UNIVERSITAT DE
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The Pyrenean mires

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Les molleres pirinenques

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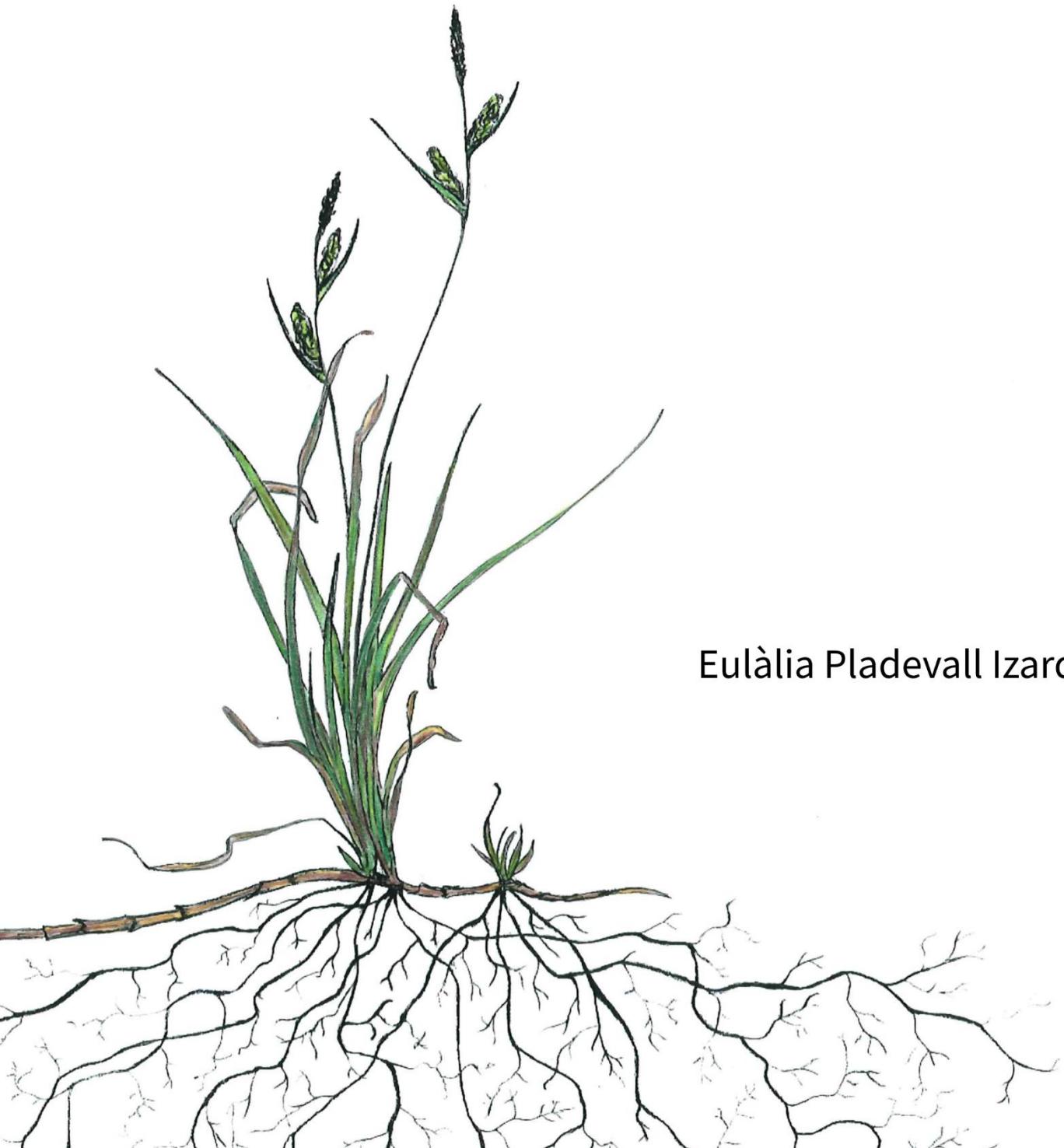
Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals

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Memòria presentada per Eulàlia Pladevall Izard per optar al grau de

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La doctoranda:
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Agraïments

Tenia tantes ganes d'escriure els agraïments! Perquè em sento profundament agraïda! Perquè seran sincers, sense hipocresia. Com els dies bons.

Aaron, aquesta tesi és teva. Des de la primera a la última reunió, des que et vaig demanar que fossis el meu codirector, a la sala de lupes, fins la trucada amb rialles d'aquest migdia; totes les decisions les hem pres junts. No tindria sentit fer una llista del que has fet perquè aquest conjunt de papers un dia s'imprimeixin. M'has mantingut dempeus i m'has ensenyat milions de coses (i moltes plantes, unes quantes vegades cadascuna d'elles). Només diré tres coses: gràcies per treballar junts; gràcies per tot allò que no és feina; i no et desfaràs de mi tan fàcilment.

Pep, gràcies per comptar amb mi. Sé que t'he fet patir, però ja arribem a port. Com un pare que fa veure que no vigila les criatures, m'has deixat fer el que he volgut i has procurat que no em faltés de res, guiant-me quan era necessari sense que ho hagués de demanar. El somriure amb el que em reps quan fa dies que no ens veiem no té preu. Gràcies per deixar-te embolicar amb aquesta tesi i per voler-me contenta sempre.

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Tots els companys de botànica. L'Estela, que sempre s'ha assegurat que dinés bé, que ha treballat tant al capítol dels pins, i que fa que a casa seva m'hi senti tan bé. Gràcies per cuidar-me. El Jose, perquè *posa un Jose a la teva vida*; no te'n penediràs. L'Arnau, amb el millor dels humors possibles. L'Alba, que em va fer companyia al principi i que sempre, sempre que li demanes, té un bon consell. L'Albert, l'Efrem, l'Empar, i tots els altres habituals del Coffea, actuals, passats, tots. Al Coffea ric, ric molt, i de vegades dinar és el millor que em passa en tot el dia. Com una paracaigudista desubicada, vaig petar aquí. Tornaria a saltar per tornar-hi a caure.

La Maria i la Neus. Casa és *casa* perquè hi són elles. I no ho dic per dir. Sempre tinc ganes de tornar a casa per veure si us hi trobo. És que no sé com ho feu, que si arribo atabalada o trista, al cap de deu minuts ja estic contenta. Pel sol del balcó i les converses de sofà. Pels vermuts, els fideuets i la bossa d'aigua calenta. M'heu acompanyat aquests cinc anys i les hem vist de tots colors. Vau acollir a l'Elsa. Vam confinar-nos. M'heu escoltat sempre; i això són moltes vegades. Feu que tot sigui més fàcil i divertit. Gràcies, amigues.

El Nil, el millor company de campanyes de camp i el millor fotògraf. Sofert i incansable, fa que tot sigui senzill. El Jaume, que va ser el meu germà en una època molt intensa, de punts de rosada i de models mixtes. *Som un equip, lagarto*. La Cèlia, que em fa recordar que les plantes són boniques, perquè sí, i que només per això ja val la pena la resta. Llarga vida als viatges mini-botànics. L'Eva, que va posar sal i pebre a una tardor de dubtes. L'Anna Ruvi, menció d'honor a l'ajudant de camp. I també el Xavi Patxot, la Carla Cárdenas, la Gemma Domènech, el Pau Montané, el Marc Vez, la Paula Vicenç, el Pol Alemany, l'Ana García, només per dir-ne alguns. I la Carolina Doza, el Joel Rodríguez, el Marçal Galobart, el Pau Compte, el Víctor Lecegui, el Marc Arimany, la Jordina Gili, i un etcètera molt llarg. Sou molts els que heu vingut amb mi a camp, us heu ajupit al costat d'un punt de mostreig i m'heu vist nerviosa o molt cansada. Ens n'han passat unes quantes, i sense la vostra ajuda jo no hauria pogut tirar endavant. Gràcies a tots.

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La recerca t'acompanya allà on vas. Al tren, d'excursió, a Oulu, als sopars amb amics, a casa. La portes a dins i de tant en tant et crida. Forma part de tu. En algun moment, la tesi va sobrepassar límits no desitjats, i alguns amics se n'hauran ressentit. Només tenim una vida, i jo sempre l'he volguda omplir de coses, perquè hi ha moltes coses que m'agrada fer. Els equilibris són difícils, en ecologia i al dia a dia, i de vegades la balança tomba. Però a mi m'agrada viure intensament. I *i tant*, si ho he fet. Amb les amigues de l'Autònoma, que són ja un pilar i el sinònim de vida social. Amb l'Annamari i la Ruth a Oulu. Amb les noies de teles, on he tornat a vibrar. Amb les persones d'orquestra. Seria injust obviar que el Jordi em va acompanyar i ajudar moltíssim els primers anys de la tesi. Gràcies fer-me tant de costat.

Però no puc acabar sense fer uns apunts una mica més formals. Algunes persones han participat significativament als diferents capítols, i els vull agrair aquí les seves aportacions. Al capítol 1, a l'Efrem, per participar a fer el disseny experimental i ajudar a les primeres fases de l'estudi. Al Jaume, per ajudar-me a manipular les mostres i analitzar les dades. A l'Empar, mestressa de Font Grossa. Al capítol 2, al Jose, per venir amb mi a Parros i dissenyar el mostreig, i per ajudar-me a ser pràctica a les fases terminals. Al Nil, per tota la feinada amb les tanques. Impossible sense tu. Al capítol 3, a tots els coautors del treball –Estela, Marçal, Marc, Albert i Empar. També a l'Enric, per ajudar-nos a comptar anells de pins. Al capítol 4, al Janne Alahuhta i al Jani Heino per haver confiat amb mi i acollir-me a Oulu. I finalment a l'Albert, per fer uns mapes tan bonics, i a tots els que m'heu cedit fotografies. Ah, i a Erwin Lichtenegger, per dibuixar tant bé. A partir del seu dibuix em vaig atrevir a dibuixar el *Carex* de la portada. Gràcies a persones com vosaltres, la ciència és més amena i tot és una mica més agradable.

I a tots els capítols, i a tots els treballs que no formen part d'aquesta tesi, al Pep i a l'Aaron, el millor tiet i el millor amic que mai algú podrà tenir com a directors de la seva tesi doctoral. La meva sort és preuada.

Despunten crits de fulles en els arbres

Abstract

Multiple processes determine the structure and diversity of plant communities. The study of these processes, the community assembly rules, is a central part of the study of terrestrial ecology in the recent decades. In the Alpine mountains mires occupy inland insular habitats, which face natural fragmentation and variation of environmental conditions both within a mire and between distant mires. In addition, mire communities experience the effects of land use changes and climate change. In this thesis, we want to understand how these communities respond to changes of different ecological and land use factors. The results shown and discussed should enable to reveal what are the current threats of Alpine mires, and to perform science-based management decisions. Here, we studied the vegetation dynamics of Alpine mires from the Central Pyrenees at different temporal and spatial scales. More concretely, we studied the relationship between water table depth and plant-plant interactions of three engineering plant species; we assessed the responses of the vegetation under contrasting grazing conditions in a three-year experiment; we studied what bioclimatic and land use factors facilitate the mires encroachment by *Pinus uncinata*; and we studied beta diversity patterns of mire communities at a regional scale. At shoot or plant level, growth performance proved to be the basis of the competitive abilities of the three species studied, independently of the water level. Lateral expansion of clonal plants was the main mechanism in gap colonization after grazing exclusion, whereas sexual reproduction had a secondary role in short-term vegetation dynamics. The current spontaneous reforestation of the subalpine belt resonates even in the mire systems, where pine encroachment has increased at places, namely at the neighborhood of pinewoods. At regional scale, beta diversity patterns showed that each mire site harbors its floristic singularity, whereas environmental gradients are less relevant in the community assembly of these inland insular habitats. Overall, the vegetation dynamics in Alpine mires proceeds very slowly at wide geographical scales, but remarkable changes in vegetation occur in short time at detailed scale.

Sinopsi

Múltiples processos determinen l'estructura i diversitat de comunitats vegetals. L'estudi d'aquests processos és una part central de l'estudi de l'ecologia terrestre de les darreres dècades. A les muntanyes alpines, les molleres són hàbitats que es disposen en forma d'illes terrestres, i que s'enfronten a la fragmentació natural i la variació de les condicions ambientals –tant dins d'una mollera com entre molleres distants. A més, les comunitats de mollera estan exposades als canvis d'ús del sòl i al canvi climàtic. En aquesta tesi, volem entendre com aquestes comunitats responen als canvis de diversos factors ecològics i d'usos del sòl. Els resultats trobats i discutits han de permetre esbrinar quines són les amenaces actuals de les molleres alpines, i prendre decisions de gestió científicament fonamentades. Hem estudiat la dinàmica de la vegetació de les molleres alpines dels Pirineus centrals a diferents escales temporals i espacials. Més concretament, hem estudiat la relació entre la profunditat del nivell freàtic i les interaccions planta-planta de tres espècies enginyeres; hem analitzat les respostes de la vegetació sota condicions de pressió ramadera contrastades en un experiment de tres anys de durada; hem avaluat quins factors bioclimàtics i d'usos del sòl faciliten la invasió de Pinus uncinata; i hem estudiat l'estructura de la diversitat beta entre comunitats de mollera a escala regional. A nivell de planta, el creixement de les plantes va ser la base de les capacitats competitives de les tres espècies, independentment del nivell freàtic. L'expansió lateral de les plantes clonals va tenir un paper important en la colonització d'espais malmesos per la pressió ramadera, mentre que la reproducció sexual va tenir un paper secundari en la dinàmica de la vegetació a escala de detall. L'increment de pins a l'estatge subalpí de vegetació succeeix també a les molleres, on la presència de pins ha augmentat sobretot a les molleres envoltades de boscos. A escala regional, els patrons de diversitat beta van mostrar que cada mollera té una singularitat florística pròpia, mentre que els gradients ambientals són menys rellevants en la construcció de les comunitats d'aquests hàbitats a les muntanyes alpines. En global, la dinàmica de la vegetació a les molleres alpines és lenta a escales geogràfiques àmplies, però es produeixen canvis notables la vegetació en poc temps a escales detallades.

Índex

Introducció general

Trescuro. Fotografia de Nil Escolà.

Introducció general

A les regions alpines, les comunitats vegetals són, en general, poc productives, tenen un període de creixement curt i estan dominades sobretot per plantes perennes que poden viure molts anys (Körner, 2003). Això fa que davant un canvi en l'ambient, la resposta de la vegetació pugui ser aparentment lenta (Lu et al., 2021; Tasser & Tappeiner, 2002). Però, sigui quina sigui la inèrcia o la magnitud en aquesta resposta, el canvi climàtic impacta de ple en la vegetació alpina i subalpina d'Europa (Engler et al., 2011), i l'herbivorisme és un director clau en la construcció de les seves comunitats vegetals (Dullinger et al., 2003). En aquest treball ens centrem en les molleres de les muntanyes alpines, més concretament dels Pirineus, i millorem el coneixement de base sobre l'estructura i dinàmica de la seva vegetació, i sobre la vulnerabilitat d'aquests ambients als paisatges alpins.

La construcció de les comunitats vegetals

Els processos que determinen la presència i l'abundància de les espècies en una comunitat ecològica es coneixen en conjunt com la construcció de comunitats (*community assembly*). A partir d'un conjunt d'espècies que potencialment poden formar part de la comunitat (*species pool*), l'expressió que prenguin la dispersió, els filtres ambientals i les interaccions biòtiques acabaran determinant com serà la comunitat d'un lloc concret (Kraft & Ackerly, 2014). La capacitat de dispersió de les espècies determinarà la probabilitat que puguin colonitzar llocs més o menys llunyans de les seves poblacions originals, com ja apuntaven Wilson i MacArthur a la teoria de la biogeografia d'illes (1967). En segon lloc, els filtres ambientals operen sobre el fenotip de les espècies (Keddy, 1992), de manera que les que s'estableixin i persisteixin en un punt donat seran només aquelles que tinguin les característiques concretes que els permetin sobreviure a les condicions ambientals d'aquell punt (van der Valk, 1981).

En tercer lloc, les espècies que conviuen en una comunitat interaccionen, i aquestes interaccions poden modificar el creixement de les espècies positivament o negativament, fins a fer-les desaparèixer en el que es coneix com a exclusió competitiva (*competitive exclusion*) com ja proposaven Gause & Witt (1935) i posteriorment ho aplicava Diamond (1975) a la construcció de comunitats. En aquest model determinista, espècies funcionalment molt similars tendirien a no co-existir en una comunitat (*limiting similarity*, Abrams, 1983); és a dir, les espècies d'una comunitat serien menys similars entre elles que per atzar (Weiher & Keddy, 2001). Amb tot plegat, una espècie és capaç de prosperar en un conjunt de situacions ecològiques (el que es coneix com a nínxol fonamental,

fundamental niche; Hutchinson & Deevey Jr, 1949) però la distribució real de les espècies acostuma a ser més restringida degut a constriccions en la dispersió i a les interaccions biòtiques (nínxol real, *realised niche*; Colwell & Rangel, 2009).

En contrast a les teories deterministes, Hubbell (2001) proposa la teoria neutra de l'ecologia de comunitats (*neutral theory*), segons la qual tots els individus són equivalents i la composició de les espècies d'una comunitat es deu només a l'atzar (Chave, 2004). Paradoxalment, les dues visions sobre la construcció de comunitats no són mútuament excloents, sinó que, per exemple, Tilman (2004) les combina afegint el component de l'atzar a la dispersió i als filtres abiòtics i biòtics.

A una escala espacial més àmplia, comunitats similars poden estar connectades a través de la dispersió de les espècies que comparteixen, i per tant formar poblacions i comunitats interconnectades en l'espai i el temps (metapoblacions i metacomunitats). Per estudiar la construcció d'aquestes metacomunitats, Leibold et al. (2004) proposen quatre paradigmes diferents, en els que inclouen de nou tant el punt de vista determinista com el punt de vista neutralista en l'estudi de la construcció de metacomunitats.

Les molleres

Les molleres són hàbitats en què el nivell de l'aigua és molt proper a la superfície del sòl (o fins i tot la supera) durant una bona part de l'any, i per tant són una tipologia concreta d'aiguamolls. Les plantes que s'hi fan han de poder sobreviure sobre sòls amb molt baixes concentracions d'oxigen (hipòxia o anòxia) durant períodes prolongats. En aquests sòls saturats d'aigua, sovint la descomposició de la fullaraca i altra matèria orgànica que s'acumula és incompleta, i progressivament forma acumulacions de torba (Rydin & Jeglum, 2013). Les molleres on aquesta acumulació supera els 30 cm de gruix reben el nom de torberes (Joosten & Clarke, 2002). Molleres i torberes es classifiquen en dues tipologies hidrològiques principals: les minerogèniques (*fens*) reben aigua freàtica enriquida amb minerals del sòl, mentre que en les ombrogèniques (*bogs*) l'acumulació de torba aïlla l'aigua freàtica mineral de la vegetació, fent que aquesta només rebi aigua de la pluja i la neu (Rydin & Jeglum, 2013). La gran diversitat de molleres arreu del planeta es reflecteix en una bona diversitat de termes per referir-s'hi. Pérez-Haase (2016) fa una bona descripció de les tipologies de molleres dels Pirineus, a partir de la qual resumim la manera com ens hi referim al llarg de la present memòria, tant en català com en anglès (Taula 1).

Les torberes ocupen grans superfícies en climes temperats i boreals (Vitt, 2009), on el període vegetatiu no és gaire llarg, les temperatures estivals són moderades i la precipitació és notable. Ocupen grans superfícies a Canadà i a Sibèria, i a Europa són dominants sobretot a Fennoscàndia i a les illes Britàniques (Joosten & Clarke, 2002). A mesura que disminuïm en latitud, les condicions climàtiques favorables al

Taula 1. Terminologia dels hàbitats higròfils utilitzada al llarg de la present memòria, amb el significat que li'n donem.

En anglès	En català	Significat emprat en aquesta memòria
Wetland	Aiguamoll	Terme general que inclou molleres i altres hàbitats hidròfils o semi-aquàtics
Mire	Mollera	Hàbitat dominat per plantes hidròfiles i acumulador de torba. Terme general per referir-nos al conjunt d'ambients estudiats
Fen	Mollera minerotròfica	Mollera minerotròfica (majoritàries als Pirineus, sovint ens hi referim com a simplement mollera)
Spring fen	Mollera en surgències	Molleres minerotròfiques associades de manera directa al curs d'aigua superficial d'una font o surgència d'aigua
Peatland	Torbera	Mollera amb una acumulació de torba superior als 30 cm de gruix.
Bog	Torbera ombrotròfica	Torbera ombrotròfica, oligotròfica i generalment dominada per esfagnes
Sphagnum hummock	Coixí d'esfagnes	Bombament torbós en una mollera, generalment dominat per esfagnes i on el nivell de l'aigua freàtica es manté baix. Ombrotròfic o de tendència ombrotròfica.
Sphagnum carpet	Catifa d'esfagnes	Comunitat dominada per briòfits (sobretot esfagnes) i ciperàcies, que formen catifes baixes de certa extensió.

desenvolupament de molleres i torberes es limiten a zones muntanyoses per damunt dels 1.000 m d'altitud a les muntanyes alpines del sud d'Europa, o a zones amb forta influència atlàntica com Galícia o Cantàbria, entre els 200 i els 1.000 m d'altitud (de Hoyos et al., 1996; Heras et al., 2010). Als Pirineus meridionals, la majoria de molleres es troben entre els 1.500 i els 2.500 m d'altitud, coincidint força amb l'estatge subalpí de vegetació (Casanovas, 1991; Rivas-Martínez, 2011).

A les molleres hi dominen les plantes graminoides (principalment *Cyperaceae*, *Poaceae* i també *Juncaceae*), tot i que en molleres minerotròfiques la riquesa de fòrbies acostuma a ser prou elevada (Rydin & Jeglum, 2013). Algunes torberes també duen subarbustos (sobretot en llocs aixecats com els coixins d'esfagnes; per exemple, *Calluna vulgaris*, *Vaccinium myrtillus*) o poblacions esclarissades d'arbres, que fan arrels superficials per evitar penetrar en sòls permanentment saturats –per exemple, *Pinus sylvestris* o *Picea abies* en torberes de les planes europees (Edvardsson & Hansson, 2015; Freléchoux et al., 2003), i *Pinus uncinata* en algunes molleres pirinenques. Els briòfits juguen un paper estructural als hàbitats de mollera, sent les molses del gènere *Sphagnum* les principals formadores de torba. Per la seva banda, les anomenades molses brunes dominen en molleres minerotròfiques (Fig. 1).

Interaccions biòtiques i filtres ambientals a les molleres

A les comunitats vegetals, les plantes interaccionen de manera molt diversa (Connell & Slatyer, 1977). Les interaccions poden ser negatives (inhibició, competència), neutrals (tolerància) o també positives (facilitació, mutualisme). Les plantes més competitives acostumen a tenir taxes de creixement grans, a explotar eficientment els recursos de l'ambient, a tenir un vigor notable i a depositar fullaraca a la superfície del sòl (Grime, 1973). Sovint, les plantes menys competitives sobreviuen als llocs on les més competitives no poden prosperar degut a limitacions en els recursos, com s'ha observat en diferents hàbitats d'aiguamoll (Keddy, 2010). De fet, s'ha demostrat que les interaccions biòtiques juguen un paper clau en el nínxol real de les espècies de prats humits (Švamberková et al., 2017).

Més enllà de les característiques intrínseques de cada espècie, la prevalença de les interaccions positives o negatives pot variar al llarg d'un gradient d'estrès abiòtic al que estiguin sotmesos els individus (Bertness & Callaway, 1994). Segons la teoria del gradient d'estrès (stress gradient hypothesis; Brooker & Callaghan, 1998), en situacions estressants prenen importància les interaccions positives per al desenvolupament dels individus de la comunitat, mentre que en condicions amb recursos abundants i més productius augmenten les relacions de competència (Callaway & Walker, 1997; Grime, 1979). Això permetria que espècies amb nínxols similars coexisteixin en comunitats amb estressos ambientals molt forts, ja que l'exclusió competitiva hi perdria importància.

Malgrat això, diversos autors subratllen que aquest patró no sempre es compleix (Maestre et al., 2006). Aquests proposen que la facilitació només prevaldria en situacions intermèdies d'estrès per un recurs (Maestre et al., 2009) i que les interaccions variarien en funció de la naturalesa del gradient en qüestió (Kawai & Tokeshi, 2007). A més, les capacitats competitives i els requeriments abiòtics de les plantes canvien al llarg de la seva vida (Callaway & Walker, 1997; Malkinson & Tielbörger, 2010). Finalment, les característiques ambientals d'un lloc poden canviar al llarg del temps de manera gradual o de manera brusca (per exemple, després d'una pertorbació) fent que les relacions entre les espècies d'una comunitat també canviïn (Callaway et al., 2002). Tot plegat promou que les comunitats vegetals siguin en certa manera dinàmiques. Entendre aquesta dinàmica en diferents escales temporals i espacials representa un dels principals focus d'estudi de l'ecologia de les comunitats vegetals (Pickett et al., 2012).

Per entendre la resposta de les espècies a l'ambient, s'ha mostrat molt útil la consideració dels trets funcionals i de les estratègies d'aquestes espècies. Anomenem tret funcional a qualsevol característica morfològica, fisiològica, fenològica o reproductiva d'un ésser viu que tingui influència en l'èxit pel seu establiment, supervivència o reproducció (Reich et al., 2003). Per la seva naturalesa, els trets funcionals són adaptatius, de manera que les espècies d'un mateix hàbitat o nínxol comparteixen un bon nombre de trets funcionals, seleccionats pels filtres que hi operen (Kraft & Ackerly, 2014). A cada espècie, el conjunt de trets defineix la seva estratègia ecològica particular. En aquest sentit, la majoria de plantes de mollera són considerades estrès-tolerants o lleugerament competitives segons l'esquema d'estratègies de Grime (2001) i la diversitat funcional hi és baixa (E. Vojtkó et al., 2017). Per exemple, quasi totes són clonals, capaces de persistir i d'expandir-se lateralment a partir de rizomes (Moor et al., 2017; Rydin & Jeglum, 2013), ja que en climes freds, poc fèrtils i amb pH baix se seleccionen plantes que poden reproduir-se vegetativament (E. Vojtkó et al., 2017).

Tot i que les molleres resultin estressants o limitants per a la flora que no hi estigui ben adaptada, moltes espècies hi troben el seu hàbitat únic. Les plantes que hi viuen toleren l'escassetat d'oxigen als òrgans subterranis xops gràcies al desenvolupament d'aerènquima (parènquima amb espais intercel·lulars per on transportar l'aire als òrgans que no hi tenen accés) o arrels especialment superficials, a més d'una multiplicitat de respostes metabòliques (Cronk & Fennessy, 2001). Paral·lelament, conservar els nutrients adquirits els permet fer front a l'escassetat de nutrients disponibles al medi. Així, són plantes amb una baixa taxa de creixement i longeves, i utilitzen els òrgans subterranis com a reservori dels nutrients que han adquirit o que transloquen a la tardor des de les fulles per reciclar-los la temporada següent. Això els permet rebrotar a partir de la glicòlisi dels carbohidrats emmagatzemats (Cronk & Fennessy, 2001).

Dins les molleres, la distribució de les plantes i els briòfits està determinada per tres principals gradients ambientals. El primer és l'anomenat gradient pobre-ric (*poor-rich gradient*) i es relaciona amb les característiques físico-químiques de l'aigua freàtica:

Fig. 1. A les molleres hi dominen, sobretot, les plantes graminoides (a l'esquerra, una mollera dominada per *Eriophorum angustifolium*) i els briòfits (a la dreta, un coixí d'esfagnes al costat de comunitats dominades per molses brunes). Fotografies d'Albert Ferré i Nil Escolà.

la seva càrrega iònica, l'acidesa i la concentració de calci (Sjörs & Gunnarsson, 2002; Wheeler & Proctor, 2000). El segon és la profunditat de l'aigua freàtica i la seva fluctuació al llarg del temps, expressada com l'amplitud i la periodicitat en les fluctuacions (nivell freàtic o w*ater table depth*; (Hájková et al., 2004; P. Keddy & Fraser, 2000). El tercer és la fertilitat o disponibilitat de nutrients per les plantes, i es relaciona no només amb la productivitat de l'hàbitat sinó que també acostuma a anar lligat amb la seva riquesa florística. Així, en general, les molleres més oligotròfiques són més pobres en flora (Rydin & Jeglum, 2013). Altres factors ecològics rellevants en l'estructura de les comunitats de mollera són la disponibilitat de llum als diferents estrats de vegetació (Kotowski et al., 2006; Kotowski & Diggelen, 2004), la profunditat de la torba (Wheeler & Proctor, 2000) i les seves característiques fisico-químiques (Bragazza & Gerdol, 1999), i factors modulats per l'acció humana com la pastura o el dall (Bergamini et al., 2009), a més de paràmetres climàtics i biogeogràfics a escales espacials més àmplies (Jiménez-Alfaro et al., 2014; Sekulová et al., 2012).

A les molleres, també cal considerar la plasticitat fenotípica de les plantes, que és la capacitat d'un organisme –amb un genotip concret– de modular la seva organogènesi davant d'un estímul extern (West-Eberhard, 1989). Aquesta capacitat suposa un avantatge competitiu per a les plantes de les comunitats vegetals, ja que els permet adaptar-se a situacions ambientals concretes. Per això, la variabilitat intra-específica ha resultat una branca d'importància creixent en l'ecologia (Des Roches et al., 2018). Per exemple, davant una situació de competència per la llum (en llocs, per exemple, molt productius), les plantes acostumen a elongar-se (Chen et al., 2010), mentre que en condicions d'inundació permanents la producció d'aerènquima augmenta (Visser et al., 2000). Algunes plantes també poden modificar l'estructura dels seus òrgans clonals per fer front a situacions concretes (Klimešová et al., 2018). Produir rizomes llargs (estratègia *guerrilla*) permet a les plantes evitar una situació adversa o molt competitiva i colonitzar espais propers més favorables (Li et al., 2015; Tammaru et al., 2021), mentre que generar brots molt junts (estratègia *phalanx*) els du a ser més competitives en estadis avançats de la successió vegetal (Chen et al., 2011). La plasticitat fenotípica varia en funció del tret funcional, i pot diferir molt entre espècies de mollera (Moor et al., 2017).

Per tant, els filtres ambientals als hàbitats de mollera propicien comunitats amb una flora força especialitzada, amb trets funcionals que els permeten establir-se i prosperar en un ambient estressant (Rydin & Jeglum, 2013). Dins les comunitats, les interaccions biòtiques prenen rellevància en múltiples processos, que acaben determinant l'abundància de les seves espècies en funció de la competitivitat que exerceixin sota les diferents condicions ambientals, més o menys estables en el temps (Keddy, 2010). S'ha demostrat que la diversitat funcional dins de la comunitat augmenta al llarg de la successió vegetal en el desenvolupament de les torberes (Laine et al., 2018).

Les molleres a les muntanyes alpines i als Pirineus

A les muntanyes alpines, les molleres ocupen àrees petites i fragmentades, limitades als llocs on l'aigua es manté molt propera a la superfície. S'acostumen a formar molleres en cubetes de sobre-excavació dels circs glacials, sovint acompanyant estanys dels estatges de vegetació alpí o subalpí (Casanovas, 1991). També en trobem en fonts i surgències d'aigua als vessants, o vorejant rius i rierols del fons de les valls, en terrenys amb una inclinació molt variable. En aquests casos, moltes vegades els hàbitats de mollera prenen formes irregulars, dendrítiques, i poden ocupar àrees molt petites, envoltades d'altres hàbitats de muntanya, sobretot prats de pastura o boscos d'aciculifolis (Pérez-Haase, 2016).

La topografia abrupta fa que les molleres alpines sovint presentin una microtopografia complexa que deriva en la presència de comunitats vegetals contrastades dins d'una mateixa mollera (Pérez-Haase & Ninot, 2017) (Fig. 2). L'heterogeneïtat dins les molleres promou canvis en la seva biodiversitat a distàncies curtes (Hájek et al., 2009), el que s'expressa com una elevada diversitat beta, o recanvi d'espècies en passar d'una comunitat a una altra. Els gradients ambientals dins d'una mollera –i entre una mollera i els seus hàbitats limítrofs– poden ser graduals, però en

Fig. 2. El paisatge abrupte de les muntanyes fa que la majoria de molleres alpines ocupin àrees reduïdes mentre que una complexa micro-topografia promou que tinguin una bona diversitat de comunitats vegetals. A la imatge, les basses dels Estanys Roi, a la primavera poc després de la fosa de la neu. Fotografia d'Eulàlia Pladevall.

molts casos la superfície de transició entre una comunitat vegetal i una altra a l'alta muntanya és molt reduïda (Larkin, 2016). A una escala més àmplia, múltiples factors ecològics condicionen les comunitats vegetals de cada mollera al llarg del sistema muntanyós: les característiques bioclimàtiques derivades del gradient altitudinal i de la topografia (temperatura, vent, radiació, innivació, productivitat, etc.; Pérez-Haase et al., 2019), les característiques geològiques del lloc, les hidrològiques i l'acumulació de torba (Colomer et al., 2019; Pérez-Haase & Ninot, 2017) o l'antiguitat de la mollera i el seu estadi en la successió vegetal (Horsák et al., 2012). Aquesta heterogeneïtat espacial també es trasllada a les altres formacions vegetals del paisatge, que es caracteritza per un mosaic de comunitats vegetals molt divers (Ninot et al., 2017).

A les muntanyes alpines, per tant, les molleres estan més o menys allunyades entre elles en un paisatge abrupte, formant el que podem interpretar com a hàbitats distribuïts en illes terrestres (*inland insular habitats*) connectats heterogèniament a escala regional (Jiménez-Alfaro et al., 2012). Aquesta distribució en l'espai permet estudiar l'estructura de les comunitats a les molleres de l'alta muntanya des de la perspectiva de la teoria de la biogeografia d'illes (Wilson & MacArthur, 1967) o de les metacomunitats (Leibold et al., 2004). Això permet estudiar els patrons que expliquen la composició de les comunitats pels processos que ocorren a escales local i regional alhora (Chase et al., 2020).

Les espècies que puguin viure exclusivament a les molleres (especialistes) dependran de la seva capacitat de dispersió i de la connectivitat entre molleres per colonitzar hàbitats favorables i intercanviar material genètic entre poblacions de dins de l'arxipèlag d'illes terrestres (Horsák et al., 2012; Shurin et al., 2009). En canvi, aquelles espècies capaces d'establir-se en un conjunt més ampli de situacions ecològiques (generalistes) tindran menys limitacions per a la dispersar-se i colonitzar hàbitats favorables (Whittaker, 1998). Taxes de dispersió més elevades faran reduir la diversitat beta entre hàbitats similars. Conèixer la distribució de les espècies dins les metacomunitats permet prendre mesures de protecció que tinguin en compte no només els hàbitats i les espècies sota una major amenaça de conservació, sinó també quines són les seves rutes de dispersió, la connectivitat entre comunitats i la presència d'hàbitats similars susceptibles de ser colonitzats per noves poblacions d'una espècie diana (Chase et al., 2020; Legendre et al., 2005).

Tot i ocupar una superfície relativa molt petita de la serralada, als Pirineus apareixen una bona diversitat d'hàbitats de mollera, alguns d'ells inclosos dins dels Hàbitats d'Interès Comunitari europeus, dels quals molts són prioritaris (6230*, 7110*, 7140, 7220*, 7230, 7240*, 91D0*) (Pérez-Haase et al., 2019). Als Pirineus, les molleres són propenses a oscil·lacions del nivell de l'aigua freàtica acusats, estan exposades a la influència del clima mediterrani –sobretot al seu vessant meridional–, a insolacions més grans que a la seva regió principal de distribució, i a precipitacions i boires escasses durant l'època de l'any més càlida (Pérez-Haase, 2016). Molts hàbitats de mollera troben

als Pirineus el seu límit meridional de distribució a Europa, cosa que suposa no només el límit per a alguns hàbitats i formacions vegetals, sinó també per força espècies especialistes d'hàbitats de mollera. De fet, les molleres dels Pirineus es consideren un refugi per a espècies especialistes relictes, i estan geogràficament aïllades d'hàbitats similars de la serralada Cantàbrica i dels Alps. En aquest sentit, la flora de mollera, força diversa a les regions atlàntiques d'Europa i també als Alps, s'empobreix a les muntanyes del sud d'Europa com els Pirineus (Jiménez-Alfaro et al., 2012).

