Agència de Gestió d'Ajuts Universitaris i de Recerca

UNIÓ EUROPEA
Fons Social Europeu

Memòria justificativa de recerca de les beques predoctorals per a la formació de personal investigador (FI)

La memòria justificativa consta de les dues parts que venen a continuació:
1.- Dades bàsiques i resums
2.- Memòria del treball (informe científic)

Tots els camps són obligatoris

1.- Dades bàsiques i resums

Títol del projecte ha de sintetitzar la temàtica científica del vostre document.
Interaccions arbre-arbust al límit superior del bosc i efectes de gradients bioclimàtics en la vegetació

Dades de l'investigador (benficiari de l'ajut)

Nom: Oriol
Cognoms: Grau i Fernández
Correu electrònic: grau.oriol@gmail.com

Dades del director del projecte

Nom: **Josep Maria**
Cognoms: Ninot i Sugrañes
Correu electrònic: **jninot@ub.edu**

Dades de la universitat / centre al que s'està vinculat
Facultat de Biologia, Departament de Biologia Vegetal, Unitat de Botànica

Número d'expedient

Paraules clau: cal que esmenteu cinc conceptes que defineixin el contingut de la vostra memòria.
Ecologia alpina, límit del bosc, interaccions planta-planta, gradients bioclimàtics, canvi climàtic

Data de presentació de la justificació
07-11-2011

Generalitat de Catalunya
Departament d'Innovació, Universitats i Empresa

Resum en la llengua del projecte (màxim 300 paraules)

Durant el periode d'elaboració d'aquesta tesi hem aprofundit en el coneixement dels factors que controlen les dinàmiques espacio-temporals del límit superior del bosc. Aquest ecotò se situa entre el límit superior del bosc i els prats alpins i és susceptible a canvis ambientals, fet que provoca que fluctuï altitudinalment i latitudinalment en funció d'aquests canvis. Els motius d'aquesta dinàmica s'ha estudiat sovint des d'un punt de vista climàtic, però mai fins ara s'havia estudiat des d'un punt de vista de les interaccions entre organismes. Per aquest fet hem estat evaluant l'efecte de les interaccions planta-planta en la regulació de la dinàmica supraforestal.

L'estudi l'hem emmarcat en un context alpí (als Pirineus Catalans) i en un context subàrtic (Lapònia, Suècia), fet que ens ha permès fer un estudi comparatiu en dos ecotons contrastats però homòlegs ecològicament. Hem desenvolupat una sèrie d'experiments considerant diversos factors (augment de temperatura, quantitat de nutrients, presència d'arbust, posició en l'ecotò); en les dues zones d'estudi hem fet una plantació de plançons dels arbres formadors del límit del bosc en les diverses situacions derivades de la combinació d'aquests factors, i hem fet el seguiment fenològic dels plançons durant tres periodes de creixement.

Els resultats dels experiments ens han permès veure que les interaccions entre organismes tenen una gran importància en la regulació de la dinàmica supraforestal, tant als Pirineus com a Lapònia. Les interaccions planta-planta i planta-herbívors determinen el reclutament de plançons i per tant l'estructuració de les comunitats supraforestals. Per altra banda, la posició en l'ecotò evidencia la presència d'un gradient bioclimàtic; les manipulacions ambientals de temperatura i nutrients originen una resposta generalment positiva en el desenvolupament dels plançons, indicant que canvis en aquestes variables pot suposar alteracions notables de l'estructura forestal del límit del bosc.

Per altra banda en aquest projecte també hem aprofundit en temes relacionats amb l'efecte dels gradients altitudinals en la distribució de plantes vasculars als Pirineus Catalans.

Resum en anglès(màxim 300 paraules)
In this study we have gained insight into the factors controlling the spatio-temporal dynamics observed in the treeline. This limit or ecotone is situated in the transition between forest and alpine grasslands and it shows high sensitivity to environmental changes, which originates altitudinal and latitudinal shifts. The causes of these shifts have been studied from a climatic scope, although there are other controlling factors such as the interactions between organisms, which remain poorly studied. Thus, our study has focused on this issue, in order to assess the effect of plant-plant interactions as a regulating factor of treeline dynamics.
We situated our study in an alpine region (Catalan Pyrenees) and in a subarctic region (Swedish Lapland), which allowed us to perform a comparative study in two contrasting homologous ecotones. We set up a series of experiments involving several factors (increased temperature, amount of nutrients, presence of shrub, position across the ecotone); in both study regions we transplanted seedlings of the species forming the treeline, in distinct treatments derived from the combination of such factors, and we have assessed the phenological evolution of such seedlings during three growing seasons.
Our results indicate that the interactions between organisms play an important role in regulating the treeline dynamics, both in the Pyrenees and in Lapland. The plant-plant and plant-herbivore interactions determine the seedling recruitment and thus, the structure of treeline plant communities. Moreover, the position across the ecotone evidences the importance of a bioclimatic gradient. The environmental manipulations (temperature, nutrients) originate a positive response in seedling development, indicating that changes in such variables could cause noticeable changes in the forest structure at the treeline. In this project we have also gained insight into the effect of altitudinal gradients on vascular plant distribution in the Catalan Pyrenees.

2.- Memòria del treball (informe científic sense limitació de paraules). Pot incloure altres fitxers de qualsevol mena, no més grans de 10 MB cadascun d'ells.

2.1. Efecte dels arbusts en la dinàmica del límit superior del bosc en resposta a simulacions de canvis ambientals als Pirineus Centrals

Introducció

El límit superior del bosc subalpí és l'ecotò més notable a les muntanyes alpines, tot i la irregularitat del seu relleu i les modificacions del paisatge degudes a l'explotació humana. Als Pirineus centrals, aquest límit altitudinal és una estreta zona de transició en la qual es passa del bosc regular subalpí als claps dispersos d'aquest bosc alternant amb landes subarbustives, a la barreja d'aquestes landes amb prat alpí, i finalment al mosaic de prats alpins (Ninot et al. 2008). En el mateix sentit, el pi negre (*Pinus uncinata*), l'arbre subalpí per excel·lència, passa del port arbori al d'arbrets regruats (que defineixen la *treeline*, o límit de l'arbre), i finalment al de petites formes aparentment juvenils, encara que sovint prou longeves (Batllori et al. 2009).

- En la dinàmica de la vegetació del límit supraforestal hi intervenen complexos processos de colonització, i de competència i facilitació entre plantes funcionalment diferents. Els canvis climàtics, i principalment l'augment de temperatures, tenen una important incidència en tots aquests processos, tant directament sobre el desenvolupament vegetal, com sobre el balanç edàfic d'aigua i nutrients (Holtmeier & Broll 2005). Com que, a més, hi ha evidències que en temps pretèrits climàticament més càlids el límit del bosc prop de la zona d'estudi es trobava a més altitud (Cunill 2010), cal preveure que l'augment de temperatures afavoreixi l'ascens del límit del bosc.
- Tot i això, i a més tenint en compte l'important descens de l'explotació tradicional forestal i ramadera, als Pirineus no es detecta un ascens generalitzat del límit forestal les darreres dècades. Sí que es dóna en localitats concretes, i sobretot allà on el límit del bosc

havia estat abaixat per l'home. Però en altres casos s'observa més aviat una densificació d'arbres i de formes juvenils per sota del límit supraforestal, sense que aquest s'hagi desplaçat sensiblement durant les darreres dècades (Batllori & Gutiérrez 2008).

- Per altra banda, recentment s'ha documentat un increment en la densitat i productivitat de les comunitats subarbustives en algunes zones àrtiques i alpines, com a resposta al notable augment de temperatures de les últimes dècades detectat en aquestes àrees (Chapin et al. 1995, Tape et al. 2006). Cal tenir en compte que els plançons d'arbres forestals subalpins solen progressar més a redós de subarbusts o d'altres elements protectors, que exerceixen un clar efecte facilitador en front de factors d'estrès abiòtic o d'herbivorisme (Smith et al. 2003, Batllori et al. 2009).

