	15,1	OM	1,88	19	0,20	0,75	0,93
Snowbed 4	530466,63	38953,53	2350	intermediate	flat	14,69	IOM	1,62	8	0,02	0,85	0,60
Snowbed 5	530336,24	35583,75	2600	intermediate	north	12,99	IOM	2,20	13	0,23	0,64	0,76
Snowbed 6	530336,24	33583,75	2450	intermediate	north	12,99	ANOM	1,81	15	0,27	0,32	0,68
Snowbed 7	532380,1	38313,98	2325	intermediate	south	15,05	OM	1,89	13	0,24	0,47	0,86
Snowbed 8	534262,03	38826,92	2500	high	south	12,17	ANOM	2,07	14	0,34	0,49	0,68
Snowbed 9	527631,36	33702,19	2500	intermediate	south	13,51	ANOM	2,19	13	0,11	0,81	0,86
Snowbed 10	527266,6	33746,11	2650	high	south	12,56	ANOM	2,19	13	0,28	0,77	0,87
Snowbed 11	528977,76	33688,82	2500	intermediate	flat	14,18	ANOM	2,15	23	0,31	0,57	0,82
Snowbed 12	530386	34348,67	2300	intermediate	south	15,09	ANOM	2,51	15	0,41	0,06	0,72
Snowbed 13	547967,24	31648,84	2400	low	north	13,6	IOM	1,56	18	0,13	0,54	0,89
Snowbed 14	548587,44	31878,01	2410	low	north	13,88	IOM	2,21	15	0,27	0,40	0,74
Snowbed 15	529820,09	35569,38	2400	intermediate	north	13,45	IOM	1,90	10	0,11	0,45	0,79

Snowbed	UTM Coordinates		Elevation (m)	Timing of snowmelt	Exposure	Temperature (ºC)	Soil type	Shannon Index	Species Richness	FRic	FEve	FDiv
	X	**Y**										
Snowbed 16	537776,23	33147,13	2450	low	south	14,65	IOM	1,65	11	0,14	0,69	0,89
Snowbed 17	540239,06	35633,24	2550	low	south	13,2	ANOM	2,74	17	0,23	0,74	0,77
Snowbed 18	540418,28	35559,11	2480	intermediate	south	13,51	ANOM	2,59	19	0,15	0,63	0,77
Snowbed 19	540196,65	35595,97	2550	intermediate	south	13,2	IOM	2,27	15	0,14	0,62	0,78
Snowbed 20	539713,86	35829,85	2450	intermediate	flat	13,24	OM	2,34	19	0,21	0,39	0,78
Snowbed 21	526096,2	32228,85	2625	high	south	12,59	IOM	1,80	7	0,04	0,56	0,84
Snowbed 22	526234,66	32410,28	2650	high	flat	12,27	IOM	1,68	10	0,07	0,81	0,79
Snowbed 23	525777,12	31704,45	2500	low	south	13,79	ANOM	2,39	20	0,24	0,51	0,85
Snowbed 24	549261,7	27614,4	2570	low	north	13,36	OM	1,95	14	0,05	0,67	0,67
Snowbed 25	530870,21	38620,3	2460	intermediate	north	13,75	ANOM	2,43	14	0,51	0,62	0,78
Snowbed 26	531101,07	38952,63	2500	intermediate	flat	13,37	IOM	1,64	22	0,21	0,05	0,97
Snowbed 27	530682,48	38574,64	2410	low	flat	14,28	OM	1,92	20	0,20	0,15	0,98
Snowbed 28	548816,71	33806,89	2280	intermediate	north	14,75	ANOM	2,44	13	0,40	0,71	0,77
Snowbed 29	529227,01	36080,41	2540	low	south	13,36	ANOM	1,42	23	0,07	0,32	0,98
Snowbed 30	530246,14	34442,05	2350	intermediate	south	14,8	ANOM	2,56	18	0,39	0,43	0,87
Snowbed 31	529518,98	34482,49	2460	low	north	13,74	IOM	2,10	16	0,23	0,48	0,73
Snowbed 32	530571,63	34540,82	2300	low	south	15,28	OM	1,85	15	0,14	0,75	0,88

Data collection

Plant functional traits

The functional traits associated with plant strategies and reproduction were quantified in 25 plant species that were common to the 32 snowbeds (following the recommendations of Cornelissen et al. 2003). To identify the functional traits of each of the most common species, we used the Ecoflora, Leida Traitbase, Biopop, Biolflor, and Try Initiative databases, and Bolòs et. al (2005) (Table 2).

Table 2. Functional traits evaluated in snowbed plant communities in Andorra. Some traits have more than one source; in these cases, the result value was the average of the values of all of the sources.

Trait	Source of traits	Details of traits
Life form	Bolòs et al. (2005)	Categorical measures: hemicryptophyte graminoids, hemicryptophyte no graminoids, chamaephyte, therophyte
Life cycle	Bolòs et al. (2005) and Leda Traitbase	Categorical measures: perennial, annual
Growth form	Leda Traitbase and Biolflor	Categorical measures: basal, semi-basal, erect leafy, tussocks, dwarf shrubs, short succulents
Clonality	Ecoflora and Biolflor	Categorical measures: non-clonal, clonal aboveground, clonal belowground
Normal method of propagation	Biolflor and Ecoflora	Categorical measures: seed, seed and vegetative, vegetative
Pollination mode	Ecoflora, Biopop and Biolflor	Categorical measures: anemophyllous, insects, self, unspecialized zoophyllous
Corotype	Bolòs et al. (2005)	Categorical measures: Alpine (Alp.), Lateboreal subalpine (Latebor. Alp.), Pluriregional (Plurireg.), Boreo-subalpine (Bor. Alp.), South west european (SW-Europ.), Pyrenees wide distribution (Alp. Pyr..)
Height	Bolòs et al. (2005) and field measurements	Continuous measure: m
Specific leaf area	Leda Traitbase, Try Initiative and Laboratory measurements	Continuous measure: mm^2/mg
No. inflorescences	Measured in the laboratory	Continuous measure: no. infl.
No. inflorescences/stem	Measured in the laboratory	Continuous measure: no. infl./stem

In two of the snowbeds, we evaluated additional functional plant traits of the most common species (*Cardamine alpina*, *Gnaphalium supinum*, *Mucizonia sedoides*, *Poa alpina*, and *Sibbaldia procumbens*) (Table 1 and Table 5). *Sibbaldia procumbens* was very common in all of the snowbeds, except snowbed 6. The plants that were measured came from two of the snowbeds (snowbed 6, the “Arbella snowbed”, and snowbed 9, the “Cataperdis snowbed”) (Table 1), which had physiographic and climatic conditions that were similar to those in the other 30 snowbeds (see Domènech et al. submitted). To quantify the height (m), specific leaf area (mm^2/mg), number of inflorescences, and number of flowering stems of the 5 species, individuals were collected from an early snowmelt (ESM) isocline and a late snowmelt (LSM) isocline within each of the two snowbeds (10 individuals of each species at each of the four sites).

Plant height (m) (the distance between the highest photosynthetic tissue and the ground) was measured in the field at the end of the growing season. Plants that had large leaf rosettes, e.g., *Gentiana acaulis*, were measured to the top of the rosette leaves. Specific leaf area (mm^2/mg) (SLA), number of inflorescences, and number of flowering stems were measured in the laboratory. All of the plants were fully expanded and in the flowering phenophase. We collected 10 leaves per individual, which were collected with their branches, placed in plastic bags, and transported, immediately to the laboratory. The leaves were placed in water and removed individually, and the fresh mass and dimensions of each were recorded. Leaf area was calculated from images obtained using a desktop scanner and pixel-counting software (Rasband 2011). To calculate SLA, leaves were dried (usually, for 3 days) at 70 ºC until they reached a constant weight. The number of total inflorescences and the number of total flowering stems of each plant were calculated in the laboratory.

Data analysis

The relationships between snowmelt isocline on a local snowmelt gradient (LSM and ESM) and site (Cataperdis and Arbella snowbeds) on plant traits (specific leaf area, height, number Inflorescences, and number flowering stems) were evaluated in the following species: *Cardamine alpina*, *Mucizonia sedoides*, *Sibbaldia procumbens*, *Gnaphalium supinum*, and *Poa alpina*. The statistical analyses were based on the non-parametric Kruskall-Wallis Test.

Functional diversity was measured using three indices (Villeger et al. 2008): functional richness (FRic), functional evenness (FEve), and functional divergence (FDiv) because they can provide insights into various facets of the FD (Mouchet et al.