Amenaces per a les molleres en un ambient canviant

Els canvis d'usos del sòl són vectors directors de la dinàmica de la vegetació, i poden provocar canvis en l'abundància relativa de les espècies en un hàbitat, canvis en la seva riquesa i fins i tot canvis cap a altres hàbitats difícilment reversibles. Alguns dels més importants a les molleres a escala global són el drenatge per a finalitats agrícoles, l'extracció de torba i les activitats forestals (Joosten & Clarke, 2002; Raeymaekers, 2000). La freqüentació de ramats domèstics (ramaderia extensiva) té un impacte heterogeni a les molleres a escala global, però que pot ser localment molt acusat (Bergamini et al., 2009; Spitale, 2021). De fet, l'amenaça dels canvis d'usos dels sòl i canvis climàtics sobre les molleres és molt variable entre regions biogeogràfiques (vegeu, per exemple, Essl et al., 2012; Grzybowski & Glińska-Lewczuk, 2020; Poulin et al., 2004; van Diggelen et al., 2006).

Des de la segona meitat del segle XXè, hi ha hagut un abandonament progressiu de les zones de muntanya a Europa (MacDonald et al., 2000), i els estatges per on distribueixen les molleres sobretot s'han vist afectats per canvis en la ramaderia. Als Pirineus, s'ha substituït progressivament la ramaderia extensiva de ramats ovins per bovins a la majoria de valls del vessant meridional (Collantes, 2009). Les vaques en general freqüenten zones de menys altitud (sobretot a l'estatge subalpí) i amb relleus més suaus (MacDonald et al., 2000). Paral·lelament, una superfície notable de la serralada s'ha protegit gràcies a una bona xarxa de Parcs Naturals i Nacionals i de la xarxa Natura 2000. En aquestes zones, els usos del sòl s'han regulat, i l'aprofitament de la fusta s'ha limitat o en alguns casos prohibit. Tot plegat ha derivat en canvis progressius dels usos del sòl (García-Ruiz et al., 1996; Lasanta-Martínez et al., 2005) que han sigut la causa principal dels canvis en la coberta del sòl (Roura-Pascual et al., 2005). Així, s'ha registrat un increment notable de les àrees boscoses i una homogeneïtzació progressiva del mosaic de vegetació (Gracia et al., 2011), un desplaçament altitudinal del límit forestal, o treeline (Améztegui et al., 2016), i la colonització de subarbusts a les pastures, o emmatament (Nadal-Romero et al., 2018).

Paral·lelament, al llarg del segle XXè –sobretot a la primera meitat– es van construir un bon nombre de preses amb finalitats hidroelèctriques a moltes valls pirinenques (per exemple, 27 a la conca del Flamisell, a la Vall Fosca, entre el 1910 i el 1940; Boneta, 2012).

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L'aprofitament de l'aigua ha representat un benefici socioeconòmic molt important (Colino, 2015), però també ha provocat canvis bruscos als cabals i la desaparició d'algunes molleres sota pantans (Catalan et al., 1997). A dia d'avui es mantenen funcionals gairebé tots els pantans, però ja es planteja l'enderrocament d'algunes preses en un futur poc llunyà, sigui per obsolescència, sigui per interès conservacionista. En algun cas, els organismes gestors ja han retornat a l'estat original certs trams dels rius, rebaixant o eliminant preses (Ninot et al., 2019). Les àrees novament lliures d'aigües són sòls nus de vegetació, i una part és susceptible de ser repoblada per vegetació de mollera (en processos de successió facilitats o no per accions de restauració).

L'interès creixent per conèixer els processos derivats dels canvis dels usos del sòl sobre la dinàmica i composició de les molleres alpines es tradueix en la publicació recent de nombrosos treballs, relatius a la magnitud i els efectes de l'herbivorisme i el trepig per bestiar domèstic (Pérez-Haase et al., 2019; Sjögren et al., 2007; Fig. 3), a les respostes davant d'un canvi en el règim de ramaderia en els trets de les plantes (Pauler et al., 2020), a l'estructura i productivitat de la vegetació (Li et al., 2017), a la restauració mitjançant la regulació de la pastura (Graf et al., 2022), a les conseqüències del drenatge sobre la biodiversitat (Spitale, 2021), als canvis hidrològics i de biodiversitat derivats de l'entrada d'arbres a les torberes –per exemple Eckstein et al. (2011) a Alemanya, però encara poc conegut a muntanyes alpines–, a la importància del banc de llavors en els primers estadis de successió vegetal (Ma et al., 2011), etcètera.

Fig. 3. La ramaderia extensiva té efectes directes en la construcció de comunitats de mollera als Pirineus. A l'esquerra, quan animals grossos com les eugues pasturen a les molleres, s'enfonsen als llocs on el nivell de l'aigua s'acosta més a la superfície, trencant l'estructura subterrània de la vegetació i desestructurant el sòl. A la dreta, contrast de l'alçada de la vegetació herbàcia entre una zona pasturada i una zona tancada al bestiar, que afecta les interaccions biòtiques entre les plantes del lloc. Autora: Eulàlia Pladevall.

Reptes per a la investigació i gestió

Des dels inicis dels estudis de vegetació alpina als Pirineus, les molleres s'han considerat sempre formacions singulars al paisatge, tant florísticament com funcionalment (Braun-Blanquet, 1948; i també posteriorment a Carreras et al., 1993; Carrillo & Ninot, 1992; Vigo, 1996). A finals del segle XXè, la tesi doctoral de L. Casanovas (1991) representa el primer gran estudi entrat en les molleres pirinenques. L'autora hi descriu l'ecologia de diferents associacions vegetals, afegeix dades d'estructura de la vegetació i recull un bon nombre d'inventaris i cites florístiques al llarg de la serralada. Més tard, A. Pérez-Haase dedica la seva tesi doctoral (2016) també a les molleres, on destaca una anàlisi detallada sobre la resposta de les espècies (i comunitats) de mollera als gradients ecològics, incloent la dinàmica del nivell freàtic al llarg de l'estiu. Incorpora un bon nombre d'inventaris florístics i aborda alguns aspectes sobre l'estructura espacial d'aquestes comunitats vegetals. Malgrat això, resten encara per conèixer molts aspectes de les interaccions abiòtiques i biòtiques, de l'estructura espacial i de la dinàmica de la vegetació, tant mitjançant aproximacions observacionals com experimentals.

Durant les darreres dècades, ha augmentat la necessitat i voluntat de gestió dels hàbitats naturals. Cal una gestió conservativa, tal com evidencia la creació de Parcs Naturals i altres òrgans gestors, però malgrat el bon coneixement de base de les molleres (flora, distribució dels hàbitats, paràmetres ecològics...) no coneixem prou bé l'amenaça real que representen per a la seva conservació diferents factors canviants (clima, usos del sòl, hidrologia...). Per això, des d'inicis del segle XXIè, diversos projectes de recerca a les molleres combinen la diagnosi de comunitats ecològiques amb accions de conservació i monitoreig. En destaca el projecte LIFE+ LimnoPirineus (2014), que implica desviació de camins, programes pilot de restauració i monitoreig de molleres davant canvis hidrològics sobtats, programes pilot de protecció davant la pressió ramadera, etc. Poc més tard, s'inicia un programa de restauració passiva de molleres molt freqüentades pel bestiar domèstic, sumant fins a onze molleres als Pirineus Centrals catalans gràcies a la Fundació Andrena i al projecte Poctefa GREEN (Andrena, 2016; GREEN, 2014).

Amb tot plegat, la necessitat de conservació d'aquests hàbitats promou actuacions sobre el terreny sense que coneguem bé com respondrà la vegetació als canvis propiciats, és a dir, sense poder preveure els canvis en la biodiversitat i per tant l'èxit de l'acció en cada cas. És en aquest context que sorgeix la necessitat d'abordar el coneixement de base sobre els canvis en les comunitats de mollera, tant a escales de detall (expansió clonal, ocupació de l'espai en una mollera, interaccions biòtiques), com a escala local (heterogeneïtat microtopogràfica, influència d'habitats propers o del pool d'espècies local, efectes de la ramaderia), o a escales més àmplies (com operen aquests processos a l'arxipèlag de molleres de la serralada). A més, cal conèixer si aquests processos estan influenciats per l'actual canvi climàtic i els canvis en els usos del sòl, i per tant, si les molleres dels Pirineus són sensibles a canvis mesurables en un futur proper. Això ha de permetre preveure la trajectòria que puguin seguir els hàbitats de mollera

davant de canvis graduals o sobtats en les seves característiques físiques, climàtiques o ambientals. Així, davant d'una amenaça per a la conservació, es podran prendre mesures fonamentades de gestió conservativa o de restauració. És necessari aprofundir en el coneixement funcional dels sistemes de molleres pirinenques des de diversos pols relacionats amb la conservació d'uns ecosistemes relictes i en regressió, i per tant, molt valuosos.

Àrea d'estudi

L'àmbit d'estudi dels capítols d'aquesta tesi correspon principalment als Pirineus Centrals catalans, prop dels límits administratius amb Aragó i França, i incloent algun punt d'estudi a Andorra. En aquesta regió, les cotes més altes superen els 2.900 m d'altitud, i en algun cas els 3.000 m. La majoria d'aquesta àrea correspon al vessant meridional dels Pirineus, amb rius que desemboquen al Segre i posteriorment a l'Ebre, fins al mar Mediterrani, però també incloem punts de mostreig a la Val d'Aran, una comarca de Catalunya situada al vessant nord dels Pirineus, que dirigeix les seves aigües pel riu Garona fins a l'Atlàntic francès (Fig. 4). Per tant, les influències oceànica i continental varien força dins de l'àmbit d'estudi. Al nord-oest (Val d'Aran), el clima és oceànic, amb precipitacions força abundants i boires habituals que propicien una vegetació ufanosa. En canvi, a la resta de l'àrea d'estudi (Andorra, Pallars, Ribagorça) el clima és més continental, amb estius més secs i calorosos però hiverns freds (Ninot et al., 2013). A més, a les cotes baixes i mitjanes, la influència del clima mediterrani s'hi fa més acusada, amb sequeres estivals més acusades (Rivas-Martínez et al., 2017). Arreu, la durada del període vegetatiu és inversament proporcional a l'altitud, amb uns 6-7 mesos de mitjana als 1.700 m d'altitud, i 4-5 mesos als 2.500 m (Ninot et al., 2013).

Les molleres que s'han analitzat als diferents capítols van dels 1.350 m als 2.580 m d'altitud, la gran majoria situades a l'estatge subalpí de vegetació però sobrepassant aquest límit tant cap a l'estatge montà com per damunt del límit del bosc, a l'estatge alpí. El treball de camp està focalitzat sobretot en vuit molleres (entre els 1.630 m i els 2.050 m d'altitud; Fig. 4). Al capítol 1 hem dut a terme un treball experimental amb plantes trasplantades en hivernacle i a la localitat de Font Grossa, a Espot. Al capítol 2 hem realitzat seguiments periòdics de parcel·les permanents en sis molleres de característiques prou diferents, sota condicions experimentals contrastades a cadascuna (Fig. 5, 6 i 7). Al capítol 3 hem treballat amb més de 300 molleres de la regió a través de tècniques SIG, i hem analitzat mostres de pins de la mollera de Trescuro (Fig. 7). Finalment, el capítol 4 es fonamenta en més de 500 parcel·les d'estudi procedents d'un bon nombre de sistemes de mollera, amb diferents sub-ambients i incloent tots els principals hàbitats de mollera dels Pirineus Centrals (Fig. 4 i 7).
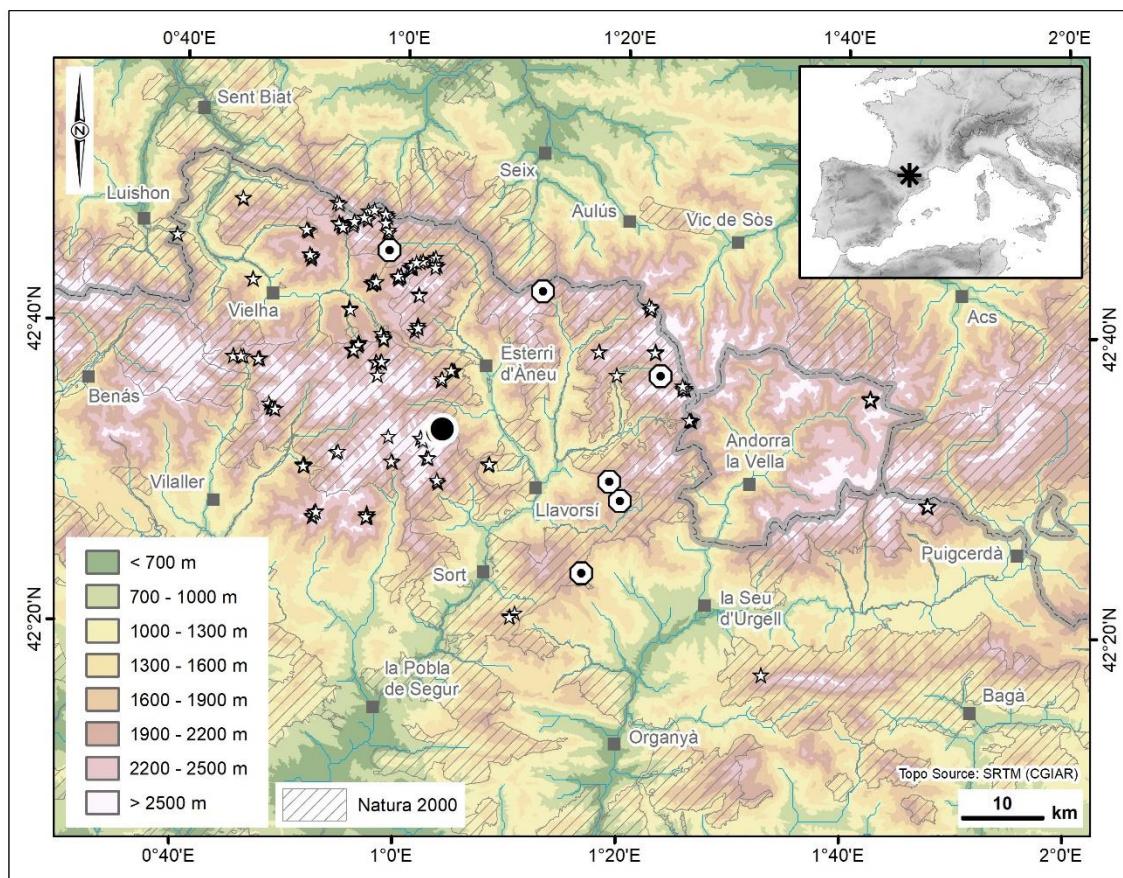
Fig. 4. Localització dels punts d'estudi en què es fonamenta aquesta tesi doctoral. En fons ratllat s'indiquen les àrees protegides per la xarxa Natura 2000. Cercle negre, localització de l'experiment de camp del capítol 1, i de la mollera mostrejada al capítol 3 (superposats). Octàgon blanc amb centre negre, molleres per a l'experimentació del capítol 2. Estrelles, punts mostrejats per al capítol 4 (molts d'ells superposats). No indiquem específicament les nombroses molleres analitzades amb tècniques SIG al capítol 3, que globalment coincideixen amb la mateixa àrea d'estudi.

Fig. 5. Fotografies de tres de les principals molleres mostrejades al capítol 2 de la tesi. De dalt a baix: Bedet, Pallerols, Parros. Fotografies de Nil Escolà, Eulàlia Pladevall i Gemma Domènech.

Fig. 6. Fotografies de tres de les principals molleres mostrejades al capítol 2 de la tesi. De dalt a baix: Boet, Burg, Montroig. Fotografies de Nil Escolà i Josep Maria Ninot.

Fig. 7. Fotografies de molleres mostrejades. A dalt, Font Grossa (capítol 1). Al mig, Trescuro (capítol 3). A baix, Montoliu (capítol 4). Fotografies de Marc Arimany, Joana Colomer, Eulàlia Pladevall.

Objectius

Pla de Boet. Fotografia de Nil Escolà.

Objectius

En aquesta tesi doctoral ens plantegem millorar el coneixement sobre la naturalesa de les comunitats vegetals de les molleres alpines i la seva dinàmica. L'objectiu principal és entendre com la construcció de les comunitats de mollera (*community assembly*) depèn de certs factors bioclimàtics, ecològics i d'usos del sòl, rellevants en el paisatge de muntanya i que poden veure's modulats pel canvi global actual. En paral·lel, volem que aquesta memòria ofereixi coneixements de base necessaris per a poder prendre mesures de conservació –o restauració– fonamentades. Abordem aquest objectiu mitjançant treballs específics tant experimentals com de diagnòstic, i a escales temporals i espacials contrastades.

Al primer capítol, volem entendre quines interaccions planta-planta s'estableixen entre espècies de mollera que són comunes i susceptibles de ser bones espècies enginyeres de comunitats de molleres alpines. Volem eixamplar i fonamentar el coneixement de base sobre l'establiment i desenvolupament d'aquestes plantes sota règims hidrològics contrastats, i així assegurar l'èxit en accions de restauració durant els primers estadis de successió vegetal. Aquest estudi inclou un experiment a camp de dos anys de durada i un experiment de curta durada en cambres experimentals controlades, i ha de permetre valorar la importància del desenvolupament dels òrgans d'expansió vegetativa en la capacitat competitiva de les plantes de mollera.

Al segon capítol, avaluem els efectes de l'eliminació de la pressió ramadera en la dinàmica de comunitats de mollera especialment freqüentades pel bestiar domèstic. Volem conèixer la velocitat de recuperació de la coberta vegetal, la importància de diferents processos de successió espontània, i els canvis que es produeixen en l'estructura i en la biodiversitat de les comunitats. Específicament, estudiem la importància relativa que hi té l'expansió clonal d'herbes perennes i la germinació de llavors, així com el paper que hi juguen els briòfits. Així, valorem l'exclusió total com a tècnica de restauració passiva a curt termini en molleres afectades per una pressió ramadera elevada.

Al tercer capítol, volem determinar quina és la incidència actual del pi negre (*Pinus uncinata*) a les molleres pirinenques, i com han evolucionat les poblacions d'aquest pi a les molleres durant les darreres dècades. A més, pretenem dilucidar quins factors ecològics i antropogènics faciliten o prevenen l'increment de pins als hàbitats de mollera. Això ha de permetre preveure l'impacte que pot tenir l'expansió del pi negre a les molleres de muntanyes alpines en un futur proper.

L'objectiu principal del darrer capítol és comprendre el paper dels gradients ambientals i dels patrons espacials en la diversitat beta entre comunitats de mollera, en l'àmbit d'un variat paisatge d'alta muntanya i a escala regional. D'aquesta manera posem de relleu la importància que té la distribució en l'espai dels hàbitats estudiats als Pirineus centrals –on les molleres formen un arxipèlag d'illes terrestres– i com hi operen els filtres ambientals –a escales local i regional. Basem l'estudi en la diversitat beta taxonòmica, filogenètica i funcional, comunitats, tant la taxonòmica com la filogenètica i la funcional, i dilucidem les diferències observades entre les espècies considerades especialistes d'hàbitats humits i les espècies generalistes.

Capítol 1

Font Grossa. Fotografia d'Empar Carrillo.

Experimental trials highlight the relevance of plant-plant interactions in the early successional stages of wetland communities

Estudis experimentals subratllen la importància de les interaccions planta-planta durant els primers estadis successionals a les comunitats de mollera

Abstract

Wetland communities are highly dependent to the water regime. So, any drastic change in the water table, as the rise that occur when a reservoir is constructed, cause the surrounding wetlands to disappear. After a conservation action consisting in the removal of a dam, denuded areas emerge. In these areas, primary succession processes start and gives way to new wetland communities. Here, we study the performances of three common Alpine wetland species, with different but overlapping niches (*Carex nigra, Carex rostrata* and *Juncus filiformis*) under different plant-plant interactions and water table depths. Experiments were replicated at short-term under controlled chamber conditions and in a field experiment in the Pyrenees. The results highlight the competitive ability of *C. rostrata* and its preference for flooded soils. *Juncus filiformis* was not competitive in bispecific pots but showed high growth rates at both high and low water tables. This postulates *J. filiformis* as a good pioneer species to initiate primary succession. More, *C. nigra* showed moderate competitive abilities in the different bispecific combinations and experiments, and developed a large rhizome and an important bud bank at mid-term, thus demonstrating a strong potential for clonal expansion in just two growing seasons. Additionally, *C. nigra* seedlings only survived and grew in non-flooded areas without plant competition. Overall, we detected no changes in plant-plant interactions according to water level, and a higher plant growth at high water levels. Improving the ecological basis on plant establishment, performance, and interactions of common species in Alpine wetlands will enable well-founded restoration actions to be planned in the face of hydrological changes in river basins.

Introduction

Alpine mires occupy geographical fragmented areas in Alpine mountains such as the Pyrenees (Jiménez-Alfaro et al., 2012). They are strongly constrained by the mountain physiography and cover small surfaces that occur scattered on the landscape (Ninot et al., 2017; Pérez-Haase, 2016). At the same time, mires consist of the unique suitable habitats for some rare specialist plants (Jiménez-Alfaro et al., 2012), and mires in the Pyrenees are the southern distribution limit for some Habitats of Community Interest in Europe (HCI; Pérez-Haase et al., 2019).

During the last 100 years, many small and medium-sized reservoirs have been built in the Pyrenees (Catalan et al., 1997; Colino, 2015; Rodríguez, 2012). Their main use is power generation, but many are devoted to recreational and angling purposes (Miró & Ventura, 2013). In recent times, there has been a growing concern on impacts of dam raising and water level regulation on natural communities, namely rivers, reservoirs and wetlands (Hirsch et al., 2017; McCartney, 2009; Spitale et al., 2015). Thus, land managers in natural areas are prone to restore damaged habitats, but found little knowledge regarding the best practices to undertake conservation or mitigation actions (Schletterer et al., 2021; Shuman, 1995).

Dam removal results in a sudden decrease on the water level and the emergence of denuded soils open to plant colonization and primary succession. In this scenario, appropriate management actions can improve wetlands restoration success according to abiotic site characteristics (Zedler, 2000). Many studies approached wetland restoration and recreation (Moreno-Mateos et al., 2015; Quinty & Rochefort, 2003) and wetland primary succession processes (Mitsch et al., 2012), but only few dealt with Alpine mountain mires (Schletterer et al., 2021). As for science-based restoration of wetlands, ecological knowledge on plant colonisation and patch occupation is very useful (Caldwell et al., 2011). In that sense, there is a need to enhance the ecological basis on plant establishment, performance and plant-plant interactions in the environmental conditions resulting from a removal of a dam.

Plants in waterlogged soils experience belowground anoxia and low oxidation-reduction potential (Wheeler, 2005). The hydrological regime (water table depth, oscillation, seasonality) drives plant establishment, growth, biomass allocation, aerenchyma development and shoot density among other morphological traits in wetland plants (Visser et al., 2000; Webb et al., 2012). Consequently, hydrological regime in wetlands determines community assembly and species composition, and it is

considered as one of the main ecological drivers on plant zonation (Bragazza & Gerdol, 1999; P. A. Keddy, 2010; Raulings et al., 2010; Weiher & Keddy, 1995).

Plant-plant interactions can be classified as competitive, neutral or positive (i.e., facilitative), and play a key role on community assembly and functional diversity (Kotowski et al., 2010; Soliveres & Maestre, 2014). Importantly, the importance of competition in plant communities varies along environmental gradients, whether they are resource (fertility, light) or non-resource gradients (salinity, soil structure) (P. A. Keddy, 2010; Maestre et al., 2009). In that sense, water regime can modulate wetland plant interactions by promoting morphological adaptations to water regime that would eventually modify plant competitive ability and plant-plant interactions (Davis et al., 2009; Jung et al., 2009; Kotowski et al., 2001; Webb et al., 2012). Moreover, plants interact aboveground and belowground at the same time, and biomass allocation in the two compartments may respond to different resource limitations, non-resource gradients or competitive relations (P. A. Keddy, 2010; Ottaviani et al., 2020). Thus, plant responses – morphological and physiological– to biotic and abiotic conditions are interconnected (Li et al., 2015). Moreover, transitions from facilitation to competition between specific plants may vary according to the response variable considered (Maestre et al., 2005), the experimental manipulation of abiotic conditions in experiments (Corcket et al., 2003), and the plant life stage (positive interactions are more common at early life stages, and competition increments with the plant age; Malkinson & Tielbörger, 2010). Thus, specific experiments are needed to disentangle the role of the water regime onto particular species interactions and environmental conditions (P. A. Keddy, 2010; Wheeler, 2005).

Grassy ecosystems as wetlands have particularly high belowground biomass in relation to the aboveground biomass (Klimešová, Mudrák, et al., 2021; Mokany et al., 2006). In fact, almost all wetland plants are perennial and clonal, and the majority of them are herbaceous (hemicryptophytes). Vegetative spreading helps generate new sprouts under adverse scenarios thanks to carbohydrate storage and bud banks (Klimešová et al., 2018). Parental connections can last long, and facilitate easier access to resources for new sprouts than germinated seedlings (Klimešová, Ottaviani, et al., 2021). Moreover, plants in waterlogged soils may depend on anaerobic metabolism for over-wintering and resprouting in absence of aerated organs (Crawford, 1996). While vegetative spreading has a primary importance on plant response before a limiting factor, very few experiments consider non-acquisitive subterranean organs (i.e., rhizomes and other clonal growth organs; Ottaviani et al., 2021). Taking into account clonal growth organs in parallel to aboveground organs in plant interaction experiments contribute to a more holistic understanding on plant strategies and to a better community dynamics prediction (Klimešová, Ottaviani, et al., 2021). Nevertheless, clonal growth organs, carbohydrates storage and bud banks development require several years, and in short-term pot experiments are not well-formed (Ottaviani et al., 2021). However, sampling of clonal growth organs in natural ecosystems (or even field experiments) is complicated

due to intermingled clonal growth organs and roots of different species and soil (Klimešová et al., 2018).

As for seed and seedling ecology, seed germination success on wetland herbaceous communities is directly hampered by vegetation density (Kotowski et al., 2010). In that sense, light limitation can become a major constraint for seedling establishment in wetlands (Kotowski et al., 2010). More, waterlogging has a negative effect on the seedlings growth rate in many wetland species (Fraser & Karnezis, 2005). Although most wetland species have transient or short-term persistent seed banks (Maas & Schopp-Guth, 1995; Poschold, 1995), seed dissemination and artificial sowing may become relevant in mire restoration actions (Fernández-Pascual, 2016). Combining both life stages in experiments (sexual and clonal reproduction) enable to compare plant performance and dynamics for different dissemination strategies on the same target species.

Altogether, multiple factors should be taken in account facing restoration purposes in damaged wetlands. The prediction of seedling establishment success, rhizome development, plant distribution along gradients and interactions between plants will allow for proper management actions in the first stages of plant succession in Alpine wetlands. Regarding restoration through rhizome transplantations, species involved must be common to ensure the collection of enough plant material (in affordable time) (Török et al., 2011). *Carex nigra* is a common and ubiquitous plant that dominates many mire habitats in the Pyrenees, and so it could be a good candidate for restoration actions. It can thrive under contrasting hydrological regimes from lake shores with high water table to wet grasslands, and in different stages of the vegetation succession. *Juncus filiformis* and *Carex rostrata* were also selected since they are equally common hemicryptophytes in Pyrenean wetlands. They have different but overlapping niches and usually act as pioneers, and coexist with *C. nigra* in natural communities. *Juncus filiformis*, usually behaves as a pioneer colonizer in sandy shores or temporal ponds, and so it tolerates groundwater fluctuations. It can also live in open lawns of species-poor communities. *Carex rostrata* is a robust sedge that creates open communities – sometimes monospecific– in shallow water, thus penetrating Alpine lakes through sandy or muddy shores (Casanovas, 1991; Colomer et al., 2019; Pérez-Haase, 2016; Pérez-Haase et al., 2010; Pérez-Haase & Ninot, 2017) (see Study species section for a morphological description of species).

In this study, we aim to understand the plant-plant interactions of three engineering plants along a water table depth gradient, with the purpose of planning management actions in the first stages of vegetation succession for wetland restoration. The ultimate goal is to establish the best plant combinations to promote wetland communities' assemblies. Thus, we carried out a chamber experiment and a pilot trial of a mire restoration in a field experiment. We studied the aboveground and rhizome growth in monospecific pots and different bispecific combination pots, and considering

two contrasted groundwater levels. Both seedlings and adult plants were considered. According to our hypotheses: i) *C. rostrata* and *J. filiformis* will perform higher growth rates under high water table levels, based on their ecological preferences; ii) a positive interaction between high water table levels and competition will be registered in *C. rostrata*; iii) both *Carex* species will demonstrate higher competitive abilities than *J. filiformis*, which never dominates in rich communities; iv) seedlings will only thrive under low water table levels; and v) rhizome biomass and vegetative spreading differences among treatments will only be detected in the field experiment thanks to the longer duration of the experiment.

Materials and methods

Study species

We selected three wetland plant species specialists. These three species are herbaceous perennials whose aboveground leaves and stems fall in autumn. Resprouting happens at the beginning of the growing season (right after snow melt), and it leads to lateral expansion of the overwintering rhizome. Although their ecological preferences are slightly different (Bolòs et al., 2005; Luceño et al., 2008; Zarco et al., 2010), they are common in Pyrenean fens and even frequently coexist in the same plant communities. According to these Floras, to Schweingruber et al. (2020) and to own observations on populations found nearby to the study area, the three species may be characterized as follows.

Carex nigra (L.) Reichard is a ubiquitous wetland sedge. In subalpine fens it forms single or tufted stems, the maximum height reached by their leaves varied between 7.5 and 25 cm. *Carex nigra* forms rhizomes with long (few cm) internodes, creating moderate- to high-density lawns of tillers with few leaves each. *Carex rostrata* Stokes is a robust sedge with erect stems and leaves, these reaching 40-110 cm height in the field site nearby populations. It thrives from very robust rhizomes with long internodes (10-40 cm). *Juncus filiformis* L. is a slender rush with a strong rhizome of 1.5-2 mm width and very short internodes (1-2 cm). Tillers consist in cylindrical stems 0.5-0.9 mm in diameter, stem-like leaves and short scale-like leaves. *Juncus filiformis* produces large numbers of small seeds and forms open lawns 20 to 36 cm height.

Plant material harvesting

On September 2014 we collected adult plants of *C. nigra*, *C. rostrata* and *J. filiformis*, and seeds of *C. nigra* in the Peguera valley, Central Pyrenees (see Field experiment for further information). We prepared uniform transplants by selecting apical segments, 2-4 cm long, of rhizomes, and we planted them in a mixture of peat and vermiculite in a greenhouse (Experimental Fields Service, University of Barcelona). After

five months growing under mild Mediterranean winter conditions, we selected the most uniform plants of each species according to the number of sprouts and leaves, to start the chamber experiment and three months later, the field experiment. At the same time, we set *C. nigra* seeds to germinate in Petri dishes with an always wet tissue paper (16 hours at 20 °C, 8 hours at 15 °C). From the developing seedlings, we selected those with leaves reaching approximately 5 cm and with roots about 5 cm long to be planted in the chamber experiment.

Chamber experiment

You can look up to Fig. 1.1 for a schematic overview of the two experimental designs. This experiment took place in a controlled conditions chamber, where we simulated the climatic conditions of a subalpine Pyrenean summer season by providing a daily cycle of 16 hours of light at 22 °C and 8 hours of darkness at 15 °C. We performed a factorial experiment as it follows. We settled eight different combinations of species interactions in flowerpots (9 cm diameter, 8 cm height): *C. nigra* & *C. rostrata*; *C. nigra* & *J. filiformis*; *C. nigra* seedlings & *C. rostrata*; *C. nigra* seedlings & *J. filiformis*; and the monospecific controls for the adults of the three species and for the *C. nigra* seedlings. There were three individuals of each species in each pot, therefore there were pots with three or six individuals depending on holding one or two species, respectively. We placed a replicate of each flowerpot type in ten plastic trays. In five of them we kept a low water table (*low WT*), with the water level 45 mm below-ground, and in the other five we kept
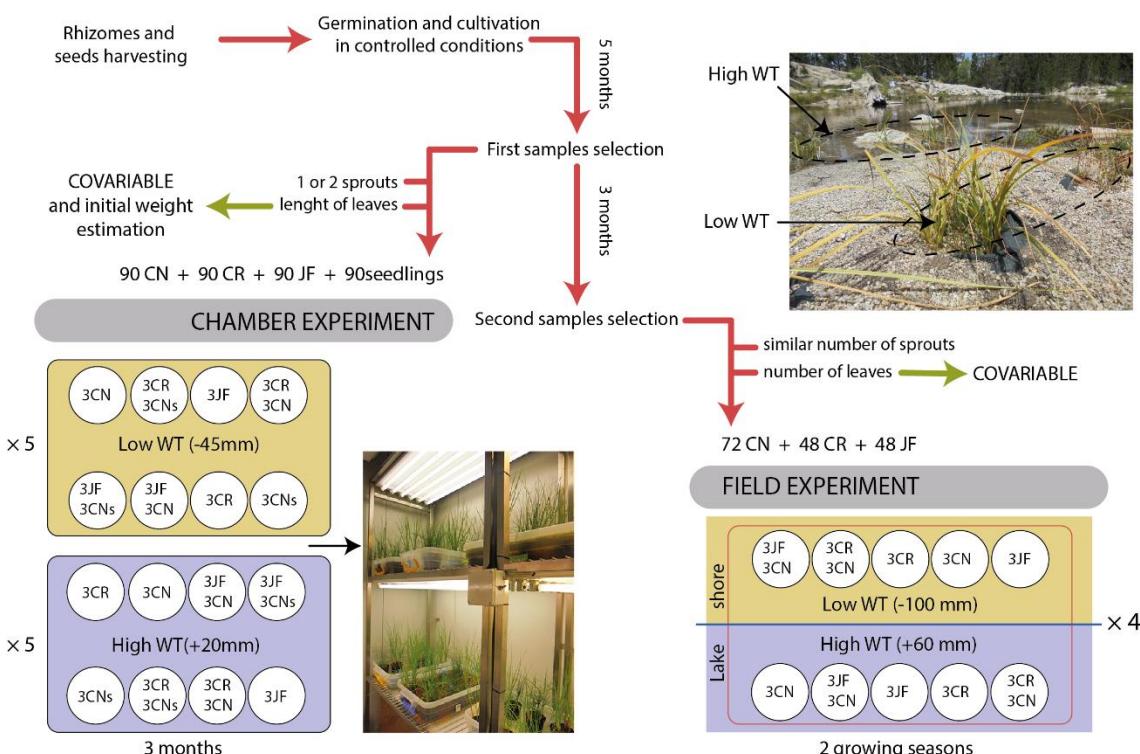
Fig. 1.1. Chart of the experimental design. CN, *Carex nigra*; CR, *Carex rostrata*; JF, *Juncus filiformis*; CNs, *Carex nigra* seedlings.

a high water table (*high WT*), with the water level constantly maintained at 20 mm above-ground.

The substrate was a commercial peat with vermiculite, and the water used was distillate water with Hoagland's nutritive solution 1:622 times dissolved (Hoagland & Arnon, 1950). This solution is similar to lake natural water mineralization on granodiorite (Pla et al., 2003). We watered the trays every 48 h to maintain the correct phreatic level, and replaced the water every 3 weeks to prevent spontaneous algae to become invasive. At the same time, we randomly interchanged the position of the pots within each tray, and the location of the trays within the chamber every 3 weeks. The experiment lasted 91 days, although the acclimation of the plants in flowerpots began 21 days before (thus, competitive relations recreated since 21 days before hydrological regimes).

Before the beginning of the experiment, we measured the length of all the leaves from all the adult plants to estimate the initial aboveground dry weight. To do so, we computed a linear regression between the length and the dry weight of a number of leaves (*C. nigra*, $R^2 = 0.851$; *C. rostrata*, $R^2 = 0.868$; *J. filiformis*, $R^2 = 0.846$). At the end of the experiment, we recorded the plant mortality and we labelled the aboveground part and the rhizome of each different species from each flowerpot (discarding roots). We recorded the dry biomass per pot and species after 48 h at 60 °C (accuracy 1 mg). Then, we calculated the *growth rate* (GR) as $= \frac{DW_1 - DW_0}{DW_0}$; where DW is the aboveground dry weight of plants at the end of the experiment (DW_1) or estimated at the beginning (DW_0). For the adult *Carex* plants, we also recorded the number of sprouts per pot and species. Finally, we calculated the aboveground:rhizome ratio as a simple coefficient between the two weights.