Per tot això, es preveu que els canvis ambientals i d'ús del sòl influeixin en el funcionament i en la posició del límit supraforestal, però no pas directament, sinó modelats per processos de facilitació i de competència existents entre la comunitat forestal i l'arbustiva que afecten la germinació i l'establiment de plançons de *Pinus uncinata*. Partim de la hipòtesi que aquestes interaccions poden canviar de positives a negatives en funció de l'estrès abiòtic i biòtic present al llarg de l'ecotò bosc-prats alpins .

En aquest estudi ens proposem investigar les interaccions ecològiques entre plançons de pi negre (*Pinus uncinata*) i matolls d'abarset (*Rhododendron ferrugineum*) a través d'una experiència en què intervenen diferents factors binaris. El seguiment detallat dels plançons al llarg de tres anys ha de permetre evidenciar com aquests factors poden controlar l'evolució espacio-temporal de l'ecotò bosc-prat alpí dels Pirineus.

Material i mètodes

Es van establir unes parcel·les d'estudi al Serrat de Capifonts (Pallars Sobirà, Catalunya), localitat representativa d'un ecotò en situació poc antropitzada. La *treeline* s'hi situa a uns 2.400 m d'altitud, en un vessant esquistós regular, on el període vegetatiu es pot estimar en uns 170 dies, i la temperatura mitjana del mes més càlid, el juliol, és d'11 °C. El

bosc subalpí és una forma típica del *Rhododendro-Pinetum uncinatae*, el prat alpí correspon al *Hieracio-Festucetum supinae*, i les landes que clapegen l'ecotò pertanyen al *Saxifrago-Rhododendretum ferruginei* i al *Cetrario-Loiseleurietum procumbentis*.

- Vam establir un total de 64 petites parcel·les de seguiment (de vora 1,3 m^2 cadascuna), corresponents a una experiència factorial de quatre factors binaris (16 combinacions), amb quatre rèpliques per a cada combinació. Els factors es van establir simulant diferents situacions ambientals , concretament:
- a) situació respecte de l'ecotò (la meitat dins del bosc, i l'altra meitat al mosaic obert)
- b) temperatura (protegides per cambres de metacrilat - *open top chambers*, OTC - del tipus ITEX, que incrementen la temperatura estival a ran del sòl entre 1 i 2 °C, o a l'aire lliure).
- c) situació respecte de mates de *Rhododendron ferrugineum* (a redós, o bé allunyades)
- d) fertilització (amb addició d'un compost d'NPK, o sense).
- A cada petita parcel·la, l'estiu de 2006 varem trasplantar-hi 6 plançons de *Pinus uncinata* provinents de viver, de tres anys de vida (sí?) i procurant seleccionar-los d'un interval de mides prou regular. Des de llavors i fins a 2009 hem avaluat cada estiu la supervivència, la longitud de tiges i fullatge, el grau de ramificació, i els efectes d'herbivorisme o de danys per fred hivernal en tots els plançons (en total, 384).
- En l'anàlisi de les dades, hem considerat cada petita parcel·la (grup de sis plançons) com una mostra, i els quatre factors binaris com a factors independents. Les respostes de cada mostra les hem analitzat emprant models linears mixtos.

Resultats i discussió

La supervivència dels plançons ha estat molt elevada al llarg de l'experiència, però molts plançons situats sobre del bosc i allunyats de *Rhododendron* vàren veure's greument

afectats durant el primer hivern, que va ser especialment dur. La manca de neu va propiciar greus efectes de dessecació hivernal a un 55 % dels plançons (Ninot et al. 2008).

La taula 1 resumeix els efectes que mostren diferències significatives lligades a les diferents condicions que els plançons han trobat a les parcel·les. Entre les variables mesurades, l'alçada de la tija dels plançons resulta força indicadora de les diferents situacions experimentals. En concret, ha mostrat increments clarament superiors en les situacions a tocar de *Rhododendron*, en les diferents condicions experimentades, i també ha respost positivament a l'addició de nutrients i a l'increment de temperatura (Fig. 1).

Els plançons situats a redós de *Rhododendron* van evidenciar un efecte facilitador molt marcat per part d'aquest arbust, a través de millor estructura funcional i de més protecció en front a herbivorisme (Fig. 2) i a danys hivernals. Aquest efecte pot ajudar a explicar la densificació d'arbres joves observada al límit forestal, a través de més reclutament i de millor creixement dels pinets en presència d'arbusts. Les interaccions positives de *Rhododendron* envers els pinets són generals tant per sobre del límit forestal com dins del bosc, tot i que la facilitació per sobre el bosc es més evident i generalitzable a escala regional, i on l'estrès abiòtic és més notable.

Els efectes de la temperatura van ser notables en els plançons després d'estar dos períodes vegetatius dins de les cambres OTC. Al contrari, la fertilització es va notar ja al primer any, però els seus efectes van durar poc ja que no es va tornar a aplicar el fertilitzant, de manera que els plançons fertilitzats aviat van deixar de diferenciar-se.

En general, doncs, els canvis ambientals simulats i les interaccions entre les mates de *Rhododendron ferrugineum* i els plançons de *Pinus uncinata* es manifesten com a importants factors claus en la regulació de la dinàmica de l'ecotò que separa el bosc subalpí de les pastures alpines dels Pirineus, fins i tot en un període força curt. Esperem que el seguiment durant un període més llarg, i altres variables encara en estudi, com són la concentració foliar d'isòtops estables del carboni i del nitrogen, permetran perfilar millor el paper de les interaccions estudiades en la dinàmica de la *treerline*.

Conclusions

Aquest estudi confirma el paper facilitador dels arbusts en la densificació d'individus juvenils d'arbres forestals al límit superior del bosc. Aquesta mena d'interaccions és general a tot l'ecotò, amb poca diferenciació entre els ecosistemes forestal i alpí, tot i que els processos que s'hi donen són diferents. Els canvis ambientals analitzats produeixen efectes significatius en el desenvolupament dels plançons forestals. Per això, esdevenen importants factors reguladors de la dinàmica de la *treeline*.

Figures i taules

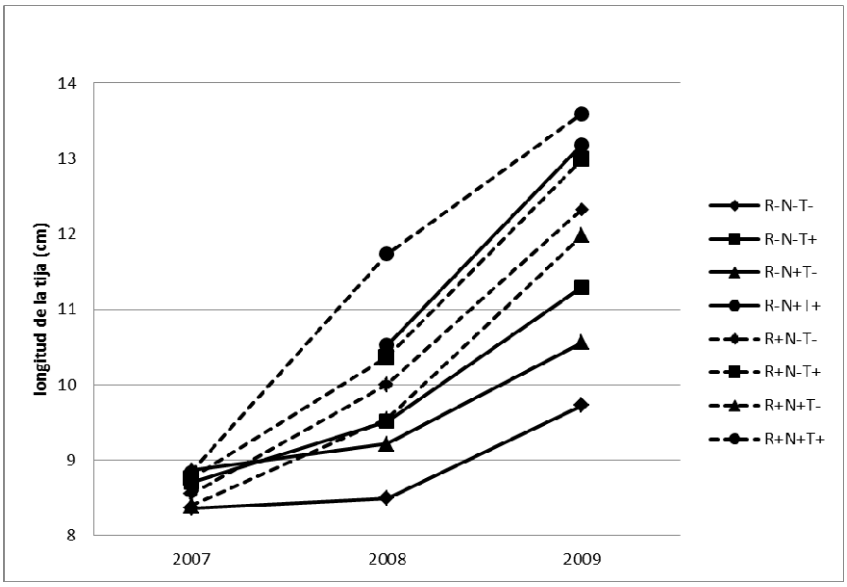

Figura 1a.