2010). FRic is the functional space occupied by the community (in this case, snowbeds). FEve is a measure of the regularity of the distribution of trait abundance within the functional space. FEve tends to be low when the functional space is irregularly occupied. FDiv describes the divergence in the distribution of species traits within a community, and a high FDiv indicates very dissimilar traits among the most abundant species and high niche differentiation among the species in a given habitat. FRic is independent of species abundance, but FEve and FDiv include relative species abundance, and values range from 0 to 1. FRic does not have an upper limit. The indices were computed using the *dfFD* function in the FD package (Laliberté and Shipley, 2011) in R version 2.14.0 (R Development Core Team 2011). Before being subjected to analyses, the functional traits data were transformed using the *gowdis* function (to compute the Gower Dissimilarity Matrix) because the variables were numeric, ordered, and factor, and NA's were present in the trait matrix.

Typically, phylogenetically analogous species share traits because they have a common evolutionary history, and they tend to occupy similar niches (Harvey and Pagel, 1991). In addition, phylogeny can distort measures of functional diversity because of a particular assemblage pattern (Mouchet et al, 2010, Spasojevic and Suding, 2011, in which case a "phylogenetic correction" can be applied (Desdevises et al, 2003). To prevent phylogeny from having an effect on he analyses of the similarities among the traits of species, the correlations between plant phylogenetic distance and plant functional distance were performed using a Mantel Test. The phylogenetic distances were obtained from the phylogenetic tree generated by Phylomatic (Webb and Donogue, 2005), and the mean pairwise distance between the 25 species was calculated using the function *cophenetic* in the picante package (Harvey et al, 2012). The functional distance between plants was based on the Gower Dissimilarity Matrix. A Mantel Test with 999 permutations was performed between the two matrixes and, because the correlation was not statistically significant (Z=17,30), no phylogenetic correction was used in the FD analyses.

To characterize the snowbeds and the traits of their plants, based on species abundance, functional diversity, and environmental factors, the data were subjected to a redundancy analysis (RDA). The factors included soil type, timing of snowmelt, exposure, temperature, plant traits (numerical and categorical), and functional diversity (FRic, Fdiv, and FEve). Categorical factors were converted into dummy variables. The species composition data were transformed using a logarithmic transformation. To test the significance of the axis, all of the species data were permuted using a global permutation test (Monte Carlo Test) with 999 permutations. All of the statistical analyses were performed using the CANOCO 4.5 software program, SAS 9.2 software, or R version 2.14.0.

RESULTS

General patterns in the traits of snowbed vegetation

In the snowbeds in Andorra, the most common life form was the hemicryptophyte life form (in terms of number of taxa and relative plant cover) and chamaephyte life forms (see Table 3 and 4). Most of the taxa and the plant cover were perennials that had semi-basal or basal leaves and clonal aboveground as their main form of clonality. The most common mode of propagation was by seed and vegetative propagation in the same plant. Insect and anemophyllous pollination were the most predominant modes of pollination. Although most of the taxa had insect pollination, the most abundant taxa had anemophyllous pollination. Boreo alpin and alpin (> 70%) were the most common corotypes (in diversity and in plant cover).

Table 3. Species in the plant communities in snowbeds in Andorra. Life form (hemicryptophyte non-graminoids (Hcng), hemicryptophyte graminoide (Hcg), chamephyte (Ch), therophyte (Th)), life cycle (perennial (P), annual (A)), Growth form (basal (b), semi-basal (sb), erect leafy (el), tussocks (t), dwarf shrubs (ds), short succulents (s)), clonality (non-clonal (nc), clonal aboveground (ca), clonal belowground (cb)), normal method of propagation (seed (se), vegetative (ve) and (seed and vegetative (seve)), Pollination mode (anemophyllous (ane), insects (in), self, unspecialized zoophyllous (zoo)), Corotype, height (m) and Specific leaf area (SLA) (mm2/mg).

Species	Life form	Life cycle	Growth form	Clonality	Method propagation	Pollination mode	Corotype	Height	SLA
Agrostis rupestris	Hcg	P	t	cb	se	ane	Alp.	0,125	15,50
Arabis alpina	Ch	P	sb	ca	se	in	Latebor. Alp.	0,3	26,32
Armeria maritima alpina	Hcng	P	b	nc	se	in	Plurireg.	0,225	16,42
Cardamine bellidifolia alpina	Hcng	P	sb	ca	se	in	Alp.	0,05	21,31
Carex pyrenaica	Hcg	P	t	cb			Plurireg.	0,15	17,97
Cerastium cerastoides	Ch	P	el	ca	seve	in	Bor. Alp.	0,1	26,13
Doronicum grandiflorum	Hcng	P	sb	cb	seve	in	Alp.	0,25	
Epilobium anagallidifolium	Hcng	P	el	ca	seve	self	Bor. Alp.	0,095	22,49
Festuca eskia	Hcg	P	t	cb	seve	-	Alp. Pirinenca	0,4	-
Gentiana acaulis	Hcng	P	b	ca	seve	in	Alp.	0,15	15,02
Gnaphalium supinum	Hcng	P	sb	cb	seve	self	Bor. Alp.	0,07	27,00
Hieracium gr. *pilosella*	Hcng	P	b	cb	seve	in	SW-Europ.	0,175	19,25
Jasione crispa	Ch	P	sb	cb	-	-	Plurireg.	0,075	-
Leucantemopsis alpina	Hcng	P	sb	cb	seve	in	Alp.	0,125	15,73
Mucizonia sedoides	Th	A	s	nc	se	in	Plurireg.	0,04	15,58
Murbeckiella pinnafitida	Hcng	P	sb	-	-	-	Alp.	0,125	-
Nardus stricta	Hcg	P	t	cb	ve	ane	Bor. Alp.	0,25	11,09
Oreochloa disticha	Hcg	P	t	cb	se	ane	Alp.	0,175	9,20
Phyteuma hemisphaericum	Hcng	P	sb	ca	seve	in	Alp.	0,09	-
Poa alpina	Hcg	P	t	ca	seve	ane	Bor. Alp.	0,25	18,80

Species	Life form	Life cycle	Growth form	Clonality	Method propagation	Pollination mode	Corotype	Height	SLA
Salix herbacea	Ch	P	ds	cb	ve	zoo	Bor. Alp.	0,175	19,54
Sedum alpestre	Ch	P	s	ca	seve	in	Alp.	0,05	14,10
Sibbaldia procumbens	Hcng	P	sb	cb	seve	in	Bor. Alp.	0,035	15,96
Trifolium alpinum	Ch	P	sb	cb	seve	zoo	Alp.	0,085	17,38
Veronica alpina	Hcng	P	el	ca	seve	self	Bor. Alp.	0,1	26,58

Table 4. Proportions (%) of traits in the snowbed vegetation in the Andorran Pyrenees.

Categorical functional traits	Classes present in vegetation surveys	Proportion of number of taxa (%)	Relative cover (%)
Life form	Hemicryptophyte graminoide	24	48,38
	Hemicryptophyte no graminoide	48	32,36
	Chamaephyte	24	17,47
	Therophyte	4	1,77
Life cycle	Perennial	96	98,23
	Annual	4	1,77
Growth form	Basal	12	4
	Semi-basal	40	35,35
	Erect leafy	12	4,27
	Tussocks	24	48,38
	Dwarf shrubs	4	4,21
	Short succulents	8	3,77
Clonality	Non-clonal	8.33	3,84
	Clonal aboveground	37.5	17,57
	Clonal belowground	54.16	78,57
Normal method of propagation	Seed	28.57	23,09
	Seed and vegetative	61.90	46,40
	Vegetative	9.52	30,50
Pollination mode	Anemophyllous	20	38,41
	Insects	55	16,66
	Self	15	15,06
	Unspecialized zoophyllous	10	29,86
Corotype	Alp.	40	37,71
	Latebor. Alp.	4	0,26
	Plurireg.	16	3,59
	Bor. Alp.	32	46,20
	SW-Europ.	4	7,07
	Alp. Pyr.	4	5,17

Relationships between site-specific factors and intraspecific plant traits in snowbeds

Cardamine alpine, *Gnaphalium supinum*, and *Mucizonia sedoides* did not differ significantly between ESM and LSM isoclines; however, the height and number of inflorescences of *C. alpina*, *M. sedoides*, and *Poa alpina* were greater in the Cataperdis snowbed (snowbed 9) than they were in the Arbella snowbed (snowbed 6) (Table 5). The height and number of inflorescences of *Poa alpina* and *Sibbaldia procumbens* were differed significantly between snowmelt isoclines. In those species, the number of flowering stems and number inflorescences were significantly higher in LSM isoclines than they were in the ESM isoclines. *P. alpina* were tallest in the ESM isoclines, and *S. procumbens* were tallest in LSM isoclines. The SLA of *C. alpina*, *S. procumbens*, *G. supinum,* and *M. sedoides* did not differ between snowmelt isoclines and sites, but the SLA of *P. alpina* differed significantly between the two snowbeds.