Field experiment

We settled the field experiment in Font Grossa, a small reservoir (570 m^2; 2,010 m a.s.l.) surrounded by fen habitats and pine forests in the Peguera valley, Central Pyrenees (42° 33′ 18″ N, 1° 03′ 46″ E). This valley is located in the Aigüestortes i Estany de Sant Maurici National Park, and thus subject to nature protection rules and to restoration actions where necessary. Font Grossa is a good example of subalpine mire systems in the Pyrenees according to vegetation and its bioclimatic features (mean annual temperature, 3.1 °C; mean annual precipitation, 1650 mm, provided by Meteorological Service of Catalonia; Meteocat, 2020).

In 2012, a narrow sandy area emerged after the 80 cm lowering of the reservoir dam. We used this area in June 2015 to set the factorial experiment, as it was still very poorly vegetated and thus could be used as arena for a primary succession experience. We set up four blocks (1.5 × 1.5 m) along the shore. At each block we set ten plots along two rows, the upper one about 10 cm above the water level in June (hereafter *low WT*), and the lower one about 6 cm below (hereafter *high WT*). At each block, each row

consisted in five plots (14 cm diameter, 12 cm depth) corresponding to five different species combinations: *C. nigra* & *C. rostrata*; *C. nigra* & *J. filiformis*; and the three monospecific plots *C. nigra*; *C. rostrata*; and *J. filiformis* (in all cases, with three individuals of each species per plot as in the chamber experiment).

In order to maintain the plant individuals closely related during all the experiment, we used pots made of geotextil fabric, buried in the soil. This material allows the groundwater flow but prevent the roots and rhizomes from escaping through. The substrate was directly obtained from the study site, consisting in granitic sand with fine mineral particles and humus, and was sterilized during 120 min at 80 °C and 60 min at 110 °C previously to be used. We performed the field experiment from June 2015 to September 2016 (16 months, including two growing seasons).

At the end of the experiment we harvested the plant below- and aboveground organs and classified them in three functional groups: *grown sprouts* (those bearing fully-developed leaves in *Carex,* or stems in *Juncus*), *young sprouts* (those bearing only juvenile leaves or stems, usually completely under the ground and not photosynthetically functional yet), and *rhizomes* (discarding the roots). We counted the number of young and grown sprouts for each species and plot, and we weighted the aboveground organs and the rhizome separately (48 h at 60 °C, accuracy 1 mg). Finally, we calculated the aboveground:rhizome ratio in the same way as in the chamber experiment.

Statistical analyses

We measured the plant performance as multiple response variables for both experiments: i) aboveground biomass (i.e., all photosynthetic and sexual organs); ii) rhizome biomass; iii) its ratio; iv) number of sprouts; and additionally in the chamber experiment v) growth rate; vi) seedlings survival; and vii) seedlings aboveground biomass. We modelled all response variables with linear mixed effect models, using *hydrological regime* (low or high WT) and *competitive relation* (species interaction or control) as fixed effects. We analyzed every species and variable separately, and we always added a covariate evaluating the plant size at the beginning of the experiment (not for seedlings). More concretely, in the chamber experiment the covariate was the sum of the length of all the leaves of the three individuals from each flowerpot, while in the field experiment we used the number of leaves (or stems, in *J. filiformis*) in each plot. Both covariates were scaled. Additionally, we set nested data structures as random effects: 10 trays in the chamber experiment, and 8 rows distributed in 4 blocks in the field experiment. As no effect was detected from seedlings to adult plants performance, the coexistence of adult plants with *C. nigra* seedlings in the chamber experiment was considered as a control situation for *C. rostata* and *J. filiformis* plants.

On every response variable we removed outliers according to Grubbs test (1950) before model selection. We modelled the quantitative responses using normal

distributions (biomass, growth rate, biomass ratio), whereas we modelled the count responses using Poisson distributions (number of sprouts), and seedlings survival using a Bernoulli distribution. We first selected the best random-effects structure using the most complex fixed-effects structure and according to the AICc criterion (using Restricted Maximum Likelihood, REML, for quantitative responses). Then, we selected the best fixed-effects structure using the chosen random-effects structure and Maximum Likelihood (ML). The final model was that containing all fixed variables that appeared in the model with the lowest AICc or in all models with a difference on AICc lower than 2 points, and using REML or ML depending on quantitative or count responses, respectively. We examined all residuals to avoid the violation of normality and homoscedasticity. A constant variance function structure was added in models were we found heterogeneity (weighted linear regressions), and some variables were log-transformed to deal with non-normality. Finally, negative binomial distributions were implemented in models for count variables that denoted overdispersion.

Overall, we performed 32 modeling procedures, thus obtaining one best model for each response variable and species. All the variables retained in a best model were considered to be relevant for the response variable. Moreover, we performed Tukey HSD multiple comparisons to test significant differences between the different levels from these fixed effects, and R^2 was computed for every model. All analyses were carried out in R (R Core Team, 2021) using *nlme, lme4, MuMIn, glmmADMB* and *multcomp* packages (Barton, 2020; Bates et al., 2014; Fournier et al., 2012; Hothorn et al., 2008; Pinheiro et al., 2021).

Table 1.1. Mean and standard deviation for each response variable and species in the chamber and the field experiments. The Growth rate expresses the quotient between the increment on dry weight and the initial dry weight; only aboveground organs.

| Species | Chamber experiment | | | | |
	Aboveground biomass (g)	Rhizome biomass (g)	Num. of sprouts or stems	Growth rate	Abovegr. : rhizome ratio
Carex nigra	2.76 ± 0.58	0.5 ± 0.18	12.76 ± 1.98	0.97 ± 0.38	5.95 ± 1.86
Carex rostrata	3.34 ± 0.48	1.04 ± 0.28	13.5 ± 3	1.34 ± 0.28	3.4 ± 0.76
Juncus filiformis	1.9 ± 0.38	0.87 ± 0.2	NA*	2.05 ± 0.58	2.17 ± 0.38

| Species | Field experiment | | | | |
	Aboveground biomass (g)	Rhizome biomass (g)	Num. of young sprouts or stems	Num. of grown sprouts or stems	Abovegr. : rhizome ratio
Carex nigra	3.06 ± 1.39	4.79 ± 2.26	26.05 ± 11.86	13.95 ± 5.04	0.69 ± 0.23
Carex rostrata	7.34 ± 6.88	5.01 ± 3.07	8.67 ± 5.09	21.73 ± 10.04	1.35 ± 0.43
Juncus filiformis	6.70 ± 3.37	3.47 ± 1.20	298.40 ± 117.52	170.21 ± 56.23	1.74 ± 0.2

* We did not counted the number of stems of *Juncus filiformis* in the chamber experiment.

Results

All three species grew considerably in chamber and field experiments, and in the different hydrological and competitive regimes. In the chamber experiment, all adult plants grew successfully but 15 *C. nigra* seedlings (out of 90) died. Contrastingly, in the field experiment plants in four plots died, two of *C. nigra*, one of *C. rostrata* and one of *J. filiformis*. The 94% of *Carex* plants in the chamber experiment developed new sprouts during the three months under experiment conditions, and all plants in the field experiment developed new sprouts or stems during the two growing seasons under experiment, excepting one *J. filiformis* sample that showed a slight size decrease (Table 1.1). Additionally, most *C. nigra* and *J. filiformis* flourished during the second summer in the field experiment. Table 1.2 summarizes the effects of hydrological regime and competitive relation factors over all response variables for the three species and the two experiments.

Above- and belowground growth of adult plants

Plant-plant interactions caused relevant constraints for aboveground and rhizome biomass formation in the three species (Fig. 1.2 b and d; Table 1.3). That is, all them performed better in monospecific pots than in bispecific pots. More concretely, *C. nigra* and *C. rostrata* were detrimental each other when they coexisted, *C. nigra* growth was not affected when coexisting with *J. filiformis,* and *J. filiformis* growth was. Competitive relations in the field experiment were weaker than in the chamber experiment. In fact, in the field experiment, the competitive relation was significant only in the *C. nigra* models (p=0.03 and p=0.002 for the coexistence with *C. rostrata* in aboveground and rhizome biomass respectively; Table S1.1 in the Supplementary Material). *Juncus filiformis* developed smaller belowground organs and fewer sprouts on average when coexisting with *C. nigra* in the field (Table 1.2).

Globally, all species performed similarly or better under high water table (WT) conditions (Table 1.2). *Carex* species responded significantly to the hydrological regime after two growing seasons in the field experiment, whereas in the chamber experiment they tolerated similarly low and high WT conditions (Fig. 1.2 a and c). Similarly, aboveground biomass of *J. filiformis* was higher in flooded soils, although only significantly in the chamber experiment.

Aboveground and rhizome dry weights were somewhat correlated in the chamber experiment and clearly correlated in the field experiment (spearman's Rho: *C. nigra*, r_s = 0.79; *C. rostrata*, r_s = 0.81; *J. filiformis*, r_s = 0.95; Table S1.2 and S1.3 in the Supplementary Material). Plants in the field experiment accumulated significantly more perennial rhizome structures in relation to the aboveground biomass, which is replaced annually, and that resulted into a lower aboveground:rhizome ratio than in the short-term chamber experiment (Fig. 1.2 e). Differences between experiments stood out in *C. nigra*, with a

Table 1.2. Summary table including the statistically significant results (p-value < 0.05) found for all species in the two experiments. Arrows indicate an increase (↑) or a decrease (↓) on the response variable under the situation indicated in the first column. Text in parentheses show that the fixed effect was retained in the best model (thus considered relevant) but its estimate had a p-value > 0.05. ab:rhiz ratio = Aboveground:rhizome biomass ratio; bm = biomass

	Chamber experiment			
	Carex nigra	*Carex rostrata*	*Juncus filiformis*	*C. nigra* seedlings
In bi-specific pots	↓ abovegr. bm (↓ rhiz. bm) ↓ growth rate	↓ abovegr. bm ↓ rhizome bm ↓ growth rate (↓ sprouts) (↑ ab:rhiz ratio.)	↓ abovegr. bm ↓ rhizome bm ↓ growth rate	↓ abovegr. bm
In high water table pots	(↑ rhiz. bm) ↑ growth rate	(↑ abovegr. bm) (↑ growth rate)	↑ abovegr. bm ↓ rhizome bm ↑ growth rate ↑ ab:rhiz ratio	↓ abovegr. bm
	Field experiment			
	Carex nigra	*Carex rostrata*	*Juncus filiformis*	*C. nigra* seedlings
In bi-specific spots	↓ abovegr. bm ↓ rhizome bm ↓ young sprouts		↓ grown sprouts (↓ rhiz. bm) (↓ young sprouts) (↑ abovegr. bm)	(not studied)
In high water table spots	↑ abovegr. bm ↑ rhizome bm ↑ young sprouts	↑ abovegr. bm ↑ young sprouts ↑ ab:rhiz ratio (↑ rhiz. bm) (↑ grown sprouts)	(↑ abovegr. bm)	(not studied)

scanty growth of rhizome in the chamber experiment but a noticeable growth in the field (Table 1.1). At the same time, aboveground:rhizome ratios tended to be higher at high WT conditions, were plants boosted aboveground organs. However, competitive relations did not affect aboveground:rhizome ratios, what may be evidence that interspecific interactions concerned similarly above and belowground plant structures (Fig. 1.2 f).

Additionally, we computed the growth rate of aboveground biomass for plants in the chamber experiment. Consistent results confirm higher growth rates for plants under high WT (significant for *C. nigra* and *J. filiformis*) and in pots without interspecific interactions (significant for all species; Fig. 1.3 and Table 1.3).

Belowground expansion

We estimated the plant clonal reproduction investment as the number of final sprouts. In the field experiment the developed (*grown*) and the preformed (*young*) sprouts were counted separately. As in dry weight variables, we found a significant effect of the water table into plants vigour. More concretely, *Carex* species produced significantly more young sprouts under high WT that under low WT (*C. nigra*, p = 0.03;
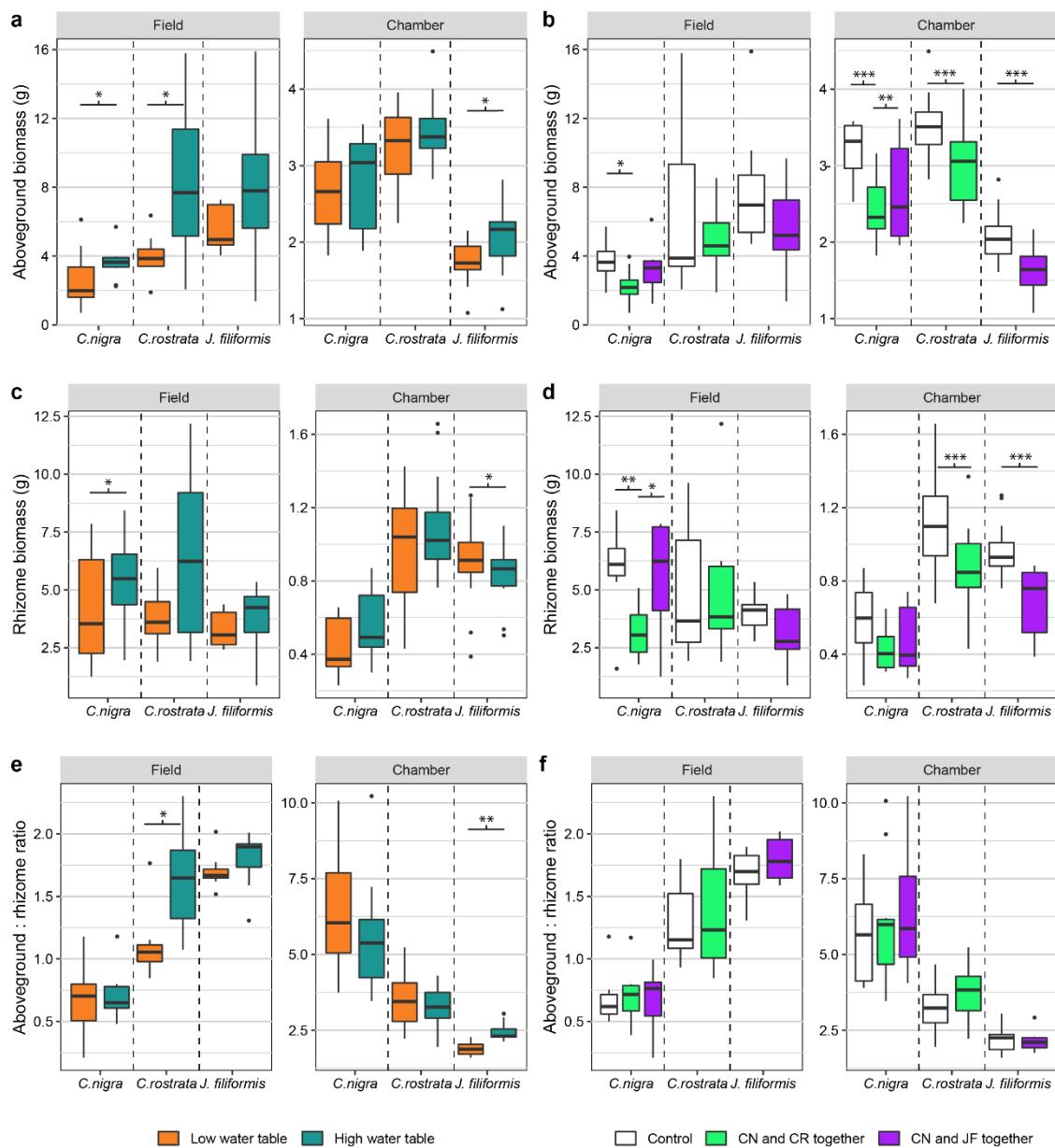
Fig. 1.2. Dry weight of the three species in the two experiments and (only adult plants). For all variables, we show significant results for each species and treatment: *, p<0.05; **, p<0.01; ***, p<0.001. Model variable significances are summarized in Table 1.3 and Table S1.1 of the Supplementary Material.

C. rostrata, p-value < 0.001; Fig. 1.4 a and Fig. S1.1 in the Supplementary Material). As in aboveground and rhizome biomass, low WT conditions for a period of two growing seasons limited *Carex* clonal reproduction. Besides, *C. nigra* formed less young sprouts when coexisting with *C. rostrata* (p-value < 0.001), whereas *C. rostrata* was not affected in high-density bispecific pots (Fig. 1.4 b). Finally, competition was detrimental for *J. filiformis* in the field experiment (grown sprouts, p-value < 0.001), and no significant results were obtained in the chamber experiment.

Table 1.3. Linear models estimates (z) and significances (p) for the different response variables and the three species in the chamber experiment (one model per variable and species). We show the R^2 and the number of samples (N) used in each model. CN = *C. nigra*; CR = *C. rostrata*; JF = *J. filiformis*; Control = monospecific pots; - = discarded variables in the selection model procedure.

| *Carex nigra*	Aboveground biomass (g)		Rhizome biomass (g)		Number of sprouts		Growth rate		Aboveground : rhizome ratio	
	z	p	z	p	z	p	z	p	z	p
Competitive relation:										
withCR versus Control	-4.44	**<0.001*****	-2.00	0.11	-	-	-5.73	**<0.001*****	-	-
withJF versus Control	-0.94	0.62	-1.45	0.31	-	-	-1.97	0.12	-	-
withJF versus withCR	2.94	**0.01****	0.49	0.88	-	-	3.60	**<0.001*****	-	-
Hydrological regime:										
High versus Low WT	-	-	1.87	0.06.	-	-	2,15	**0.03***	-1.10	0.27
Initial size of plants	3.90	**<0.001*****	-	-	1.57	0.12	-	-	1.06	0.30
R^2 *of the selected model*	0.59		0.24		0.08		0.61		0.09	
N	30		29		29		29		28	

Carex rostrata	Aboveground biomass (g)		Rhizome biomass (g)		Number of sprouts		Growth rate		Aboveground : rhizome ratio	
	z	p	z	p	z	p	z	p	z	p
Competitive relation:										
withCN versus Control	-5.19	**<0.001*****	-2.83	**0.01****	-1.55	0.12	-4.89	**<0.001*****	1.42	0.15
Hydrological regime:										
High versus Low WT	1.37	0.17	-	-	-	-	1.37	0.17	-	-
Initial size of plants	6.03	**<0.001*****	2.37	**0.03***	2.36	**0.02***	-1.18	0.25	-	-
R^2 *of the selected model*	0.72		0.33		0.22		0.51		0.07	
N	30		30		30		30		30	

Juncus filiformis	Aboveground biomass (g)		Rhizome biomass (g)		Number of stems		Growth rate		Aboveground : rhizome ratio	
	z	p	z	p	*Not studied*	z	p		z	p
Competitive relation:										
withCN versus Control	-7.74	**<0.001*****	-6.99	**<0.001*****	NA	NA	-5.14	**<0.001*****	-	-
Hydrological regime:										
High versus Low WT	2.12	**0.03***	-2.28	**0.02***	NA	NA	2.90	**0.004****	4.77	**0.001****
Initial size of plants	3.93	**0.001****	4.10	**0.004****	NA	NA	-2.33	**0.03***	-	-
Random effects	0.06.		-		NA		-		0.10.	
R^2 *of the selected model*	$R^2m = 0.60$		0.69		NA		0.66		$R^2m = 0.58$	
	$R^2c = 0.80$								$R^2c = 0.73$	
N	30		29		NA		30		28	
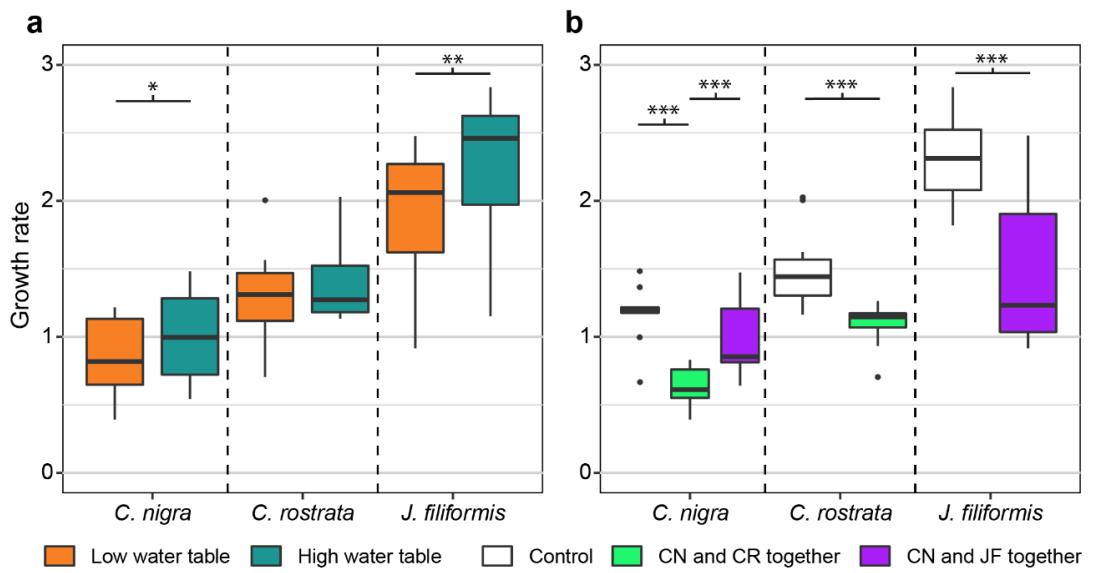
Fig. 1.3. Growth rate of the aboveground organs of the three species in the chamber experiment represented as boxplots (increment on dry weight: initial dry weight, only aboveground organs). We show significant results for each species and treatment: *, $p<0.05$; **, $p<0.01$; ***, $p<0.001$. Model variable significances are summarized in Table 1.3.

Performance of seedlings

As for seedling growth, the only successful treatment for *C. nigra* seedlings was the control condition –i.e., without *C. rostrata* nor *J. filiformis* adults– in combination with low WT ($p<0.001$; Fig. 1.5). Indeed, seedlings in high WT did not grow and eventually died, this being one of the main limitations for sexual reproduction (Table S1.4 of the Supplementary Material). In addition, the co-occurrence of *J. filiformis* caused a more important restriction to seedlings growth (p-value < 0.001 versus control conditions) than *C. rostrata* (p-value < 0.001 versus control conditions; but less restrictive than *J. filiformis*, p = 0.049) (Fig. 1.5 and Table S1.5 of the Supplementary Material).
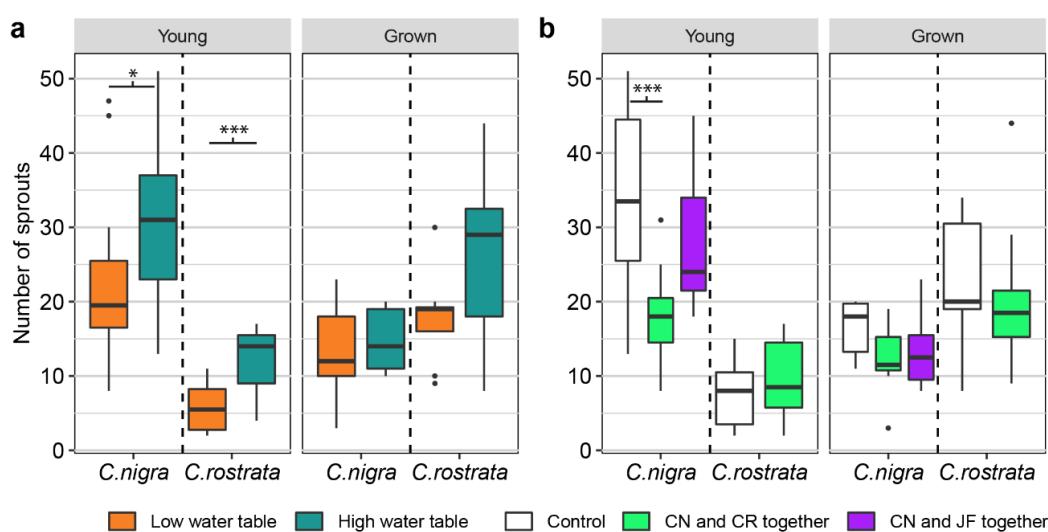
Fig. 1.4. Number of sprouts of *C. nigra* and *C. rostrata* at the end of the field experiment represented as boxplots. We show significant results for each species and treatment: *, $p<0.05$; **, $p<0.01$; ***, $p<0.001$. Model variable significances are summarized in Table S1.1 of the Supplementary Material.

Discussion

Biotic interactions

Interspecific competition slowed down the development of the three species, and we found no facilitative interactions. Globally, *Carex rostrata* was the most competitive species, as it was not affected by plant interactions after two growing seasons but caused a negative effect on *Carex nigra* growth (biomass and young sprouts). In the short-term chamber experiment, both *Carex* species had smaller biomasses and growth rate when coexisting in bispecific pots. In turn, *C. nigra* negatively affected the biomass and the growth rate of *Juncus filiformis* in the chamber experiment, whereas *J. filiformis* did not affect *C. nigra* development in any experiment. Hence, *J. filiformis* is the less competitive species, and smaller plastic pots in the chamber experiment enabled stronger plant competition for resources.

Contrastingly, interspecific competition did not affect *J. filiformis* development in the field experiment, were *C. nigra* individuals developed short aboveground biomass (although having higher rhizome biomass). This lead the rush to thrive with lower or negligible light limitations in comparison to the chamber experiment. Thus, our results suggest noticeable competition for light resource where this was limiting, since shading may hinder the occurrence of poorly competitive species in productive sites within fens and meadows (Kotowski & Diggelen, 2004) as observed for *J. filiformis* (Blackstock, 1981). These results concur with the hypothesis according to which *J. filiformis* would demonstrate little competitive abilities. However, *J. filiformis* reached higher growth rates than other species, and developed considerable aboveground biomass in the field experiment besides extensive flowering. Thus, the rush proved good adaptive responses to both chamber and field experiments and to different water levels. High growth rates lead to high nutrient loss and low nutrient retention in plants (Aerts, 1999), what may cause competitive disadvantages in nutrient-poor habitats. In natural populations, *J. filiformis* only dominates in poor communities with low total plant cover and so low competition for resources, whereas in species-rich communities is scarce or absent (Blackstock, 1981; Pérez-Haase et al., 2010; Richards, 1943). Thus, according to our results *Juncus filiformis* behaved as a pioneer species in Alpine wetlands. Consequently, *J. filiformis* would be a suitable species to use in the first stages of plant succession in wetlands restoration.

However, *C. rostrata* behaved as a better competitor, being the most vigorous species under study. This result agrees with Gaudet & Keddy (1988) who found that bigger plants tend to be better competitors. This sedge had a considerable competitive influence over *C. nigra* –which showed lower growth rates, lower biomass, and fewer young sprouts than in control conditions–, whereas *C. rostrata* was only negatively affected by species interactions in the chamber experiment (showing lower biomass and growth rate when coexisting with *C. nigra*; Table 1.2). According to the limiting similarity theory, closely related taxa are likely to occur together less than by chance (Violle et al.,

2011). Watterway et al. (2016) demonstrated that *Carex* species co-occurred less than by chance in fens, and more significantly between species from the same subclade. Results point at mutual growth exclusion between *C. nigra* and *C. rostrata* during the first weeks of interacting establishment (chamber experiment), but at stronger competitive effect of *C. rostrata* over *C. nigra* along consecutive growing seasons.

Surprisingly, although *C. rostrata* is the most robust species, it had the lowest number of young sprouts in the field experiment, thus showing a smaller bud bank. This is not adaptive under changing ecological conditions since plants with bigger bud banks can resprout more successfully after disturbances in the vegetation succession (Klimešová & Klimeš, 2007). Nevertheless, *C. rostrata* had many grown sprouts in autumn (Fig. 1.4 and Table 1.1), showing a noticeable vigour and vegetative reproduction efforts. In fact, *C. rostrata* sprouts last 1.9 years on average (Saarinen, 1998). Thus, results point *C. rostrata* to be a good competitor that limit the development and clonal expansion of closely related species, and could eventually drive out other species through interspecific interactions at mid or long term vegetation succession.

Moreover, *Carex nigra* was sharply affected by the interaction with *C. rostrata* but not by *J. filiformis*. *Carex nigra* had the lowest growth rate and a faint rhizome development in the chamber experiment. According to Aerts (1999), low growth rates of species in nutrient-poor habitats can be a consequence of high nutrient retention. Contrastingly, after two growing seasons in the field experiment, *C. nigra* developed less
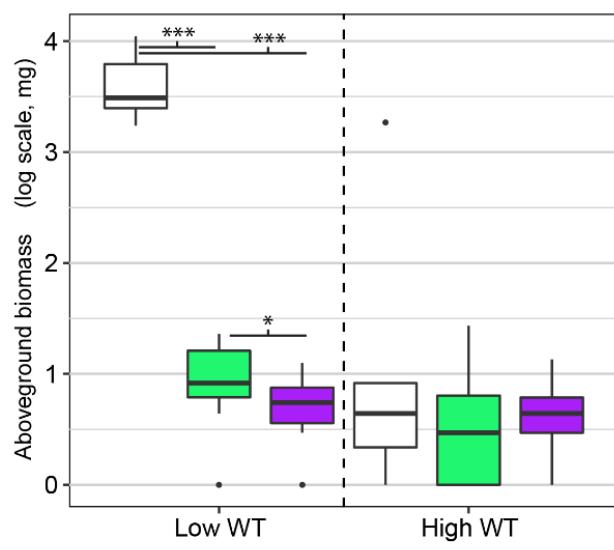
Fig. 1.5. Dry weight (in logarithm scale) of the aboveground biomass of *Carex nigra* seedlings according to the competitive relations in the two hydrological regimes in the chamber experiment. We show significant results for each species and treatment: *, p<0.05; **, p<0.01; ***, p<0.001. Model variable significances are summarized in Table #modHPL_BM in th Supplementary Material.

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photosynthetic structures but considerable rhizome biomass and a higher number of young sprouts, thus an important bud bank and good potential for clonal reproduction (Table 1.1). It is relevant to note that *C. nigra* reacted differently to *C. rostrata* than to *J. filiformis* in the chamber and the field experiments. So, our experimental design discerned between concrete interspecific relations rather than just between plant densities (see Davis et al. (2009) for a deeper discussion on plant density and interspecific competitions). These results suggest that *C. nigra* competitive responses arise after a slow acclimation to biotic and abiotic conditions. That is, an individual that survives the first years after transplantation should develop storage and clonal growth organs to ensure plant survival and population expansion. In fact, *C. nigra* is usually dominant in many Alpine wetland communities, but at the same time, it co-occurs with a number of forb and graminoid species forming rich communities where it is often not dominant (Colomer et al., 2019; Ninot et al., 2000; Pérez-Haase et al., 2010). Finally, *C. nigra* may curb other species growth, but it is not expected to displace other species.

As for belowground and aboveground growth, interspecific relations affected both compartments proportionally, since aboveground:rhizome biomass ratio was quite constant for each species and experiment. According to the game theory, plants would stimulate root growth in interspecific competition to achieve competitive superiority for nutrient resources (McNickle & Dybzinski, 2013; Padilla et al., 2013). Opposite trends have been reported for *C. rostrata* under competitive situations (Kennedy et al., 2003). Here, aboveground:rhizome ratios were constant among competitive relations in the three species and the two experiments (Fig. 1.2 e and f). Our results are in line with Tammaru et al. (2021), who studied the performance of seven *Carex* species under interspecific competition and found significant reductions in the rhizome growth but no differences on root:shoot ratios.

Moreover, some *Carex* species can change their growth strategy from *phalanx* (clump ramets) to *guerrilla* (spreading ramets) to avoid abiotic stress and to find more suitable micro-environments (Chen et al., 2011; Li et al., 2015). Although we did not measure the internodal length, rhizome biomass did not point at growth plasticity on lateral expansion between experimental conditions. Finally, the aboveground:rhizome ratio changed drastically within a species depending on the duration of each experiment (Table 1.1). More concretely, the development of sedge rhizomes incremented after two growing seasons, and thus it is risky to deduce clonal growth investment in plants only from short-term experiments (Ottaviani et al., 2021; Sorrell et al., 2012). Indeed, Paradis et al. (2014) advocate that the competitive abilities of species with vegetative spreading should not be testeduntil an appropriate plant age.

Water table depth

The water table depth did not affect the competitive ability in our case study. We expected *C. rostrata* to be more competitive under flooded conditions, as it is often dominant in flooded lake shores, but we reject this hypothesis on the grounds of our results. In fact, many studies find such factor interactions in wetland and meadow plants (see, for example, Budelsky & Galatowitsch, 2000; Jung et al., 2009; Kennedy et al., 2003).

Overall, all three species tolerated both water table depths although showing higher growth at high water tables. This validates our first hypothesis for *C. rostrata* (observed in the field) and *J. filiformis* (observed in the chamber), which was also applicable for *C. nigra*. Plants performed better under higher water tables, chiefly by developing larger aboveground structures. In fact, some plants can elongate shoots in response to flooding (Jackson & Colmer, 2005; Webb et al., 2012), a trait that although not measured in the present experiments, concur with the higher biomass or higher growth rates registered in our study. All three species are able to keep aerobic metabolism on flooded soils since they develop aerenchyma (Schweingruber et al., 2020; Visser et al., 2000; Wheeler, 2005). Altogether, plant performance at contrasting water tables vary along time as found also in previous studies (Feng et al., 2020; Miller & Zedler, 2003). In our study, while interspecific competition prevailed over water table depth for *J. filiformis* development, the opposite response was seen for *C. rostrata*. Previous studies already demonstrated that *C. rostrata* thrives largely on partially submerged soils and that release oxygen into the soil (Mainiero & Kazda, 2005; Visser et al., 2000). In this study, we demonstrated that *C. rostrata* is the most competitive plant, and that it thrives better in flooded soils. At the same time, it never dominates species-rich communities, especially in habitats with low water tables during the summer (Colomer et al., 2019; Pérez-Haase et al., 2010), so it suggests *C. rostrata* has a narrow water table niche where it is a good competitor.

Rhizome biomass response to flooding was unclear. In plants with vegetative spreading, biomass allocation to rhizomes and other storage organs vary depending on the hydroperiod (Moor et al., 2017), water fluctuations (Sosnová et al., 2010) and taxa (Webb et al., 2012). Contrastingly, the number of sprouts responded significantly to different factors. First, in the chamber experiment the number of sprouts depended mainly on the initial size of each plant –according to Kikvidze et al. (2006), ignoring initial biomass can cause systematic bias. Second, in the field experiment the number of grown sprouts in the second growing season did not show a clear trend. And third, the number of young sprouts (that is, the plant investment in bud bank after two growing seasons) depended on the water table depth. Wetland specialist plants invest notable resources to produce buds when living under flooded conditions (Deng et al., 2016; Yang & Kim, 2016). In that way, plants ensure resprouting after flooding and to recover growth the next year (Ding et al., 2019).

Plant establishment

Most wetland plants have transient or short-term persistent seed banks (Maas & Schopp-Guth, 1995; Poschold, 1995). In a preliminary study in Font Grossa, the seed bank in unvegetated sandy soils –four years after a dam removing– gave a poor response in terms of emerging species. 94% of seedlings belonged to *Juncus articulatus*, while the rest belonged to a few *Carex spp.* or mire generalists (own results, not shown here). Thus, the passive restoration through seed bank may be much slow and ill-directed to guarantee quick habitat restoration in alpine wetlands, also considering that land managers appreciate the fast recovery of the landscape aesthetic values. Nevertheless, rhizome establishment evidenced promising results through resprouting in some cases –as reported in Steed & DeWald (2003)– while seed sowing would entail a useful strategy for enhancing community richness in restoration actions (Neff et al., 2009).

Previous studies evidenced that *Carex* seedlings do not tolerate neither water saturated soils nor flooding during the first growing season (Araki & Kunii, 2013; Budelsky & Galatowitsch, 2004; Neff et al., 2009). Here, we detected slight negative effects of high water tables on *Carex nigra* seedlings survival and drastic effects on seedlings growth. Also, light limitation from neighbour plants determined significant constraints for seedling growth –as observed in Kotowski et al., (2010). Thus, at low water tables the co-occurrence with adult plants hindered seedlings development, a competence that was even more drastic when it coexisted with *J. filiformis* than with *C. rostrata*. The former produces denser populations that would shade seedlings more effectively than the latter (Schweingruber et al., 2020). Thus, competition and water level are crucial factors to ensure seedling establishment after the first growing season (Budelsky & Galatowitsch, 2000). Overall, we only think sowing is a useful action when the area to restore is unvegetated and vegetative propagules are hard to collect.