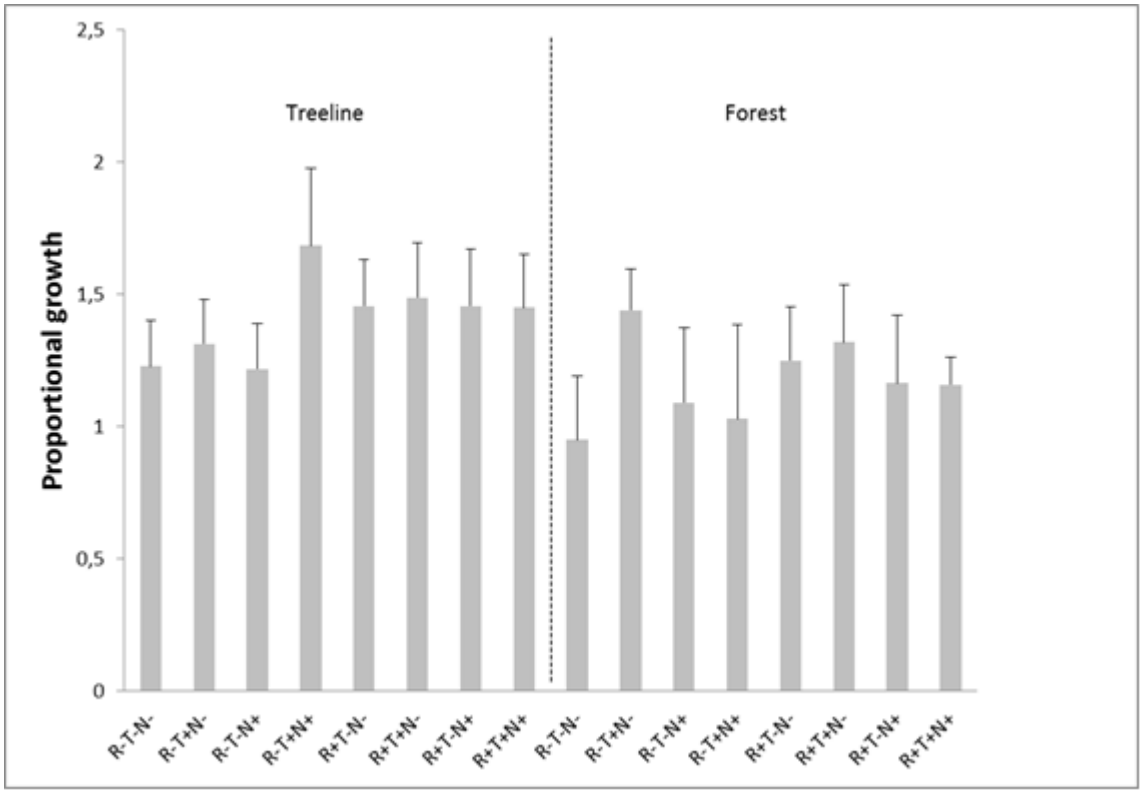

Figura 1b

Figura 1. a) Variació de la longitud de la tija dels plançons de *Pinus uncinata* durant el període d'experimentació al límit supraforestal. **b)** Creixement proporcional durant el periode 2007-2009 per tots els tractaments inclosos en l'estudi.

Les abreviatures fan referència a tres dels factors estudiats, concretament a la proximitat de *Rhododendron* (R), a l'addició de fertilitzant (N) i al sobreescalfament amb *open top chambers* (T); els símbols + i – signifiquen l'aplicació del tractament o no, respectivament.

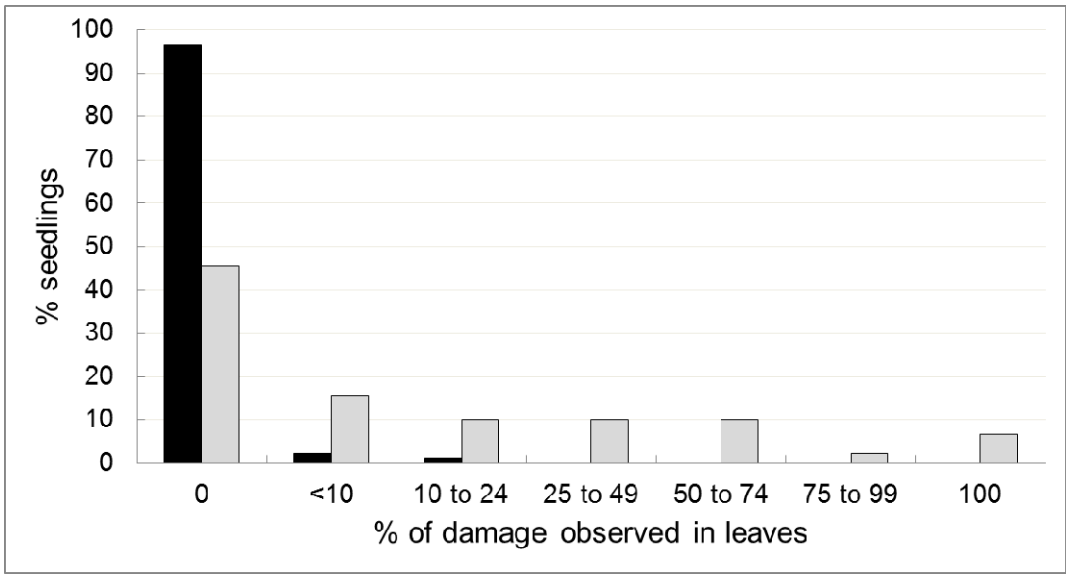

Figura 2. Percentatge de plançons vs percentatge de dany originat per l'herbivorisme del gall fer durant 2007-08.

Taula 1. Resum dels principals resultats que diferencien significativament els plançons segons els factors considerats, respecte dels seus oposats, durant els tres anys de mostreig.

	2007	2008	2009
Sota *Rhododendron*	↓ dany hivernal (fora del bosc)	↓ ramificació ↓herbivorisme per *Tetrao urogallus* (exclusivament al bosc)	↑ creixement proporcional de la tija ↑ fullatge
Dins del bosc	↑ alçada general sense dany hivernal	↓ ramificació	
Fertilització	↑ alçada general (menys evident amb *Rhododendron*)	↑ ramificació	efectes anteriors poc evidents
Dins de cambra OTC	sense efectes visibles	sense efectes visibles	↑ creixement proporcional de la tija

Bibliografia

Batllori, E., Camarero, J.J., Ninot, J.M. & Gutiérrez, E. 2009. Seedling recruitment, survival and facilitation in alpine Pinus uncinata tree line ecotones: implications and potential responses to climatic warming. *Global Ecol. Biogeogr.* 18: 460-472.

Batllori, E. & Gutiérrez, E. 2008. Regional treeline dynamics in response to global change in the Pyrenees. *J. Ecol.* 96: 1275–1288.

Chapin III, F.S., Shaver, G.R., Giblin, A.E., Nadelhoffer, K.J. & Laundre, J.A. 1995. Responses of arctic tundra to experimental and observed changes in climate. *Ecology* 76, 3.

Cunill, R. 2010. *Estudi interdisciplinar de l'evolució del limit superior del bosc Durant el període holocènic a la zona de Plaus de Boldís-Montarenyo, Pirineu central català*. Tesi doctoral. Universitat Autònoma de Barcelona.

Holtmeier, F.-K. & Broll, G. 2005. Sensitivity and response of northern hemisphere altitudinal and polar treelines to environmental change at landscape and local scales. *Global Ecol. Biogeogr*. 14: 395-410.

Ninot, J.M., Carrillo, E., Font, X., Carreras, J., Ferré, A., Masalles, R.M., Soriano, I. & Vigo, J. 2007. Altitude zonation in the Pyrenees. A geobotanic interpretation. *Phytocoenologia* 37: 371-398.

Ninot, J.M., Grau, O., Batllori, E., Camarero, J.J. & Carrillo, E. 2008. Winter drought impairs pine regeneration at the Pyrenean treeline. In: *Droughts: Causes, Effects and Predictions*. Nova Science Publishers.

Smith, W.K., Germino, M.J., Hancock, T.E., & Johnson, D.M. 2003. Another perspective on altitudinal limits of alpine timberlines. *Tree Physiol.* 23: 1101-1112.