Table 5. General Linear Model of numerical plant traits with each of the explanatory factors: timing of snowmelt (late snowmelt (LSM) isoclines and early snowmelt (ESM) isoclines and site (Cataperdis and The Arbella snowbeds) in Andorra. *Mucizonia sedoides* has one flowering stem. To test for significant differences in species traits we used Tukey's HSD Comparisons Test. Traits values are the mean measured in the summer 2011. P-values for significant terms are indicated in bold.

Numerical plant traits		**Timing of snowmelt**				**Site**			
		Chi-value	**P-value**	**Values from LSM sites**	**Values from ESM sites**	**Chi-value**	**P-value**	**Values from C**	**Values from A**
Cardamine alpina	Height (m)	1,87	0,1713	0,0385	0,0462	**8,89**	**0,002**	0,0537	0,0310
	Specific leaf area (mm^2/mg)	0,02	0,8711	23,07	22,81	0,57	0,4488	22,11	23,77
	No. inflorescences	2,43	0,188	6,60	8,57	**6,85**	**0,008**	9,94	5,30
	No. Flowering stems	0,10	0,7469	1,65	1,78	0,19	0,6559	2,00	1,45
Gnaphalium supinum	Height (m)	0,00	0,9675	0,0480	0,0512	**10,08**	**0,001**	0,0622	0,0370
	Specific leaf area (mm^2/mg)	0,53	0,4652	26,34	27,19	2,54	0,1105	27,76	25,77
	No. inflorescences	**3,77**	**0,049**	7,40	5,60	0,80	0,3706	10,05	4,75
	No. Flowering stems	0,37	0,5398	2,10	2,40	**6,37**	**0,011**	3,12000	1,50
Mucizonia sedoides	Height (m)	2,01	0,1471	0,0255	0,0342	**9,13**	**0,002**	0,0362	0,0235
	Specific leaf area (mm^2/mg)	0,32	0,5700	15,29	16,65	0,65	0,4171	16,00	15,94
	No. inflorescences	1,36	0,2423	3,50	3,80	**5,02**	**0,024**	4,10	2,90
	No. Flowering stems	-	-	-	-	-	-	-	-
Poa alpina	Height (m)	**4,29**	**0,038**	0,169	0,297	**14,07**	**<0,001**	0,031	0,0149
	Specific leaf area (mm^2/mg)	1,05	0,3037	29,83	25,31	**22,18**	**<0,001**	33,14	22,08
	No. inflorescences	**10,12**	**0,001**	83,10	31,90	**4,06**	**0,043**	92,10	22,90
	No. Flowering stems	1,09	0,2960	3,85	1,50	3,80	0,051	3,85	1,50
Sibbaldia procumbens	Height (m)	**6,29**	**0,012**	0,038	0,025	-	-	-	-
	Specific leaf area (mm^2/mg)	0,20	0,6501	14,55	14,94	-	-	-	-
	No. inflorescences	**9,60**	**0,001**	107,90	31,30	-	-	-	-
	No. Flowering stems	**5,51**	**0,018**	27,90	7,30	-	-	-	-

Relationships between functional diversity, environment factors, and plant traits

The first two components of the RDA explained 29,9% of the variance in the species data, environmental factors, functional diversity, and plant traits (Figure 2). The first canonical axis (F-ratio=0,982; P-value=0,032) and all canonical axes combined (F-ratio=1,605; P-value=0,008) were statistically significant. FDiv was highest on northern and flat exposures and, to a lesser extent, associated with high temperatures and soils that had consistent organic matter. Height had the highest values along with anemophyllous pollination mode and specific leaf area (SLA) and, to a lesser extent, with the tussock growth form and vegetative mode of propagation. In contrast, FEve was strongly correlated with high snow cover (HSC) and, to a lesser extent, the highest elevations, non-graminoid hemicryptophyte life form, and self-pollination, and inversely correlated with temperature and SLA. FRic was positively correlated with intermediate snow cover (ISC) isoclines, almost non-existent organic matter (ANEOM), and elevation. Species those are typical of snowbed habitat (which belong to *Salicetea herbacea* class) such as *Cardamine alpina*, *Cerastium cerastoides*, *Sedum alpestre*, and *Poa alpina* predominated in this abiotically constrained group. Species richness was weakly correlated with Fric, the joint seed and vegetative mode of propagation and, to a lesser extent, self-pollination.

Low snow cover (LSC), high temperature, and soils that had consistent organic matter occupied one functional space, which was correlated with high SLA, the predominance of chamaephyte life forms, below-ground clonality, and an unspecialized zoophyllous pollination mode. Species typical of high mountain grasslands, e.g., *Trifolium alpinum*, *Hieracium pilosella*, and *Gentiana acaulis* were common and FEve was lowest in that combination of abiotic conditions. The second functional space was strong correlated with northern exposures and high temperatures, and was dominated by anemophyllous pollination, hemicryptophyte graminoid life forms, tussock growth forms, and the tallest plants within species. In that functional space, species from high mountain grasslands, e.g., *F. eskia* or *N. stricta* predominated. Poor organic soils, high elevation, high snow cover, and low temperatures occupied the third functional space, which had the highest FEve and FRic. In that space, species typical of snowbed communities (*Salicetea herbacea* class) predominated.

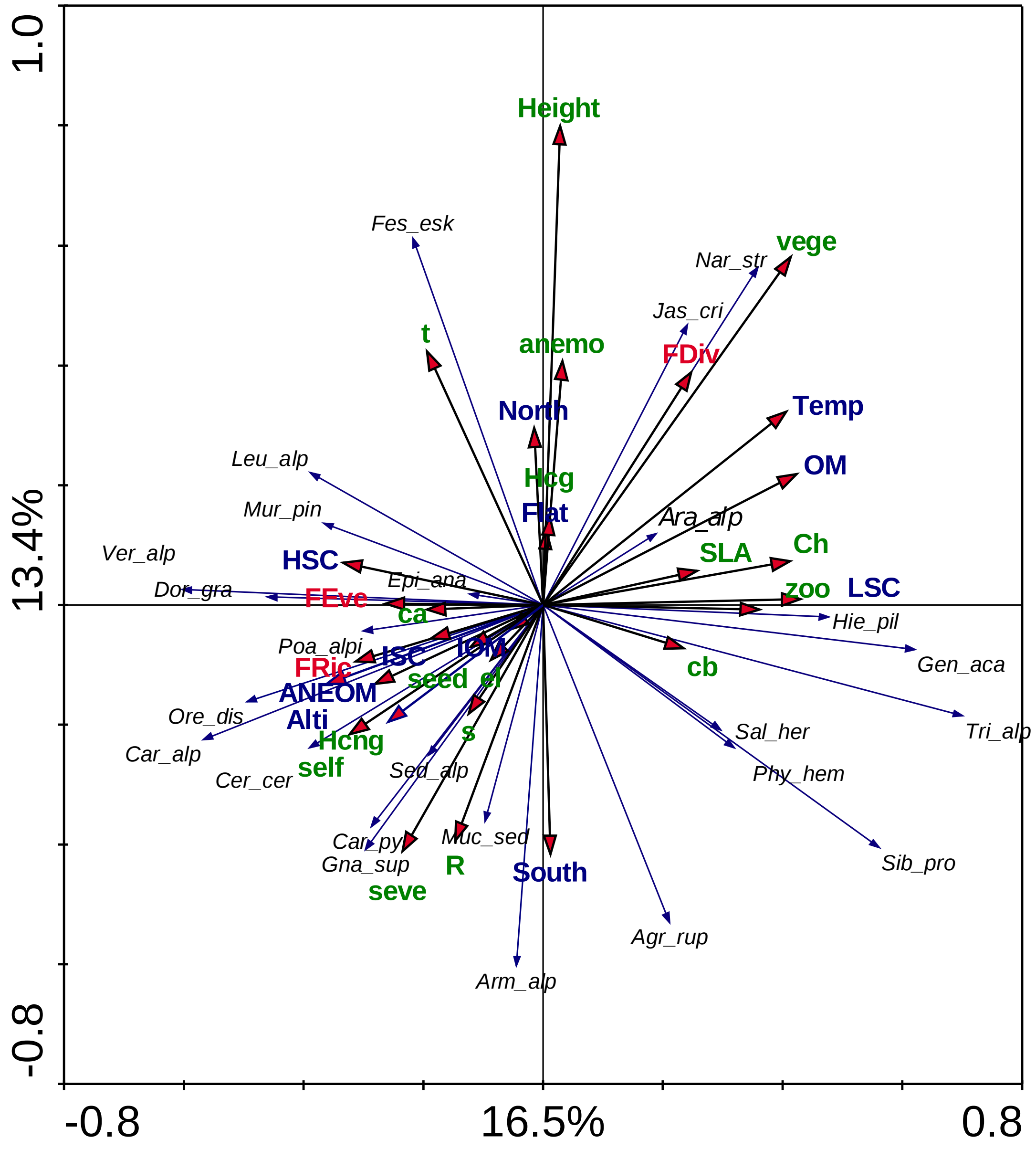

Figure 2. Redundancy Analysis (RDA) (constrained linear ordination method) of the environmental variables (elevation (Alti). snow cover (high (HSC). intermediate (ISC) and low (LSC)). exposure (northern. southern and flat). temperature (temp). and soil type (IOM. ANEOM. OM). species richness (R). Functional diversity (FDiv. FEve and FRic). functional traits: life form (hemicryptophyte no graminoide (Hcng). hemicryptophyte graminoide (Hcg). chamephyte (Ch). therophyte (Th)). growth form (basal (b). semi-basal (sb). erect leafy (el). tussocks (t). dwarf shrubs (ds). short succulents (s)). clonality (non-clonal (nc). clonal aboveground (ca). clonal belowground (cb)). normal method of propagation (seed (seed). vegetative (vege) and (seed and vegetative (seve)). Pollination mode (anemophyllous (anemo). insects (in). self. unspecialized zoophyllous (zoo)). height and specific leaf area (SLA). and all the species of the samples: Agr_rup (*Agrostis rupestris*). Ara_alp (*Arabis alpina*). Arm_alp