Implications for restoration

The removing of reservoir dams in the Pyrenean chain gives an opportunity to convert unvegetated emerged areas into wetlands. In areas that are not subjected to flooding periods, natural germination of the local seed bank is expected to be insufficient for plant colonization rates (P. Keddy, 1999), but seed sowing entails promising results. Even though, seedling growth rates are subject to adult plant occurrence, resulting from clonal reproduction of nearby populations (Qi et al., 2021) or by manual transplantation (Steed & DeWald, 2003). In the present study we transplanted adult shoots and rhizomes, which showed good survival rates on distinct biotic and abiotic conditions. In the case of transplantation of rhizome pieces, successful plant survival is expected to be higher in the beginning of the growing season than in autumn (Yetka & Galatowitsch, 1999), and flooding conditions would be detrimental in any case (Budelsky & Galatowitsch, 2000).

According to the present study, *Carex nigra* is a moderate competitor that successfully thrives in a range of water table depths and that partly prevent the development of other rhizomatous plants through mutual growth exclusion. It generates high belowground biomass that may stabilize soils in the first steps of vegetation succession, together with a high vegetative expansion that will ensure its population viability. Besides, *C. rostrata* behaved as a stronger competitor adapted to high water tables, what makes it an appropriate plant to stabilize soils in lake shores. Finally, *J. filiformis* showed weak competitive abilities, in spite of its high growth rates and good adaptation to different water tables. Thus, results agree with the pioneer behaviour of this rush in wetland vegetation succession. Overall, this study underscores that all three studied species are suitable to be used in the first stages of plant succession in lake shores, but different competitive abilities will affect vegetation dynamics along time. That is, *J. filiformis* is a good pioneer that will allow other species colonization (although shading germinated seedlings); *C. rostrata* should be used gingerly since it may prevent competitive exclusion at mid-term in flooded areas; and *C. nigra* tolerates different plant interactions and water levels but show a slower growth rate. Understanding the plant ecology and plant interactions of obtainable species is crucial to making sound decisions in initiating plant succession processes for restoration purposes (Temperton et al., 2016; Young et al., 2005).

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Supplementary Material from Chapter 1

Table S1.1. Linear models estimates (z) and significances (p) for the different response variables and the three species in the field experiment (one model per variable and species). We show the number of samples (N) used in each model and the R^2 (except for models with negative binomial family of residuals). CN = *C. nigra*; CR = *C. rostrata*; JF = *J. filiformis*; Control = monospecific plots; - = discarded variables in the selection model procedure.

Carex nigra	Aboveground biomass (g)		Rhizome biomass (g)		Num. of young sprouts		Num. of grown sprouts		Abovegr. : rhizome ratio	
	z	p	z	p	z	p	z	p	z	p
Competitive relation:										
withCR versus Control	-2.55	**0.03***	-3.43	**0.002****	-3.60	**<0.001*****	-	**-**	-	-
withJF versus Control	-1.02	0.56	-0.23	0.97	-1.05	0.53	-	-	-	-
withJF versus compCR	1.42	0.33	2.44	**0.04***	1.81	0.16	-	**-**	-	-
Hydrological regime:										
High versus Low WT	2.03	**0.04***	2.18	**0.03***	2.12	**0.03***	-	**-**	-	-
Initial size of plants	1.03	0.22	-	-	-	-	1.32	0.19	1.36	0.19
R^2 of the selected model		0.42		0.40		NA		NA		0.08
N		22		22		21		20		22

Carex rostrata	Aboveground biomass (g)		Rhizome biomass (g)		Num. of young sprouts		Num. of grown sprouts		Abovegr. : rhizome ratio	
	z	p	z	p	z	p	z	p	z	p
Competitive relation:										
withCN versus Control	-	-	-	-	-	-	-	-	-	-
Hydrological regime:										
High versus Low WT	2.07	**0.04***	1.72	0.09	3.73	**<0.001*****	1.74	0.08	2.95	**0.01***
Initial size of plants	-	-	-	-	-1.62	0.11	-	-	-	-
R^2 of the selected model		0.32		0.20		0.73		NA		0.40
N		14		15		15		15		15

Juncus filiformis	Aboveground biomass (g)		Rhizome biomass (g)		Num. of young stems		Num. of grown stems		Abovegr. : rhizome ratio	
	z	p	z	p	z	p	z	p	z	p
Competitive relation:										
withCN versus Control	-	-	-1.53	0.13	-1.28	0.20	-5.92	**<0.001*****	1.18	0.24
Hydrological regime:										
High versus Low WT	1.38	1.17	-	-	-	-	-	-	-	-
Initial size of plants	-	-	-	-	-	-	-	-	-	-
Random effects		-		-		-		**<0.001*****		-
R^2 of the selected model	0.14			0.16		NA		R^2m = 0.06		0.096
								R^2c = 0.98		
N		15		15		15		14		15

Table S1.2. Spearman's rho correlations of the response variables considered in the chamber experiment for each species (only adult plants).

Carex nigra	Aboveground biomass	Rhizome biomass	Number of sprouts	Growth rate
Rhizome biomass	0.450			
Number of sprouts	0.259	0.131		
Growth rate	0.754	0.363	-0.007	
Aboveground : rhizome ratio	0.172	-0.778	0.064	0.096

Carex rostrata	Aboveground biomass	Rhizome biomass	Number of sprouts	Growth rate
Rhizome biomass	0.483			
Number of sprouts	0.613	0.308		
Growth rate	0.580	0.441	0.330	
Aboveground : rhizome ratio	-0.097	-0.900	-0.110	-0.212

Juncus filiformis	Aboveground biomass	Rhizome biomass	Number of sprouts*	Growth rate
Rhizome biomass	0.533			
Number of sprouts*	NA	NA		
Growth rate	0.786	0.317	NA	
Aboveground : rhizome ratio	0.471	-0.390	NA	0.484

* We did not counted the number of stems of *Juncus filiformis* in the chamber experiment.

Table S1.3. Spearman's rho correlations of the response variables considered in the field experiment for each species.

Carex nigra	Aboveground biomass	Rhizome biomass	Num. of young sprouts	Num. of grown sprouts
Rhizome biomass	0.793			
Num. of young sprouts	0.968	0.909		
Num. of grown sprouts	0.470	0.486	0.477	
Aboveground : rhizome ratio	-0.595	-0.942	-0.750	-0.616

Carex rostrata	Aboveground biomass	Rhizome biomass	Num. of young sprouts	Num. of grown sprouts
Rhizome biomass	0.807			
Num. of young sprouts	0.775	0.685		
Num. of grown sprouts	0.600	0.834	0.252	
Aboveground : rhizome ratio	-0.581	-0.937	-0.621	-0.719

Juncus filiformis	Aboveground biomass	Rhizome biomass	Num. of young stems	Num. of grown stems
Rhizome biomass	0.948			
Num. of young sprouts	0.850	0.720		
Num. of grown sprouts	0.052	0.315	-0.250	
Aboveground : rhizome ratio	-0.410	-0.668	-0.147	-0.866

Table S1.4. Linear model estimates (z) and significances (p) for the *C. nigra* seedlings survival in the chamber experiment (binomial response). We show the R^2 and the number of samples used (N). CR = *C. rostrata*; JF = *J. filiformis*; Control = pots without competition; - = discarded variables in the selection model procedure. The interaction of fixed effects was not selected.

Carex nigra seedlings	Survival	
	z	p
Competitive relation:		
withCR versus Control	-	-
withJF versus Control	-	-
withJF versus withCR	-	-
Hydrological regime:		
High versus Low WT	-1.957	0.05
R^2 of the selected model		0.073
N		87

Table S1.5. Linear models estimates (z) and significances (p) for the *C. nigra* seedlings biomass in the chamber experiment. We show the R^2 and the number of samples used (N). CR = *C. rostrata*; JF = *J. filiformis*; Control = pots without competition. The interaction of fixed effects was selected and thus we represent the effects in two columns.

Carex nigra seedlings		Aboveground biomass (log scale, mg)	
Interaction factor 1	*Interaction factor 2*	z	p
Hydrological regime:	Competitive relation:		
High	withCR versus Control	-1.01	0.57
High	withJF versus Control	-0.73	0.73
High	withJF versus compCR	0.30	0.95
Hydrological regime:	Competitive relation:		
Low	withCR versus Control	-22.49	**<0.001*****
Low	withJF versus Control	-24.83	**<0.001*****
Low	withJF versus compCR	-2.35	**0.049***
Competitive relation:	Hydrological regime:		
Control	High versus Low WT	-12.56	**<0.001*****
Competitive relation:	Hydrological regime:		
WithCR	High versus Low WT	-2.76	**0.01***
Competitive relation:	Hydrological regime:		
withJF	High versus Low WT	-0.56	0.56
R^2 of the selected model			0.86
N			88

Capítol 2

Estany de Mollàs. Fotografia d'Eulàlia Pladevall.

Small scale vegetation shifts after livestock grazing cessation: a short-term experiment in Pyrenean fens

Canvis en les comunitats vegetals en cessar l'activitat ramadera. Un experiment de curta durada en molleres pirinenques

Abstract

Livestock grazing and trampling have a major impact on fen conservation worldwide. Grazing causes changes on plant above and belowground productivity, biomass accumulation, community structure and sensitivity to other environmental factors. In the Pyrenean range, cattle trampling and pugging creates muddy areas of bare soil and often is the main habitat disturbance. Under this scenario, livestock exclusion could be a useful passive restoration strategy for overgrazed Alpine fens, although the vegetation dynamics in these ecosystems at short- and mid-term is poorly understood. In this study, we aimed at analysing plant succession at short term in overgrazed fens. To meet this goal, we surveyed 120 plots of 50 × 50 cm size and 180 plots of 10 × 20 cm size in six fens along three consecutive years. We distinguished between dense plant communities, small gaps made by hoof prints and severely trampled areas (pugged). We prevented livestock grazing in half of the plots from the second year onwards by exclosures. We analysed the bare soil colonization process recording adult and seedling plant species occurrence and cover, and vascular plant and bryophyte species abundance change at each plot. Moreover, we analysed plant community dynamics through beta diversity calculations. Results showed a sharp increase in vascular plant and bryophyte cover in small gaps both inside and outside the exclosures, but livestock exclusion effects became more apparent in pugged areas. Thus, we detected a clearer increase in vascular plant richness and abundance inside than outside the exclosures, and beta diversity was higher in ungrazed plots only in some study sites. We concluded that at short-term, livestock grazing cessation accelerates revegetation of bare soil with concomitant plant composition changes, but we detected no changes neither in community composition nor species richness in dense plant communities.

Introduction

During the twentieth century, extensive pastoralism in the Pyrenees decreased significantly, with a sharp decline in sheep herds and transhumance (Collantes, 2009). However, land use intensification is observed in more appropriate areas for cattle (and horse) grazing (IDESCAT, 2019; Lasanta-Martínez et al., 2005). A similar trend also occurs in other Alpine ranges in Europe (MacDonald et al., 2000). Smooth mountain reliefs are frequently overgrazed , and most often include dry grasslands and meadows, while steep slopes at high altitudes or with difficult access are abandoned (MacDonald et al., 2000). Thus, both grazing abandonment and overgrazing coexist at regional scale, with contrasting consequences on biodiversity conservation (Galop et al., 2011).

Two mechanisms drive community changes in grasslands: grazing avoidance – favouring non-palatable species or those with morphological defences– and grazing tolerance –giving advantage to species able to resprout rapidly after grazing– (Augustine & McNaughton, 1998). Vegetation dynamics due to these processes would differ according to the grazing regime and intensity (Bullock et al., 2001). Moreover, forage selection by cattle influences vascular plant species composition and dynamics in grasslands (Díaz et al., 2007; Pauler et al., 2020). Grazing favours shorter-lived and smaller plants, whereas litter accumulation and tall herbs development promote competition for light between species under grazing exclusion (Kotowski et al., 2006). Additionally, in overgrazed areas, plant species produce smaller rhizomes, and their belowground biomass is more influenced by grazing regimes than aboveground biomass (Kauffman et al., 2004; Ottaviani et al., 2021).

Overgrazing is a common disturbance in fens worldwide (Keddy, 2010). Bovine and equine livestock use to frequent fens, since they find there green pastures and water during the whole growing season. In fact, cattle trampling has been identified as the main impact factor on Alpine mire conservation (Spitale, 2021). Trampling can hinder plant growth in fens, or even destroy plant or moss cover, and provokes mechanical compaction of peaty soils (Sjögren et al., 2007) and soil pugging, particularly under shallow water tables (Morris et al., 2013). Moreover, trampling also alters fen hydrological properties, such as water retention and surface runoff.

Most vascular plants in fens are graminoid hemicryptophytes (Cronk & Fennessy, 2001; Illa et al., 2006; Rydin & Jeglum, 2013), and clonal reproduction prevails over sexual reproduction, which is more prevalent in disturbed conditions (Klimkowska et al., 2019). Moderate grazing pressure may benefit some grasses and sedges, as they can produce new leaves faster than forbs (Grime, 2001). Moreover, light grazing regimes or livestock

exclusion allow the cover increase of tall plants, and may be detrimental to bryophyte populations due to light competition (Jasmin et al., 2008; Peintinger & Bergamini, 2006; Sundberg, 2012), although conflicting results are reported in the literature (Watts et al., 2019).

Soil disturbances from trampling favour seedling recruitment in grasslands (Kahmen & Poschlod, 2008). In Alpine grasslands, vascular plant recovery is mainly reached by plants with small seeds, unspecialized seed dispersal and a persistent seed bank (Kohler et al., 2006) and often by plants with strong vegetative spread (Cichini et al., 2011). However, little is known about soil recovery in fens as a result of cattle trampling (but see Stammel & Kiehl, 2004). In Alpine mountains, including the Pyrenees, the need for extensive livestock management has emerged to tackle ecosystem disturbance with the restoring of traditional land uses, which includes reshaping the intensity of cattle grazing. Therefore, livestock exclusion emerges as a passive restoration management strategy for overgrazed fens, even though the poor knowledge on vegetation dynamics in these ecosystems is far from allowing a prediction on vegetation responses at short- and mid-term after such sudden change in land use.

Here, we wanted to analyse the first stages and processes in plant succession in overgrazed, trampled fen vegetation after a sudden livestock exclusion. With the aim of recording the ecosystem recovery, we set up a field experiment in six study sites in the Pyrenees along an elevational gradient. We recorded vegetation dynamics at detailed scales in permanent plots, which were monitored for three years, the first under livestock grazing and trampling pressure, and the following two growing seasons under livestock exclusion. In parallel, control plots under livestock pressure permitted to compare vegetation changes according to the grazing regime. The questions we addressed here were: i) How does livestock exclusion modify vegetation structure in fen plant communities?; ii) What are the roles of mosses and vascular plants in gap colonization processes? And of sexual and clonal reproduction in vascular plants?; and iii) How does vary plant succession between small gaps (i. e., hoof prints) and larger areas of bare soil?

Methods

Study area

We conducted this study in the central Catalan Pyrenees (Fig. 2.1). Fens in the Pyrenees are chiefly related to springs, rivulets or tarn lakes. They occupy small areas, usually less than 5000 m^2, constrained by the mountain physiography in a patchy landscape (Ninot et al., 2017). Most fens are treeless and subject to extensive grazing during the summer, mainly by cattle and secondarily by equine and ovine livestock. Grazing and trampling pressures can be locally very high, where bare soil and peat occupy patches of a few square meters, particularly in areas with shallow water table. We conducted the field work in six fens on different valleys. The sites have varying geological
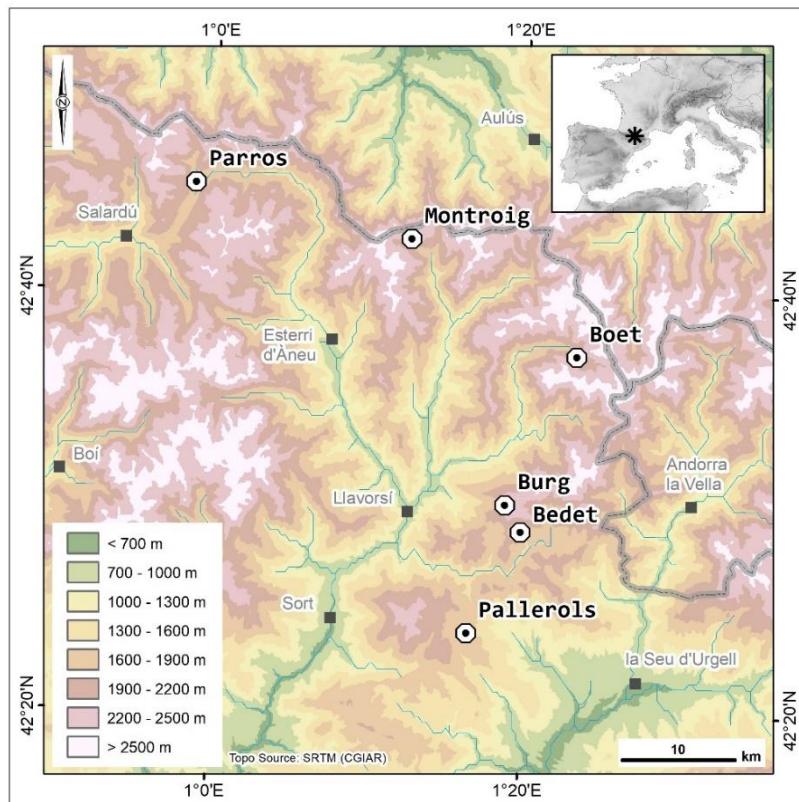
Fig. 2.1. Central Catalan Pyrenees and the six study sites, near to Andorran and French borders (grey lines).

and groundwater characteristics, and encompass most of the fen habitat types of the region. All sites are currently experiencing overgrazing and over-frequentation of livestock, and show disturbed soils by trampling and pugging. They are all located in the subalpine belt, along an elevational gradient of 400 m (Table 2.1).

Study design and field sampling

First, we classified the vegetation and soil disturbance in two categories or trampling levels, i. e. *severely trampled* and *moderately trampled*. The severely trampled areas show pugged soils without a continuous plant cover. The moderately trampled areas show high plant cover, but obvious signs of trampling evidenced by deep hoof prints with bare soil in the bottom (Fig. S2.1 of the Supplementary Material). During the summer of 2017, we set up ten permanent study points in five study sites, five in severely trampled areas and five in moderately trampled areas. All points in moderately trampled areas included one deep hoof print. Every permanent study point had two nested plot sizes.

The *big plots* were a 50 × 50 cm (0.25 m^2) square subdivided into 25 subplots of 10 × 10 cm each, from which we sampled 12 of them alternatively (Fig. 2.2). In every subplot we recorded all vascular plant species and their cover by a semi-quantitative scale: 1) up to 10% of the subplot; 2) between 11 and 33%; 3) more than 33%.

Table 2.1. Main geographic, ecologic and grazing characteristics of the study sites.

	Bedet	Pallerols	Parros	Boet	Burg	Montroig
Elevation (m)	1630	1670	1770	1860	2010	2010
Coordinates	42.479, 1.332	42.398, 1.276	42.752, 0.977	42.618, 1.389	42.501, 1.315	42.710, 1.210
Fen area (m^2)	6180	22010	28490	2460	6925	8325
Fenced area (m^2)	758	665	520	589	842	724
Sampling years	2017, 2018, 2019	2017, 2018, 2019	2017, 2018, 2019	2017, 2018, 2019	2018, 2019	2017, 2018, 2019
HCIs	7230	-	7230	7110*	7230	6230* 7110*
Mean water table depth (cm)	-17.4 ± 5.6	-8.5 ± 6.6	-10.5 ± 5.8	-19.3 ± 9.2	-15.7 ± 7.9	-11.6 ± 6.2
Mean pH	6.53 ± 0.31	5.82 ± 0.43	6.72 ± 0.18	5.10 ± 0.56	7.00 ± 0.21	5.89 ± 0.39
Mean electrical conductivity (µS/cm)	240.6 ± 80.4	125.2 ± 85.3	270.3 ± 76	140 ± 40.9	336.5 ± 75.5	131.8 ±70
Kinds of livestock	Bovine, equine	Bovine, equine	Bovine	Bovine, equine	Bovine, equine	Bovine, equine, ovine
Number of excrements per area	High	Moderate	Moderate	Moderate	High	High
Grazing intensity	Very high	High	Moderate	Very high	Very high	High
Trampling intensity	High	Very high	Very high	High	High	High

Additionally, we registered with the same scale the bare soil cover, the litter cover and the cover of the main bryophyte functional groups (i.e., acrocarpous mosses, pleurocarpous mosses, *Polytrichum spp*., *Sphagnum spp.* and liverworts).

We placed fifteen *small plots*, of 10 × 20 cm (0.02 m^2), nested within the ten big plots. More concretely, in the moderately trampled big plots, we set five small plots on the deep hoof prints (*small gaps*). In the severely trampled big plots, we set five small plots in the middle, so corresponding to the maximum trampling level (*bare soil*), and we set the other five limiting with extant vegetation (*bare soil edge*). Each small plot was subdivided into 32 subplots of 2.5 × 2.5 cm each (Fig. 2.2), and we recorded the presence of taxa that rooted on every subplot. Also, for each record, we distinguished between adults at species level, seedlings down to the lowest taxonomic level possible, and we again recorded the bryophyte functional groups.

During the spring of 2018, before livestock grazing season, we put up a livestock exclusion fence (hereinafter, an exclosure) in all the study sites enclosing all the permanent study points. During the summer of 2018 we resurveyed the plots, and we added ten extra permanent study points outside the exclosures, and so they corresponded to the control plots under grazing pressure (ten big plots and fifteen small plots nested to big plots) (Fig. S2.2 of the Supplementary Material). Additionally, also in 2018 we added a sixth study site (Burg fen; Table 2.1). During the summer 2019 we resurveyed all the plots under grazing and under grazing exclusion.
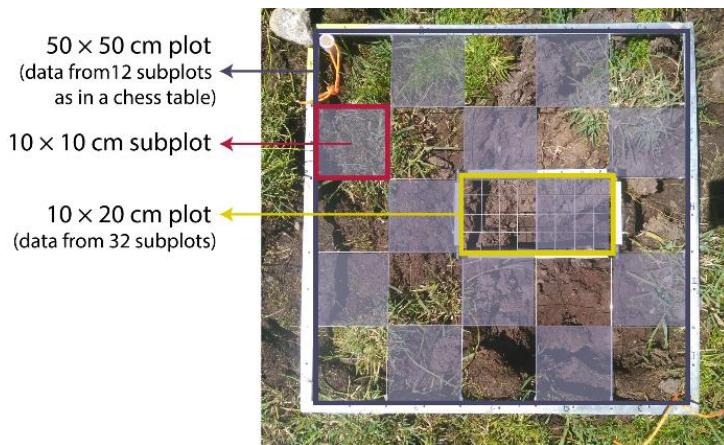
Fig. 2.2. Permanent study point showing the three plot sizes used. The data from the big plots (50 × 50 cm) come from the sum of the species percentage cover on the 12 subplots (10 × 10 cm). The data from the smallest plots (10 × 20 cm) are made up by the sum of the species occurrences on 32 subplots.

To sum up, we sampled: i) ten study points at five sites in 2017 (50 big plots of 50 × 50 cm size and 75 small plots of 10 × 20 cm size), which would be enclosed by the exclosure the following spring; and ii) ten study points at six sites inside the exclosure and ten study points outside the exclosure in 2018 and 2019 (i. e. two times 120 big plots and 180 small plots).

Data analysis

We analysed the data at three scales, and we kept separately the information of three groups, adult plants, seedlings and bryophytes. First, for the 10 × 20 cm small plots we summed all the occurrences in the 32 subplots to obtain the total abundance and the percentage of subplots where the groups were recorded. Additionally, we computed the adult plant richness of every small plot. Second, we analysed separately every 10 × 10 cm subplot from the 50 × 50 cm big plots through four variables: adult plant richness, and the sum of covers of adult plants, seedlings and bryophytes (separately). Previously, we transformed semi-quantitative cover data (1, 2 and 3 values) into percentages using the midpoint of each cover interval: 5, 22 and 66%, respectively. Third, we calculated two variables at the 50 × 50 cm big plots: Shannon index of diversity of plants and plant beta diversity (compositional change) at the same plot between two consecutive years. We calculated these variables according to the total sum of vascular plant covers for the 12 subplots together, and using the Bray Curtis dissimilarity for beta diversity (*vegdist* function from *vegan* package; Oksanen et al., 2020). Finally, we computed the total bare soil cover, as the average of each subplot cover, and the percentage of subplots with adult plants or bryophytes.

We analysed all response variables for all plot scales in the way as follows. First, we tested for differences across the three study years for each plot (2017 under livestock pressure, and 2018 and 2019 under livestock exclusion; five sites). To do so, we computed

non-parametric Friedman tests of repeated measures and Kendall's W statistic (using *agricolae* and *rstatix* packages; de Mendiburu, 2021; Kassambara, 2021). We performed all analyses taking into account the trampling level of each plot. We repeated the procedure considering all five sites together and separately to look for pattern differences between study sites. Second, we checked if vegetation response variables depended on grazing regime. To do so, we computed the magnitude of change between 2018 and 2019 at each plot and variable as a simple subtraction –we did this calculation for each variable apart from beta diversity, and in all six study sites. Then, we used this magnitude of change as a response variable, and we tested if it differed depending on the grazing regime by non-parametric Kruskal-Wallis tests. We performed all analyses considering all six sites together and separately, and taking into account the trampling level of each plot.

Results

Short-term vegetation dynamics after livestock exclusion

Results showed significant differences over time for most response variables analysed and at all plot scales (Tables 2.2, 2.3 and 2.4) and study sites (Tables S2.1, S2.2 and S2.3 of the Supplementary Material). Thus, permanent plots inside the exclosures experienced vegetation changes along the three growing seasons sampled (2017 under livestock pressure, and 2018 and 2019 under permanent livestock exclusion).

In the big plots (50 × 50 cm), we observed contrasting results according to the trampling level. The plots in severely trampled areas experienced a progressive decrease in the bare soil cover, chiefly drove by the increase in the percentage of subplots with bryophytes and with vascular plants (Fig. 2.3). However, we did not detect changes on these variables in plots in moderately trampled areas, since the bare soil cover was very low since 2017 (Fig. 2.3 b). Regarding vascular species, the Shannon diversity index increased at both trampling levels (Table 2.2). At more detailed scales (10 × 10 cm

Table 2.2. Summary of the results of plots of 50 × 50 cm. Friedman tests of plots under livestock exclusion along three growing seasons. All tests have two degrees of freedom. Multiple comparisons are represented by letters (different letters refer to different groups). See in Table S2.1 of the Supplementary Material the Friedman tests of each site separately.

Response variable	Chi^2	p	Kendall W	2017	2018	2019
Moderate trampling						
Shannon index	23.52	**<0.0001**	0.560	a	b	c
% of subplots with vascular plants	4	0.135	0.095	a	a	a
% of subplots with bryophytes	0.261	0.877	0.006	a	a	a
Bare soil cover (%)	26.63	**<0.0001**	0.634	a	a	b
Severe trampling						
Shannon index	22.52	**<0.0001**	0.490	a	b	c
% of subplots with vascular plants	21.88	**<0.0001**	0.476	a	b	c
% of subplots with bryophytes	28.32	**<0.0001**	0.616	a	a	b
Bare soil cover (%)	30.52	**<0.0001**	0.664	a	b	c

Table 2.3. Summary of the results of subplots of 10 × 10 cm. Friedman tests of plots under livestock exclusion along three growing seasons. All tests have two degrees of freedom. Multiple comparisons are represented by letters (different letters refer to different groups). See in Table S2.2 of the Supplementary Material the Friedman tests of each site separately.

Response variable	Chi^2	p	Kendall W	2017	2018	2019
Moderate trampling						
Vascular plant species richness	182.2	**<0.0001**	0.362	a	b	c
Vascular plant cover	207.5	**<0.0001**	0.412	a	b	c
Seedling cover	11.5	**0.003**	0.023	a	b	b
Bryophyte cover	36.51	**<0.0001**	0.072	a	b	c
Severe trampling						
Vascular plant species richness	353.9	**<0.0001**	0.641	a	b	c
Vascular plant cover	389.3	**<0.0001**	0.705	a	b	c
Seedling cover	50.07	**<0.0001**	0.091	b	c	a
Bryophyte cover	175.4	**<0.0001**	0.318	a	a	b

subplots, and 10 × 20 cm plots), adult vascular plant richness and cover increased during the experiment in all trampling levels (Fig. 2.4; Tables 2.3 and 2.4). Thus, we did not detect that proximity to clonal plant populations accelerated the growth of vascular plants in the plots by lateral spreading (*bare soil edge* plots showed same results than *bare soil* plots).

Table 2.4. Summary of the results of plots of 10 × 20 cm. Friedman tests of plots under livestock exclusion along three growing seasons. All tests have two degrees of freedom. Multiple comparisons are represented by letters (different letters refer to different groups). See in Table S2.3 of the Supplementary Material the Friedman tests of each site separately.

| Response variable	Chi^2	p	Kendall W	2017	2018	2019
Small gap						
Vascular plant species richness	30.304	**<0.0001**	0.722	a	b	c
Vascular plant abundance	31.143	**<0.0001**	0.741	a	b	c
Seedlings abundance	2.141	0.343	0.051	a	a	a
Bryophyte abundance	30.096	**<0.0001**	0.717	a	a	b
% of subplots with vascular plants	37.062	**<0.0001**	0.882	a	b	c
% of subplots with seedlings	4.137	0.126	0.098	a	a	a
% of subplots with bryophytes	31.876	**<0.0001**	0.759	a	a	b
% of subplots with plants or bryophytes	23.025	**<0.0001**	0.548	a	a	b
Bare soil edge						
Vascular plant species richness	22.641	**<0.0001**	0.492	a	a	b
Vascular plant abundance	24.198	**<0.0001**	0.526	a	b	c
Seedlings abundance	4.517	0.104	0.098	ab	a	b
Bryophyte abundance	20.584	**<0.0001**	0.447	a	a	b
% of subplots with vascular plants	25.694	**<0.0001**	0.559	a	b	c
% of subplots with seedlings	3.886	0.143	0.084	a	a	a
% of subplots with bryophytes	24.295	**<0.0001**	0.528	a	a	b
% of subplots with plants or bryophytes	32.721	**<0.0001**	0.711	a	b	c
Bare soil						
Vascular plant species richness	27.026	**<0.0001**	0.588	a	b	c
Vascular plant abundance	37.153	**<0.0001**	0.808	a	b	c
Seedlings abundance	3.553	0.169	0.077	a	a	a
Bryophyte abundance	22.027	**<0.0001**	0.479	a	a	b
% of subplots with vascular plants	31.506	**<0.0001**	0.685	a	b	c
% of subplots with seedlings	5.452	0.065	0.119	ab	a	b
% of subplots with bryophytes	25.127	**<0.0001**	0.546	a	a	b
% of subplots with plants or bryophytes	27.573	**<0.0001**	0.599	a	b	c
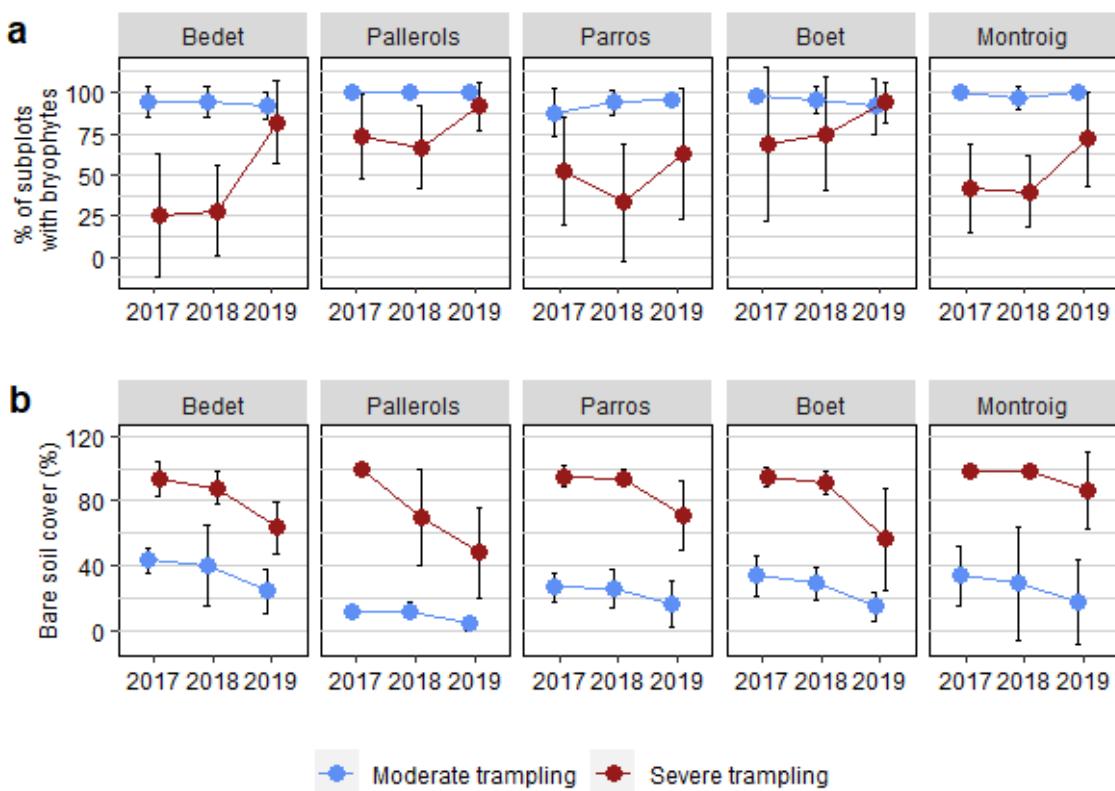
Fig. 2.3. Soil cover changes on big plots (50 × 50 cm) along three years under livestock exclusion at two trampling intensities in five study sites: a) Percentage of subplots hosting bryophytes; b) Percentage of bare soil in plots. P-values and differences for all study sites among years are showed in Table 2.2. P-values and differences for each site among years are showed in Table S2.1 of the Supplementary Material.

With regard to bryophytes, we barely detected their cover changes after the first year of exclusion, but we clearly noted it after the second year at both plot scales (Fig. 2.3 a and 2.5 a). We recorded significant increments in bryophyte cover and in the percentage of subplots with bryophytes between 2018 and 2019 in all trampling levels and scales studied (Tables 2.2, 2.3 and 2.4). Conversely, plant seedlings did not show a particular trend under livestock exclusion. Although we detected a general increase of seedlings abundance in small plots (10 × 20 cm) in Bedet, the shift was not significant when considering all the study sites (Fig. 2.5 b; Table 2.4 and Table 2.3 of the Supplementary Material).