Tape, K., Sturm, M. & Racine, C. 2006. The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. Global Change Biology 12: 686-702.

2.2. Comparació dels efecte dels arbusts en la dinàmica del límit superior del bosc en resposta a simulacions de canvis ambientals a Lapònia i als Pirineus.

(per a més informació consultar la versió publicada a Grau et al., Oikos, in press)

Introduction

Various studies have analysed changes in vegetation in several arctic, subarctic and alpine areas during the last decades, suggesting that climate changes may influence treeline dynamics.

In some northern areas there has been an increase in birch seedling recruitment above the timberline, as in the Abisko region, in northern Sweden (Dalen & Hofgaard 2005, Sunqvist et al 2008) or a densification of the ecotone (Tømmervik et al 2004) in a context of a warmer climate.
In some areas in the Pyrenees, a recent tree densification in the forest-alpine pasture ecotone has been described (Batllori & Gutiérrez 2008), under a warming climate and significant changes in land use.

Moreover, an increase in productivity of shrub communities has been detected recently at higher altitudes and latitudes, in areas where temperatures have increased noticeably, as in the Arctic (Chapin et al 1995, Tape et al 2006) and in the Alps (Dullinger et al 2003).
Shrubs seem to play a key role in the processes and interactions observed in the forest-tundra or forest-alpine grassland ecotones. Such interactions may involve facilitation processes from shrubs to tree seedlings under unfavourable climatic conditions (Brooker & Callaghan 1998), which may help these juveniles to resist winter damage and summer drought. Nevertheless, such interactions between advancing forest and shrub communities may also be affected by changing environmental conditions.

We hypothesise that facilitative effects of shrubs may regulate the tree recruitment and forest densification observed at the timberline, and that the environmental changes may modify the interactions between shrubs and trees along stress gradients.

Material and methods

Two treeline examples were studied in two different areas. At Abisko, in the subarctic Scandes, we chose *Vacciniium myrtillus* shrubs and deciduous *Betula pubescens* tree seedlings in the experiments. At Serrat de Capifonts, in the central Pyrenees, *Rhododendron ferrugineum* shrubs and evergreen *Pinus uncinata* seedlings were used instead.

A seedling transplantation experiment was started in both areas in 2006. A full factorial experimental design was set up involving four factors with four replicates each: 1) position across the ecotone (above /below the timberline); 2) temperature (+/- Open Top Chambers, OTC); 3) changes in shrub community (presence /absence of shrub); and 4) availability of nutrients (+/- NPK fertiliser, only recorded in the Pyrenees).

Seedling survival and phenology were recorded in summer 2007, and a linear mixed model was used to analyse the results.

Results and discussion

Our results at Abisko (see table 1) suggest that *Vaccinium* has facilitated *Betula* seedlings by enhancing their survival significantly. In this experiment, *Vaccinium* is comparatively more important in terms of facilitation when it is located above the timberline, as it is the only protection that seedlings can get above the timberline. They also suggest that the upslope expansion of seedling recruitment and the ecotone densification recently observed in the Scandes (Dalen & Hofgaard 2005, Tømmervik et al 2004) may be partially regulated by low shrubs like *Vaccinium*.

After only one growing season we cannot know if the studied factors induce a net production increase, although all the factors studied promoted crucial changes in the development of *Betula* seedlings throughout the growing season. Moreover, *Betula* showed big plasticity and fast susceptibility to the changes induced, as observed in previous studies (ex. Weih & Karlsson 2000).

At the Pyrenees (see table 2), the seedling survival was very high (about 98%); however, facilitation was also an important process, as *Rhododendron* protected *Pinus* seedlings from winter damaging northern winds, by promoting snow accumulation. In this experiment, the presence of shrubs is comparatively more important above the timberline in terms of facilitation, as *Pinus* seedlings can only be protected by shrubs in this site. Such results suggest that the densification in the forest-alpine grassland observed in the Pyrenees (Batllori & Gutiérrez 2008) could be partially regulated by shrubs like *Rhododendron ferrugineum*.

Conclusions

After one growing season, we observed that facilitation from shrubs may have a clear effect on the observed processes in the studied ecotones (recruitment and densification of tree juveniles) both in the Scandes and in the Pyrenees. Moreover, facilitation becomes more important above the timberline, where abiotic stress is stronger.

The temperature and the interactions between shrubs and seedlings are important regulating factors of the dynamics of the forest-tundra ecotone in the Scandes, and the effects are clearly visible after one year of growth in the field.

Although environmental changes caused a slower response in the Pyrenees, they are also key factors of the evolution of the forest-alpine grassland ecotone, and more precisely of the interactions between shrubs and tree seedlings.

Table 1. Main trends observed after the transplantation experiment at Abisko, in the subarctic Scandes.

Factors	Responses of *Betula* seedlings in June 2007	Responses of *Betula* seedlings in August 2007
Shrub: presence of *Vaccinium*	Enhanced survival Longer stems (etiolation) Bigger leaves	Enhanced survival Lower number of leaves/seedling (changes in resource allocation) Decreased effects of excessive sun radiation
Site: below the timberline	Bigger leaves (little availability of light)	Enhanced survival Stronger herbivory (more attractive to herbivores)
Temperature: with OTC	Bigger leaves	Lower number of leaves/seedling (changes in resource allocation)

Table 2. Main trends observed after the transplantation experiment at Serrat de Capifonts, in the central Pyrenees.

Factors	Responses of *Pinus* seedlings in summer 2007
Shrub:	
presence of *Rhododendron*	Longer stems
absence of *Rhododendron*	Very marked winter damage
Site: below the timberline	Longer stems Absence of winter damage
Temperature: +OTC	No effect
Fertiliser: with NPK	Increased needle length

Literature

Batllori E & Gutiérrez E (2008) Regional tree line dynamics in response to global change in the Pyrenees. Journal of Ecology 96: 1275-1288.

Brooker RW & Callaghan TV (1998) The balance between positive and negative plant interactions and its relationship to environmental gradients: a model. Oikos 81: 196-207.

Chapin III FS, Shaver GR, Giblin AE, Nadelhoffer KJ & Laundre JA (1995) Responses of arctic tundra to experimental and observed changes in climate. Ecology 76: 3.

Dalen L & Hofgaard A (2005) Differential regional treeline dynamics in the Scandes Mountains. Arctic, Antarctic, and Alpine research 37(3): 284-296.

Dullinger S, Dirnböck T & Grabherr G (2003) Patterns of shrub invasion into high mountain grasslands of the northern calcareous Alps, Austria. Arctic, Antarctic, and Alpine Research 35(4): 434-441.

Sunqvist MK, Björk RG & Molau U (2008) Establishment of boreal forest species in alpine dwarf-shrub heath in subarctic Sweden. Plant Ecology and Diversity 1: 67-75.

Tape K, Sturm M & Racine C (2006) The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. Global Change Biology 12: 686-702.

Tømmervik H, Johansen B, Tombre I, Thannheiser D, Hogda KA, Gaare E, & Wielgolaski FE (2004) Vegetation changes in the Nordic mountain birch forest: the influence of grazing and climate change. Arctic, Antarctic, and Alpine Research 36(3): 323-332.

Weih M & Karlsson PS (2000) Growth and nitrogen utilization in seedlings of mountain birch (*Betula pubescens* ssp. *tortuosa*) as related to plant nitrogen status and temperature: A two-year study. Ecoscience 4(3): 365-373.

2.3 Trends in altitudinal distribution of plant species richness in the Catalan Pyrenees

Introduction

Understanding the mechanisms behind broad scale patterns in species diversity has been a main topic for ecologists for a long time (Grytnes & McCain 2007). Studies of altitudinal variation in species richness represent a unique opportunity to test hypotheses on plant diversity (Nogués-Bravo et al. 2008), because there exist many independent altitudinal

transects in the world. Relating these patterns to physiography and to taxonomic, functional or distributional plant groups provides very valuable information about species distribution, adaptation and speciation (Körner 2000, Lomolino 2001, Rahbek 2005).