(*Armeria maritima alpina*) Car_bel (*Cardamine alpina*). Car_pyr (*Carex pyrenaica*). . Cer_cer (*Cerastium cerastoides*). Dor_gra (*Doronicum grandiflorum*). Epi_ana (*Epilobium anagallifolium*). Fes_esk (*Festuca eskia*). Gen_aca (*Gentiana acaulis*). Gna_sup (*Gnaphalium supinum*). Hie_pil (*Hieracium* gr. *pilosella*). Jas_cri (*Jasione crispa*). Leu_alp (*Leucantemopsis alpina*). Muc_sed (*Mucizonia sedoides*). Mur_pin (*Murbeckiella pinnatifida*). Nar_str (*Nardus stricta*). Ore_dis (*Oreochloa disticha*). Phy_hem (*Phyteuma hemisphaericum*). Poa_alp (*Poa alpina*). Sal_her (*Salix herbacea*). Sed_al (*Sedum alpestre*). Sib_pro (*Sibbaldia procumbens*). Tri_alp (*Trifolium alpinum*) and Ver_alp (*Veronica alpina*).

DISCUSSION

Patterns in plant traits in Andorran snowbeds

In the Andorran snowbeds, where the growing season is very short (Bolòs et al. 2005), hemicryptophyte life forms predominated (> 70% of taxa and plant cover). Chamaephyte life forms, which were somewhat common in Andorran snowbeds (24% of taxa and 17% of plant cover), might have been favored by low perturbation regimes (e.g., grazing), which enable plants to maintain their perennial structures above ground for many years (Illa et al. 2006, Gerbol et al 2000). *M. sedoides* was the only annual species, although it can be a perennial (Lluent 2007).

Plants that have semi-basal leaves or a tussock growth form predominated in the snowbed vegetation, and dwarf shrubs and short succulents were minor groups. Plants that have semi-basal leaves and tussocks might gain protection against freezing temperatures and might be able to store detritus-bound nutrient pools and moisture and harbor microbial life (Körner 2003), which might help plants adapt to poor soils, which are common in snowbeds (Björk et al. 2007).

Seed and vegetative reproduction in the same plant was the most common mode of propagation. Inter-annual variation in climate, which is very marked in the mountain belt with Mediterranean influence (Tomaselli 1991), might affect plant strategies. In that region, plants have to cope with inter-annual differences in the length of the growing season, temperatures, and precipitation. Species that use both seed and vegetative propagation increase the probability that they will establish populations in that habitat.

Most of the species used insect pollination, but species that used anemophylous pollination contributed the most to the plant cover, which might have been because of the fewer insects at high elevations (Mosquin 1966). Therophyte life forms, succulents, and dwarf shrubs appeared to be unsuited to snowbed conditions.

Relationships between site-specific factors and intraspecific plant traits in snowbeds

Most (e.g., *S. procumbens*, *P. alpina*, and *G. supinum)*, but not all (e.g., *C. alpina* and *M. sedoides)* of the species exhibited intraspecific plasticity adaptations to site-specific factors, especially timing of snowmelt, which reflects the capacity of some species to acclimatize to changes in environmental conditions (e.g., changes in inter-annual climate variation. *C. alpina* and *M. sedoides*, however, might have traits that have not yet adapted to changes in the environmental. For example, *M. sedoides*, produces many seeds, which gives it the capacity to colonize other areas. In addition, *C. alpina* was one of the species that reached peak flowering early. If that is normal, that species could cope with inter-annual variation in climate without much plasticity. In general, intraspecific plasticity was species-specific.

All of the species, except *S. procumbens*, exhibited intraspecific plasticity adaptations. Overall height and number of inflorescences were the traits that exhibited the highest plasticity, especially at LSM sites and in the Cataperdis snowbed (snowbed 9). The shifts in intraspecific traits might affect the response of functional diversity to changes in environmental conditions of a community. Some species will respond with plasticity and others will not. Therefore, quantifying that functional plasticity should be integrated in the multifunctional space habitat.

Relationship between functional diversity and the environment

As in snowbeds elsewhere (Grime 2006, Spasojevic and Suding 2011), in the snowbeds of Andorra, the functional diversity reflected the importance of assembly processes in limiting similarity and facilitating among functional plants traits. In our study, the highest FDiv occurred in the least stressful abiotic conditions (high temperature, low elevation, and organic soils, which reflected an increase in the competition between species for light or in facilitation. The high plant height and specific leaf area (SLA) and FDiv were weakly correlated, which reflects a response by plants to competition for light. Hemicryptophyte graminoids from high mountain grasslands predominated under those conditions and, therefore, anemophillous pollination and vegetative propagation were the most common traits.

Functional Evenness (FEve) was highest in sites that had stressful abiotic conditions (high snow cover and elevation and low temperatures and low presence of organic soils). Species abundances were concentrated within a small portion of the functional gradient, which reflects a high degree of habitat filtering (Mouchet et al. 2010, Pakeman et al. 2011). In addition, the inverse correlation between FEve and FDiv suggests that abiotic filtering might reduce functional divergence and productivity through a reduction in high standing biomass (low SLA, and plant height and Feve correlated). Pakeman et al. (2011) found that a reduction in standing biomass was correlated with an increase in FEve. Non-hemicryptophyte graminoids, short plants that have low SLA, specifically, typical snowbed species (in the *Salicetea herbaceae* class) predominated under those conditions.

As it has been noted in Pakeman et al. (2011) work, in the Andorran snowbeds FRic and productivity (above ground biomass) were negatively correlated.

The combination of three independent indices provided a means of examining the mechanisms that link biodiversity to ecosystem functioning. Specifically, this study showed that FEve indicated strong pressure by environmental filters and FDiv indicated a shift in the intensity of competitive interactions (see also Cornwell et al. 2006, Mason et al 2007, 2008). Thus, habitat-specific factors enhanced functional diversity in snowbed plant communities in the Pyrenees because of a variety of environmental factors and stressful conditions that provide the basis for multiple uses of the functional space, which might lead to an increase in the capacity of snowbed ecosystems to respond to perturbations, specifically, changes in climate because functional divergence increases at high temperatures and low snow cover. The results from using functional diversity indices in Pyrenean snowbeds argue for the use of functional diversity as an indicator of processes that drive community assembly. The functional diversity in Andorran snowbeds, like snowbeds elsewhere (see Grime 2006, Spasojevic and Suding 2011), indicated the importance of assembly processes in limiting similarity and conducting facilitation among different and facilitating among functional plants traits.

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CONCLUSIONS

In 32 snowbeds in the Andorran Pyrenees, (1) the most relevant plant traits were perennial plants with chamaephyte life forms that exhibited semi-basal and basal leaves, and clonal aboveground as its main type of clonality, and had insect and anemophyllous pollination, (2) site-specific factors has caused shifts in intraspecific plant traits, (3) specific leaf area and chamaephyte life form were strongly associated with high temperatures, low elevations, low snow cover, and the presence of the organic soils, while hemicryptophyte non-graminoid life forms and aboveground clonation were associated low temperatures and high elevations, high snow cover, and non-organic soils), and (4) FRic, Feve, and FDiv helped to understand the complex relationship between biodiversity and environment factors in Andorran snowbeds. FEve indicated a strong pressure by environmental filters in most snowed and coldest snowbeds, and FDiv indicated a shift in the intensity of competitive interactions in the lowest, least snowed and warmest snowbeds. Thus, site-specific factors enhanced functional diversity in the snowbeds plants communities in the Pyrenees because of the variety in environmental factors and the stressful conditions there that provide the opportunity for multiple uses of the functional space.