Changes in vegetation in relation to grazing regime

We compared the vegetation change from 2018 to 2019 in plots inside the exclosures versus control plots, and we detected noticeable changes in vegetation variables in both grazing regimes. In areas moderately trampled at the beginning of the experiment, vegetation dynamics was similar inside and outside the exclosures and mainly depended on the study site. For instance, vascular plant cover change did not depend on the grazing regime (except for Pallerols), and vascular plant richness in Burg
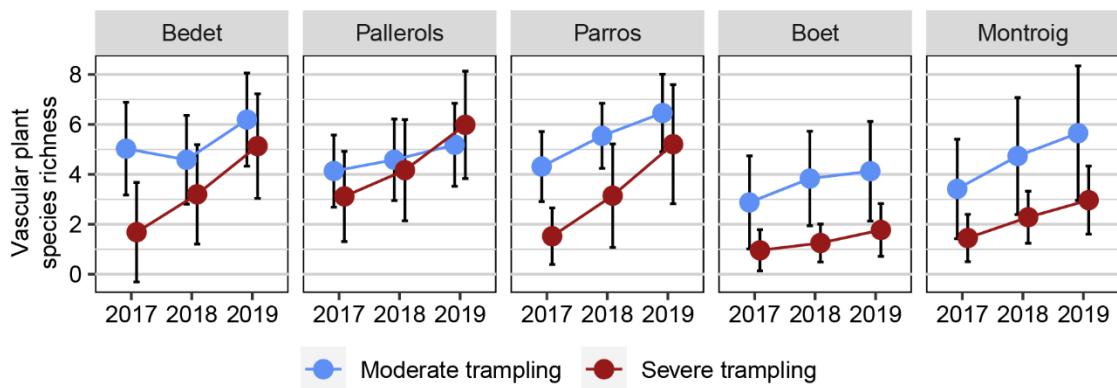
Fig. 2.4. Plant species richness in subplots of 10 × 10 cm along three years under livestock exclusion at two trampling intensities in five study sites. P-values and differences for all sites among years are showed in Table 2.3. P-values and differences for each study site among years are showed in Table S2.2 of the Supplementary Material.
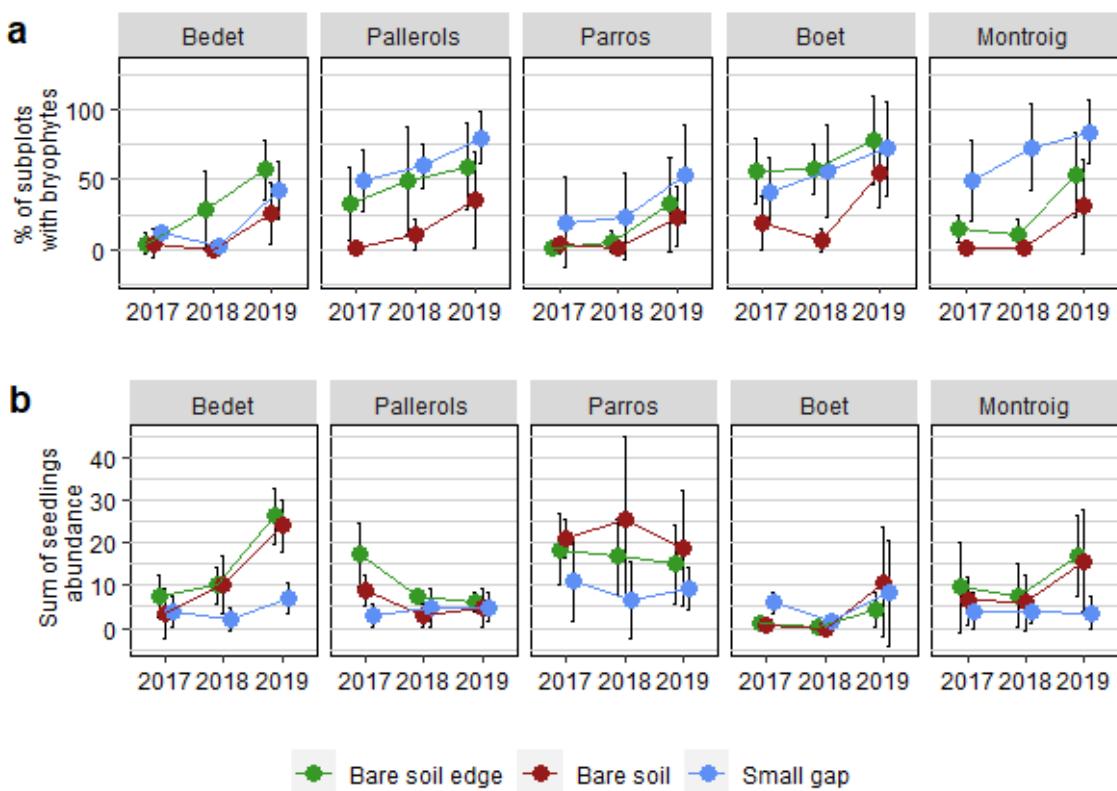
Fig. 2.5. Vegetation changes at small plots (10 × 20 cm) along three years under livestock exclusion at three trampling intensities in the five study sites: a) Percentage of subplots hosting bryophytes; b) Sum of seedling taxa in all subplots. P-values and differences for all study sites among years are showed in Table 2.4. P-values and differences for each study site among years are showed in Table 2.3 of the Supplementary Material.

increased more inside the exclosures than outside; but opposite trends were observed in Pallerols and Parros. Moreover, the bryophyte cover in Burg and Bedet sites decreased in subplots inside the exclosures and increased under grazing pressure (Table 2.5).

Table 2.5. Summary of the results in subplots of 10 × 10 cm. Kruskal Wallis tests of the change on cover variables between 2018 and 2019 comparing the trampling levels. All tests have one degree of freedom.

Change on the	All sites		Bedet		Pallerols		Parros		Boet		Burg		Montroig	
	Chi²	p	Chi²	p	Chi²	p	Chi²	p	Chi²	p	Chi²	p	Chi²	p
Moderate trampling														
Plant richness	3.28	0.070 ..	1.84	0.175	5.96	**0.015** *	4.34	**0.037** *	0.26	0.614	4.75	**0.029** *	0.2	0.657
Plant cover	0.09	0.767	0.31	0.578	10.6	**0.001** **	0.36	0.548	3.57	0.059 .	2.03	0.155	0.74	0.390
Seedling cover	0.36	0.548	3.98	**0.046** *	6.13	**0.013** *	1.77	0.183	1.77	0.184	0.93	0.336	0.42	0.519
Bryophyte cover	5.21	**0.022** *	3.97	**0.046** *	0.14	0.712	2.05	0.152	0	0.989	3.9	**0.048** *	0.05	0.821
Severe trampling														
Plant richness	36.1	**<0.0001** ****	1.88	0.170	23.6	**<0.0001** ****	11.3	**<0.001** ***	0.47	0.494	6.79	**0.009** **	1.21	0.271
Plant cover	32	**<0.0001** ****	2.01	0.156	10.4	**0.001** **	32.4	**<0.0001** ****	2.23	0.135	10.9	**<0.001** ***	0.74	0.388
Seedling cover	3.48	0.062 .	19.7	**<0.0001** ****	3.19	0.074 .	4.13	**0.042** *	17.7	**<0.0001** ***	1.98	0.160	5.97	**0.015** *
Bryophyte cover	27.2	**<0.0001** ****	6.91	**0.009** **	21.3	**<0.0001** ****	3.19	0.074 .	9.27	**0.002** **	3.77	0.052 .	6.32	**0.010** *

Contrastingly, areas severely trampled experienced larger changes under livestock exclusion than in control plots. More concretely, vascular plant richness and cover increased faster inside the exclosures, a process that was significant in Pallerols and Parros (Fig. 2.6 a; Table 2.5), and the bryophyte cover increase was higher inside the exclosures than in control plots (Table 2.5). Moreover, the bare soil cover change in severely trampled plots depended on the grazing regime in all study sites except for Montroig (p < 0.1 or 0.5 depending on each study site; Table S2.4 of the Supplementary Material). That is, while we detected small changes in bare soil cover outside the exclosures, the bare soil cover decreased sharply in all plots inside the exclosures (Fig. 2.6 b).

In the small plots (10 × 20 cm), we obtained only slight differences on the vegetation dynamics between fenced plots and control plots, and most of them occurred in the plots in the most severe trampling level (*bare soil* plots). There, vascular plant and bryophyte abundances increased more sharply in fenced plots than in control plots (Table S2.5 of the Supplementary Material).
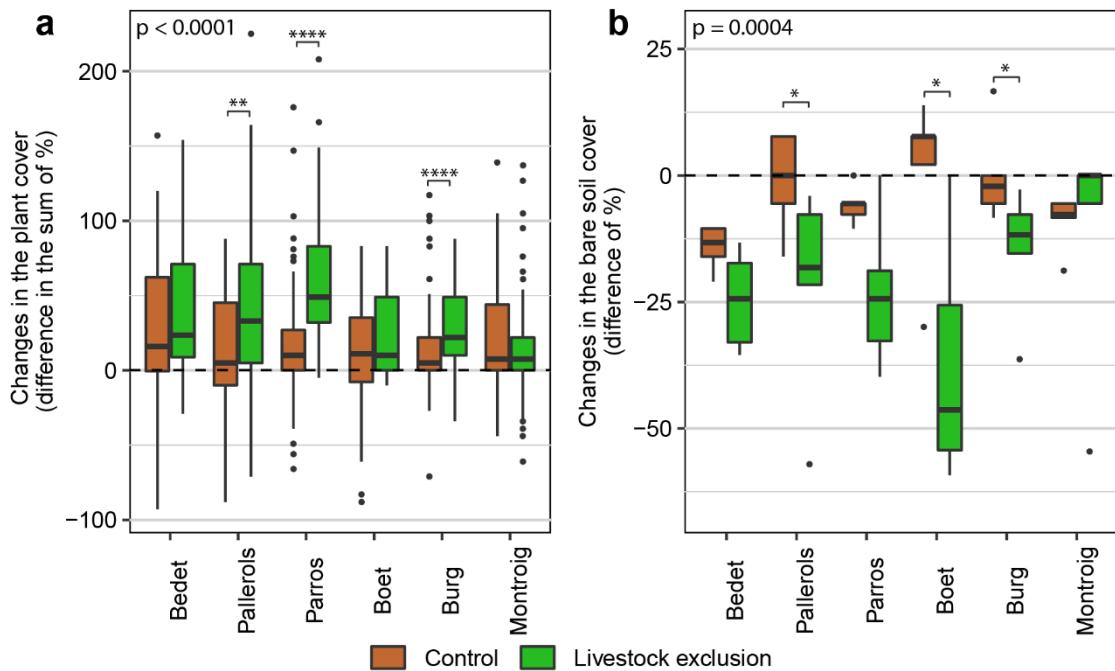
Fig. 2.6. Sum of plant species covers in subplots of 10 × 10 cm size (a) and percentage of bare soil in plots of 50 × 50 cm size (b) Changes observed between 2018 and 2019 under severe trampling according to livestock regime and study site. Positive values indicate an increase and negative values indicate a decrease. We indicate the p-value accounting for all study sites together; p-values and differences for each study site are showed in Table 2.5 for the plant cover, and in Table S2.4 of the Supplementary Material for the bare soil cover.

Finally, the beta diversity of vascular plants between 2018 and 2019 in moderately trampled plots was similarly low inside and outside the exclosures. However, severely trampled plots showed higher beta diversity figures under livestock exclusion than in control conditions (Fig. 2.7; Table S2.4 of the Supplementary Material), and Shannon index increased similarly regardless of the grazing regime.

Discussion

Gap colonization after livestock disturbance

Cattle trampling in fens impacts plant communities by creating gaps (hoof prints and pugged soil areas), which gives way to various response mechanisms by vegetation (M. B. Collantes et al., 2013; Graf et al., 2022; Milligan et al., 2016). Through sampling in detail the first stages of plant succession, we clearly observed gap colonization processes, both in areas under cattle grazing and in excluded areas. Short-term vegetation dynamics on bare soil drove to a rapid bare soil decrease as found by other authors (Merriam et al., 2018). Unexpectedly, we found no differences in the colonization of small gaps (hoof prints up to 20 cm length) in relation to the grazing regime. Similar results are given by

Kohler et al. (2006) in Alpine grasslands, were trampling, manuring and mowing simulations only act as secondary filters in the gap colonization process. According to this and to our results, livestock grazing cessation would not make a difference to small gaps colonization but would only prevent small gaps creation.

As for the bryophytes, they are not directly affected by grazing as they are not a food source for cattle, but are directly affected by trampling and by nutrient increase from manuring (Spitale, 2021). In our study bryophytes needed two growing seasons of complete livestock exclusion to start colonizing severely trampled areas, where they achieved a dominance comparable to that of moderately trampled plots. These results support previous works that bring to light the vulnerability of mosses to trampling (Sjögren et al., 2007). Also, point that their response to land use changes may be slower than that of vascular plants. At the same time, our results highlight the importance of mosses onto vegetation recolonization in disturbed fens, as stated in other studies (Arnesen, 1999; Graf et al., 2022).

Sexual and clonal reproduction in gap colonization

Gaps created by livestock act as microsites that promote seedling germination (Isselstein et al., 2002) and recruitment (Eskelinen & Virtanen, 2005). Seedling establishment has been reported to depend on the gap size (Okada et al., 2012) and on the soil moisture and the type of plant community in fens (Mayer & Erschbamer, 2011). In fact, trampling effects on germination go in opposite directions. On the one hand, trampling can cause severe negative effects on seedling survival in fens (Stammel et al., 2006). On the other hand, germination is hindered by the accumulation of litter (Diemer et al., 2001; Mayer & Erschbamer, 2011), a fact favoured by livestock exclusion, and seedling recruitment is higher where the moss layer is removed (Špačková et al., 1998). In the present study, however, we could not find any effect of livestock exclusion or trampling level on seedlings abundance nor richness over time. However, even if germination is successful, establishment could fail, as previous studies in fens have reported. Stammel & Kiehl (2004) found that more than half of the species that germinate in hoof prints disappear during the first two years. Moreover, Kladivová & Münzbergová (2016) found that grazing in xerothermic grasslands has a positive effect on seedling emergence but has no effect on seedling establishment. In our study, plant establishment from germination could be also hindered by trampling and grazing. However, we did not evaluate the seedling establishment over time.

As for vascular plant dispersal abilities, previous studies found that successful plant gap colonizers in pastures have small seeds, no seed dispersal strategy, and a persistent soil seed bank (Kohler et al., 2006). These traits are mainly shared for the most common species that germinated in our study (like *Juncus articulatus*; Table S2.6 of the Supplementary Material). Besides, species abundances at each site determine their seed
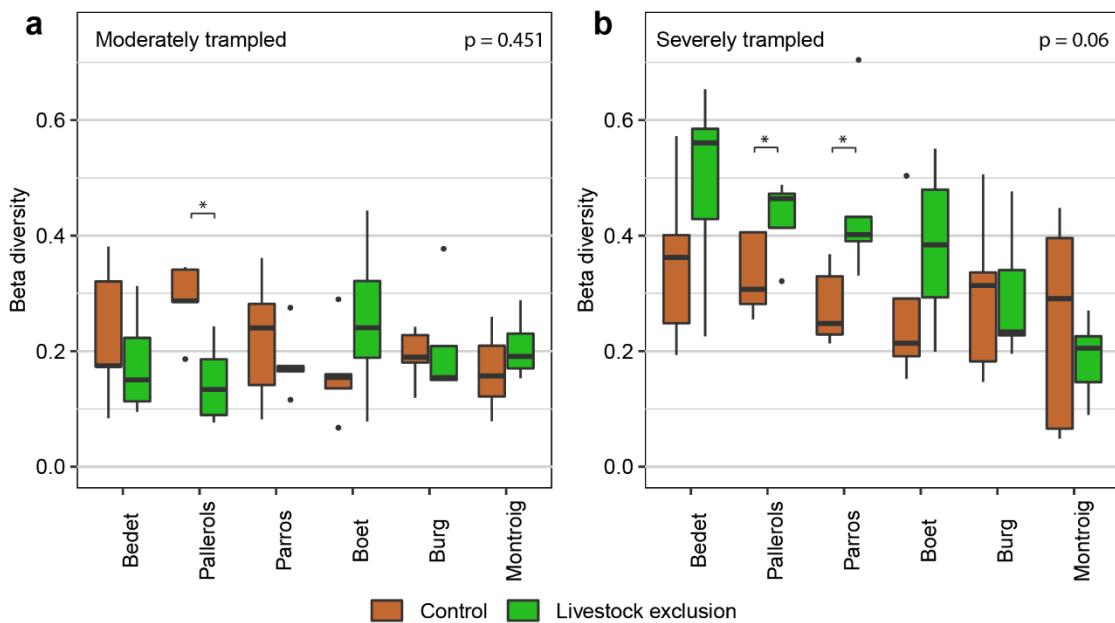
Fig. 2.7. Plant community change –beta diversity– between 2018 and 2019 for each plot of 50 × 50 cm (computed as Bray Curtis dissimilarity of vascular species percentage covers) according to livestock regime and study site. a) Moderately trampled plots; b) Severely trampled plots. We indicate the p-value accounting for all study sites together; p-values and differences for each study site are showed in Table S2.4 of the Supplementary Material.

rain (Marteinsdóttir, 2014; Urbanska & Fattorini, 2000) and it is correlated to germination (Salonen, 1987). It may be the case of *Carex* seedlings that prevailed over forbs as sedges were more abundant –except for the *Carex* seedlings in Boet, where the local abundance of adult sedges was low. Moreover, *Juncus articulatus* has a long-lived seed bank of very small seeds (0.02 mg; Royal Botanic Gardens Kew, 2022), dominates fen seed banks (Stammel & Kiehl, 2004; and Chapter 1) and is a characteristic species at the first successional stages of wetlands (Smith & Brock, 1998). So, local plant abundances are good predictor for seedling communities (Marteinsdóttir, 2014), although species associated with soil disturbance may be disproportionately represented (Klimkowska et al., 2019).

As for clonal gap colonization, adult plants sharply increased everywhere, which was mainly due to lateral spreading of rhizomes of clonal species, as it takes more than two years to develop an adult fen plant from a seed (so in our study we considered all adult plants to come only from adult plants). Interestingly, vegetative spreading was of major importance both in small gaps and in severely trampled areas through all study sites. We expected the clonal growth to be more important in colonizing the gaps at their edge (limiting with extant clonal plants) than on their centre (on bare soil), but we did not find significant differences. Nevertheless, the vascular plant cover in pugged areas and hoof prints was still low after two years of monitoring, as found Stammel & Kiehl (2004). Nevertheless, it is likely a matter of scale because the role of clonal growth in gap

colonization is expected to be less important as the surface of pugged soil increases (Lembrechts et al., 2015).

Some studies point that vegetation gaps favour opportunistic species, since there is less competition and their environmental conditions differ from those in the surrounding close vegetation (Lembrechts et al., 2015; Vandvik, 2004). However, in the present study we did not find opportunistic species to have a relevant role. The main colonizing species were also among the most common in the study sites (see Table S2.7 of the Supplementary Material): *Carex nigra*, *Juncus* (*J. articulatus* or *J. alpinoarticulatus* according to the fen) and *Agrostis* (*A. capillaris*, *A. canina* or *A. stolonifera* according to the fen) among others. *Agrostis capillaris* has been identified as a good gap colonizer in grasslands, tolerant to grazing and trampling (Kohler et al., 2006), while *Agrostis stolonifera* has the ability to increase the rhizome length under grazing cessation in order to enhance the spatial propagation and to escape from aerial competition (Amiaud et al., 2008). In fact, only few species became more frequent in severely trampled plots in the exclosures than in the surrounding non grazed vegetation and also than in grazed plots. Thus, gaps had some impact on vegetation dynamics and on relative abundance composition of species in the community, but did not significantly favour vascular plant species richness in the studied fens (as also found in Stammel & Kiehl, 2004).

Vegetation dynamics in grazed and ungrazed areas

Fen vegetation changed notably in only one year, particularly in severely trampled plots. Thus, livestock exclusion accelerated plant succession, that promoted a sharp decrease on the bare soil cover after only two years of complete grazing exclusion (Fig. 2.8). These results are in line with other studies on Alpine bogs, where bare peat can be almost recolonised within a decade (Graf et al., 2022). However, we found no significant vegetation changes in plots affected by moderate trampling. Thus, short-term wetland monitoring programs would find vegetation changes only after the cessation of severe disturbances. This might be the case of previous works, which found differences in only one year (Collantes et al., 2013; Merriam et al., 2018). However, sometimes more time is needed to assess plant community trajectories after a change in the grazing regime (Bullock et al., 2001). Moreover, inter-annual variation in climate and plant phenology can blur directional plant cover changes (Rudolf, 2019), and slight errors in quadrat placement may similarly inflate beta diversity inside and outside exclosures. Also, high mountain plant communities tend to respond slowly to land use changes (Peintinger & Bergamini, 2006), and so the vegetation recovers slowly after fen restoration as registered before in boreal peatlands (Arnesen, 1999; Haapalehto et al., 2011). Overall, this study highlights that the best way to assess the early stages of succession is by studying the patterns at detailed scales, as seen thanks to the results obtained in the small plots (10 × 10 cm and 10 × 20 cm).
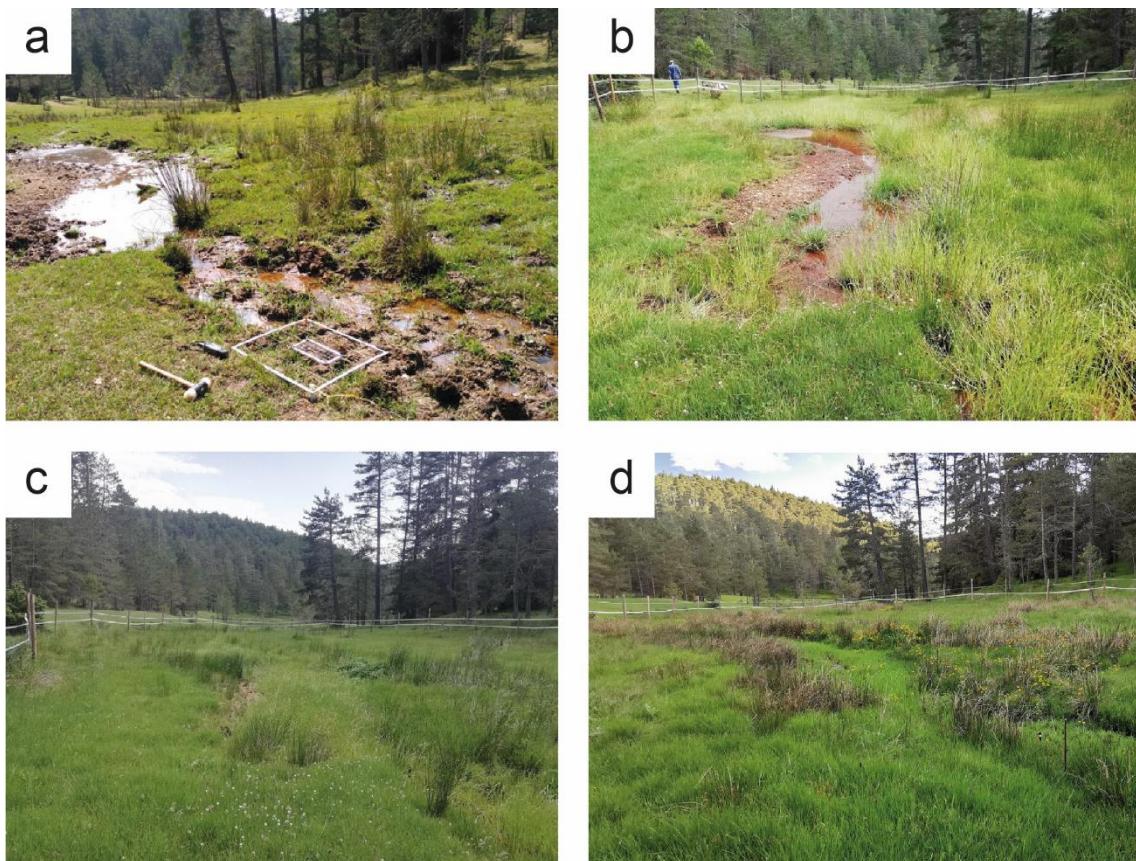
Fig 2.8. Pallerols study site over time. a) September 2017 (with a plot of 50 × 50 cm and of 10 × 20 cm in the foreground); b) July 2018, already fenced; c) July 2019; d) June 2021. Photos by Eulàlia Pladevall-Izard and Marc Garriga Lujan.

Besides, at short-term we also found important ecosystem processes like vascular plant growth and height, and measured a sharp increase of litter accumulation inside the exclosures in all the study sites (Fig. S2.3 of the Supplementary Material). These changes were not uniform, as study sites at higher elevations showed shorter plant height and fewer litter accumulation. Diemer et al. (2001) observed that litter mass depend on community productivity instead of on the time since the cessation of grazing or mowing, so litter accumulation would depend strongly on site fertility and temperature. Litter tends to cover low prostrate forbs, bryophytes and seedlings, thus directly affecting the community composition (Diemer et al., 2001; Mayer & Erschbamer, 2011; Peintinger & Bergamini, 2006). Probably related to litter accumulation, we found that moderately trampled plots outside the exclosures were more prone to have higher moss cover than plots under livestock exclusion. According to some studies and our preliminary results, we expect the reduction of the bryophyte layer in ungrazed plots within the following years (Bergamini et al., 2001; Diemer et al., 2001).

As for interactions between plants, grazing and trampling reduce the importance of competitive species chiefly through the increase of light incidence to the vegetation lowest strata (Fossati & Pautou, 1989; Schrautzer et al., 2013). Also, in ungrazed areas, we expect a clonal organ recovery in vascular plants (Ottaviani et al., 2021). If livestock

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exclusion is maintained over time, diversity may decrease as a result of competition for light (Watts et al., 2019) and a resulting competitive exclusion by vigorous species (Schultz et al., 2011). In this sense, Golodets et al. (2010) detected an increasing similarity between vegetation from different recently fenced sites. In fact, we did not identify such trends after two years, and we only expect to find clear competitive exclusion at mid-term in the highest productive sites (Rydin & Jeglum, 2013), where we already recorded an increase in generalist tall herbs (*Filipendula ulmaria* and *Cirsium palustre*) or in tussocky sedges (*Carex paniculata*).

Implications for conservation

Most Alpine mires are disturbed by trampling in the Southern Alps (Spitale, 2021), in the Central Pyrenees (Pérez-Haase et al., 2019) and in other Iberian peatlands as blanked bogs in the Cantabrian Mountains (Chico et al., 2019). Livestock exclusion in fens drives significant vegetation recovery at short-term, and provides floral resources for pollinators and allows annual seed dispersal (Filazzola et al., 2020). Our study demonstrates that livestock exclusion accelerates vascular plant and bryophyte colonization of pugged areas, and that the majority of the colonizer plants in gaps are fen specialists. Although we observed plant succession processes in the first year of cattle exclusion, full recovery of vegetation in trampled fens may take several decades (Arnesen, 1999). Nevertheless, it has to be considered that a permanent removal of livestock may be unfavourable for the proper conservation of fen vegetation. Several studies (Merriam et al., 2018; Middleton et al., 2006) point that the competition for light would prevent non-competitive species to persist in high-productive zones (Kotowski et al., 2006) and some woody species may become eventually invasive (van Diggelen et al., 2006).

Overall, low-intensity grazing would be highly recommended to keep litter accumulation at low levels in productive grazed fens, and also to prevent pugging (Middleton et al., 2006). In order to prevent soil pugging and even hoof print gaps, a transition from cattle to sheep would be advisable since sheep are lighter and generally avoid water-dependent vegetation (Reeves & Champion, 2004).

Concerning highly disturbed fens, short-term permanent exclosures –or grazing cessation for few growing seasons– would be highly recommended as a passive restoration action to improve their conservation status. Finally, this study stresses the potentiality of livestock management in preserving fen vegetation, and the importance of protecting pristine fens in Alpine mountains from cattle trampling. We strongly recommend monitoring Alpine fens under livestock exclusion for longer periods to better predict plant succession in the face of land use changes.

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Supplementary Material from Chapter 2
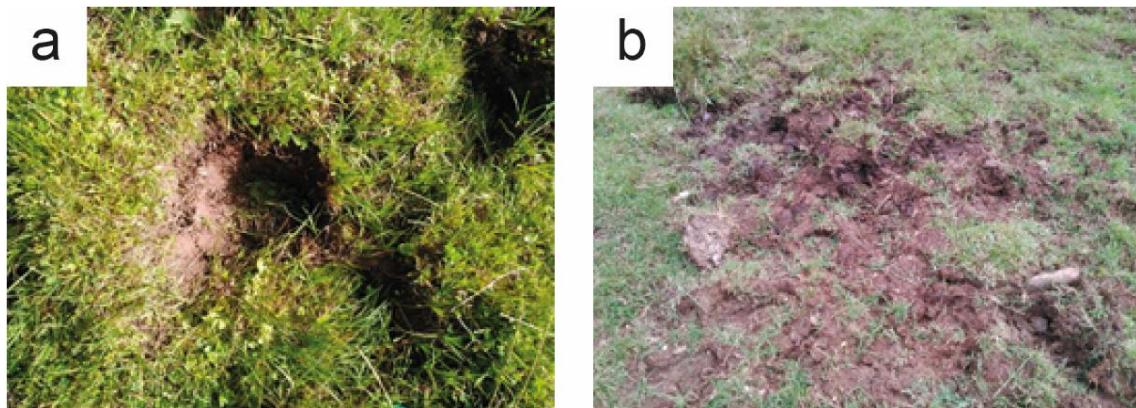
Fig S2.1. Field images of the two trampling levels studied. a) Moderately trampled (small gaps corresponding to hoof prints); b) Severely trampled (puuged). Photos by Eulàlia Pladevall-Izard.
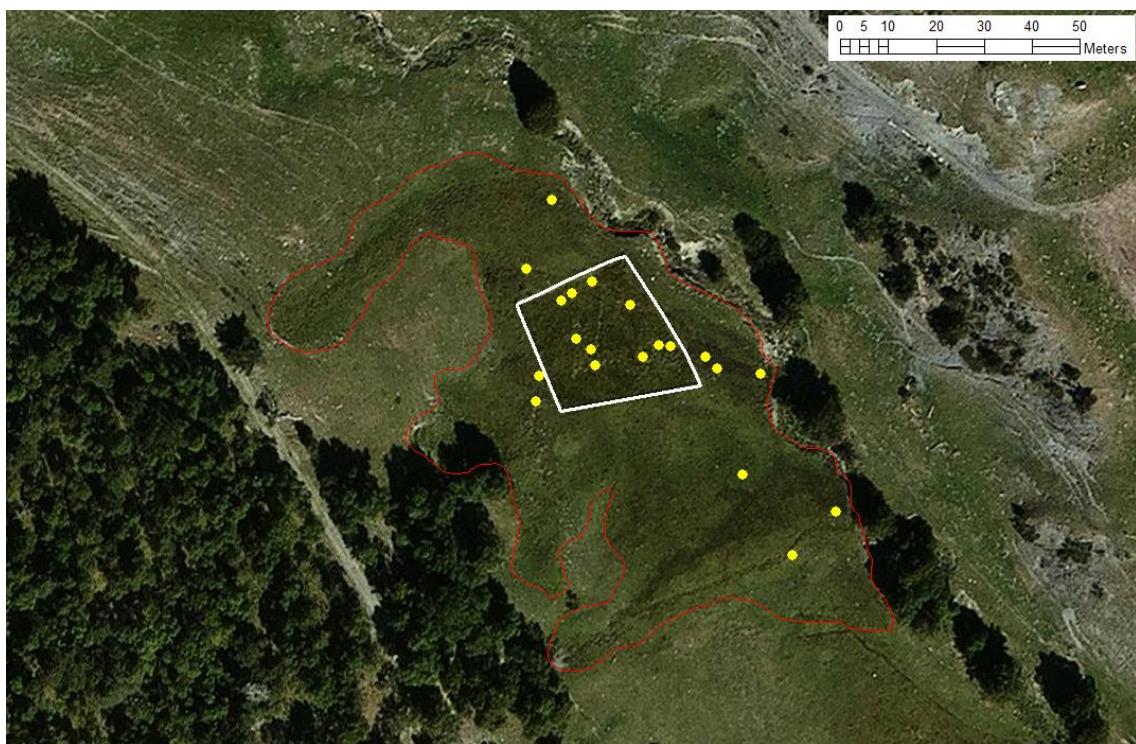
Fig S2.2. Orthoimage of the Bedet study site. The exclosure is outlined in white and permanent plots are marked as yellow points. We delimited the fen area with a thin red line.

Table S2.1. Summary of the results in plots of 50 × 50 cm for each study site. Friedman tests of plots under livestock exclusion along three growing seasons. All tests have two degrees of freedom. Multiple comparisons are represented as letters (different letters refer to different groups).

Response variable	Bedet						Pallerols						Parros					
	Chi^2	p	Kendall W	2017	2018	2019	Chi^2	p	Kendall W	2017	2018	2019	Chi^2	p	Kendall W	2017	2018	2019
Moderate trampling																		
Shannon index	0.667	0.717	0.111	a	a	a	7.6	**0.022**	0.760	a	b	b	8	**0.018**	1	a	b	c
% of subsamples with vascular plants*	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	2	0.368	0.250	a	a	a
% of subsamples with bryophytes*	0	1	0	a	a	a	NA	NA	NA	NA	NA	NA	2	0.368	0.250	a	a	a
Bare soil cover (%)	4.667	0.097	0.778	a	a	b	8.444	**0.015**	0.844	a	a	b	3.5	0.174	0.438	a	a	a
Severe trampling																		
Shannon index	10	**0.007**	1	a	b	c	4.8	0.090	0.480	a	a	b	6	**0.049**	0.750	a	b	b
% of subsamples with vascular plants	7.248	**0.024**	0.743	a	b	b	2	0.368	0.200	a	a	a	3	0.223	0.375	a	a	a
% of subsamples with bryophytes	8.4	**0.015**	0.840	a	a	b	4.933	0.085	0.493	ab	a	b	6.5	**0.039**	0.812	a	b	a
Bare soil cover (%)	8.316	**0.016**	0.832	a	a	b	10	**0.007**	1	a	b	c	5.6	0.061	0.700	a	a	b

Response variable	Boet						Montroig					
	Chi^2	p	Kendall W	2017	2018	2019	Chi^2	p	Kendall W	2017	2018	2019
Moderate trampling												
Shannon index	4.5	0.105	0.562	a	ab	b	7.6	**0.022**	0.76	a	b	b
% of subsamples with vascular plants*	2	0.368	0.250	a	a	a	NA	NA	NA	NA	NA	NA
% of subsamples with bryophytes	0.286	0.867	0.036	a	a	a	2	0.368	0.20	a	a	a
Bare soil cover (%)	3.5	0.174	0.438	a	a	a	7.6	**0.022**	0.76	a	a	b
Severe trampling												
Shannon index	0.5	0.778	0.063	a	a	a	8.4	**0.015**	0.84	a	a	b
% of subsamples with vascular plants	6.615	**0.036**	0.827	a	b	b	3.5	0.174	0.35	a	a	a
% of subsamples with bryophytes	5.6	0.061	0.700	a	a	b	7.6	**0.022**	0.76	a	a	b
Bare soil cover (%)	4.667	0.097	0.583	a	ab	b	3	0.223	0.30	a	a	a

* NA when all the plots had the same value on the variable.

Table S2.2. Summary of the results in subplots of 10 × 10 cm for each study site. Friedman tests of plots under livestock exclusion along three growing seasons. All tests have two degrees of freedom. Multiple comparisons are represented as letters (different letters refer to different groups).

Response variable	Bedet						Pallerols						Parros					
	Chi^2	p	Kendall W	2017	2018	2019	Chi^2	p	Kendall W	2017	2018	2019	Chi^2	p	Kendall W	2017	2018	2019
Moderate trampling																		
Vascular plant species richness	23.63	**<0.0001**	0.328	a	a	b	23.9	**<0.0001**	0.199	a	b	c	52.81	**<0.0001**	0.550	a	b	c
Vascular plant cover	21.57	**<0.0001**	0.300	a	a	b	34.17	**<0.0001**	0.285	a	b	b	56.34	**<0.0001**	0.587	a	b	c
Seedling cover	15.14	**<0.001**	0.210	a	b	c	13.0	**0.001**	0.109	a	b	b	7.381	**0.025**	0.077	a	b	ab
Bryophyte cover	0.958	0.619	0.013	a	a	a	5.793	0.055	0.048	a	ab	b	19.62	**<0.0001**	0.204	a	b	b
Severe trampling																		
Vascular plant species richness	93.91	**<0.0001**	0.783	a	b	c	87.75	**<0.0001**	0.731	a	b	c	69.51	**<0.0001**	0.724	a	b	c
Vascular plant cover	93.0	**<0.0001**	0.775	a	b	c	91.6	**<0.0001**	0.763	a	b	c	73.31	**<0.0001**	0.764	a	b	c
Seedling cover	75.28	**<0.0001**	0.627	a	b	c	64.72	**<0.0001**	0.539	a	b	b	1.633	0.442	0.017	a	a	a
Bryophyte cover	60.78	**<0.0001**	0.506	a	a	b	34.32	**<0.0001**	0.286	a	a	b	23.23	**<0.0001**	0.242	a	a	b

Response variable	Boet						Montroig					
	Chi^2	p	Kendall W	2017	2018	2019	Chi^2	p	Kendall W	2017	2018	2019
Moderate trampling												
Vascular plant species richness	35.44	**<0.0001**	0.369	a	b	b	75.35	**<0.0001**	0.628	a	b	c
Vascular plant cover	33.15	**<0.0001**	0.345	a	b	b	7.919	**<0.0001**	0.666	a	b	c
Seedling cover	6.018	**0.049**	0.063	a	b	ab	4.282	0.118	0.036	a	a	a
Bryophyte cover	3.976	0.137	0.041	a	a	a	21.45	**<0.0001**	0.179	a	a	b
Severe trampling												
Vascular plant species richness	27.11	**<0.0001**	0.282	a	b	c	80.89	**<0.0001**	0.674	a	b	c
Vascular plant cover	59.86	**<0.0001**	0.624	a	b	c	78.71	**<0.0001**	0.656	a	b	c
Seedling cover	47.25	**<0.0001**	0.492	a	b	c	19.43	**<0.0001**	0.162	a	a	b
Bryophyte cover	25.43	**<0.0001**	0.265	a	a	b	39.9	**<0.0001**	0.332	a	a	b

Table S2.3. Summary of the results in plots of 10 × 20 cm for each study site. Friedman tests of plots under livestock exclusion along three growing seasons. All tests have two degrees of freedom. Multiple comparisons are represented as letters (different letters refer to different groups).