Altitudinal plant diversity patterns in the Catalan Pyrenees have not been described in detail yet, although there are some studies which describe the effect of altitude on vegetation patterns (Ninot et al., 2007 and references therein) and on aspects of plant diversity in some Pyrenean regions (Gómez et al. 1997, Petit & Thompson 1999, Villar et al. 2001, Ninot & Ferré 2008, Nogués-Bravo et al. 2008).

The aim of this study is to describe the species richness patterns in vascular plants along the altitudinal gradient of the Catalan Pyrenees by using an extensive compilation of observations, which includes the registered records of the last 126 years. We also analyse the factors determining the altitudinal pattern of species richness by separating the species into taxonomic, functional and distributional groups.

Methods

The study area

The Pyrenees are a typical interzonal mountainous range, with Mediterranean, Atlantic and high mountain bioclimates. The high mountain zone (from 1,600-1,800 m a.s.l. upwards) has a typically Alpine landscape and a flora mostly composed by Boreo-Alpine and orophytic (Alpine, Pyrenean or Mediterranean) taxa. The intermediate elevations (from 700-900 m a.s.l. to the high mountain) correspond to a medio-European zone and host a strong physiographic and bioclimatic diversification. The landscape is typically Atlantic on the northern and western sides of the range, with preeminent montane medio-European flora. The southern and eastern sides are characterised by a transitional sub-Mediterranean landscape, where medio-European and Mediterranean vegetation and flora constitute a complex patchwork subjected to local physiography. At lower altitudes, the bioclimatic, floristic and

landscape variability is even greater between Atlantic and Mediterranean sides (Ninot et al., 2007).

Other enviromental factors influencing the local flora are the continentality gradient towards inner valleys, the phylogeographic influence of other mountain ranges (such as the Alps or the Cantabrian mountains), and the complex shifts between siliceous and carbonated substrata. Also, the human influence is especially noticeable in the lowlands, where old land use has produced generalised landscape changes, and decreases towards higher areas, still affected by extensive farming activities (Lasanta 1990).

The Catalan Pyrenees roughly correspond to the eastern half of the Iberian Pyrenees (41º53'12"-42º54'9" N, 0º35'22"-3º10'17" E), which include most of the south-facing valleys stretching from the vicinity of the highest Aneto massif to the Mediterranean coast, and also one north-facing valley (Val d'Aran) (Fig. 1). This area forms an entire physiographic unit, as defined in Bolòs et al. (2005). However, given the size of the UTM squares used in the analyses (10 x 10 km), some surrounding areas beyond the Catalan Pyrenees have also been included (small parts of Aragón, Andorra and southern France). For simplicity reasons, we will refer our study area to as Catalan Pyrenees hereafter.

Data sources and analysis

The data we used to quantify the richness patterns of the flora were obtained from the Biodiversity Data Bank of Catalonia (Font 2008). They correspond to plant citations coming from a wide scope of papers (local floras, floristic notes or phytosociological works), from personal contributions, and from herbarium records. Each plant citation includes the elevation and the coordinates within the UTM grid of 10 x 10 km. We selected the data belonging to any of the squares included totally or partially within the Catalan Pyrenees. We rejected some low-quality data, such as imprecise taxonomical identifications or wrong altitudinal information, and we reduced the data at species level. In that way we built a regional flora of

2,491 species, according to the taxonomy stated in Bolòs et al. (2005), obtained from more than 300,000 citations.

We analysed the altitudinal species richness for the entire flora, and then for different taxonomic, functional and distributional groups, as defined by Bolòs et al. (2005). The species richness was estimated for each 100 m altitudinal band, from sea level up to 3,404 m, which is the highest point in the Pyrenees. We used the interpolation method as an approximation to the species richness pattern, which assumes the occurrence of a given species along the interval defined by the maximum and minimum altitudes where it has been observed. This may cause an artificially humped pattern if sampling is not complete (Grytnes & Vetaas 2002, Grytnes & Romdal 2008), but given the amount of citations we used, anomalies may be expected only at the edges of the altitudinal gradient.

Results and discussion

The number of observations varies very much along the altitudinal gradient, with approximately 2,300 citations at the lowest interval (0-100 m), a maximum of 21,223 citations between 1,200 m and 1,300 m, and less than 200 citations above 3,000 m (Fig. 2). This humped pattern is very similar to that of the area occupied by each elevational interval, although the peak maximum area is reached at around 1,000 m of altitude.

Species richness

The altitudinal species richness pattern shows a very marked humped response, with a maximum of 1,666 species of vascular plants at 1,000 m (Fig. 3). There is a very fast increase from sea level to 400 m, and then a moderate increase up to 1,000 m. At higher altitude, there is a marked linear decrease of species richness from 1,400 m to 3,000 m, with an average reduction of 90 species approximately per 100 m interval within this range.

From a taxonomical point of view, larger families such as Asteraceae, Poaceae and Fabaceae have a similar pattern to that of the whole flora (Fig. 4), which means that broad

taxonomical groups within Spermatophyta have presumably experienced similar ecological diversification processes than the entire flora. In smaller families the distribution may be more or less contrasting. Their richness decreases with increasing altitude, in relation to their Mediterranean or late-tropical optimum, whereas the maximum may occur at relatively high altitudes in particular families and in Pteridophyta.

The unimodal pattern for the entire flora and for larger groups is a very common trend in altitudinal or latitudinal gradients (e.g. Odland & Birks 1999, Bhattarai et al. 2004, Hillebrand 2004, Romdal et al. 2005, Grau et al. 2007). It is also very similar to those described in the Aragón Pyrenees (Villar et al. 2001), where the species richness is also highest from 800 to 1,300 m a.s.l. approximately.

The humped patterns obtained in this study, with maximum richness at a low-intermediate elevations, could be partially explained by the mid-domain effect hypothesis (MDE; Colwell et al. 2004), which states that mid-elevation habitats have a relatively higher diaspore input than areas close to the end points of the elevational gradient, which mostly have diaspore input from one direction only (Grytnes 2003). But since there is strong variation depending on the taxonomic, functional and distributional groups analysed (see later), the variations from the general pattern will indicate that climatic, spatial, biotic, historical or evolutionary factors may be also involved in defining the diversity pattern along the elevational gradient (see Grytnes & McCain 2007).

As for climatic and physiographic factors, low and medium altitudes clearly host a greater diversity of soils, outcrops, and landforms, which create a remarkable physiographic diversity. At small and medium scales, such physiographic diversity creates a high diversity of habitats and of local floristic pool (Pausas et al. 2003), which may in turn enhance the asymmetry of species richness along the altitudinal gradient. Also, climatic variability is stronger at low altitudes, since there is a greater variability of annual rainfall, spring rainfall, and summer temperature (Ninyerola et al. 2000).

Therefore, low altitudes include markedly Mediterranean areas, and from 600 m a.s.l. upwards, there are also areas with strong Atlantic influence, connected by transitional conditions in intermediate areas. This strong phytogeographic variability decreases with increasing altitude, with varied medio-European flora (ranging from sub-Mediterranean to Atlantic) at mid altitude, and Alpine flora upwards (Ninot et al. 2007). This may help in explaining the displacement of the maximum species richness towards low-medium altitudes. Besides, a considerable proportion of medio-European plants may develop in locally humid habitats within Mediterranean lowlands, such as riverbanks or in particularly mild areas. Also, although a number of temperate species may reach the high mountain, their favourable habitats (south-facing, thermal slopes) decrease rapidly above 2,200 m.

Moreover, traditional anthropogenic activities such as agriculture, farming and forest exploitation have created spatial heterogeneity at low and medium altitudes in the Pyrenees (Lasanta 1990), which in turn increases habitat diversity and species richness in these areas.

Biogeographical groups

When the flora is divided into different range size (Fig. 5), we observe a very interesting pattern in the species richness. The number of endemics of small to medium range (117 sps., 5%) peaks at 2,000 m, whereas the endemics of large range (361 sps.) reach the highest richness at 1,500 m; the number of species occurring over a large area (1,163 sps.) peaks at 1,000 m, and the species of very large range (850 sps) reach their maximum at 600 m. The percentage of endemic species increases markedly with altitude, with a percentage of more than 30% of endemics of large range and more than 10% of endemics of small range above 2,600 m.