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CAPÍTOL 5: Site-specific factors influence the richness and phenology of snowbed plants

Site-specific factors influence the richness and phenology of snowbed plants

ABSTRACT

Although the timing of snowmelt and growth temperature appears to be the main factors that influence the species richness and phenology of snowbed plants, site-specific characteristics might play a role in modifying the effects of the timing of snowmelt and temperature. In this study, the effects of site-specific factors on species richness and plant phenology were evaluated in 72 plots in two snowbeds in the Andorran Pyrenees. Snowmelt patterns influenced the spatial distribution of species richness and abundance. Site-specific factors had significant effects on the responses of species (shortening or lengthening the duration of the phenophase) and on the extent to which the timing of snowmelt influenced leaf expansion and flowering. Notably, the highest rates of leaf expansion occurred at the late snowmelt isoclines, where on the contrary, the period to reach peak flowering was significantly longer than in the early snowmelt isoclines. The results of this study highlight that in addition to the effects of inter-annual variability in climate, site-specific factors can have a significant effect on the phenology and reproductive success of the most common plants in the snowbed communities of the Pyrenees.

KEYWORDS: snowbeds, phenology, Andorra, especies richness, Pyrenees, climate change.

INTRODUCTION

Climate change is a threat to alpine plants (Theurillat and Guisan 2001, Grabherr 2003, Huelber et al. 2006), especially, those that depend on snow cover for protection against harsh weather (Schöb et al. 2009, Björk and Molau 2007, Nagy 2006) such as snowbed plants. Global circulation models have forecasted an increase in temperatures of between 1.4 ºC and 5.8 ºC (IPCC 2007) during the 21st Century. In the Pyrenees, the average annual temperature is expected to increase by 2.5 to 5 ºC (AEMET 2008). Ambient temperature has a significant effect on the timing of snowmelt and most studies have reported reductions in or the disappearance of snow cover in alpine habitats (EEA 2004, Stanton et al 1994, Walker 1993, Beniston et al. 2003, Muñoz et al. 2007).

Numerous studies related the influence of the timing of snowmelt and the temperature over the richness and plant cover plants in snowbeds (Lluent 2007, Orjan Totland et al 2002, Hülber et al. 2011). Climate change effects will probably modify the current physical conditions of snowbed habitats (for example timing of snowmelt and temperature), affecting richness and plant cover there.

The timing of snowmelt (Galen and Stanon 1995, Körner 2003, Hülber et al. 2010, Hülber et al. 2006, Totland and Alatalo 2002) and the temperature during the growing season (Kudo and Hirao 2006, Molau et al. 2005, Hülber et al. 2006, Körner 2003) have a significant effect on plant development and phenology in alpine snowbeds. Although those factors appear to have the greatest influence on the phenology of snowbed plants, site-specific factors might modify (exacerbate or diminish) the effects of the timing of snowmelt and temperature. Few studies have examined the influence of site-specific factors such as microtopography and snow origin on the phenology of alpine plants (Kudo and Hirao 2006, Hülber et al. 2010, Lluent 2007). Locally, the effects of climate change might be distributed unevenly and the intensity might differ among snowbeds depending on site-specific conditions.

To gain a full understanding of the impacts of climate change on the cover, the richness and the phenology of alpine plants of snowbed communities, it is important to know whether changes in phenologies and variations in patterns of species richness can be attributed to site-specific factors. Those issues are particularly important on the Iberian side of the Pyrenees, where global warming is predicted to have a specially significant effect (Lluent 2007), and where snowbeds are being reduced and disappearing as the range of the Mediterranean climate expands (Tomaselli 1991).

Furthermore, the Pyrenees are at the southern limit of the distribution of most of the snowbed alpine plants and, therefore, the snowbed habitat of these mountains is particularly vulnerable to the effects of climate change.

In this study, we addressed the following specific questions: How do site-specific factors influence plant cover and species richness in snowbeds? Do site-specific factors influence the date of snowmelt and the microclimate in snowbeds? Do the effects of snowmelt on plant phenology (leaf expansion and flowering) differ between early and late snowmelt sites? Do the phenologies of snowbed plant species differ in their responses to the timing of snowmelt?

METHODS

Study site

The study was conducted in two snowbeds in the northwest of the alpine region of Andorra: the Cataperdis snowbed (1º 28' 48.1079''; 42º 37' 1.7774'') at an elevation of 2525 m.a.s.l., and the Arbella snowbed (1º 29' 24.1448''; 42º 39' 3.2380'') at an elevation of 2475 m (Figure 1).

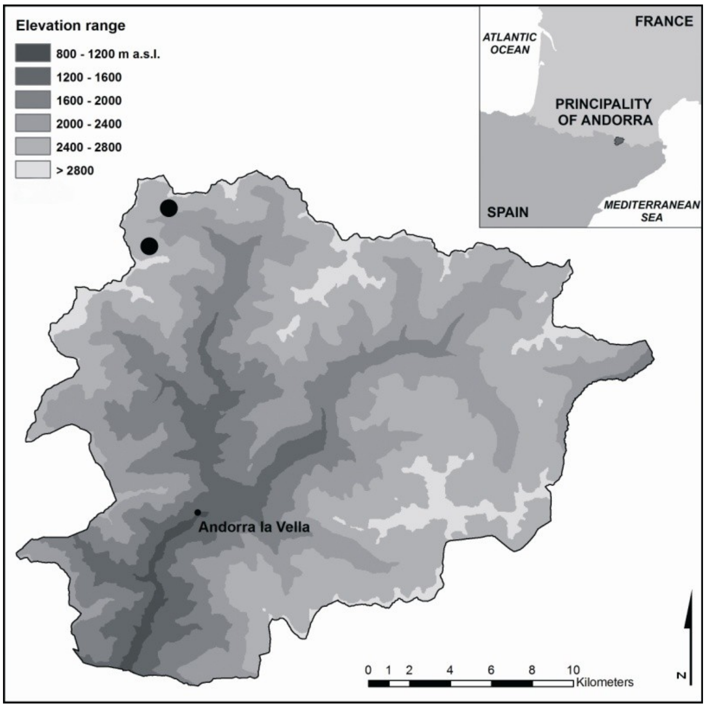

Figure 1. Location of the two snowbeds in the Andorran Pyrenees (black dots).

The soils are acidic and on gneiss, granodiorite, or granite rock, and the snowbeds have the same geological substrata; however, they differ in the origin of the snow. Cataperdis accumulates snow primarily because of the topography and the Arbella snowbed accumulates snow from avalanches. The Cataperdis and the Arbella snowbeds have slope aspects of 15-22 (degrees) and 20-30 (degrees), respectively. The snowbeds had continuous snowmelt gradients from concaves form to moderately exposed slopes. The area has a cold continental climate with a Mediterranean influence. In the Central Pyrenees (Andorra), 2009 was warm and dry, 2010 was cold and wet, and 2011 was warm and wet (Servei Meteorològic de Catalunya, 2012).

Data collection

In 2009, we established 36 permanent plots (50*50 cm) in each of the two snowbeds: 12 each on late-snowmelt (LSM) isoclines, intermediate-snowmelt (ISM) isoclines, and early-snowmelt (ESM) isoclines. All of the 12 plots were within a 20-m^2 area. To monitor snowmelt patterns, since 2009, the snowbeds have been visited weekly in Jun, Jul, and Aug.

In 2010 and 2011, the timing of snowmelt was documented for the 72 plots. We assumed that the growing season was the period between snowmelt and the next snow period.

Temperature data loggers (n=6) (Temperature logger i-button-Maxim Integrated Products, Sunnyvale, USA, range -40º to +85º) were placed on each of the three isoclines in each snowbed. From June 2010 to October 2011, readings were taken at the soil surface at 3-h intervals.

Species and plant cover

During the growing season from early Jul to early Oct, the plant species and the amount of plant cover of all of the vascular plants and bryophytes in each plot were recorded weekly (14 times per year). The main plant phenological sequences of each species were recorded weekly throughout the growing season, which included the two following phenophases: cessation of leaf expansion and main peak flower opening. In addition, we documented the abundance of the four most common species that occurred in both of the snowbeds; viz., Sedum *alpestre*, *Mucizonia sedoides*, *Gnaphalium supinum,* and *Poa alpina*. Plants species identification and nomenclature followed Bolòs et al. (2005).