Response variable	Bedet Chi^2	p	Kendall W	2017	2018	2019	Pallerols Chi^2	p	Kendall W	2017	2018	2019	Parros Chi^2	p	Kendall W	2017	2018	2019
Small gap																		
Vascular plant species richness	4.666	0.097	0.778	a	a	b	9	**0.011**	0.900	a	b	c	6.5	**0.039**	0.812	a	a	b
Vascular plant abundance	4.666	0.097	0.778	a	a	b	2.8	0.247	0.280	a	a	a	8	**0.018**	1	a	b	c
Seedlings abundance	2.667	0.264	0.444	a	a	a	1.5	0.472	0.150	a	a	a	0.933	0.627	0.117	a	a	a
Bryophyte abundance	6	**0.049**	1	a	b	c	7.6	**0.022**	0.760	a	a	b	6.533	**0.038**	0.817	a	a	b
% of subplots with vascular plants	4.666	0.097	0.778	a	a	b	7.444	**0.024**	0.744	a	a	b	7.6	**0.022**	0.95	a	b	c
% of subplots with seedlings	2.667	0.264	0.444	a	a	a	1.733	0.420	0.173	a	a	a	1.5	0.472	0.188	a	a	a
% of subplots with bryophytes	6	**0.049**	1	a	b	c	7.6	**0.022**	0.760	a	a	b	7.429	**0.024**	0.929	a	b	c
% of subplots with plants or bryophytes	4.667	0.097	0.778	a	a	b	4.8	0.091	0.480	a	a	b	4.5	0.105	0.562	ab	a	b
Bare soil edge																		
Vascular plant species richness	7.444	**0.024**	0.744	a	b	b	7.6	**0.022**	0.760	a	a	b	5.692	0.058	0.712	a	a	b
Vascular plant abundance	3.895	0.143	0.389	a	a	a	7.6	**0.022**	0.760	a	b	b	6.5	**0.038**	0.812	a	a	b
Seedlings abundance	7.6	**0.022**	0.760	a	a	b	6.632	**0.036**	0.663	a	b	b	0	1	0	a	a	a
Bryophyte abundance	10	**0.007**	1	a	b	c	2.842	0.241	0.284	a	a	a	6.533	**0.038**	0.817	a	a	b
% of subplots with vascular plants	3.895	0.143	0.389	a	a	a	8.444	**0.015**	0.844	a	b	b	7.6	**0.022**	0.950	a	b	c
% of subplots with seedlings	8.316	**0.016**	0.832	a	a	b	6.632	**0.036**	0.663	a	b	b	0.5	0.779	0.063	a	a	a
% of subplots with bryophytes	10	**0.007**	1	a	b	c	3.263	0.196	0.326	a	a	a	6.533	**0.038**	0.817	a	a	b
% of subplots with plants or bryophytes	9.579	**0.008**	0.958	a	b	c	9.5	**0.009**	0.950	a	b	b	3.333	0.189	0.417	a	a	a
Bare soil																		
Plant richness	9	**0.011**	0.900	a	b	c	3.176	0.204	0.318	a	a	a	7.6	**0.022**	0.950	a	b	c
Vascular plant abundance	9.579	**0.008**	0.958	a	b	c	7.6	**0.022**	0.760	a	a	b	8	**0.018**	1	a	b	c
Seedlings abundance	6.4	**0.041**	0.640	a	ab	b	3.111	0.211	0.311	a	a	a	2	0.368	0.250	a	a	a
Bryophyte abundance	7.538	**0.023**	0.754	a	a	b	6.632	**0.036**	0.663	a	b	b	2.714	0.257	0.339	a	a	a
% of subplots with vascular plants	9.579	**0.008**	0.958	a	b	c	2.8	0.247	0.280	a	a	a	8	**0.018**	1	a	b	c
% of subplots with seedlings	8.4	**0.015**	0.840	a	ab	b	4	0.135	0.400	a	b	ab	2	0.368	0.25	a	a	a
% of subplots with bryophytes	7.538	**0.023**	0.754	a	a	b	8.588	**0.014**	0.859	a	b	c	2.714	0.257	0.339	a	a	a
% of subplots with plants or bryophytes	9.579	**0.008**	0.958	a	b	c	3.263	0.196	0.326	a	a	a	3.5	0.174	0.438	a	a	a

Response variable	Chi²	p	Kendall W	2017	2018	2019	Chi²	p	Kendall W	2017	2018	2019
		Boet						**Montroig**				
Small gap												
Vascular plant species richness	2.286	0.319	0.286	a	a	a	9.579	**0.008**	0.958	a	b	c
Vascular plant abundance	8	**0.018**	1	a	b	c	10	**0.007**	1	a	b	c
Seedlings abundance	5.733	0.057	0.717	a	b	ab	0.615	0.735	0.062	a	a	a
Bryophyte abundance	6.5	**0.039**	0.812	a	a	b	8.4	**0.015**	0.840	a	b	b
% of subplots with vascular plants	8	**0.018**	1	a	b	c	10	**0.007**	1	a	b	c
% of subplots with seedlings	5.733	0.057	0.717	a	b	ab	0.133	0.936	0.013	a	a	a
% of subplots with bryophytes	6	**0.049**	0.775	a	a	b	9.579	**0.008**	0.958	a	b	c
% of subplots with plants or bryophytes	5.571	0.062	0.696	a	a	b	5.444	0.066	0.544	a	a	b
Bare soil edge												
Vascular plant species richness	4.769	0.092	0.596	ab	a	b	1.714	0.424	0.171	a	a	a
Vascular plant abundance	3.5	0.174	0.438	a	a	a	6.4	**0.041**	0.64	a	ab	b
Seedlings abundance	5.571	0.062	0.696	a	b	a	0.4	0.819	0.040	a	a	a
Bryophyte abundance	1.5	0.472	0.188	a	a	a	7.684	**0.021**	0.768	a	a	b
% of subplots with vascular plants	5.2	0.074	0.650	a	ab	b	5.444	0.066	0.544	a	a	b
% of subplots with seedlings	5.571	0.062	0.696	a	b	a	1.2	0.549	0.120	a	a	a
% of subplots with bryophytes	2.533	0.282	0.317	a	a	a	7.684	**0.021**	0.768	a	a	b
% of subplots with plants or bryophytes	6	**0.049**	0.750	a	a	b	8.4	**0.015**	0.840	a	a	b
Bare soil												
Vascular plant species richness	3.714	0.156	0.464	a	a	a	6.632	**0.036**	0.663	a	b	b
Vascular plant abundance	5.636	0.059	0.705	a	ab	b	7.684	**0.021**	0.768	a	b	b
Seedlings abundance	3.5	0.174	0.438	a	a	a	4.105	0.128	0.411	a	a	a
Bryophyte abundance	6.533	**0.038**	0.817	a	a	b	3.5	0.174	0.350	a	a	a
% of subplots with vascular plants	5.636	0.059	0.705	a	ab	b	7.684	**0.021**	0.768	a	b	b
% of subplots with seedlings	3.5	0.174	0.438	a	a	a	3.111	0.211	0.311	a	a	a
% of subplots with bryophytes	6.533	**0.038**	0.817	a	a	b	3.5	0.174	0.350	a	a	a
% of subplots with plants or bryophytes	6.533	**0.038**	0.817	a	a	b	8.4	**0.015**	0.840	a	b	b

Table S2.3. (cont.)

Table S2.4. Summary of the results in plots of 50 × 50 cm. Kruskal Wallis tests comparing the trampling levels. Response variables are: the changes on the Shannon index between 2018 and 2019, beta diversity of plots over time (Bray Curtis dissimilarity), the change in the percentage of subplots hosting vascular plants and hosting bryophytes, and the change in the bare soil cover. All tests have one degree of freedom.

	All sites		Bedet		Pallerols		Parros		Boet		Burg		Montroig	
Change on the	Chi^2	p	Chi^2	p	Chi^2	p	Chi^2	p	Chi^2	p	Chi^2	p	Chi^2	p
Moderate trampling														
Shannon index	0.42	0.515	0.10	0.754	0.01	0.917	0.10	0.754	0.27	0.602	1.32	0.251	0,27	0,602
Beta diversity (of vascular plants)	0.57	0.451	0.53	0.465	5.77	**0.016** *	0.27	0.602	1.84	0.175	0.10	0.754	0,88	0,347
% of subplots with vascular plants*	1.00	0.317	NA	NA	NA	NA	NA	NA	1.00	0.317	NA	NA	NA	NA
% of subplots with bryophytes	1.53	0.217	0.41	0.521	0.41	0.521	0.15	0.700	2.79	0.095 .	1.95	0.163	1,80	0,180
Bare soil cover (%)	2.19	0.139	0.01	0.917	0.10	0.753	0.54	0.463	2.46	0.117	0.10	0.754	0,89	0,346
Severe trampling														
Shannon index	0.66	0.416	0.54	0.465	0.27	0.602	0.88	0.347	0.01	0.917	2.46	0.117	2,46	0,117
Beta diversity (of vascular plants)	3.53	0.060 .	1.84	0.175	4.81	**0.028** *	5.77	**0.016** *	1.84	0.175	0.10	0.754	0,27	0,602
% of subplots with vascular plants	0.88	0.348	0.80	0.371	0.42	0.519	0.41	0.520	1.44	0.230	4.06	**0.044** *	0,43	0,513
% of subplots with bryophytes	9.64	**0.002** **	6.99	**0.008** *	2.21	0.138	2.18	0.140	0.00	1.000	0.29	0.588	3.25	0,071 .
Bare soil cover (%)	12.33	**0.0004** ***	3.58	0.058 .	3.96	**0.046** *	2.83	0.093 .	4.84	**0.027** *	3.94	**0.047** *	1.62	0.203

* NA when all the plots had a null change over time, thus all values were zero.

Table S2.5. Summary of the results in plots of 10 ×20 cm. Kruskal Wallis tests of the change on variables between 2018 and 2019 in relation to the grazing regime. All tests have one degree of freedom.

	All sites		Bedet		Pallerols		Parros		Boet		Burg		Montroig	
Increase on the	Chi²	p	Chi²	p	Chi²	p	Chi²	p	Chi²	p	Chi²	p	Chi²	p
Small gap														
Vascular plant species richness	0.52	0.471	0.72	0.396	0.12	0.735	0.01	0.915	1.01	0.314	1.61	0.205	1.44	0.230
Vascular plant abundance	0.66	0.416	0.28	0.597	1.84	0.175	0.01	0.917	0.55	0.459	1.10	0.293	1.10	0.295
Seedlings abundance	0.83	0.362	1.11	0.292	0.18	0.675	0.10	0.735	3.60	0.058 .	0.89	0.346	0.55	0.458
Bryophyte abundance	3.29	0.070 .	1.33	0.249	0.10	0.754	4.84	**0.028** *	1.86	0.173	0.18	0.675	0.01	0.917
% of subplots with vascular plants	0.71	0.398	0.01	0.916	2.15	0.143	0.40	0.527	0.71	0.401	2.63	0.112	0.88	0.347
% of subplots with seedlings	1.31	0.253	0.41	0.522	0.28	0.596	0.54	0.462	3.60	0.058 .	0.18	0.671	0.29	0.590
% of subplots with bryophytes	1.70	0.192	1.34	0.248	0.11	0.747	6.99	**0.010** **	0.04	0.834	0.28	0.598	0.10	0.753
% of subplots with plants or bryophytes	0.03	0.853	0.10	0.753	0.90	0.343	2.58	0.108	0.28	0.600	0.05	0.830	0.18	0.673
Bare soil edge														
Vascular plant species richness	2.91	0.088 .	0.19	0.664	2.65	0.104	0.90	0.344	0.32	0.572	0.01	0.906	0.19	0.661
Vascular plant abundance	1.18	0.277	1.32	0.251	2.46	0.117	0.54	0.463	1.86	0.173	0.04	0.833	0.40	0.527
Seedlings abundance	0.62	0.432	6.86	**0.009** **	4.90	**0.030** *	2.47	0.116	2.52	0.113	0.04	0.834	0.90	0.344
Bryophyte abundance	1.22	0.270	1.10	0.293	0.28	0.599	0.05	0.829	0.54	0.463	0.54	0.465	1.58	0.209
% of subplots with vascular plants	0.51	0.477	1.35	0.245	1.59	0.207	0.00	1	2.16	0.141	0.01	0.916	0.71	0.401
% of subplots with seedlings	0.19	0.667	6.82	**0.009** **	4.04	**0.049** *	3.17	0.075 .	2.53	0.112	0.28	0.597	0.91	0.340
% of subplots with bryophytes	1.53	0.216	1.58	0.209	0.28	0.600	0.40	0.528	0.18	0.671	0.54	0.462	1.34	0.247
% of subplots with plants or bryophytes	1.03	0.310	0.89	0.346	2.63	0.105	1.34	0.247	1.32	0.251	0.10	0.753	1.34	0.248
Bare soil														
Vascular plant species richness	4.77	**0.030** *	0.18	0.671	0.05	0.823	7.31	**0.010** **	0.29	0.591	1.38	0.240	0.10	0.747
Vascular plant abundance	6.87	**0.010** **	0.88	0.347	0.28	0.598	6.82	**0.010** **	0.00	1	2.21	0.138	0.10	0.753
Seedlings abundance	0.26	0.609	3.15	0.076 .	1.13	0.287	1.32	0.251	1.87	0.172	0.18	0.675	0.18	0.674
Bryophyte abundance	4.49	**0.030** *	1.67	0.196	0.01	0.916	3.56	0.059 .	0.54	0.465	0.28	0.597	0.90	0.344
% of subplots with vascular plants	3.13	0.077 .	0.18	0.675	0.70	0.402	6.86	**0.010** **	0.56	0.456	1.62	0.203	0.54	0.462
% of subplots with seedlings	0.63	0.428	3.31	0.069 .	0.55	0.458	0.27	0.600	1.87	0.172	0.18	0.675	0.10	0.753
% of subplots with bryophytes	5.19	**0.020** *	1.98	0.160	0.11	0.746	3.99	**0.050** *	0.54	0.465	0.28	0.596	0.70	0.402
% of subplots with plants or bryophytes	0.02	0.900	0.18	0.675	2.47	0.116	1.58	0.209	0.27	0.602	0.54	0.462	0.10	0.752

Table S2.6. List of the most frequent taxa recorded as seedlings in plots of 10 × 20 cm recorded in 2019. We show the total number of subplots where plants were found, at each site (seven records or more) and for all sites together (twenty records or more).

Bedet	Pallerols	Parros	Boet	Burg	Montroig	All sites
Dicotyledons; 102	Poaceae; 36	*Carex* sp.; 77	Poaceae; 45	*Carex* sp.; 42	*Juncus articulatus*; 74	*Juncus articulatus*; 201
Succisa pratensis; 47	*Juncus articulatus*; 31	*Juncus articulatus*; 63	Dicotyledons; 22	Poaceae; 36	*Glyceria fluitans*; 36	*Carex* sp.; 200
Potentilla erecta; 34	*Carex* sp.; 20	Poaceae; 42	*Saxifraga stellaris*; 20	Dicotyledons; 27	*Carex* sp.; 34	Poaceae; 200
Carex sp.; 26	*Potentilla erecta*; 12	*Potentilla erecta*; 40	*Scorzoneroides duboisii*; 12	*Cardamine pratensis*; 17	Poaceae; 15	Dicotyledons; 199
Poaceae; 26	*Viola palustris*; 12	Dicotyledons; 35	*Ochlopoa supina*; 11	Monocotyledons; 13	*Potentilla erecta*; 13	*Potentilla erecta*; 108
Juncus articulatus; 25	*Cardamine pratensis*; 10	*Valeriana dioica*; 21	*Viola palustris*; 9	*Selinum pyrenaeum*; 11	*Scorzoneroides duboisii*; 8	*Glyceria fluitans*; 52
Lotus corniculatus; 25	*Glyceria fluitans*; 10	Monocotyledons; 13		*Juncus articulatus*; 8	*Juncus alpinoarticulatus*; 7	Monocotyledons; 50
Cardamine pratensis; 19	Dicotyledons; 7	*Parnassia palustris*; 12		*Potentilla erecta*; 8		*Succisa pratensis*; 50
Cerastium fontanum; 14		*Cerastium fontanum*; 11		*Caltha palustris*; 7		*Cardamine pratensis*; 46
Monocotyledons; 12		*Cirsium palustre*; 10		*Ranunculus* sp.; 7		*Scorzoneroides duboisii*; 32
Pedicularis sylvatica; 10						*Lotus corniculatus*; 26
Ranunculus sp.; 9						*Cerastium fontanum*; 25
Scorzoneroides duboisii; 8						*Viola palustris*; 24

Table S2.7. List of the most frequent species of vascular plants recorded as adults in severely trampled plots (50 × 50 cm) and inside exclosures; recorded in 2019. We show the total number of subplots where plants were found, at each study site (ten records or more) and for all sites together (forty records or more).

Bedet	Pallerols	Parros	Boet	Burg	Montroig	All sites
Juncus articulatus, 33	*Agrostis canina*, 52	*Juncus articulatus*, 55	*Agrostis capillaris*, 51	*Carex nigra*, 41	*Carex nigra*, 45	*Carex nigra*, 203
Ranunculus repens, 30	*Glyceria fluitans*, 49	*Carex flava*, 42	*Saxifraga stellaris*, 21	*Agrostis stolonifera*, 30	*Juncus alpinoarticulatus*, 39	*Juncus articulatus*, 131
Agrostis stolonifera, 28	*Carex nigra*, 47	*Carex nigra*, 42	*Ochlopoa supina*, 17	*Carex davalliana*, 29	*Carex echinata*, 18	*Glyceria fluitans*, 78
Carex nigra, 27	*Juncus articulatus*, 41	*Trifolium repens*, 18		*Juncus alpinoarticulatus*, 22	*Juncus filiformis*, 13	*Agrostis stolonifera*, 70
Carex davalliana, 20	*Trifolium repens*, 25	*Carex echinata*, 14		*Briza media*, 15	*Cerastium cerastoides*, 12	*Carex flava*, 65
Potentilla erecta, 19	*Stellaria alsine*, 20	*Glyceria fluitans*, 14		*Carex flava*, 14	*Glyceria fluitans*, 12	*Carex davalliana*, 62
Lotus corniculatus, 18	*Montia fontana*, 19	*Veronica beccabunga*, 14		*Potentilla erecta*, 10		*Juncus alpinoarticulatus*, 61
Carex panicea, 14	*Carex curta*, 18	*Carex davalliana*, 13				*Agrostis capillaris*, 59
Juncus effusus, 14	*Carex echinata*, 16					*Agrostis canina*, 52
Carex disticha, 12	*Juncus effusus*, 15					*Trifolium repens*, 50
Carex paniculata, 12	*Sagina procumbens*, 14					*Carex echinata*, 48
Festuca rubra, 10	*Veronica beccabunga*, 10					*Ranunculus repens*, 44
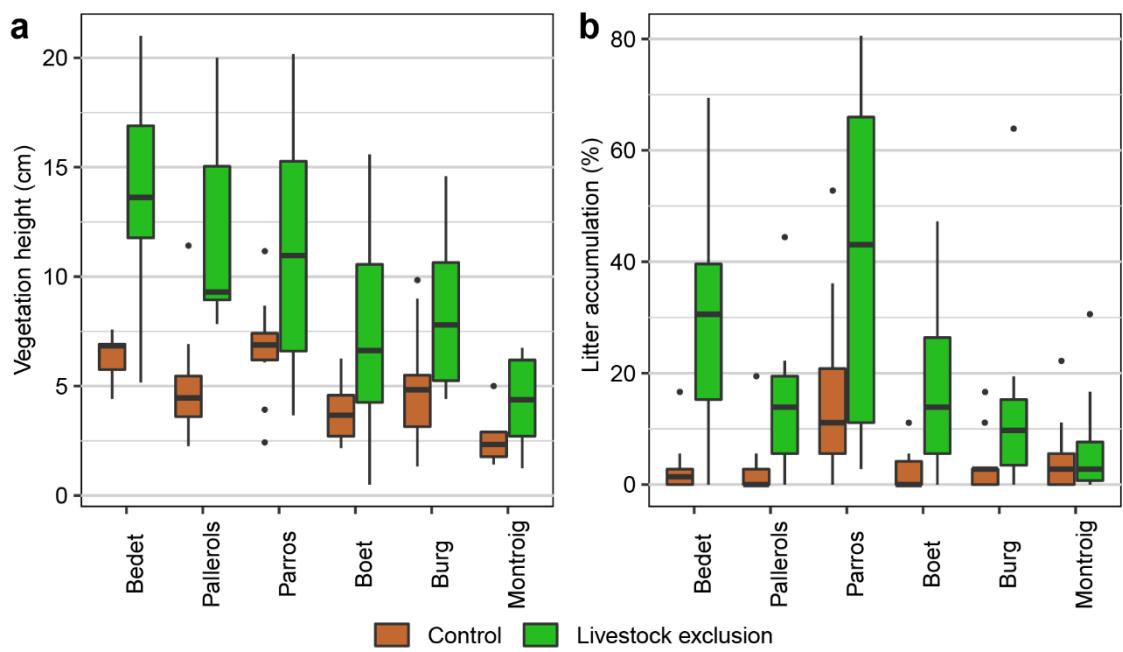
Fig S2.3. Herbaceous plant heigh (a) and litter accumulation (b) in plots of 50 × 50 cm size according to livestock regime and study site; July 2019.

Capítol 3

Trescuro. Fotografia de Pep Ninot.

Climate and landscape predictors of pine encroachment of high-mountain mires

Embosquinament per l'establiment de pins en molleres d'alta muntanya. Predictors climàtics i de paisatge

Abstract

The abandonment of agricultural and livestock activities in European mountainous landscapes has contributed to an increase in forested areas during the last decades. Pine encroachment in mires leads to environmental changes that bring with changes in species distribution and diversity at landscape level through habitat homogenisation. This can turn into a conservation threat if mires are small and scattered as in the Pyrenees. In this study we tackle the natural pine encroachment of the bog pine (*Pinus uncinata*) in Pyrenean mires during the last half century, and we address which ecological and land-use factors facilitate –or prevent– this trends in Alpine mires. We assessed the presence and density of pines in 228 mires through GIS photointerpretation of orthoimages from 1956 and 2011. We then modelled pine occurrence and pine densification in relation to elevation, mediterraneity and continentality indexes, the cover of pine forest around each mire, and the distance to the nearest path and building. Results underscore that pine colonization occurred in 16% of the mires, and that 27% of the mires were forested in 2011. Pine densification was positively correlated with the cover of pine forest around mires, while the likelihood of containing pines was slightly lower on mires located near livestock corrals or cottages. Importantly, pine density and densification trends decreased along the elevation and mediterraneity gradients. This study emphasises that landscape and land-use variables allow predicting the likelihood of pine encroachment in mires in the near future, and postulates pine encroachment as a key factor when planning conservation actions in Alpine mires.

Introduction

During the last decades, European rural landscapes in mountainous areas are experiencing progressive pine encroachment (Gerard et al., 2010; Wieser, 2020) due to the decrease in agricultural and livestock activities (MacDonald et al., 2000) and due to temperature rise within climate change (Ameztegui et al., 2016; Camarero & Gutiérrez, 2004). Indeed, in southern European mountains, traditional economic activities have progressively become economically not viable and their abandonment has contributed to the current noticeable increase in forested areas (Ameztegui et al., 2016; Chauchard et al., 2007; García-Ruiz et al., 2020; Taillefumier & Piégay, 2003). Although spontaneous tree colonization and densification affect mainly grasslands, it can occur in a variety of open habitats such as mires and peatlands worldwide (Gunnarsson & Rydin, 1998).

At least 20-25% of global peatland area is forested and potentially exploitable for forestry activities. Although environmental filters such as soil anoxia and oligotrophy constrain tree development in mires (Rydin & Jeglum, 2013), land use and climatic changes may favour the establishment of trees in not forested mires. Indeed, grazing cessation has been related to facilitation of tree establishment in mires (Bart, 2021), and repeated summer dry spells -such as those predicted by climate change scenarios (Meehl & Tebaldi, 2004)- could foster the establishment of woody plants (Breeuwer et al., 2009). Tree encroachment has been largely documented in boreal and Atlantic wetlands in relation to declines in the water table depth (Berg et al., 2009; Breeuwer et al., 2009; Ratcliffe et al., 2017), mainly as a consequence of man-induced drainage (Littlewood et al., 2010), but also due to climate change (Kapfer et al., 2011). In Alpine mires, shrub, bush and tree encroachment has been documented in research and conservation projects (Binnert, 2012; Langanke et al., 2007; Waser et al., 2008). However, little is known about tree encroachment in mires influenced by the Mediterranean climate, where higher evapotranspiration and less precipitation during summer could facilitate tree recruitment (Colomer et al., 2019).

Pine encroachment triggers significant environmental shifts in mires. First, trees reduce the wind influence and incidental solar radiation on the mire surface. Second, trees contribute to soil drying by intercepting precipitation and fostering water drainage (Limpens et al., 2014). Third, pine encroachment together with water table drawdown provides a supplementary amount of litter, which induces higher soil organic matter accumulation (Straková et al., 2012). At the same time, it implies not only changes in local environmental conditions, but triggers vegetation succession and habitat changes, and therefore shifts in local biodiversity (Eckstein et al., 2011; Frankl & Schmeidl, 2000; Ohlson

et al., 2001). Indeed, pine encroachment may be one of the major threats to the ombrotrophic mire conservation in Europe (Raeymaekers, 2000).

In European Alpine mountains, mires cover small areas on flat valleys, around alpine lakes and springs (Payne, 2018), and are surrounded by drier mountain habitats in a patchy landscape (Ninot et al., 2017; Pérez-Haase, 2015). Alpine mires host a large number of specialist bryophytes and vascular plants (Molina, 2017; Pérez-Haase, 2015; Pérez-Haase & Ninot, 2017). Therefore, mountain mires contribute significantly to beta and gamma diversity at landscape scale (Flinn et al., 2008). Some mire systems bear natural communities of woody species, such as sparse and poorly grown conifer stands (e.g. *Picea abies* and *Pinus uncinata*; Reille 1991). At the same time, the mire systems and neighbouring rangeland in the Pyrenees currently bear from moderate to strong grazing pressure, mainly by cattle (Pérez-Haase et al., 2019).

In the Pyrenean subalpine belt, *Pinus uncinata* is the dominant tree, where it forms forests in most ecological conditions: from rocky dry shelves to moist slopes, and even to mires (Ninot et al., 2007). In the last decades, *P. uncinata* populations have largely expanded, including an ascent of the upper treeline (Batllori & Gutiérrez, 2008; Ninot et al., 2017). Land-use changes rather than climate change lead to an expansion of forested areas (Ameztegui et al., 2016; Gracia et al., 2011). Indeed, the drastic decline over the last two centuries of sheep, horses and goats that historically maintained slope grasslands, has led to shrub and pine encroachment on slopes, whereas the huge increase of cattle herd, which graze mainly in valley bottoms, has resulted in overgrazing in valley bottoms (García-Ruiz et al., 2020; Montserrrat, 2009).

Although in the southern Alpine ranges forest expansion mainly affects grasslands, which occupy broad areas throughout the mountain range (Ameztegui et al., 2021), little is known about pine encroachment in Alpine mountain mires. Also, it is unknown what ecological factors may facilitate –or prevent– pine colonisation in mires, and what consequences it entails for biodiversity conservation. This study delves into the establishment and development of pinewoods in mire systems of the central Pyrenees, by means of GIS generated information approaches and trees age estimations. The two main objectives of this work are: i) to quantify the cover density of *Pinus uncinata* and the pine encroachment (densification) in Pyrenean mires during the last half century (1956-2011); and ii) to elucidate what ecological and land-use factors play a role in the presence, density and encroachment of *Pinus uncinata* in the Pyrenean mires.

Given the land use changes, we hypothesise that the recruitment and area of occupancy of pines have grown since 1956. We also expect elevation to be negatively related to the presence and densification of pines mires, as the current treeline is lower than the higher mires in the studied area, whereas Mediterranean climatic influence may deepen the summer water table drawdown and, therefore, facilitate pine establishment in mires. Furthermore, mires in forested landscapes may be more prone to contain pines and undergo densification. Finally, we expect to find a negative relationship between

human activities and pine encroachment in mires, since logging may modify the pace of apparent encroachment.

Material and methods

Study area

We studied the mire systems found in the central Catalan Pyrenees (Fig. 3.1 a), where they mainly occur in the subalpine and low alpine belts –i.e., from about 1500 to 2700 m a.s.l. (Casanovas, 1991; Pérez-Haase, 2015)–, and are strongly constrained by the complex physiography of these high mountains (Ninot et al., 2017). They are related to surface waters, such as alpine lakes, rivulets, and springs, thus they are mostly soligenous, and occupy reduced surfaces. The main environmental gradients in the study area correlates to elevation (chiefly through the shortening of the growing season upwards; (Ninot et al., 2013). Moreover, the Pyrenees are influenced by Atlantic and Mediterranean climates, the former penetrating from northern and western areas and producing milder, wetter summers; and the later more influential in the southern areas in the form of dryer summers, which include irregular drought events (Rivas-Martínez, 2007).

A particular field sampling was carried out in the pinewood of Trescuro, a mire of high natural interest in the central Pyrenees, located at 2045 m a.s.l. in a northeast facing valley of Peguera river (42°33'07.3"N 1°03'23.9"E). This mire system is a complex mire mosaic surrounding two mountain lakes that encompasses a wide array of hydrologic conditions. It is highly biodiverse and gather different CORINE biotopes and HCIs (Colomer et al., 2019), such as small *Shpagnum* hummocks (the southernmost representation of ombrogenous habitats) and a *Pinus uncinata* scattered population, being one of the few good examples of Pyrenean bog woodland. According to past and current orthoimages, pine density has increased over the last 70 years.

Selection of mires

We used a specific mire cartography previously elaborated in a LIFE+ project (LimnoPirineus; Pérez-Haase el al. 2020), where mires were delimited based on the orthoimages of year 2011 with a pixel of 0.25 m (obtained from the Institut Cartogràfic i Geològic de Catalunya; from now on, ICGC, 2014). For this current study, we excluded mires smaller than 2500 m^2 to ensure reliable estimates of pine densification obtaining a dataset of 683 mires (Fig. 3.1). Finally, in order to reduce the total number of mires to analyse, we performed a random resampling to obtain a subset of 228 mires spread all along the main gradients. Those selected mires were found from 1500 to 2580 m a.s.l., where together they cover a noticeable area (Fig. 3.1 b and c).
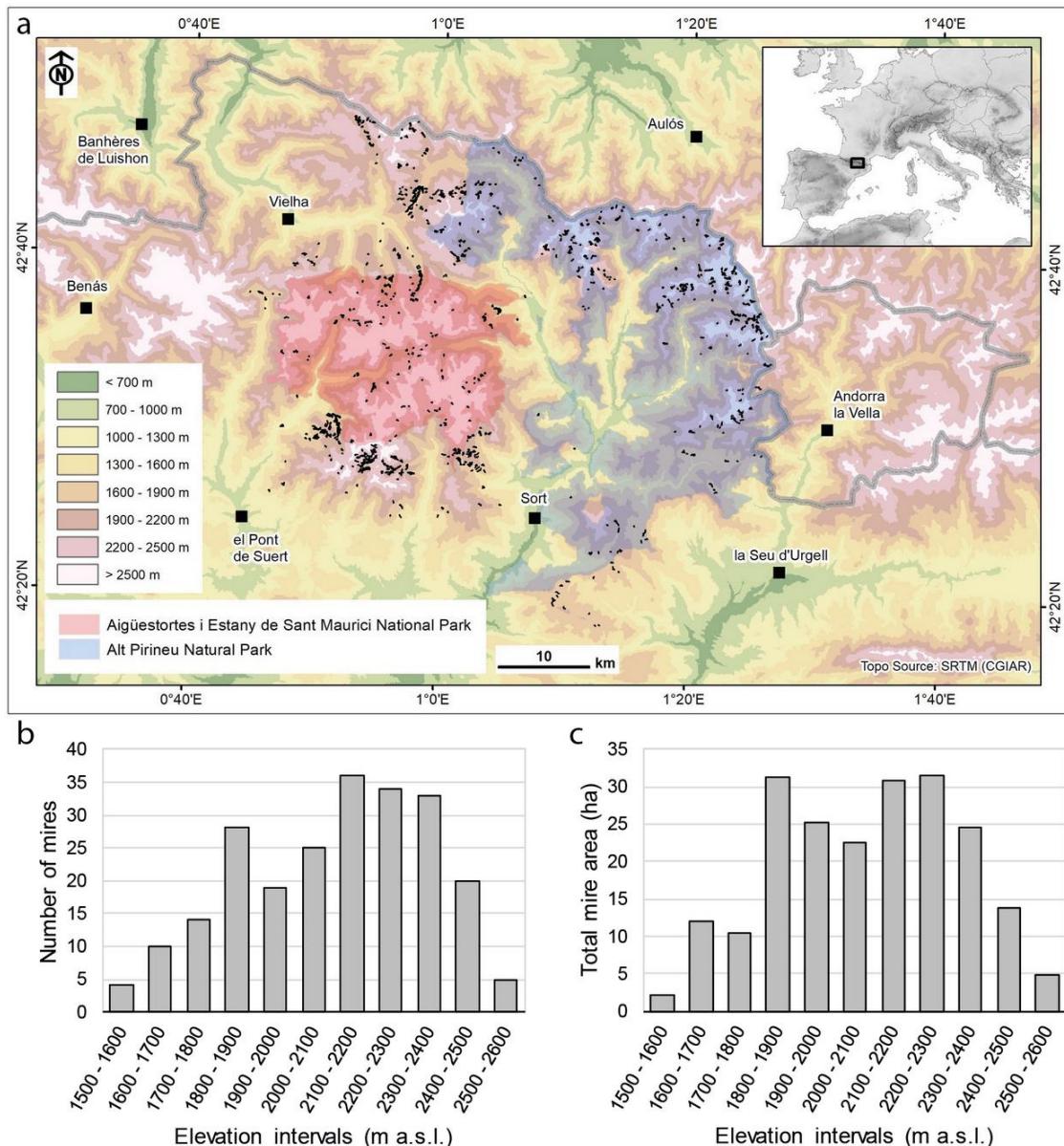
Fig. 3.1. a) Location of 683 mire systems larger than 2500 m2 mapped in the study area (black spots); b) Distribution of the 228 mire polygons selected, through 100 m altitude intervals; c) Total area of these mire polygons through 100 m altitude intervals.

Evaluation of pine density and canopy cover change

We used current (2011) and past (1956) orthoimages obtained from the ICGC (2014) to evaluate pine cover and densification in mires. These times were selected for the availability and the quality of the images, and for the relatively long period elapsed between them. The past images are the oldest but still reliable aerial images took by the United States Army Map Service. They are in black-and-white and have a scale of 1:33.000 and a pixel of 1 m. Aerial images from 2011 are near-infrared (NIR) orthoimages that have a scale of 1:1250 and a resolution of 25 cm, and were selected for their quality and the absence of pine canopy shading. Also, NIR images allow distinguishing pines from other deciduous tree species. Moreover, we validated the presence and correct identification of trees in some of the mire locations, where the only tree species seen was

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Pinus uncinata. In both series of orthoimages, only adult pines were considered, with a well-developed and detectable canopy, in order to avoid bias for small ones due to the different quality of the orthoimages.

After, we quantified the density of pines in each mire for both times of study. For that purpose, we projected a regular orthogonal cloud of points onto the mire cartography, with a distance of 5 m between them. To calculate the pine density for each mire polygon, we counted the number of points that intercepted any canopy of an adult pine, and divided them by the polygon total number of points. Then, we computed the pine densification as the density difference between 2011 and 1956.