These results reinforce the hypothesis that higher degree of isolation generally creates endemism, by means of promoting isolated habitats and speciation (Vetaas & Grytnes 2002). Broad-scale climatic dynamics strongly affects vascular flora, as they facilitate hybridisation between previously isolated populations followed by polyploidisation, which may result in

new species adapted to new conditions following climatic change (Stebbins 1984, Petit & Thompson 1999). Higher endemic proportion with increasing altitude has been also stated in other mountainous ranges also affected by strong glacial periods and climate changes, as in the Himalayas, in the Andes, in the Alps or in Sierra Nevada (Kessler 2000, Vetaas & Grytnes 2002, Casazza et al. 2005, Giménez et al. 2004, Grau et al. 2007). From a regional scale, the Catalan Pyrenees share many species with close mountain ranges such as the Alps or the Cantabrian range, which may explain that large range endemics are more abundant than short range endemics along the altitudinal gradient).

As for biogeographical types (Fig. 6), the species classified as Alpine and Boreo-Alpine are especially abundant between 1,600 m and 2,500 m. The medio-European species are the most abundant and have the widest altitudinal range in general, and they reach their maximum between 1,000 and 1,500 m. The Mediterranean species are very common from the sea level to 600 m, and show a marked and linear decrease upwards. The introduced species are not very common, although a considerable amount is found up to 1,000 m approximately. Thus, these groups respond to the three main altitude units found in the Catalan Pyrenees: high mountain, intermediate altitudes and low altitudes (Ninot et al. 2007).

Functional groups

The distribution of each life form shows a humped pattern, but except for geophytes and deciduous phanerophytes, it clearly differs from that of the whole flora (Fig. 7). This reinforces the hypothesis that life forms correspond to a marked adaptation to different bioclimatic areas and ecological niches (Raunkiær 1934).

Hemicryptophytes is the larger group, and extends abundantly up to very high elevations. Their capacity to actively regenerate most of the above ground structures during the favourable vegetative period in many contrasting bioclimates makes them very abundant along the whole altitudinal range. The ability of therophytes growing under an irregular climatic seasonality or in areas affected by marked disturbance (Grime 2001) explains their

high richness towards lower altitudes. Chamaephytes are very widely distributed along the altitudinal gradient and their relative importance increases at higher altitude. The stress-tolerant strategy dominant in this form (Grime 2001) allows them to thrive in a wide scope of unfavourable habitats, such as rocky slopes, in the understorey of dry forests and shrubs, and in open and unfertile vegetation units, which often become dominant in the higher Alpine zone.

Geophytes and deciduous phanerophytes follow the general pattern, which means that their life strategy is neutral concerning the altitude gradient, whereas evergreen phanerophytes are concentred at lower altitudes, mostly related to Mediterranean climate.

Conclusions

Species richness of vascular plants in the Catalan Pyrenees follows an asymmetric unimodal distribution, as described in other ranges, concerning the whole flora and larger subgroups. Such asymmetry may be partially explained in terms of higher physiographic heterogeneity, climatic variability, biogeographic diversity and anthropisation at lower altitudes.

The contrasting patterns observed in the subgroups considered (families, life forms, biogeographic groups) reveal adaptive strategies or historical traits exclusive to the Pyrenees.

References

Bhattarai, K.R., Vetaas, O.R. & Grytnes, J.A. 2004. Fern species richness along a Central Himalayan elevational gradient, Nepal. *J. Biogeogr.* 31: 389–400.

Bolòs, O. de, Vigo, J., Masalles, R.M. & Ninot, J.M. 2005. *Flora manual dels Països Catalans*. 3rd edn. Pòrtic, Barcelona.

Casazza, G. Barberis, G. & Minuto, L. 2005. Ecological characteristics and rarity of endemic plants of the Italian Maritime Alps. *Biol. Conserv.* 123: 361–371.

Colwell, R.K., Rahbek, C. & Gotelli, N.J. 2004. The mid-domain effect and species richness patterns: What have we learned so far? *Am. Nat.* 163: E1-E23.

Font, X. 2008. *Mòdul de Flora, Banc de Dades de Biodiversitat de Catalunya (BDBC).* Generalitat de Catalunya & Universitat de Barcelona. http://biodiver.bio.ub.es/biocat/homepage.html

Giménez, E., Melendo, M., Valle, F., Gómez-Mercado, F. & Cano, E. 2004. Endemic flora biodiversity in the south of the Iberian Peninsula: altitudinal distribution, life forms and dispersal modes. *Biodivers. Conserv.* 13: 2641–2660.

Gómez, D., Sesé, J.A., Ferrández, J.V. & Aldezabal, A. 1997. Altitudinal variation of floristic features and species richness in the Spanish Pyrenees alpine belt. *36th Symposium of IAVS. Serie Informes* 40: 113-123. Univ. de la Laguna, Tenerife.

Grau, O., Grytnes J.A. & Birks H.J.B. 2007. A comparison of altitudinal species richness patterns of bryophytes with other groups in Nepal, Central Himalaya. *J. Biogeogr.* 34: 1907–1915.

Grime, J.P. 2001. *Plant Strategies, Vegetation Processes and Ecosystem Properties*. John Wiley & Sons, Chichester.

Grytnes, J.A. 2003. Ecological interpretations of the mid-domain effect. *Ecol. Lett.* 6: 883-888.

Grytnes, J.A.& Vetaas, O.R. 2002. Species richness and altitude, a comparison between simulation models and interpolated plant species richness along the Himalayan altitudinal gradient, Nepal. *Am. Nat.* 159: 294–304.

Grytnes, J.A. & McCain C.M. 2007. Elevational patterns in species richness. In: Levin S.A. (ed), *Encyclopedia of biodiversity*, online enhancement: 1-8. Elsevier, New York.

Grytnes, J.A. & Romdal, T.S. 2008. Using Museum Collections to Estimate Diversity Pattern along Geographical Gradients. *Fol. Geobot.* 43(3): 357-369.

Hillebrand, H. 2004. On the generality of the latitudinal diversity gradient. *Am. Nat.* 163: 192-211.

Kessler, M. 2000. Elevational gradients in species richness and endemism of selected plant groups in the Central Bolivian Andes. *Plant Ecol.* 149: 181–193.

Körner, C. 2000. Why are there global gradients in species richness? Mountains might hold the answer. *Trends Ecol. Evol.* 15: 513–514.

Lasanta, T. 1990. Diversidad de usos e integración especial en la gestión tradicional del territorio en las montañas de Europa Occidental. In: García Ruiz J.M. (ed) *Geoecología de las áreas de montaña*: 235-266. Geoforma Ediciones, Logroño.

Lomolino, M.V. 2001. Elevation gradients of species-richness, historical and prospective views. *Global Ecol. Biogeogr.* 10: 3–13.

Ninot, J.M. & Ferré, A. 2008. Plant diversity across five vegetation belts in the Pyrenees (Catalonia, Spain). *Collect. Bot.* (Barcelona) 27: 67-76.

Ninyerola, M.., Pons, X. & Roure, J.M. 2000. A methodological approach of climatological modelling of air temperature and precipitation through GIS techniques. *Int. J. Climatol.* 20: 1823-1841.

Nogués-Bravo, D., Araújo, M.B., Tomdal, T. & Rahbek, C. 2008. Scale effects and humn impact on the elevational species richness gradients. *Nature* 453: 216-220.

Odland, A. & Birks, H.J.B. 1999.. The altitudinal gradient of vascular plant species richness in Aurland, western Norway. *Ecography* 22: 548–566.

Pausas, J.G., Carreras, J., Ferré, A. & Font, X. 2003. Coarse-scale plant species richness in relation to environmental heterogeneity. *J. Veg. Sci.* 14: 661-668.