Data analysis

The factors affecting timing of snowmelt (days since snowmelt ended) and accumulated temperature during the growth period (ºC) were evaluated separately using a General Linear Model procedure, with year (2010 and 2011), site (Cataperdis and Arbella snowbeds), and snowmelt isoclines (LSM, ISM and ESM) as the explanatory variables. To test for normality, the data were subjected to a Kolmogorov-Smirnov Test. To estimate the independent explanatory power of each predictor variable, we used hierarchical partitioning (Chevan and Sutherland 1991). We used the “hier.part” procedure of the “hier.part” package (Mac Nally and Walsh 2005) in R, and obtained a measure of the independent contribution of each variable as a proportion (%) of the total explained variance (Mac Nally and Walsh 2005). The statistical significance of the amount of variance explained by each variable was tested using a Randomization Test based on 100 randomizations of each of the independent variables. To test for significant differences in the timing of snowmelt and accumulated temperature among the different levels of the environmental factors, Tukey-HSD Tests were performed. To assess the co-linearity between timing of snowmelt and accumulated temperature, we used a Pearson Chi-squared Test.

Species richness and amount of plant cover were subjected to an analysis of variance that included the following explanatory factors: snowmelt isocline (LSM, ISM, and ESM), site (Cataperdis and Arbella snowbeds), year (2010 and 2011), and plot within the isocline in a General Linear Model. To test for normality, the data were subjected to a Kolmogorov-Smirnov Test. To test for significant differences in species richness and plant cover, we used Tukey’s Post-hoc Multiple Comparisons Test.

The effects of snowmelt isocline, site, year, and plot on the number of days before each phenophase was reached were evaluated for all of the species, collectively, and for the following species, individually: *Mucizonia sedoides*, *Sedum alpestre*, *Gnaphalium supinum*, and *Poa alpina*. The analysis was performed using the non-parametric Kruskall-Wallis Test. To quantify the explanatory power of each variable (site, year, and snowmelt isocline) on the response variables (the timing of snowmelt and accumulated temperature), we used hierarchical partitioning. All of the analyses were performed using the SAS statistical package (SAS 9.0, SAS Institute, 2003) and the R (version 2.12.1; R Development Word Team, 2010).

RESULTS

Timing of snowmelt and accumulated temperature

The earliest snowmelt occurred at Cataperdis on 6 July 2010, and the latest began at Arbella on 24 August 2010; thus, the two snowbeds differed substantially (49 days) in the timing of snowmelt. The average length of the growing season differed significantly among the snowmelt isoclines (ESM sites = 77.5 d, ISM sites = 61.75 d, and LSM sites = 47.75 d). The timing of snowmelt did not vary significantly between years (F= 2.59; p<0.15); however, the timing differed significantly between snowbeds (F= 23.28; p<0.002) and snowmelt (F= 22.66; p<0.001). Snowmelt occurred 18 d later in the Arbella snowbed than it did in the Cataperdis snowbed. On average, the snow melted 30 days later at the LSM isocline sites than it did at the ESM isocline sites, but the timing of snowmelt did not differ significantly between the ISM and the LSM sites.

Accumulated temperature ranged from 184ºC (desv=3.77ºC) at an LSM site to 1150 ºC (desv=7.01ºC at a LSM site (Table 2), but did not vary significantly among years (F= 1.1; p<0.33) or between snowbeds (F= 0.62; p<0.46); however, the accumulated temperatures of the snowmelt isoclines differed significantly (F= 56.18; p<0.0001).

Table 1. Timing of snowmelt (Julian date) and accumulated temperature (ºC) at three snowmelt isoclines in two snowbeds in the Andorran Pyrenees.

Site	Year	Snowmelt isoclinel	Snowmelt timing (day of the year)	Temperature accumulated (ºC)
Cataperdis	2010	ESM	188	1150
Cataperdis	2010	ISM	209	572
Cataperdis	2010	LSM	230	184
Cataperdis	2011	ESM	195	978
Cataperdis	2011	ISM	202	668
Cataperdis	2011	LSM	209	336
Arbella	2010	ESM	209	941
Arbella	2010	ISM	230	513
Arbella	2010	LSM	237	212
Arbella	2011	ESM	202	923
Arbella	2011	ISM	223	744
Arbella	2011	LSM	237	284

The timing of snowmelt and accumulated temperature during the growing period were significantly correlated (r=0.965; p<0.001). Snowmelt isocline and site explained 57.7% and 36.3% of the variance in the timing of snowmelt, respectively. Snowmelt isocline explained a substantial amount (96%) of the variance in accumulated temperature over the growing season (Table 2).

Table 2. Hierarchical partioning analiysis of the factors considered (year, site and snowmelt isocline explaining the variance (%) in snowmelt date and accumulated temperature at two snowbeds in the Andorran Pyrenees. Significant factors (p<0.05) are given in bold.

	Hierarchical partitioning			
	Variance explained (in %)	Year	Site	Snowmelt level
Snowmelting date	**15.2**	6.0	**36.3**	**57.7**
Accumulated temperature	**16.6**	1.5	2.5	**96.0**

Species richness and plant cover

Thirty-four plant species were found in the two snowbeds (28 species in the Cataperdis snowbed and 33 in the Arbella snowbed) (Table 3). The species richness among vascular plants (mainly forbs) was much higher than the richness of bryophytes (Table 4). Overall, average plant cover was 87.54% and ranged from 14% in the LSM site in the Arbella snowbed to 100% in the ESM site of the Cataperdis snowbed. Plant cover varied significantly between years (F=16.12; p<0,001), sites (F=39.11; p<0.001), and snowmelt isoclines (F=22.59; p<0.001), but did not vary significantly among plots (F=0.14; p<0.8679). Species richness varied significantly between years (F=18.13; p<0.001), sites (F=111.46; p<0.001), and snowmelt isoclines (F=80.84; p<0.001), but not among plots (F=0.51; p<0.5810). Plant cover and species richness were highest in the ESM isocline (average richness per plot= 9.64±2.06 species, average plant cover per plot=84.04%±38.72) and were lowest in the LSM isocline (average richness per plot=4.77±1.70 species, average plant cover per plot=57.59%±28.12).

The species richness of vascular plants, especially grasses (e.g., *Poa alpina*, *Agrostis rupestris*, and *Nardus stricta*), was significantly higher in the ESM isoclines (average richness per plot=2.10±desv=1.10) than it was in the LSM isoclines (average richness per plot=0.37±desv=0.60); but, the species richness of bryophytes was significantly higher in the LSM sites than it was in the other isoclines.

Table 3. Species recorded in the two snowbeds studied in the Andorran Pyrenees in 2010 and 2011. The species that were present in the Cataperdis snowbed, only, are indicated by a superscript C and the species present in the Arbella snowbed, only, are indicated by a superscript A.

Species	
Agrostis rupestris	*Mucizonia sedoides*
Arabis alpina	*Murbeckiella pinnatifida*
Armeria maritima	*Nardus stricta*
Androsace carnea	*Polytrichum sexangulare*
Alopecurus gerardii^{A}	*Polytrichum piliferum*
Anthelia juratzkana	*Pohlia drumondi*
Cardamine bellidifolia	*Kiaeria starkei A*
Carex pyrenaica	*Oreochloa disticha*^{A}
Cerastium cerastoides	*Poa alpina*
Cryptogama crispa^{A}	*Polytrichum piliferum*
Epilobium anagalifolium	*Polytrichum sexangulare*
Festuca glacialis^{C}	*Sedum alpestre*
Gnaphalium supinum	*Sagina saginoides*
Hieracium gr. pilosella	*Saxifraga stellaris*^{A}
Leucanthemopsis alpina	*Sibbaldia procumbens*
Luzula alpinopilosa^{A}	*Veronica alpina*
Minuartia recurva	*Veronica nummularia*

On average, the Cataperdis snowbed had significantly higher richness per plot (8.83 species) and greater plant cover (94.29%) than did the Arbella snowbed (5.52 species, 66.80% plant cover). Average richness per plot and average plant cover were significantly higher in 2010 (7.84 species, 86% plant cover) than they were in 2011 (6.51 species and 64.22% plant cover).

Table 4. Average richness and standard deviation per plot of all species, vascular plants, bryophytes, and grasses in two snowbeds in the Andorran Pyrenees.

	Averages richness per plot±desv	**Averages richness in Cataperdis**	**Averages richness in Arbella**
All species	7.19±desv=3.25	8.83±desv=2.97	5.52±desv=2.64
Vascular plants	5.34±desv=3.09	6.56±desv=2.61	4.12±desv=3.08
Bryophytes	1.85±desv=1.03	2.33±desv=0.95	1.37±desv=0.87
Grasses	1.43±desv=1.28	1.81±desv=0.93	1.06±desv=1.48

Growth and flowering phenology

All of the plots in the ESM isoclines reached the cessation of leaf expansion and flowering phenophases. In the ISM isoclines, plants in 96% and 85% of the plots reached the cessation of leaf expansion phenophase and the flowering phenophase, respectively; however, in the LSM isoclines, only 68% and 50% of the plots reached the cessation of leaf expansion and the flowering phenophases.