Predictor variables

To assess the factors that influence the presence, density and densification of pines, we obtained bioclimatic, topographic, ecological and land-use variables for each mire (Table 3.1). We chose the mediterraneity and the thermal continentality indexes as the most influential bioclimatic variables. Mediterraneity index purport the summer water deficit while Continentality index express the annual thermal amplitude. To compute these variables we first obtained monthly temperatures and precipitations for each mire from the digital climatic atlas of Catalonia with 180 m resolution (Ninyerola et al., 2000), and we calculated summer PET using the Thornthwaite method (1948). At the same time, we obtained mire Elevation by combining our mire cartography with a 5 × 5 m digital elevation model (DEM) from the ICGC (2014).

Regarding the ecological variables, we calculated the cover percentage of *P. uncinata* forest surrounding each mire polygon within a buffer of 100 m around each mire (hereinafter, the Rim forest cover). Specifically, we calculated for each buffer the percentage of the area occupied by *P. uncinata* habitats according to the cartography of CORINE habitats of Catalonia (Gencat, 2012). Moreover, we categorized the continuous variable of the Rim forest cover into a binary variable, which simply accounted for the occurrence of pines in the surrounding area (the Rim forest occurrence variable). Finally, in the Mire typology variable we classified all mires into two groups: valley mires (mires on flat areas or on very gentle slopes, where water is stagnant or slowly flowing), and sloping mires (where water runs off).

The land-use variables considered were the assumed impacts of livestock and logging, estimated through the distance from the mire systems to human related-structures. To account for livestock pressure, we calculated the distance in meters between each mire and the closest structure (in use or abandoned) used for livestock management, i.e., cottages, corrals, folds or refuges (the Distance to buildings variable). To account for logging activities, we calculated the distance from mires to paths, considering the closest path as a hauling road related to logging (the Distance to paths variable). This information was extracted from the topographic layer of Catalonia at scale

Table 3.1. Description and preparation of all predictor variables for the data analyses.

Predictor variable	Data origin	GIS layers	Procedure	Data used in analyses
Mediterraneity index	Ninyerola et al. 2000	Temperature and Precipitation (June, July, August)	PET (Potential Evapotranspiration of Thornthwaite) / Precipitation PET_{summer}/P_{summer}	Normalized
Continentality index	Ninyerola et al. 2000	Temperature (January, July)	$\left[\bar{X}\left(max.T_{Jul}\right)\right]-\left[\bar{X}\left(min.T_{Jan}\right)\right]$	Excluded for VIF collinearity
Elevation	ICGC 2014	5 × 5 m Digital Elevation Model	-	Normalized
Rim forest cover	Gencat 2012	CORINE habitats version 2	% of forest in a 100 m buffer	Normalized
Rim forest occurrence	Gencat 2012	CORINE habitats version 2	Presence of forest in a 100 m buffer	Presence / Absence
Mire typology	ICGC 2014	Near-infrared (pixel = 0.25m)	Interpretation of orthoimages and topological maps	Sloping mire / Valley mire
Distance to buildings	ICGC 2014	Topographic 1:5000	Interpretation of orthoimages and toponymy	Normalized
Distance to paths	ICGC 2014	Topographic 1:5000	Interpretation of orthoimages and toponymy	Normalized

1:5000 obtained from the ICGC (2014). Cartographic data were processed using ArcMap10.6 (ArcGIS, intellectual property of ESRI Spatial Analyst, ESRI 2011).

Statistical analyses

We modelled the effect of the predictor variables for three response variables related to pine encroachment in mires: i) the current presence of pines in mires; ii) the current density of pines; and iii) the densification during the last half century (55 years).

The sample size for modelling the presence of pine consisted of 228 mires, but since *Pinus uncinata* rarely constitutes forests at elevations higher than 2300 m a.s.l., we also analysed separately the subset of 170 mires below this elevation to exclude a potential effect of the forest elevation limit. In both cases we used generalized linear models (glm) with all the set of predictor variables and a binomial response variable (absence or presence of pines).

To determine the variables that influence pine density, we retained only those mires with presence of pines in 2011, which accounted 54. Among them, we excluded two extremely large mires (more than 48 000 m^2) since they potentially included varying ecological situations and could not be included into a single category. Thus, the final sample size for the pine density analysis included 52 mires. For the analysis of pine densification, we used the same samples but excluding a sole polygon where

densification was slightly negative, most probably due to anthropic deforestation. In both cases, we used a linear regression model (lm), and we transformed the response variable to a logarithmic scale to fulfil the normality and homoscedasticity requirements of the residuals.

In all analyses, we first tested the collinearity between the predictor variables through the variance inflation factor (VIF), and Continentality was in all cases rejected due to collinearity with both Elevation and Mediterraneity. After that, all the continuous variables were normalized. Then, for each analysis we built the most complex model considering four different variations: with and without meaningful interactions between predictor variables, and alternatively with the Rim forest cover or the Rim forest occurrence (numerical or categorical variable respectively). We retained the model with the lowest corrected Akaike Information Criterion (AIC$_c$), which was then subjected to an automatic simplification. After that, we retained all the resulting simplified models with AIC$_c$ differences lower than or equal to 2 (as recomended in Mazerolle, 2006). To better assess the importance of each predictor variable, we accounted for the model uncertainty by performing model averaging of coefficients of the retained models, including zeros as coefficients for predictor variables when not considered in some of the models (Burnham & Anderson, 2002). Finally, we also evaluated the importance of each predictor variable based on the relative weight (w_{ip}), which is the sum of Akaike weights for the models where the variable appears, and ranges from 0 (none of the models) to 1 (all of them). We considered a predictor variable to be significant when the 95% confidence interval (CI) of the model-average estimate did not include zero. A schematic view of the statistical procedure is supplied in Fig S3.1 of the Supplementary Material.

Statistical analyses were carried out with the R software (R Core Team 2020), using *car* (Fox & Weisberg, 2019), *vegan* (Oksanen et al., 2020) and *MuMIn* (Barton, 2020) packages.

Cambial age of trees

In 2016, we carried out a field sampling in Trescuro site with the main objective to delving into the forest dynamics in a model mire. Four plots of 100 m^2 were distributed across the site, at least 60 m separated from each other (Fig. S3.2 of the Supplementary Material). In each plot, we measured the basal diameter, breast height diameter, and total height of 10 pines, which were cored near the base. All 40 selected individuals were alive, measured over 1.30 m, and were representative of the different tree sizes found in each plot. After the extraction of wood cores, we determined the age of each pine counting the rings with a stereomicroscope. For those cores where the chronological centre of the tree was missing, we estimated the age using the method described in Batllori & Gutiérrez (2008).

Results

Most of the mire polygons studied (73% of the 228 samples) did not include any pine in the two times considered. Photointerpretation evidenced that only 11% of the sampled mires hosted at least one pine in 1956, whereas pine colonisation occurred in 16% of mires until 2011. Among the 52 mires with pines in 2011, 30 had been colonised during the considered period, and only 22 already hosted pines in 1956. From these, 18 experienced positive pine densification, 3 maintained the same pine density and 1 experienced deforestation.

Presence of Pinus uncinata

We obtained six different models with an AIC_c index <2, explaining presence of pines. All of them had an R^2 value around 38.50% (Table S3.1 of the Supplementary Material), and included all the predictor variables except the Mire typology and the Distance to paths (Table 3.2). The model-average coefficients revealed that the presence of *Pinus uncinata* in mire systems depended mainly on the occurrence of a Rim forest (a positive relationship). In addition, the model averaging suggested that the Distance to buildings may also play a noticeable role in determining the presence of pines, as mires with buildings at shorter distances had lower probabilities to contain pines (w_{ip} of 0.71 out of 1, Table 3.2 and Fig. 3.2 a). Furthermore, mires with greater Mediterraneity index were more prone to contain pines.

After excluding mires above 2300 m a.s.l., we obtained a subset of nine models with an AIC_c index <2 (R^2 around 37.50%). The resulting model-average showed that only the Rim forest occurrence around mires was significantly correlated with the presence of pines inside (Table 3.2). The Distance to buildings, though not being significant, had a high relative weight (w_{ip} of 0.53, Table 3.2 and Fig. 3.2 b), and other predictor variables showed non-significant confidence intervals.

Density and densification of Pinus uncinata *cover*

We obtained two different models explaining pine density in forested mires with an AIC_c index <2, which had an R^2 around 63% (Table S3.1 of the Supplementary Material). The confidence intervals and model-average coefficients showed that the most important predictor variables determining pine density were the Rim forest cover, the Mediterraneity index and the Elevation (Table 3.2). The more forest cover of *P. uncinata* around mires, the greater pine density within mires (Fig. 3.3 a), whereas Elevation and Mediterraneity index negatively influenced the pine density (Fig. 3.4). Moreover, Mire typology had also a high relative weight, valley mires having lower pine densities than sloping mires (Fig. 3.5 a).

As for the densification (pine canopy cover change), we obtained two different models with an AIC$_c$ index <2, with an R^2 around 58% (Table S3.1 of the Supplementary Material). The model-average coefficients revealed the importance of Rim forest cover, Elevation, Mediterraneity and Mire typology to explain the pine densification in mires (Table 3.2). As in the pine density model, the Rim forest cover had a positive relation to densification (Fig. 3.3 b), whereas Elevation and Mediterraneity index had a negative relation. The negative relation between Mediterraneity index and pine densification is an effect of this factor in mires at low altitudes (i. e. below approximately 2100 m. a.s.l.), where Elevation itself did not show a direct relationship with pine densification (Fig. S3.3 of the Supplementary Material). Nevertheless, no significant interactions were found between the two predictor variables. Finally, valley mires experienced less pine densification than sloping mires (Fig. 3.5 b).

Table 3.2. Model-average summaries, showing for each predictor the estimated value (Estimate), the 95% confidence interval (CI 95%) and the relative weight (wip) within each model-average. Background shading indicates significant variables which its CI 95% did not include zero. Note that Mire typology is represented as the effect of valley mires with regards to sloping mires.

Response variable	Predictor variable	Estimate	CI 95%	w$_{ip}$
Presence of pines	Intercept	-2.54	-3.21 to -1.99	–
	Rim forest occurrence	3.46	2.64 to 4.30	1.00
	Distance to buildings	0.28	0.02 to 0.93	0.71
	Mediterraneity index	0.16	-0.19 to 0.84	0.49
	Elevation	-0.07	-0.70 to 0.39	0.26
Presence of pines below 2300 m a.s.l.	Intercept	-2.27	-3.09 to -1.60	–
	Rim forest occurrence	3.36	2.48 to 4.28	1.00
	Distance to buildings	0.18	-0.11 to 0.84	0.53
	Elevation	0.06	-0.33 to 0.87	0.24
	Distance to paths	0.05	-0.26 to 0.63	0.22
	Mediterraneity index	0.05	-0.18 to 0.95	0.18
	Mire typology	0.01	-0.96 to 0.92	0.07
Pine density	Intercept	1.66	1.42 to 2.01	–
	Rim forest cover	0.91	0.69 to 1.15	1.00
	Mediterraneity index	-0.39	-0.68 to -0.11	1.00
	Elevation	-0.36	-0.64 to -0.05	1.00
	Mire typology	-0.30	-0.87 to 0.01	0.69
Pine densification	Intercept	1.45	1.16 to 1.73	–
	Rim forest cover	0.69	0.48 to 0.92	1.00
	Mire typology	-0.45	-0.87 to -0.02	1.00
	Mediterraneity index	-0.42	-0.73 to -0.10	1.00
	Elevation	-0.40	-0.67 to -0.09	1.00
	Distance to buildings	-0.05	-0.37 to 0.10	0.35

Pine population structure

In the Trescuro mire, the field sampling revealed high pine age diversity in every plot. Overall ages ranged between 30 and 500 years old (Fig. 3.6), with a mean of 115 years. We recorded a continuous establishment of pines since 1816 onwards, with 52.5% of individuals being established during the last century. In general, adult pines had a small breast height diameters considering their age (between 12.3 and 18.9 cm on average depending on the plot, see Table S3.2 of the Supplementary Material). The correlation between cambial age and basal diameter showed an R^2 value of 0.4 (details not shown), indicating highly variable growth rates within small plots. Additionally, pine stands were globally small-sized, as 59% of pines in sampled plots were shorter than 1.30 m, and tallest pines only reached 6 m.

Discussion

Local forest dynamics

The analysis of the orthoimages allowed consistently evaluating and quantifying the density of *Pinus uncinata* in high-mountain Pyrenean mires. Although most of the studied mires remained treeless throughout the studied period, some of them were colonised by few pine individuals or hosted a growing pine cover. The increase of mires hosting pines from 1956 to 2011 (from 22 to 52 mires in our dataset, a 136.6% more) evidences a general trend of *Pinus uncinata* colonisation and densification during the last century. Moreover, as in this study we only considered adult pines, the results imply that recruitment success of pine seedlings increased in the last decades.

The presence, density and densification of *P. uncinata* in mires showed a strong relationship with the occurrence and cover of pine forest around the mire systems (Rim forest). That is, mires surrounded by pine forests are more prone to become forested in the near future. Forest expansion at a regional scale in the Pyrenees show an aggregation
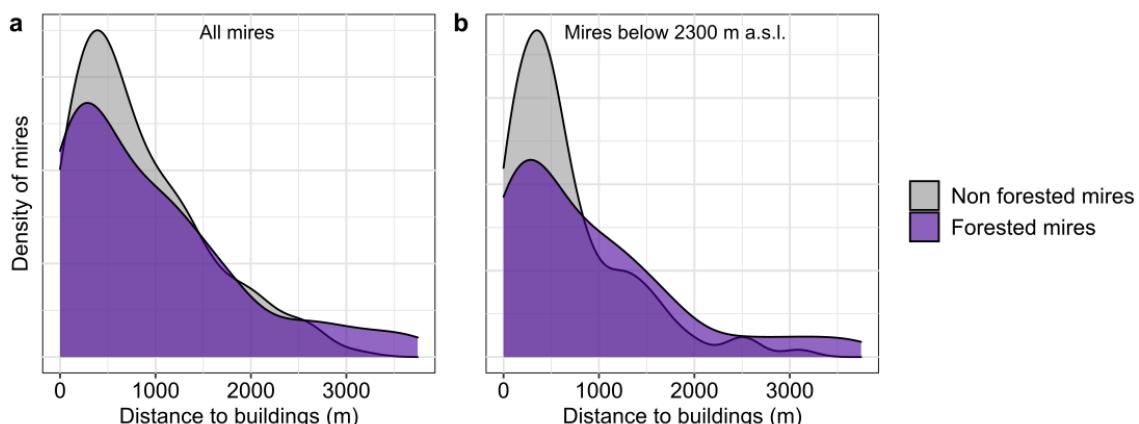
Fig. 3.2. Gaussian smoothed distribution of the Kernel density estimation for the distance to the nearest building from each mire, according to the presence of pines in mires. a) All mires; b) Only mires below 2300 m a.s.l.
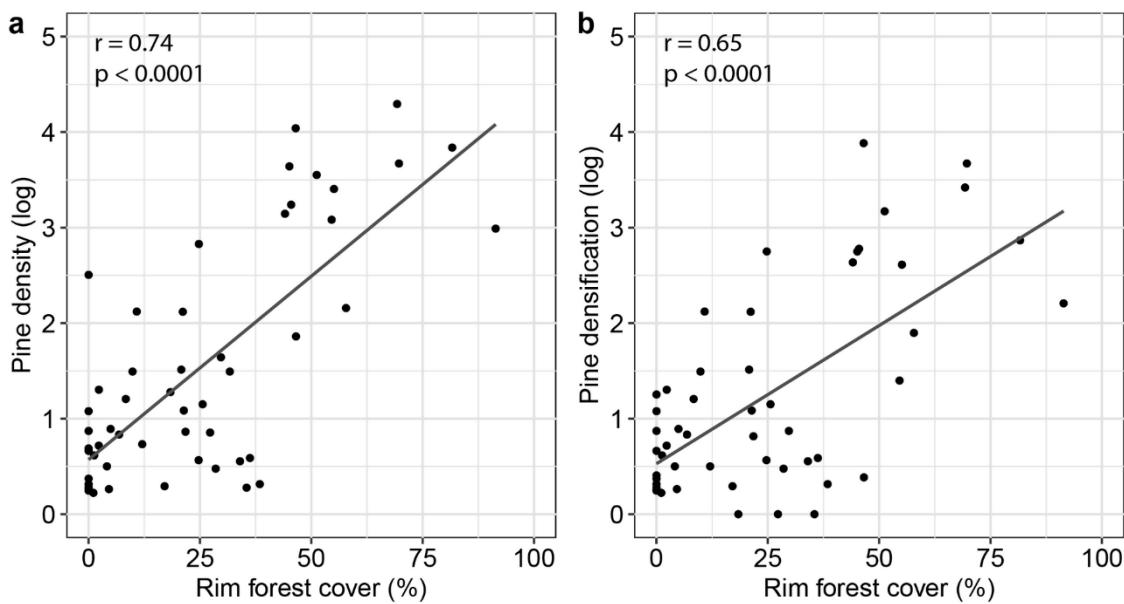
Fig. 3.3. Relation between the Rim forest cover (in %) and the a) Pine density (expressed as the percentage of the points in the grid that intercepted an adult pine canopy; log transformation); b) Pine densification (density change between 1956 and 2011, log transformation).

trend of small forest patches that promotes landscape homogenization (Ameztegui et al., 2021; Carrillo et al., 2009). According to our results, this process affects not only grasslands and pastures, but also mires, regardless of physiological and ecological limitations for pines to thrive in flooded or water-saturated soils. In short, Rim forest is one of the main causal factors of pine densification in mires, especially considering that, although pine seeds are winged, long-distance colonisation hardly occurs (Anadon-Rosell et al., 2020). This causal relationship improves habitat-change predictions and reinforce planning conservation and management actions in order to preserve unique mires of special interest.

The process observed in Pyrenean mires agrees with that documented for other habitats in the region (Puente et al., 2011; Roura-Pascual et al., 2005) and are related to the decrease of logging, grazing and farming activities (Ameztegui et al., 2021; Améztegui et al., 2010). Indeed, the same processes have also been described for the majority of the European mountain ranges (Cudlín et al., 2017). In this study, we observed a higher impact of grazing and farming activities than logging, as the nearer the buildings to the mire, the lower the probability for a mire to be forested. That is, mires below the treeline were more prone to bear pines when they were located farther from buildings (cottages or corrals), which in these high mountain areas have been always related to traditional livestock management. Since the second half of the twentieth century, the abandonment of transhumance of sheep herds, the increase of cattle herds, and the implementation of new technologies in livestock management, led to the abandonment of some of these constructions and to a decline in livestock overall pressure (García-Ruiz & Lasanta-Martínez, 1990; Lasanta-Martínez et al., 2005). These changes, together with a reduction in forestry activities, led to an increase of forested areas over grasslands and
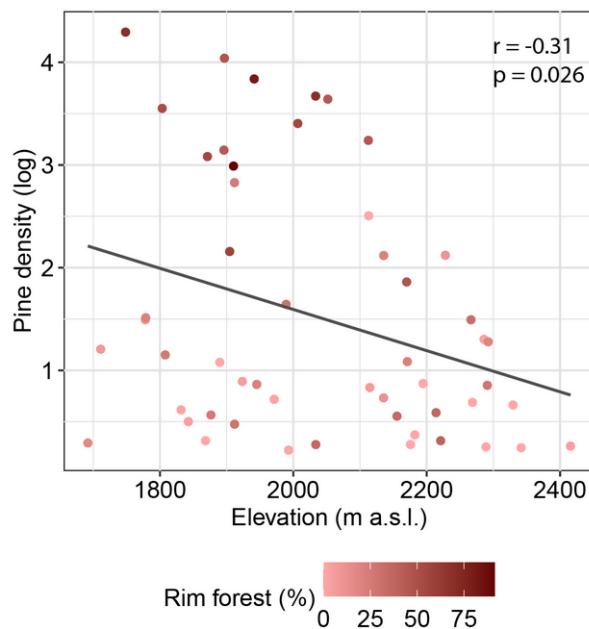
Fig. 3.4. Linear regression between pine density in forested mires (logarithm transformation) and Elevation. We indicate the Rim forest cover (in %) on each mire as red intensity.

shrublands (Gracia et al., 2011), an elevation ascent of the treeline, and a densification of the upper subalpine forest (Améztegui et al., 2010; Batllori & Gutiérrez, 2008). Hence, pinewood expansion patterns observed in mires are a particular case of general forest dynamics on the surrounding landscape.

We observed different pine densification rates depending on Mire typology. In particular, sloping mires experienced higher densification rates than valley mires. We relate this trend to the changes in livestock pressure associated with the substitution of sheep by cattle herds. Indeed, while sheep graze on hillsides and slopes in spring and autumn, cattle graze in more easily accessible pastures or meadows at lower altitudes (García-Ruiz et al., 1996; Lasanta-Martínez et al., 2005). Therefore, pine seedlings in sloping mires may have higher survival rates than those in valley mires, under stronger pressure by current cattle grazing. Besides, mountain sloping mires are dendrite-shaped and usually encompass strong variations in water table depth at short distances or along the margins, which may be undetectable at the photointerpretation scale (snaky surface watercourses, tiny peat depths, rocky outcrops, etc.). Thus, they include microhabitats where pines may easily thrive (Colomer et al., 2019).

Functional basis for forest expansion in mires

According to our results and confirming the hypotheses, high elevation constrained pine density and densification in mires. The effect of Elevation as a predictor variable in the models reflects a set of related abiotic and biotic factors that play a key role in mountain plant biodiversity. High elevation accounts for bioclimatic constraints such as lower temperatures, greater annual snowfall and later snow melting, shorter growing season, greater radiation or greater wind influence (Nagy & Grabherr, 2009). These environmental conditions translate into slower pine growth at higher elevations, along with generalized slower response to land-use changes. Thus, pine encroachment in mires at high-altitude areas is not expected to occur in the near future, although climate change may accelerate this process as documented for alpine grasslands (Batllori & Gutiérrez, 2008).

Some studies have pointed to a decrease in the water table as one of the key ecological factors of pine establishment in bogs (Frankl & Schmeidl, 2000; Gunnarsson et al., 2002; Holmgren et al., 2015), a fact that is expected to occur more frequently as a consequence of summer higher temperatures and drought events linked to climate change. In this sense, we hypothesised that mires with a greater mediterranean influence would be more prone to bear pines and more sensitive to higher densification rates in the short term. However, we did not find any evidence to support this hypothesis, which suggests that the depth of the water table in mires responds more to local geological and topographic characteristics than to the water availability at a catchment scale. Therefore, local hydrological dynamics may be more relevant than bioclimatic gradients, which would act on a broader scale.

In that sense, tree recruitment is higher in drier microhabitats within mires (Gunnarsson & Rydin, 1998). In this study, pine population structure in the Trescuro mire showed highly variable pine growth rates, so the ecological conditions experienced by established pines vary over short distances, even abruptly. Indeed, the pine expansion
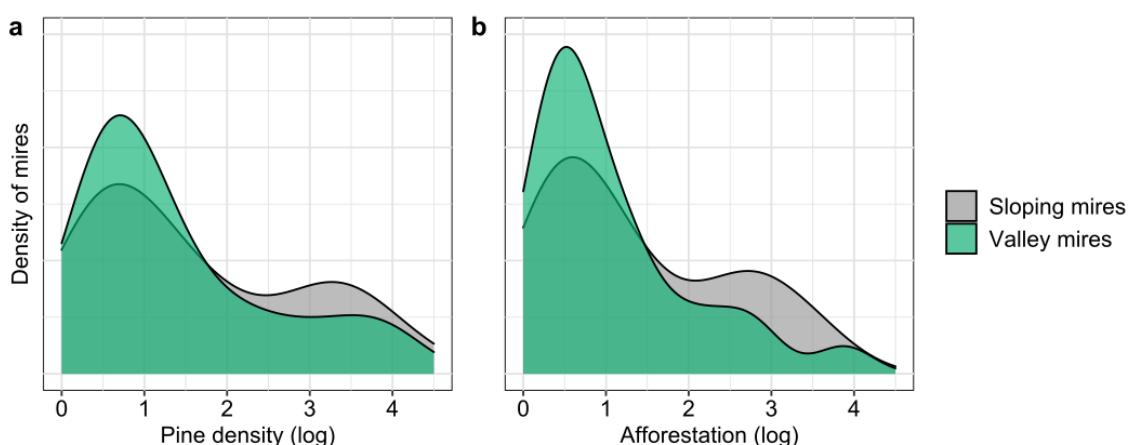
Fig. 3.5. Pine density and densification (canopy cover change) in forested mires according to the Mire typology, expressed as Gaussian smoothed distribution of the Kernel density estimation. a) Pine density (logarithm transformation); b) Pine densification (logarithm transformation).
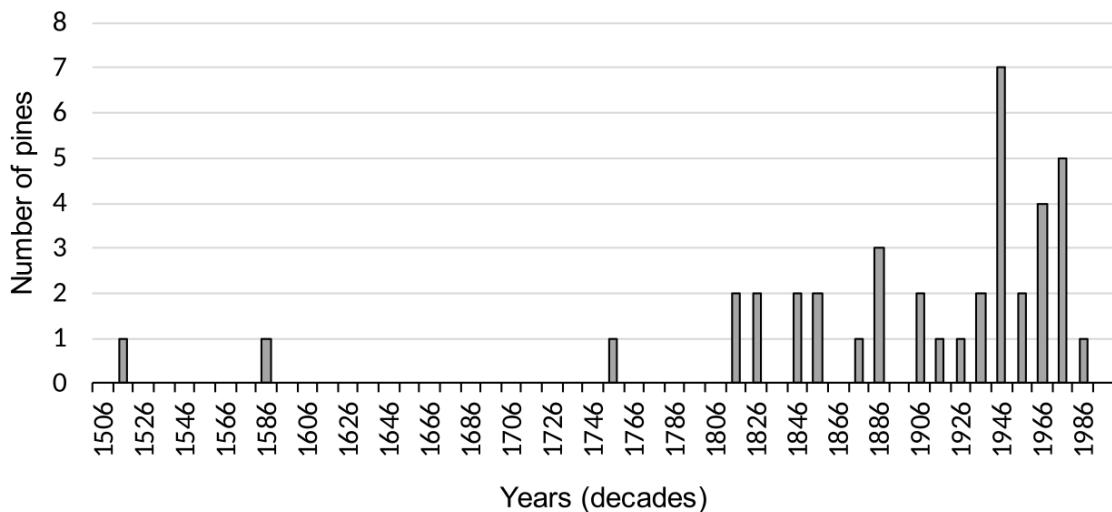
Fig. 3.6 Age structure of the pine population in the Trescuro mire (based on 40 adult individuals taller than 1.30 m).

was heterogeneous throughout the mire. In this sense, Freléchoux et al. (2003) observed that pine encroachment proceeds distinctly along a mire: where the water table level remains high, pine settlement is slow and pines have a long life span, whereas where the water table and soil moisture levels are lower, pines grow faster and have a shorter life span. Furthermore, tree encroachment entails soil drying in mires (Limpens et al., 2014), which may favour the growth of younger neighbouring trees (Gunnarsson & Rydin, 1998) in a positive feedback..

Pine encroachment is seen as a threat for mire conservation in Europe, in particular for blanked bogs, aapa mires and raised bogs (Raeymaekers, 2000). In our case study sampled pine stands were thin (and small) considering age, thus showing lower pine growth rates in mires than in other nearby habitats and under the same climatic conditions (Batllori & Gutiérrez, 2008; Camarero et al., 1998). Therefore, although pine populations have increased in Pyrenean mires during the last century, the field sampling in this study evidences that *Pinus uncinata* habitat preferences are far from mires, and that pine encroachment would proceed at very slow rates and showing heterogeneous spatial patterns. Thus, pine encroachment dynamics is apparently slow and uneven. However, continuous successional processes such as those documented here for the last few decades could turn into noticeable habitat changes in high-mountain mires.

Mid-term to long-term effects on biodiversity

Complex Pyrenean mire systems have co-occurred with pinewoods for the last 10 millennia (Garcés-Pastor et al., 2017; Reille, 1991). Rough topography in these high mountain complexes may promote contrasting hydrological conditions at detailed-scale, thus maintaining changing mosaic patterns across long-term scales in environmental conditions (Pérez-Haase & Ninot, 2017). Noteworthy, the pine encroachment observed

during the past half century in mires is comparatively fast (82% of mires hosting *P. uncinata* stands in 1956 experienced an increase in pine density).

Pine encroachment in treeless mires leads to changes in species richness and diversity through habitat homogenisation towards forested peatlands. Through these dynamics, light-dependent mire species, high water table specialists, and locally threatened heliophile species could lose considerable favourable habitat area (Kapfer et al., 2011; Pinceloup et al., 2020; Woziwoda & Kopeć, 2014).

In the Pyrenees, where many European mire habitats are at their south-western distribution limit (Jiménez-Alfaro et al., 2012), mires occur as small, scarcely connected islands in a patchy landscape. Their pine densification could lead to a decline in some of these habitats, due to the reduction in size of the larger treeless systems, and the vanishing of the smaller ones. According to our results, treeless mire regression is expected to be more pronounced at hillsides (spring fens and other sloping mires) than at valley bottoms (transition mires or bogs). Cartwright and Johnson Cartwright & Johnson (2018) suggest that spring fens –mainly those with large discharge volumes and long groundwater residence– are more resilient to dry spells and climate warming, and are expected to maintain its ecohydrological function in a warmer and drier climate. Thus, they would act as refugia for mire species in a climate change scenario, and pine encroachment would represent an additional threat here. Thus, to preserve these potential refugia, policy makers should consider pine encroachment control as a key factor in planning conservation actions in Pyrenean mires.

This study emphasises that landscape and land-use variables allow predicting the probabilities for mires to bear pine densification in the near future. In that sense, mires surrounded by pine populations in the subalpine belt and far from corrals or cottages are more prone to be colonized by pines, while mires in the alpine belt would be less sensitive to pine recruitment. At the same time, for a suitable management of high-mountain mires it is necessary to delve into the knowledge of their pine encroachment dynamics on a regional scale and through complementary methods, including a precise evaluation of the water balance at plot scale. This would allow a better understanding of the significance of this process in the current context of both land-use and climate changes.

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Supplementary Material from Chapter 3

Table S3.1. Set of models with an AIC_c index <2 for each response variable evaluation. Δ_i indicates the differences of the AIC_c index between models within each set, and w_{ip} indicates the weight of each model. Predictor variables are: rim.forest.pr = Presence of *Pinus uncinata* forest around the mire; rim.forest.cov = Cover of *Pinus uncinata* forest around the mire within a buffer of 100 m; build.dist = Distance between the mire and the nearest building; medit = Mediterraneity index; elev = Elevation; path.dist = Distance between the mire and the nearest path; mire.type = Mire typology (represented as the effect of valleys mire with regards to sloping mires)

Response variable	Model	Predictor variables	AIC_c	Δ_i	w_{ip}	R^2
Pine presence	1	rim.forest.pr + build.dist + medit	169.08	0.00	0.27	39.25
	2	rim.forest.pr	169.86	0.79	0.18	37.40
	3	rim.forest.pr + build.dist	169.92	0.85	0.18	38.15
	4	rim.forest.pr + build.dist + elev	170.27	1.20	0.15	38.80
	5	rim.forest.pr + build.dist + medit + elev	170.85	1.77	0.11	39.37
	6	rim.forest.pr + medit	170.96	1.89	0.11	37.76
Pine presence below 2300 m a.s.l.	1	rim.forest.pr + build.dist	142.15	0.00	0.18	37.67
	2	rim.forest.pr	142.29	0.14	0.17	36.66
	3	rim.forest.pr + path.dist	143.02	0.87	0.12	37.27
	4	rim.forest.pr + build.dist + medit	143.25	1.10	0.11	38.13
	5	rim.forest.pr + elev	143.30	1.14	0.10	37.15
	6	rim.forest.pr + build.dist + path.dist	143.32	1.16	0.10	38.10
	7	rim.forest.pr + build.dist + elev	143.96	1.81	0.07	37.81
	8	rim.forest.pr + build.dist + elev + medit	144.12	1.96	0.07	38.71
	9	rim.forest.pr + mire.type	144.15	1.99	0.07	36.76
Pine density	1	rim.forest.cov + elev + medit + mire.type	128.03	0.00	0.69	64.43
	2	rim.forest.cov + elev + medit	129.64	1.61	0.31	61.46
Pine densification	1	rim.forest.cov + mire.type + elev + medit	121.18	0.00	0.65	57.06
	2	rim.forest.cov + mire.type + elev + medit + build.dist	122.43	1.25	0.35	58.26

Table S3.2 Description of sizes and ages of pine populations sampled in the Trescuro mire. We indicate the total number of pines in each plot (in parenthesis, pines taller and shorter than 1.30 m, respectively), and mean basal diameter, mean breast height diameter and mean age of the ten sampled pines per plot (always higher than 1.30 m).