Petit, C. & Thompson, J.D. 1999. Species diversity and ecological range in relation to ploidy level in the flora of the Pyrenees. *Evol. Ecol.* 13: 45-66.

Rahbek, C. 2005. The role of spatial scale and the perception of large-scale species-richness patterns. *Ecol. Lett.* 8: 224–239.

Raunkiær, C. 1934. *The life forms of plants and statistical plant geography*. Clarendon Press. Oxford.

Romdal, T.S., Colwell, R.K. & Rahbek, C. 2005. The influence of band sum area, domain extent, and range sizes on the latitudinal mid-domain effect. *Ecology* 86: 235–244.

Stebbins, G.L. 1984. Polyploidy and distribution of the arctic-alpine flora: new evidence and new approaches. *Bot. Helv.* 94: 1–13.

Vetaas, O.R. & Grytnes, J.A. 2002. Distribution of vascular plants species richness and endemic richness along the Himalayan elevation gradient in Nepal. *Global Ecol. Biogeogr.* 11: 291–301.

Villar, L., Sesé, J.A. & Ferrández, J.V. 2001. *Atlas de la Flora del Pirineo Aragonés*. Vol. II. Instituto de Estudios Altoaragoneses & Consejo de Protección de la Naturaleza de Aragón, Jaca.

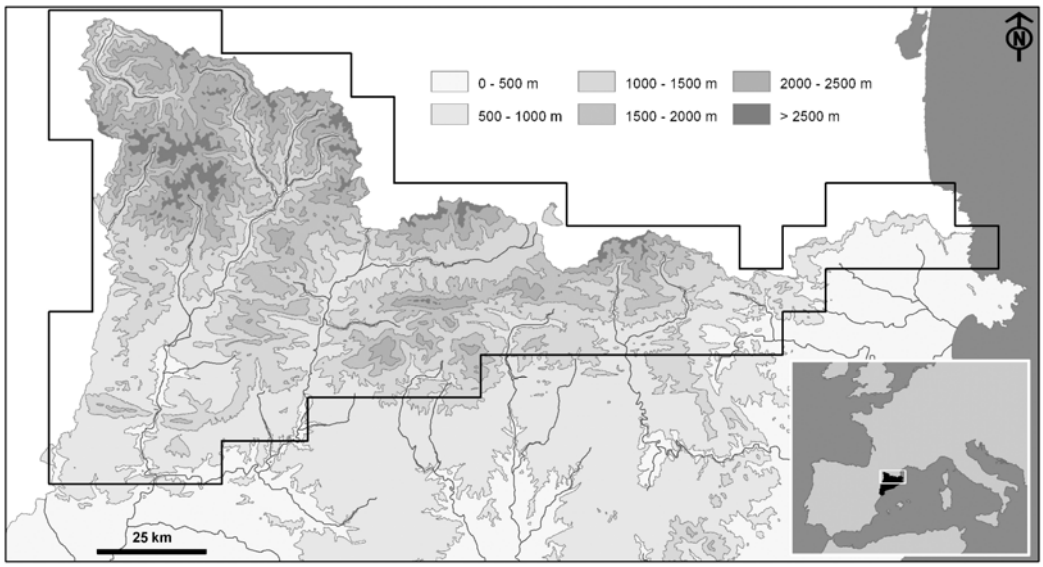

Figure 1. Area of study, defined by 10 x 10 km UTM squares in the Catalan Pyrenees.

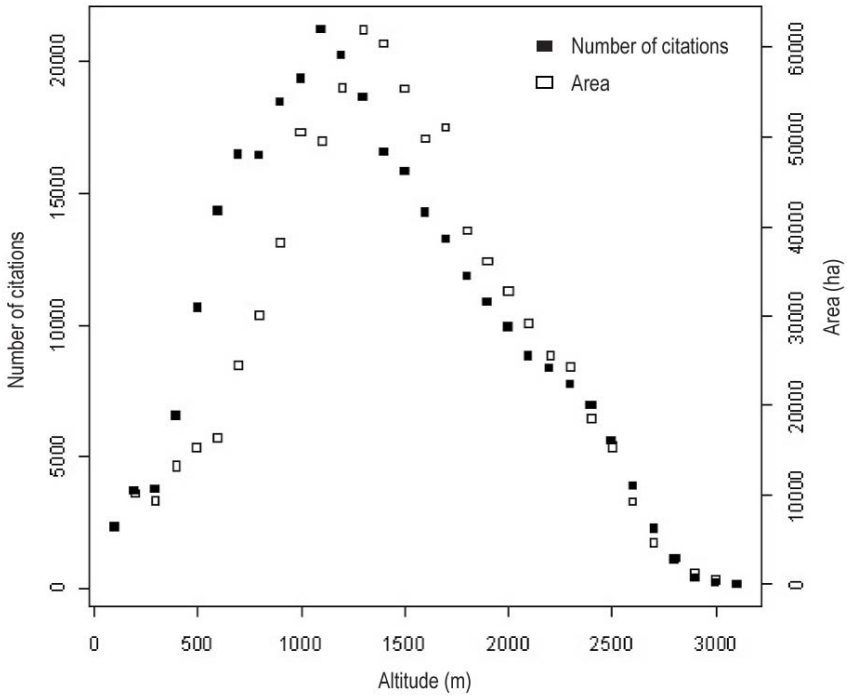

Figure 2. Number of citations (empty squares) and area in ha (filled squares) per 100 m altitudinal interval along the altitudinal gradient in the Catalan Pyrenees.

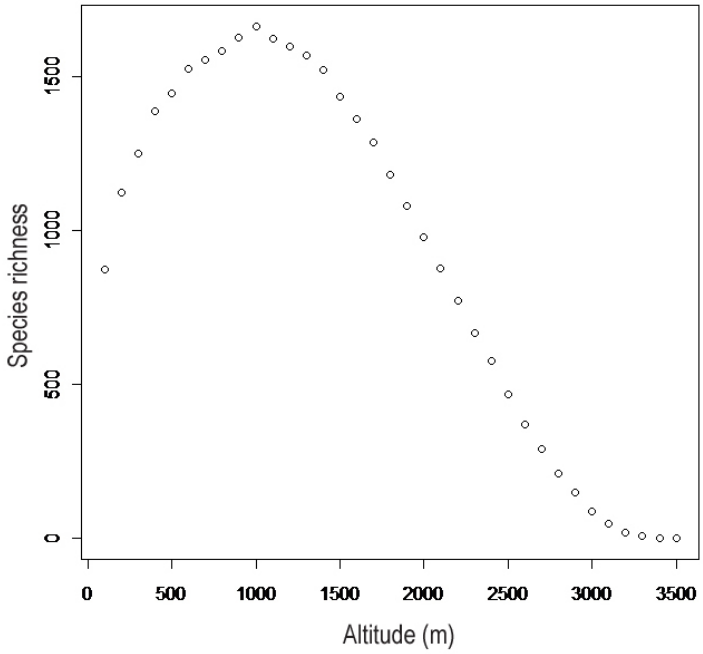

Figure 3. Altitudinal species richness pattern estimated from interpolated ranges along the altitudinal gradient in the Catalan Pyrenees.