The period from the end of snowmelt to the cessation of leaf expansion differed significantly between snowmelt isoclines (Chi=12.16; p<0,002), between years (Chi= 29.38; p<0.001), and between sites (Chi=4.19; p=0.04). That period was significantly shorter in the LSM isoclines than it was in either the ESM isoclines (4.87 d) or the ISM isoclines (6.64 d). In 2010, that period was 6.34 days longer than it was in 2011 and, on average, it was 2.49 days longer at Cataperdis than it was at Arbella.

The period from the cessation of leaf expansion to the peak flowering differed significantly between snowmelt isoclines (Chi= 8.03; p<0.01) and between years (Chi= 15.64; p<0.001), but not between sites (Chi= 0.77; p=0.37). That period was significantly longer in the LSM isoclines than it in either the ESM isoclines (8.82 d) or the ISM isoclines (6.84 d), and was 4.37 d longer in 2011 than it was in 2010.

The period from the end of snowmelt to the peak flowering differed significantly between sites (Chi=5.43; p<0.01), but not between years (Chi=1.49; p<0.22) or snowmelt isoclines (Chi=1.85; p<0.39), and was significantly shorter (4.06 d) in the plots at Arbella than in the plots at Cataperdis.

The average accumulated temperature at the cessation of leaf expansion in the ESM plots (131 ºC) was significantly (F = 4.55; p<0.01) higher than it was in the LSM plots (85ºC). The average accumulated temperature at peak flowering in the plots in the ESM isoclines (212 ºC) was significantly higher than the average in the ISM isoclines (148 ºC), but did not differ significantly from the plots in the LSM isoclines; possibly, because only 50% of plots in the LSM isoclines reached the flowering phenophase.

Peak flowering occurred earlier (Figure 2) and the number of flowering species was higher in the ESM isoclines than it was in the LSM isoclines. The flowering period was 17.5 d and 38 d shorter at the two LSM sites than it was at the ESM sites, which left very little time for the later phenophases; e.g., fructification. Peak flowering always occurred later in the Arbella snowbed than it did in the Cataperdis snowbed.

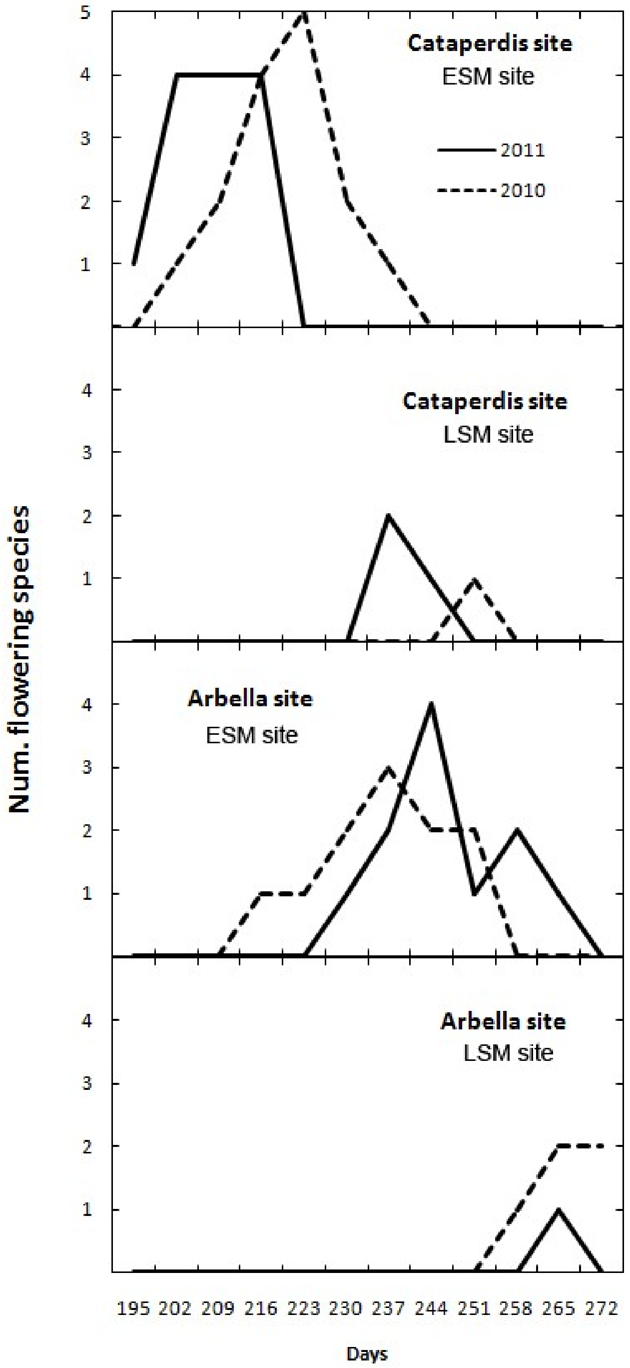

Figure 2. Flowering time course in the two snowbeds (Cataperdis and Arbella) in the Andorran Pyrenees in 2010 and 2011 and in the snowmelt gradient. Flowering duration in Cataperdis in 2010 and in the ESM sites was 49 days, 28 in 2011. Flowering duration in Cataperdis in 2010 and in the LSM sites was 14 days, 21 in 2011. Flowering duration in Arbella in 2010 and in the ESM sites was 49 days, 49 in 2011. Flowering duration in Arbella in 2010 and in the LSM sites was 21 days, 14 in 2011.

Species-specific phenological responses

The amount of variance in the time to reach the two phenophases explained by site-specific factors was very high (>35%) for all of the species except *Mucizonia sedoides* (19%) and *Gnaphalium supinum* (20%) in the flowering phenophase (Table 5). Snowmelt isoclines and year had the greatest effect on the phenologies of most of the snowbed species; however, the cessation of leaf expansion phenophase in *Sedum alpestre* was more strongly influenced by site, rather than year. The proportion of the plots in which each all species reached the flowering phase was lower than the proportion of the plots in which the plants reached the cessation of leaf expansion.

In *Sedum alpestre* and *Mucizonia sedoides*, but not *Poa alpina* and *Gnaphalium supinum,* the time needed to reach the two phenophases differed significantly among snowmelt isoclines (Table 6). *G. supinum* required more time (mean = 11 d) from the end of snowmelt to reach the flowering phase in the ESM isoclines than it did in the LSM isoclines, and *S. alpestre* and *M. sedoides* required more time (14 d and 21 d, respectively) from the end of snowmelt to reach the flowering phase in the ESM sites than they did in the LSM sites.

Table 5. Hierarchical partioning analyisis of the factors considered (year, site, snowmelt isocline, and plot) explaining the variance (%) in the time required to reach phenophases (cessation of leaf expansion, and flowering) in the four most common species *Gnaphalium supinum*, *Mucizonia sedoides*, *Poa alpina* and *Sedum alpestre* occurring in two snowbeds in the Andorran Pyrenees Significant terms ($p<0.05$) are given in bold.

				Hierarchical partitioning			
Species	**Phenology**	**n**	**Explain (in %)**	**Year**	**Site**	**Snowmelt level**	**Plot**
Gnaphalium supinum	Cessation of leaf expansion	80	37.1	**42.1**	**9.7**	**47.6**	0.6
	Flowering	57	20.0	**43.0**	**7.9**	**47.0**	2.1
Mucizonia sedoides	Cessation of leaf expansion	72	71.0	**66.2**	**7.0**	**26.7**	0.1
	Flowering	52	18.7	**59.6**	**22.4**	9.7	**8.3**
Poa alpina	Cessation of leaf expansion	42	40.1	**27.4**	**27.4**	**44.4**	0.8
	Flowering	38	36.9	**46.6**	**28.5**	**27.1**	2.8
Sedum alpestre	Cessation of leaf expansion	91	92.7	**12.9**	**48.0**	**38.9**	0.2
	Flowering	46	58.2	**56.0**	**26.8**	**16.7**	0.5

Table 6. Non-parametric one-way ANOVA of the time taken to reach each phenophase at three snowmelt isoclines in two snowbeds in the Andorran Pyrenees. P-values for significant terms

are indicated in bold. SA *Sedum alpestre*; MS *Mucizonia sedoides*; GS *Gnaphalium supinum* and PA *Poa alpina*.

Species	**Phenology (days)**	**n**	**Chi^2 value**	**P value**
SA	Snowmelt to the cessation of leaf expansion	94	36,42	**0,001**
	Leaf expansion to flowering	48	3,55	0,168
	Snowmelt to flowering	48	8,78	**0,012**
MS	Snowmelt to the cessation of leaf expansion	69	5,89	0,052
	Leaf expansion to flowering	54	12,79	**0,001**
	Snowmelt to flowering	54	14,63	**0,001**
GS	Snowmelt to the cessation of leaf expansion	79	1,22	0,542
	Leaf expansion to flowering	61	1,47	0,478
	Snowmelt to flowering	61	10,62	**0,004**
PA	Snowmelt to the cessation of leaf expansion	48	0,16	0,923
	Leaf expansion to flowering	39	5,83	0,054
	Snowmelt to flowering	39	2,63	0,268

DISCUSSION

Timing of snowmelt and accumulated temperature

In the two snowbeds in the Andorran Pyrenees, the timing of snowmelt, but not accumulated temperature, differed significantly, which suggests that site-specific factors might have had a significant effect on accumulated temperature through their localized effects on the microclimate of the snowbeds. At the Arbella snowbed, avalanches are the source of accumulated snow whereas at the Cataperdis snowbed, the micro-topography is responsible for the accumulated snow. Consequently, the volume of accumulated snow is greater and snowmelt occurs later in the former than it does in the latter. At the ESM site in the Arbella snowbed, snowmelt occurred 7 d later in 2010 than it did in 2011; consequently, the accumulated temperature was higher in 2011. At the ESM site at the Cataperdis snowbed, snowmelt occurred 7 d later in 2011 than it did in 2010, and accumulated temperature was highest. When snowmelt occurs early in the summer, the effective accumulated temperature increases gradually, initially, but the rate of increase accelerates. However, when the snow cover on a snowbed is removed after mid-summer, the effective accumulated temperature increases at a constant rate, initially, but the rate then decreases (Kudo and Hirao 2006). At the LSM sites in the Andorran Pyrenees, the accumulated temperatures were similar between sites and years, even when there were differences in the date of snowmelt. Thus, at the ESM sites, snowmelt date might have had a greater effect on phenologies than did accumulated temperature (see also Kudo and Hirao 2006).

Species richness and plant cover

In the snowbeds in the Andorran Pyrenees, the diversity of vascular plants and the amount of plant cover were correlated with the snowmelt isocline gradient; specifically, diversity and plant cover decreased between early and late snowmelt isoclines, which has been observed elsewhere (Totland et Alatalo 2002, Lluent 2007). Abiotic factors such as water content, nutrient fixation capacity, and C/N ratio can differ between snowmelt isoclines (Retzer 1956, Billings and Bliss 1959, Hülber et al. 2011). Galen et Stanton (1995) found strong correlations between the timing of snowmelt, soil quality and structure, and the productivity of alpine plants.

In our study, overall plant diversity was highest at the ESM sites in both of the snowbeds; however, the relatively low diversity at the LSM sites, where bryophytes predominated, was associated with snowbed specialists, and we did not encounter many of the species that occur in adjacent habitats (mainly grasses) (see also Stanon et al. 1994, Schöb et al. 2009). Thus, snowmelt isoclines influence and conserve the biodiversity of snowbeds. In our study, diversity per plot was higher in the Cataperdis snowbed than it was in the Arbella snowbed, probably because, at the former, the snow melted earlier and, therefore, the plants had a longer growing season than they did at the Arbella snowbed.

Species richness and plant cover were greater in 2010, which was colder and more humid, than they were in 2011; however, probably, that was a carry-over effect from 2009, which was warmer and drier, and the timing of snowmelt was earlier than it was in 2010. Presumably, the flowering season in 2009 influenced seed success in 2010 (Kudo and Hirao 2006) and, consequently, might have increased species richness and plant cover in 2010.

Plant growth and flowering phenology

In the Andorran snowbeds, accumulated temperatures were lower at the LSM sites than they were at the ESM sites; however, the highest rates of leaf expansion occurred at the LSM sites. The contrary occurred with the flowering phenophases: the period to reach peak flowering was significantly longer in the LSM isoclines than it in either the ESM isoclines. Other studies have noted this (Wipf 2010, Hülber et al. 2006, Galen and Stanton 1995). Wipf (2010) reported that early season phenophases are more strongly affected by the timing of snowmelt than by temperature; however, in later phenophases, temperature has a strong effect both in the Alps and in Andorran snowbeds.

In the Andorran snowbeds, the time between snowmelt and peak flowering did not differ significantly among snowmelt isoclines; however, the time between the cessation of leaf expansion and flowering was longer at the LSM sites than it was at the ESM sites. Plants at the LSM sites flowered in late summer when air temperatures were decreasing and accumulated temperatures were lower than they were at the ESM sites. Probably, the low input of thermal energy at the LSM sites was responsible for the delay in flowering phenophases, which compromised the success of sexual reproduction because fructification and the dispersal of fruit occurred close to the new snowfall (onset of winter). Thus, it appears that the onset of winter (a stochastic event) dictates the sexual reproductive success of plants at the LSM sites. Furthermore, Kudo and Hirao (2006) have demonstrated the importance of the minimum temperature for the onset of flowering, which might explain why only 50% of the plots at the LSM sites in the Andorran snowbeds reached the flowering phenophase.

Given that the growing season was longer at the ESM sites than it was at the LSM sites in the Andorran snowbeds, it is plausible that increases in global temperatures will led to an increase in sexual reproductive success; however, in most alpine species, most reproduction is clonal, rather than sexual (Bliss 1960, Lluent 2007) and, therefore, vegetative growth phenophases might be more important than flowering phenophases (Wipf 2010).

In our study, the differences between the three snowmelt isoclines in the durations of the phenophases (cessation of leaf expansion and flowering) probably were the result of the phenotypic plasticity of the plants and their response to environmental variability (Post et al. 2008). At the LSM sites, species have had to adapt to having relatively less time to achieve leaf expansion, but they cannot reduce the amount of time needed to reach flowering because of the decline in temperature in late summer.

Within the two Pyrenean snowbeds, the timing of snowmelt differed between snowmelt isoclines (ESM sites *vs.* LSM sites), which affected the number of species that flowered and the timing of the peak in flowering; however, there were differences between the two snowbeds. Temperature and the timing of snowmelt had a significant influence on phenologies, and site-specific factors (probably in microtopography and snow origin) were important because they influenced the timing of snowmelt and accumulated temperature.

Species-specific phenology responses

In the Andorran snowbeds, *Poa alpina*, but not *Mucizonia sedoides* and *Sedum alpestre,* was highly conservative in its phenological responses to differences in snowmelt isoclines. Probably, those species are better adapted to variation in the timing of snowmelt than is *Poa alpina*. Many studies have demonstrated the strong phenotypic responses of plant species to changes in their environment (Arft at al. 1999, Hülber et al 2006, Peñuelas and Filella 2001, Peñuelas et al. 2002) and, typically, the phenological responses are highly species-specific, even among closely related taxa (Miller-Rushing and Primack 2008).

In some of the snowbed species (*Mucizonia sedoides* and *Sedum alpestre*) the flowering period was shortest at the LSM sites, which allowed them to maximize the period for seed maturation and conferred an advantage at the sites where snowmelt occurs later in the season, but not at the ESM sites. Thus, site-specific factors such as the effects of isocline or climate in a given year on the timing of snowmelt can influence the competitive advantage of some species.

In our study, year had a significant effect on the phenologies of all of the snowbed plants evaluated and on the duration of the growing season, which indicates that inter-annual variation in climate has a significant effect on the phenology of these plants. Domènech et al. (submmited) found a close relationship between annual climate and the number and extent of snowbeds in the Pyrenees, and suggested that changes in climate will have a strong influence on the future of Pyrenean snowbeds. Inter-annual variation in climate is common in the Pyrenees (López Moreno et al. 2009) and in many other mountainous areas such as the Alps (Hülber et al. 2011) and, probably it will increase in the near future. Changes in climate (mainly, temperature and precipitation) will affect snowpack (Johnson and Billings 1962, Scott and Billings 1964, Tieszen 1975, Evans and Fonda 1990, Auerbach and Halfpenny 1991, Cess et al. 1991, Walker et al. 1993, Stanon et al. 1994) and the rate of snowmelt (affected by air temperature), which will modify the timing of snowmelt and, consequently, the nature of the growing season.

CONCLUSIONS

In the two snowbeds in the Andorran Pyrenees, (1) site-specific factors (microtopography and snow origin) had significant effects on the timing of snowmelt, (2) the timing of snowmelt had a greater effect on plant phenologies than did accumulated temperature at early snowmelting sites, (3) the timing of snowmelt had a significant effect on leaf expansion and flowering schedules, (4) species richness and abundance were greater in early snowmelt isoclines, and (5) species differed in their responses (shortening or lengthening the duration of phenophases) to differences in the timing of snowmelt, probably, because of differences in their phenotypic adaptations.

In summary, this study showed that, in addition to the effects of inter-annual variation in climate, site-specific factors had a significant affect on the phenology and reproduction of the most common plants in snowbed communities in the Pyrenees. Therefore, site-specific factors are expected to influence the effects of climate change on alpine plants.

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