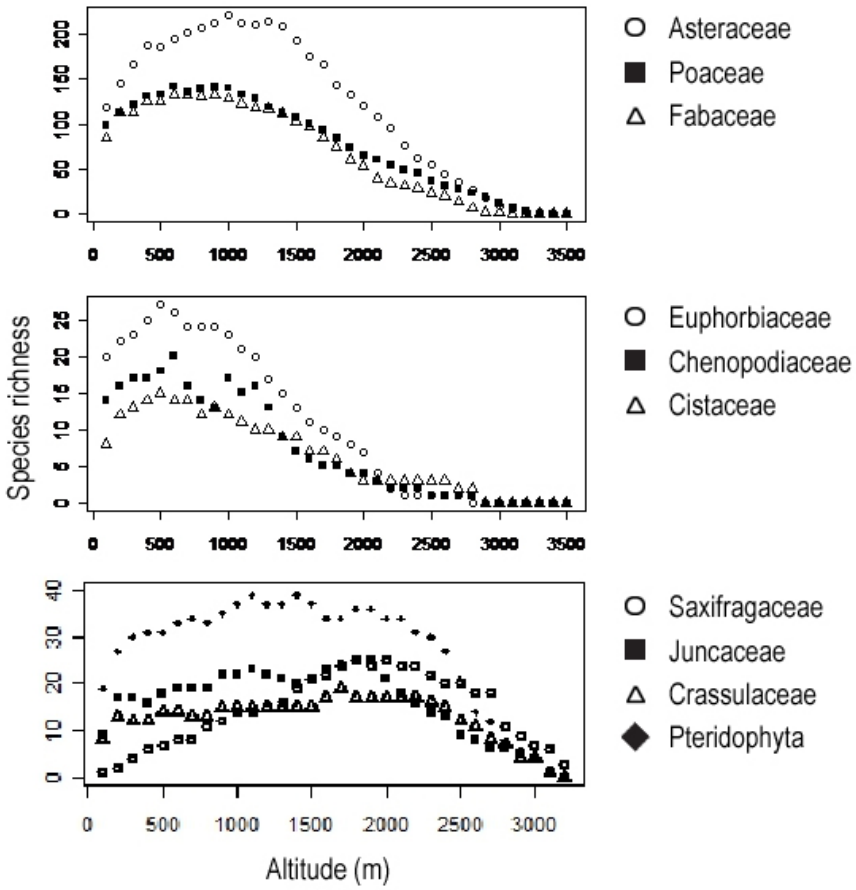

Figure 4. Species richness patterns for some plant groups (representative families and pteridophytes) along the altitudinal gradient in the Catalan Pyrenees.

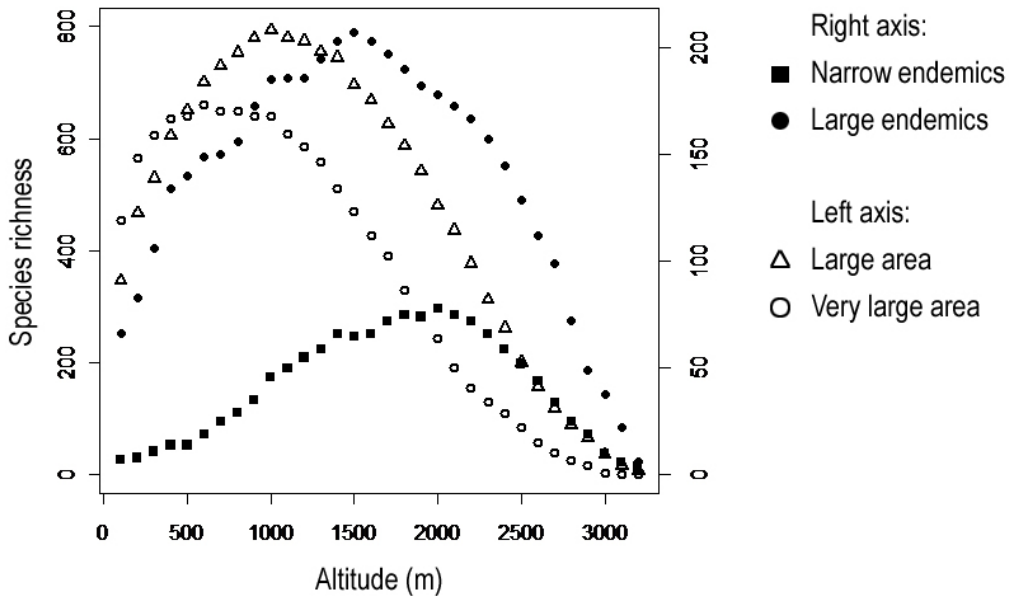

Figure 5. Species richness patterns for groups of different range size along the altitudinal gradient in the Catalan Pyrenees.

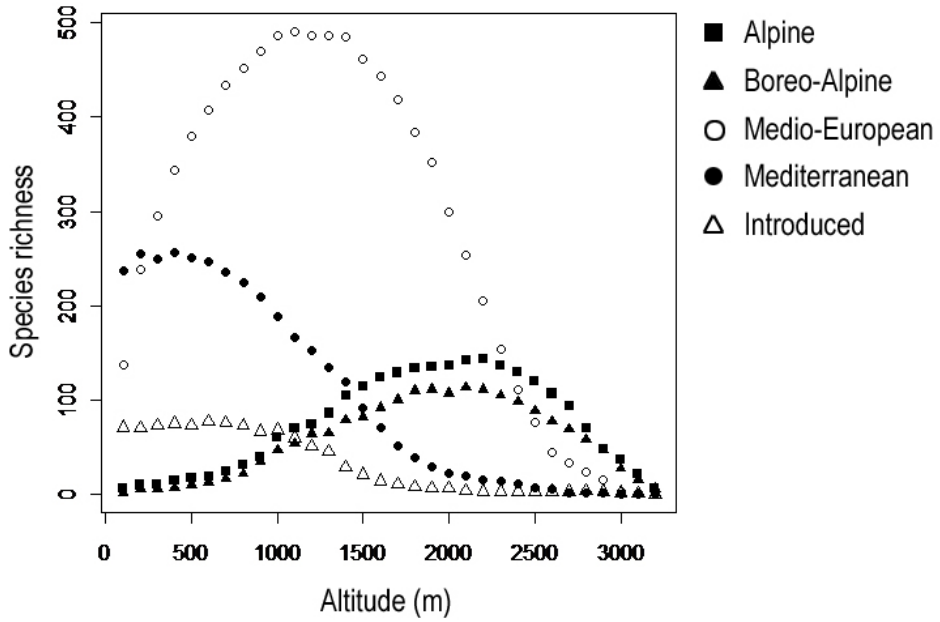

Figure 6. Species richness patterns for different biogeographical groups along the altitudinal gradient in the Catalan Pyrenees.

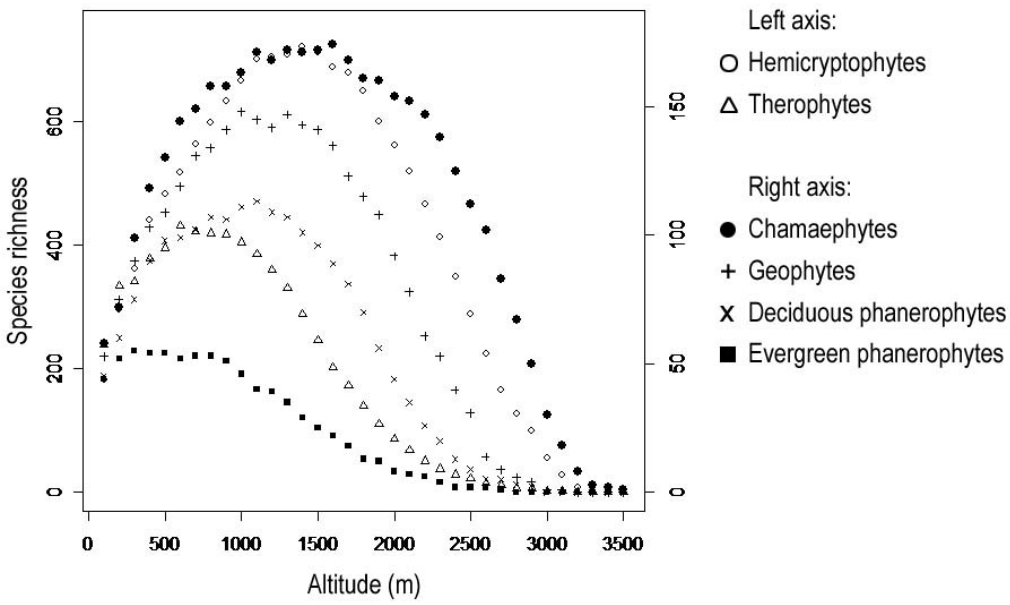

Figure 7. Species richness patterns for different life forms along the altitudinal gradient in the Catalan Pyrenees.