Plot	Total number of pines	Basal diameter (cm)	Breast height diameter (cm)	Mean age (years)
1	64 (31, 33)	24.6	17.7	100.7
2	119 (17, 102)	22.5	18.1	165.9
3	61 (39, 22)	17.4	12.3	67.8
4	73 (43, 30)	22.0	18.9	125.8
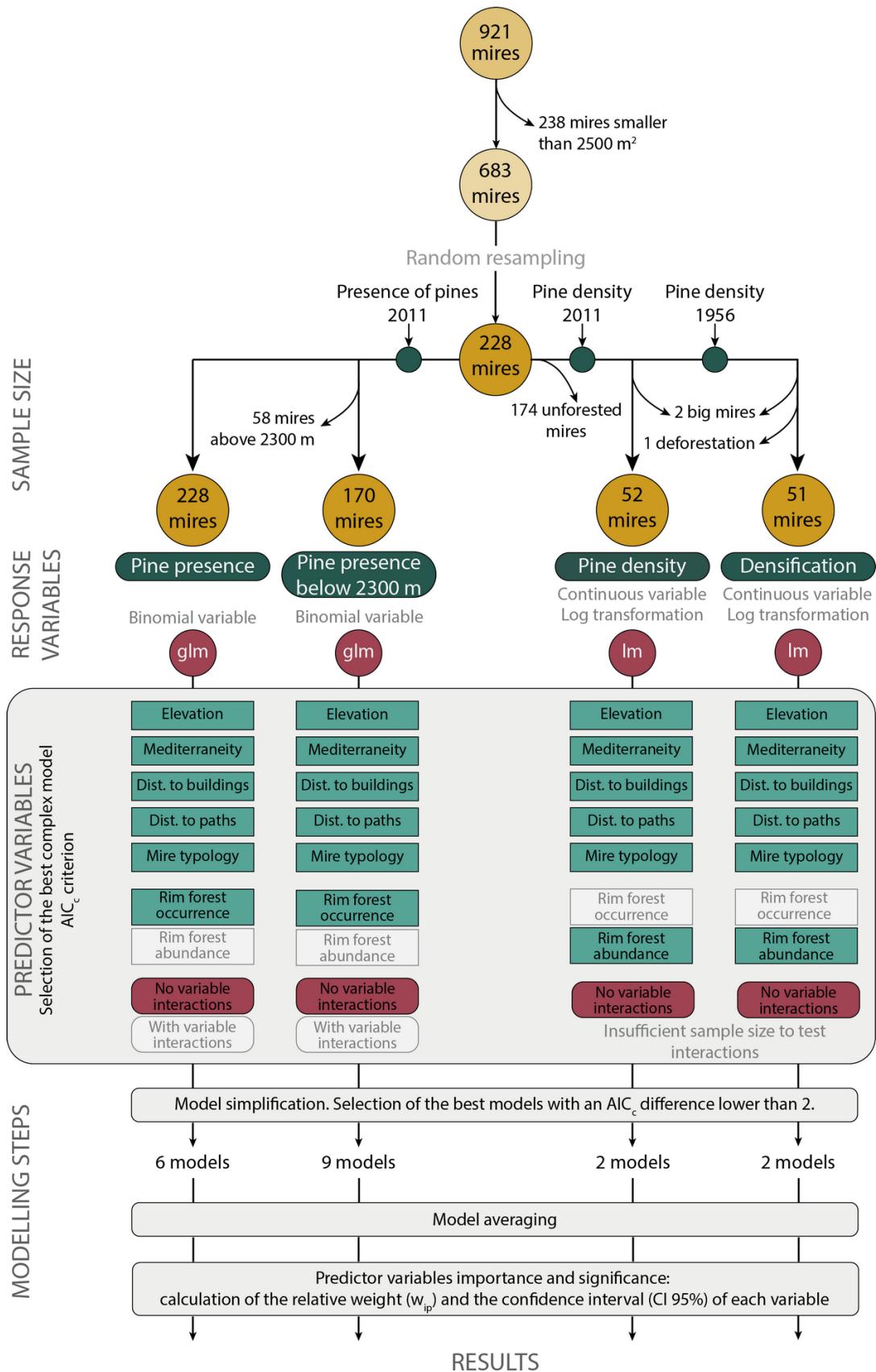
Fig. S3.1. Flowchart of the procedure and data analyses in the study. For each response variable we show the data selection, the predictor variables selected and the modelling process.
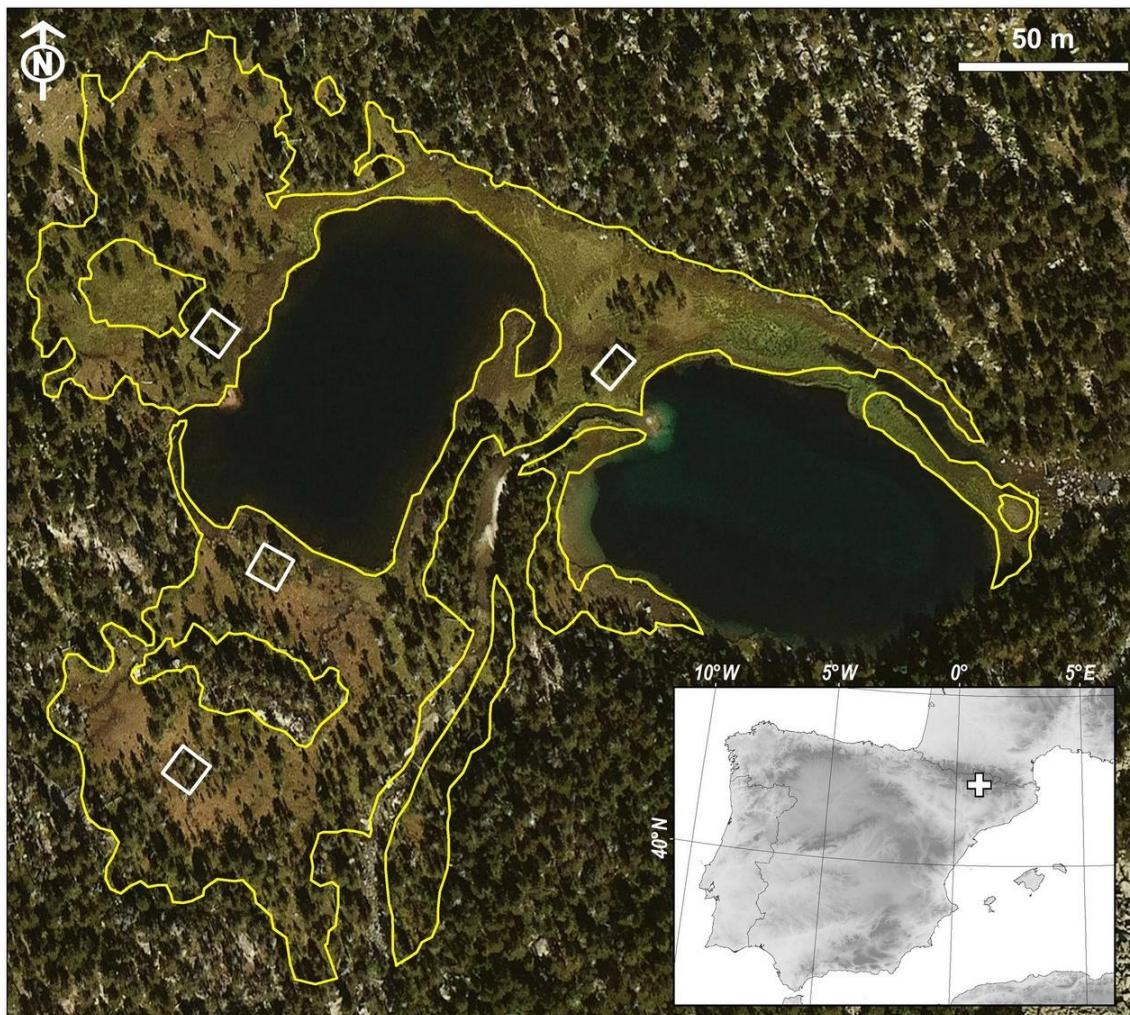
Fig. S3.2. Orthoimage of the Trescuro mire showing the situation of the four plots sampled (white squares) and the total extension of the mire (yellow line).
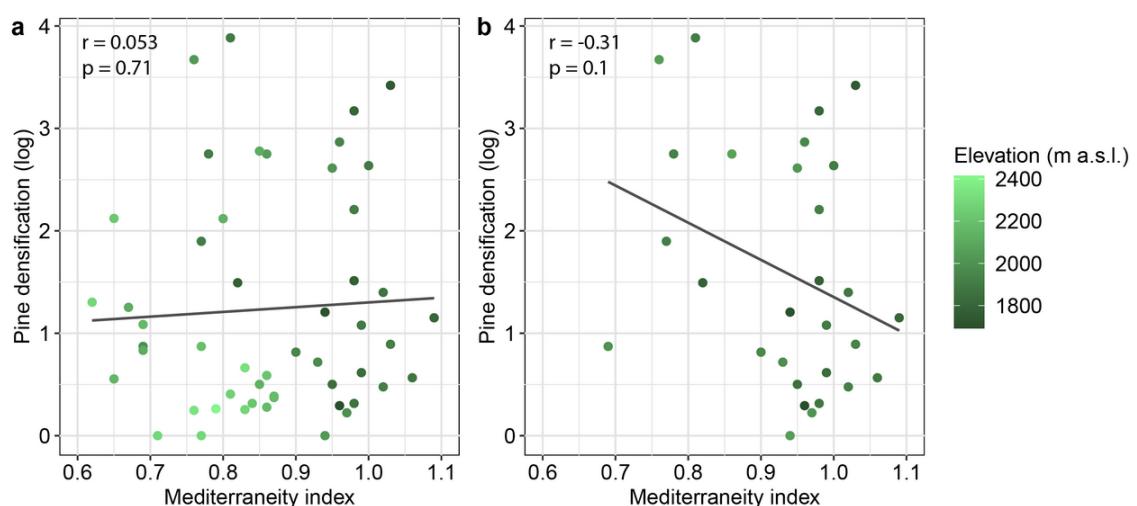
Fig. S3.3. Effect of Mediterraneity index on pine densification in mires that hosted pines in 2011. The elevation gradient is represented as varying green intensity. a) linear regression of the whole dataset (51 mires); b) linear regression of mires below 2100 m a.s.l. (i. e., in dark green; 29 mires).

Capítol 4

Vall de Montroig. Fotografia d'Eulàlia Pladevall.

The roles of environment and geographic distance to taxonomic, phylogenetic and functional beta diversity of vascular plants in Alpine mountain mires

El paper de les distàncies ambientals i geogràfiques en la diversitat beta taxonòmica, filogenètica i funcional de les plantes vasculars en molleres de muntanyes alpines

Abstract

In Alpine mountains, mires cover small areas within a patchy landscape, so they represent inland insular habitats with shared waterlogged conditions, but different site characteristics, surrounding habitats and relative isolation. Their plant communities are rich in mire specialist species, which contribute notably to gamma diversity at a regional scale. Here we studied the relevance of environmental and spatial drivers on beta diversity patterns in Pyrenean mire plant communities, both for all species dataset and only for mire specialists. Community assembly drivers of specialist plants can be different than those determining the co-existence of generalist species. We assessed the taxonomic, phylogenetic and functional beta diversity between 422 plots within 56 mire systems. After, we related beta diversity indices with geographic distances and local and regional environmental variables, carrying out variance partitioning analyses. Results showed high rates of taxonomic beta diversity, both at regional and local scales (within the same mire). Besides, both phylogenetic and functional beta diversities were lower and strongly correlated. Beta diversity accounting for all the dataset was similar to that of only specialist species, and we suggest that plant specialist distributions drove beta diversity patterns in mires. Against expectation, belonging to a given mire system explained most of the total beta diversity variance (24%), while environmental variables and spatial distances were of secondary importance for all beta diversity figures. Results highlight that each mire system has a local biodiversity beyond environmental characteristics. Also, we suggest that inhibitory priority effects may play a key role on community assembly in mires at regional scales, and different species functionally similar would play the same ecological role at distant mires. This work delves into the ecological processes that determine beta diversity rates in mountain mires, and points out the importance of making management decisions taking such processes into consideration.

Introduction

One of the main goals of biogeography and community ecology is to understand environmental drivers and spatial patterns of biodiversity change at different geographical scales, taxonomic groups and ecosystems. Most researchers deal with this subject by means of taxonomic diversity, that is, considering the taxa in a given area (Ricklefs, 2004). However, this approach does not consider that communities are made up by species with different evolutionary histories and diverse morphofunctional traits. Approaches on taxonomic diversity consider species as evolutionarily and functionally equivalent, but traits and phylogeny influence biotic and abiotic interactions in communities (Arnan et al., 2017).

Considering different facets of biodiversity provides a more thorough understanding of the processes that take place in community assembly and in vegetation succession (Cardoso et al., 2014; Heino & Tolonen, 2017). Two main dimensions of biodiversity supplement taxonomic diversity: phylogenetic diversity, which accounts for the evolutionary history in a community (Webb et al., 2002), and functional diversity, which reflects the phenotypic (morphological and physiological) and ecological traits within a community (Petchey & Gaston, 2006). Correlations and congruencies between different aspects of biodiversity vary between distinct studies, demonstrating that they are not equivalent and that they represent a useful tool in comparing multiple processes in community dynamics (Devictor et al., 2010). Thus, incorporating phylogenetic and functional biodiversity into research provides a better understanding on biodiversity structure (Pavoine & Bonsall, 2011).

Beta diversity is defined as the variation in the composition of communities among sites within a geographic area (Whittaker, 1960), and it can be partitioned into two additive dissimilarity components: species replacement and richness difference (Podani & Schmera, 2011). Species replacement (β_{Repl}) is related to the substitution of species in a given site by different species in another site, whereas richness –or abundance– difference (β_{AbDiff}) is caused by the change in species number between sites (J. C. Carvalho et al., 2012). Generally, the first correlates with environmental filters and gradients, while the second would be caused mainly by colonization and extinction processes and by dispersal limitations (J. C. Carvalho et al., 2012). Concurrently, beta diversity calculations can be performed using taxonomic (TβD), phylogenetic (PβD) or functional (FβD) diversity data, offering a new framework on ecology studies.

Recently, multiple studies addressed beta diversity patterns from the metacommunity perspective. Leibold et al. (2004) defined a metacommunity as "a set of

local communities that exchange colonists of multiple species". Four paradigms are based on the importance of the ecological processes that shape the metacommunity structure: patch dynamics, species sorting, mass effect, and neutral dynamics (Leibold et al., 2004). They all consider distinct relevance of environmental and spatial patterns. On the one hand, greater dispersal is expected to reduce beta diversity between sites. The potential of organisms to colonize suitable sites depends on the distances and connectivity between these sites (Shurin et al., 2009) and on each species dispersal ability. Many studies assume that plant dispersal is unlimited in a regional species pool, but even at local scales (given a short temporal scale) dispersal limitation can be one of the main drivers of species distribution within a metacommunity (Kraft & Ackerly, 2014). On the other hand, species composition changes along environmental gradients, and habitat filtering would reduce the range of successful strategies for a given site due to abiotic conditions (Cornwell et al., 2006). Furthermore, biotic interactions play an important role in community assembly (Kraft et al., 2015; Švamberková et al., 2017). Evidence suggests that metacommunity structure is driven by environmental and spatial patterns together, but the importance of each factor depends on multiple variables related to taxonomic group, ecosystem type, and temporal and spatial scales (Cottenie, 2005).

In the last ten years, methodological advances allowed the partitioning of beta diversity indices as a research tool (Cardoso et al., 2014). The first results evidenced that ecological processes in metacommunities translate into the relative importance of the different components and facets of beta diversity, and that all are interconnected. For example, species replacement may occur along an environmental gradient due to niche filtering according to the species traits, and in this case, functional and taxonomic replacement would respond to the same environmental driver (Leão-Pires et al., 2018).

Considering habitat indicator species (Dufrêne & Legendre, 1997), we can split species in a community into specialists and generalists (interpatch disperser species and matrix-derived species according to Whittaker, 1998). Specialists are good indicators to a specific habitat, so they only live in patches of a given specific habitat and can colonize new patches through suitable habitats. Contrastingly, generalists have broader ecological preferences, so they have the opportunity to colonize other habitats in the system (Horsáková et al., 2018; Whittaker, 1998). Therefore, dispersal limitations from species in "inland insular habitats" depend on their specificity to the system studied (Hájek et al., 2007). Nevertheless, only a minority of studies study specialist and generalist species separately (but see Horsák et al. (2012) or Horsáková et al. (2018)) and to our knowledge, no study focus beta diversity patterns neither metacommunity assembly according to a habitat specificity criterion.

In our study we focused on mires –peat-forming wetlands. Mires cover large areas in the Boreal and Atlantic zones, while in the Alpine mountains cover such smaller areas due to topographic and climatic factors. In the Pyrenees, as in many mountainous regions, most mires occupy less than 5000 m^2. They are only found on flat bottoms of

alpine cirques and bordering rivulets or lakes (Payne, 2018), and they are surrounded by drier mountain habitats in a patchy landscape (Ninot et al., 2017; Pérez-Haase, 2016). Mires cause stress for plant establishment and growth (mainly root hypoxia and oligotrophic soils (Rydin & Jeglum, 2013), so they represent inland insular habitats heterogeneously connected at landscape and regional scales. The main ecological gradients that drive species distribution within mires are: the *poor-rich* gradient (related to water pH, electric conductivity, calcium concentrations), the depth and dynamics of the water table (Bragazza & Gerdol, 1999; Økland et al., 2001), and the fertility (related to phosphorus availability and productivity (Wheeler & Proctor, 2000). Species richness in mires increases worldwide along the nutrient availability gradient from open bogs to rich fens (Rydin & Jeglum, 2013), and numerous studies addressed environmental patterns in mires and fens vegetation from local to broad scales (see, for example, Bragazza et al. (2005), Marini et al. (2008) or Pérez-Haase & Ninot (2017) at local scales in south-European mountains; Jiménez-Alfaro et al. (2012) or Rozbrojová & Hájek (2008) at regional scales; and Jiménez-Alfaro et al., (2014) or Peterka et al. (2017) at European scale).

Understanding the processes by which beta diversity is caused and maintained is a key point on making proper management decisions on ecosystem conservation and protection policies (Legendre et al., 2005). Environmental conditions often explain a noticeable proportion of the community composition variation among sites. Consequently, mires within the landscape mosaic are not equivalent, and show unique combinations of environmental characteristics (Tuomisto et al., 1995). Moreover, such differences lead to substantive spatial patterns on the community assembly (Kasel et al., 2017). In that case, natural reserves must represent the different types of habitat and the areas representing dispersion routes among them (Legendre et al., 2005).

During recent years, beta diversity approaches to biodiversity structure have increased widely focusing on ponds, streams and lakes, and have addressed the macroinvertebrate or macrophyte biodiversity over other taxonomic groups (Alahuhta et al., 2017; Hill et al., 2019; Jiang et al., 2021; etc.). However, only few studies dealing with plant species dynamics in mires include beta diversity as an analytical tool (Robroek et al., 2017; Sekulová et al., 2012; Udd et al., 2015). To our knowledge, no study addresses the different components of beta diversity in mires using a metacommunity framework on phylogenetic and functional plant biodiversity.

Here we present a regional scale investigation on high-mountain mire vegetation in the Pyrenees with the aim of delving into the environmental and spatial patterns that affect plant community assembly. We included a wide diversity of Alpine mire micro-habitats (bogs, poor and rich fens, quaking mires, springs...). More concretely, we addressed two main objectives:

i)   To determine the relative importance of replacement and abundance difference components for beta diversity indices by comparing the beta diversity between

plant communities within mire systems and between different mire systems. We considered taxonomic, phylogenetic, and functional beta diversity including both all species and only mire specialists (indicator species). We hypothesise that the replacement component will drive beta diversity because of the sharp environmental gradients studied, and that FβD will be lower than TβD due to niche filtering.

ii)   To distinguish the effects of environmental gradients from spatial patterns on beta diversity in Alpine mire plant communities. We hypothesise that environmental gradients at local scales would show strong correlations with the variation of beta diversity (and more strongly in FβD) because previous studies at local scale in the Pyrenees highlight the relevance of environmental gradients on mire biodiversity structure (Pérez-Haase & Ninot, 2017). Also, dispersal limitations between mires would be scarcely detected, although if there are, they will be stronger for specialist species.

Materials and methods

Study area

This study was carried out in mountain mire systems located in the Central Pyrenees at both Atlantic and Iberian slopes (Fig. 4.1). Although the Pyrenees belong to the Eurosiberian and Boreo-alpine biogeographical regions, they are also under the Mediterranean climate influence. Mires in the study area chiefly occur between 1500 m and 2500 m a.s.l. (Casanovas, 1991), thus within the subalpine and low alpine belts. Most of the study area is dominated by acidic substrata (mainly granites and lutites), but calcareous sedimentary rocks such as limestones also occur. Here, mires are strongly constrained by high-mountain complex physiography (Ninot et al., 2017), and usually cover small surfaces in a patchy landscape. They are most often soligenous and so related to runoff and spring waters, but limnogenous and ombrogenous mires also occur. Furthermore, mire plant communities occur scattered on the landscape, thus communities are likely to be poorly connected, even within the same valley. However, Pyrenean mire systems hold noticeably plant diversity since their microtopography is very complex and variable at detailed scales. Thus, a single mire includes a number of different habitats (Pérez-Haase, 2016).

Sampling of plant communities and local environmental variables

The data used in this study were sampled between 2005 and 2018 and consist of 422 plots heterogeneously distributed along 56 mire systems from the Catalan and Andorran Pyrenees. A mire system includes all waterlogged areas closer than 500 m. The entire dataset includes samples from all kinds of mire micro-habitats found in the study
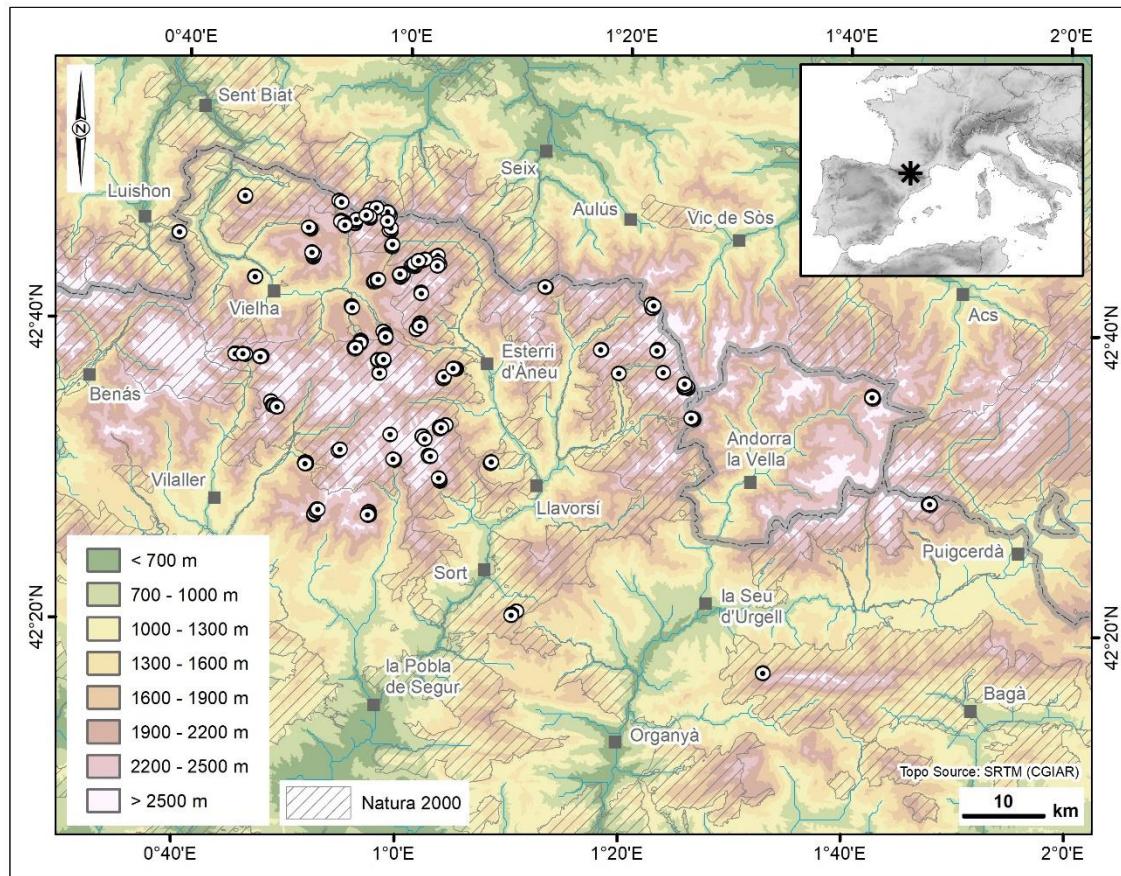
Fig. 4.1. Plot distribution in the study area. Protected are painted in a stripe pattern. In grey, country borders of France (N), Andorra and Spain (S).

area, and most mire systems comprised between three to six plots. At each 2.5 × 2.5 m plots (6.25 m^2), we recorded all vascular plant species and subspecies and we estimated their cover by the Domin scale. After, we transformed the Domin scale into cover percentages and log-transformed the resulting values. Plant nomenclature follows the The Plant List checklist (2013).

As for indicator species, we classified all species into two categories, waterlogged soil specialists (hereafter, mire specialists or simply specialists) and generalists. We included in the specialists group all indicator species of fens (*Scheuchzerio palustris-Caricetea fuscae* Tüxen 1937), bogs (*Oxycocco palustris-Sphagnetea magellanici* Br.-Bl. & Tüxen 1946) and springs (*Montio-Cardaminetea* Br.-Bl. et Tüxen ex Klika et Hadač 1944) following the criteria of Bolòs et al. (2005). Among the 254 taxa from our dataset, 103 belong to the specialists group (40.6%). The generalists group includes all other species that, despite tolerating waterlogged soil conditions, are found in a wide range of habitats or are matrix-derived species (151 taxa, 59.5%). We removed all those plots with less than three specialist species.

We undertake all field work campaigns during the second half of July to keep all the plot variables, including species, as similar as possible between areas and years. We recorded for each plot the geographic coordinates using Garmin 60CSx GPS (accuracy

<10 m) and the *Elevation* (in m a.s.l.). We measured the *Water Table Depth*, and took 100 mL of groundwater to measure the *pH* and the *Electric Conductivity* (WTW MultiLine® 3620), and we stored the sample at -20°C for further laboratory analyses. Furthermore, we measured the *Slope* inclination and *Aspect* (in degrees). After, we transformed the slope aspect into eight categories and we assigned the minimum value to plots facing the North (minimum insolation) and the maximum value to plots facing the South (in a semi-quantitative type variable. Finally, we assigned each plot to one of the following *Hydrologic Categories*: topogenous, soligenous and ombrogenous (cf. Damman et al., 1987).

Explanatory variables

We analysed the concentration of Ca, Mg, Na, K and Al by inductively coupled plasma mass spectroscopy (ICP-MS). We summed the total cation concentration into a single variable related to the water cation content (*Cation Contents*, in mEq/L). Previously, the water samples were filtered (pore Ø = 0.2 µm). Preliminary analyses of nitrate and nitrite concentrations in groundwater yielded values below detection level (<32 µeq/L of N) and ammonium yielded nearly constant values around 120 µeq/L of N, so we rejected groundwater fertility as an explanatory variable. Nevertheless, to estimate the fertility in our plots, we retrieved the soil nutrient indicator values for all plant species from Baseflor database in Catminat (Julve, 1998). After, for each plot, we computed the weighted mean of indicator values to obtain a fertility value for each plot (*CWM Nutrients*, being the weights the plant cover percentages). Moreover, to estimate the primary production, we summed all the species percentage covers in each plot (*Productivity*).

As for climatic regional variables, we used the Pyrenean Digital Climatic Atlas with 30 m resolution (Batalla et al., 2018). We retrieved mean annual *Precipitation*, annual potential solar *Radiation* and *Growing Degree Days*, and calculated the *Water Availability* (annual precipitation minus potential evapotranspiration) and the *Mediterraneity Index* (summer potential evapotranspiration divided by summer precipitation). To take *Geological Substrates* into account we used a map of lithological types at 1:50.000 scale (Conesa et al., 2010), and we assigned each plot to one of these four main groups: i) acid siliceous rocks (such as granites), ii) lutites, iii) acid or neutral sandstones and conglomerates and iv) alkaline sandstones and conglomerates.

To remove redundant variables, we checked for correlations between all explanatory variables. When Spearman's correlation test < 0.7 we kept only one variable from the pair. We removed Electric Conductivity, Aspect, Mediterraneity Index, Growing Degree Days and Water Availability Index. The variables finally selected were classed into two main groups depending on the scale of variation (local or regional). The first are the local environmental variables, which may vary at very short distance, i.e. pH, Water Table Depth, Slope, Cation Contents, Productivity, CWM Nutrients and a dummy variable

indicating if the plot is in a hummocky-like habitat or not (Hydrologic Category). The second group are the regional environmental variables, namely Elevation, Precipitation, Radiation and Geological Substrates. We centered and scaled all the numerical variables. Finally, we modelled the spatial variation with dbMEM (distance-based Moran's Eigenvector Maps; Dray et al., 2006). We used *dbmem* function from *adespatial* package (Dray et al., 2021) and we obtained 28 positive eigenvalues.

Phylogenetic and functional trait data

To calculate the phylogenetic diversity we used taxonomic hierarchies as a coarse proxy for true phylogeny (Heino & Tolonen, 2017; Li et al., 2021; Lindholm et al., 2020; Ricotta et al., 2012). We used six taxonomic levels to construct a dendrogram with equal branches length: species, genus and family collected from The Plant List (2013); and order, superorder and subclass collected from Tropicos database (2019).

To calculate the functional diversity, first we built a nine functional trait matrix related to three ecological aspects: space occupancy and competence, *in situ* persistence, and seed dispersion (Table 4.1). We log transformed canopy height and seed mass variables to normalize values distribution and we verified that no trait was correlated with others (spearman < 0.7 and Kruskal-Wallis tests). We then transformed the species × traits matrix into a dissimilarity matrix with the Gower dissimilarity measure using *gowdis* function (package *FD*; Laliberté et al., 2014). We imputed missing values with de *dissimilarity* imputation method proposed by (Taugourdeau et al., 2014) and we reduced the total number of NA's in the functional data matrix from 73 to 3 (from 3.19 to 0.13% of cells in the database; Table 4.1). Finally, we built a functional dendrogram for all species using UPGMA method.

Statistical analyses

Beta diversity calculations

We calculated taxonomic beta diversity indices (TβD) based on the percentage difference coefficient, i.e. Sørensen dissimilarity (J. C. Carvalho et al., 2012; Podani & Schmera, 2011). We used the log transformed species percentage cover to balance the contribution of the dominant vs. rare species to the results (Legendre, 2014). Then we decomposed the total beta diversity (β_{Total}) into replacement (β_{Repl}) and abundance difference (β_{AbDiff}) components, where

β_{Repl} + β_{AbDiff} = β_{Total} and

1 - β_{Total} = Similarity   which implies that

β_{Repl} + β_{AbDiff} + Similarity = 1

Table 4.1. List of functional traits used for FβD. We show the type of each variable, the data source and the number of species not assessed out of the 254 species in total (NA).

	Functional trait	Type	Number and names of levels	Data origin	NA's
Space occupancy and competence					
	Canopy height	Numerical	—	LEDA [1]	0 / 0
	SLA	Numerical	—	LEDA[2]	44 / 2
	Maximum annual clonal lateral spread	Ordinal	5 ordinal levels: 0<0.005<0,13<0,25<1	CLO-PLA	3 / 0
	Maximum annual clonal multiplication rate	Ordinal	5 ordinal levels: 0<0,5<1<6<13	CLO-PLA	13 / 1
In situ persistence					
	Principal clonal growth organ	Categorical	without clonality horizontal above-ground stem turion plantlet; epigeogenous stem hypogeogenous stem stem tuber bulb root-splitter roots with adventitious buds root tuber	CLO-PLA	0 / 0
	Perennial bud bank	Categorical	2 (yes/no)	CLO-PLA	3 / 0
	Growth form	Categorical	phanerophytes camaephytes erect hemicryptophytes basal rosette hem. cespitosus hem. stoloniferous hem. biannual hem. bulbous geophytes rhizomatous geophytes tuberous geophytes hydrophytes therophytes	Baseflor	0 / 0
Seed dispersion					
	Seed mass	Numerical	—	LEDA, SID[2]	10 / 0
	Dispersion strategy	Categorical	anemochory autochory barochory endozoochory epizoochory hydrochory myrmecochory	Baseflor	0 / 0

[1] also personal observations and herbarium consultations. / [2] and personal measuring.

We repeated the same procedure for phylogenetic (PβD) and functional (FβD) beta diversity indices, where each plot diversity is calculated from the correspondent dendrograms of the species (for both the whole dataset and for the specialists only). Subsequently, we summarized the beta diversity structure in ternary plots (Podani & Schmera, 2011). Afterwards, we performed Mantel tests with 9999 permutations to check for correlations between TβD, PβD and FβD. All beta diversity calculations were performed with *BAT* package (Cardoso et al., 2021), ternary plots with *Ternary* package (Smith, 2017) and Mantel test with *mantel.rtest* function from *ade4* package (Dray et al., 2007).

Variance partitioning of total beta diversity

We used distance-based Redundancy Analysis (dbRDA) and variance partitioning to examine the variance proportion of total beta diversity (TβD, PβD and FβD for both the whole dataset and the mire specialists) explained by groups of explanatory variables. We grouped the variables as follows: i) local environmental variables (LAND); ii) regional environmental variables and geology (REG); iii) spatial autocorrelation (dbMEM), and iv) name of each mire system (a site dummy variable, MIRE). Before any variance partitioning analysis, we selected those significant explanatory variables of each group (except for the mire system) using a forward selection procedure (*ordiR2step* function from *vegan* package with 999 permutations and reaching the Adjusted R^2 of the global model as a criterion to stop the procedure; Oksanen et al., 2020). We run dbRDA and variance partitioning by *capscale* and *varpart* functions from *vegan* package respectively, and we used square root dissimilarities to avoid negative eigenvalues (Legendre, 2014). Finally, we tested the significances of unique fractions with *anova* function. You can see a schematic flowchart of data analyses in the Fig S4.1 of the Supplementary Material.

Beta diversity differences based on the mire system site

Here we focused on the importance of the mire system site in pairwise comparisons for beta diversity. To do so, we split all distance matrices into two vectors: pairwise comparisons between plots belonging to different mire systems were allocated to the first, and those belonging to the same to the second. We saved this data as a new data frame that we used to run Welch one-way ANOVA tests and Games Howell post-hoc tests to determine significant differences between vectors. We run these tests by *rstatix* package (Kassambara, 2021).

Results

Species richness per plot (6.25 m^2) ranged from 3 to 35, and the average was 14.83 (standard deviation 6.91). Considering only mire specialists, plots hosted in average 9.18 species (± 4.47).

Beta diversity patterns

Mire vascular plant communities showed high rates of beta diversity. The mean taxonomic beta diversity (TβD) using the Sørensen family with abundance data was 0.81 (±0.15) (Table 4.2; Fig 4.2). Beta diversity values greater than 0.5 indicate that the abundance of the non-shared species between two plots is higher than twice the abundance of the shared species, so our data plant composition was noticeably different. In fact, a 9.20% of TβD reached 1, so there were no shared abundances of species between these plots. The comparison between taxonomic, phylogenetic and functional β calculations showed that the mean β$_{Total}$ was significantly higher for TβD than for PβD, and higher for PβD than for FβD. Nevertheless, all beta diversity matrices were significantly correlated according to Mantel tests (p<0.0001) and Pearson correlations (r>0.7; see Fig. S4.2 of the Supplementary Material).

As for β components, β$_{Repl}$ was larger than and β$_{AbDiff}$ in most cases. Thus, average β$_{Repl}$ represented between 55.7 to 72% of β$_{Total}$ (Table 4.2). Moreover, β$_{AbDiff}$ had the same values for TβD, PβD and FβD calculations due to numerical limitations in Sørensen abundance beta calculations (since it doubles the weight of the shared species component, using a tree or not will be the same; see *BAT* package code in https://github.com/cran/BAT/blob/master/R/BAT.R). The beta diversity of mire specialists was slightly lower than for all species (concerning TβD$_{Repl}$ and PβD$_{Repl}$) but FβD$_{Repl}$ was higher when only specialist species were considered. At the same time, β$_{AbDiff}$ showed higher rates for the specialist dataset than for all species, representing up to 44.3% in FβD$_{Total}$.

Variance partitioning of taxonomic, phylogenetic and functional beta diversity

The forward selection procedures –that preceded the variance partitioning analyses– retained almost all environmental variables and 21-24 of the 28 dbMEMs (see the selected variables for each variance partitioning and their adjusted R^2 values in Tables S4.1 and S4.2 of the Supplementary Material). All six β$_{Total}$ variance partitioning analyses showed similar results and beta diversity variation reached up to 31.62% (Fig 4.3). The mire system site represented the most important explanatory group of variables, thus explaining up to 26.50% of variance (with a pure fraction of 9.37% in TDβ of specialist plants). At the same time, the spatial variation (dbMEMs group) and the mire system variables were more relevant in TβD than in PβD and FβD. Hence, spatial distances

Table 4.2. Mean and standard deviation for beta diversity calculations (taxonomic, phylogenetic and functional) and for all its components (βTotal, βRepl and βAbDiff). We indicate values for the whole dataset and for only specialist species; and below, βRepl and βAbDiff proportions with respect to the total beta diversity.

	Taxonomic beta diversity		Phylogenetic beta diversity		Functional beta diversity	
	All species	Specialist species	All species	Specialist species	All species	Specialist species
Total	0.81 ± 0.15	0.79 ± 0.17	0.55 ± 0.12	0.54 ± 0.14	0.51 ± 0.12	0.53 ± 0.14
Replacement	0.58 ± 0.19	0.54 ± 0.22	0.33 ± 0.13	0.29 ± 0.13	0.28 ± 0.12	0.28 ± 0.13
Abundance Diff	0.23 ± 0.16	0.25 ± 0.18	0.23 ± 0.16	0.25 ± 0.18	0.23 ± 0.16	0.25 ± 0.18
Repl % of total	0.72 ± 0.19	0.68 ± 0.22	0.61 ± 0.24	0.56 ± 0.26	0.58 ± 0.25	0.56 ± 0.26
AbDiff % of total	0.28 ± 0.19	0.32 ± 0.22	0.39 ± 0.24	0.44 ± 0.26	0.42 ± 0.25	0.44 ± 0.26

may play a more relevant role in species distribution than in functional and phylogenetic diversity.

Local environmental variables showed a relevant role in PβD and especially in FβD (adj R^2 = 13.82 and 14.44 respectively) rather than in TβD (adj R^2 = 10.43; Table 4.3). Although regional environmental variables explained little variation, remarkable adjusted R^2 were shared between this variables group and the mire system variable. This should be due to the constancy or low variation of the regional environmental variables through the same mire system. Overall, regional variables were more relevant in TβD patterns (adj R^2 = 8.28) than in PβD than in FβD (adj R^2 = 6.84 and 7.67 respectively), i.e. the opposite behaviours with respect to the local variables.

Variance partitioning on specialists' beta diversity showed the same tendencies as for all-species calculations (Fig 4.3 and Table 4.3). Nevertheless, the regional environmental variables showed a slightly higher adjusted R^2 while the local environmental variables were proportionally less relevant. Finally, the mire system site was the most relevant group of explanatory variables regarding the variance partitioning on specialists' beta diversity (adj R^2 from 23.47 to 26.50).

Beta diversity patterns between plots from the same or different mire systems

The effects of the mire system site on beta diversity –through Welch one-way ANOVA tests and Games Howell post-hoc tests– gave evidence for a regional pattern. For all comparisons, a beta diversity between two plots from the same mire was more prone to be lower than a beta diversity between two plots belonging to different mires (Fig. 4.4 and Fig. S4.3 of the Supplementary Material). In fact, we always found significant differences with a p-value < 0.0001.
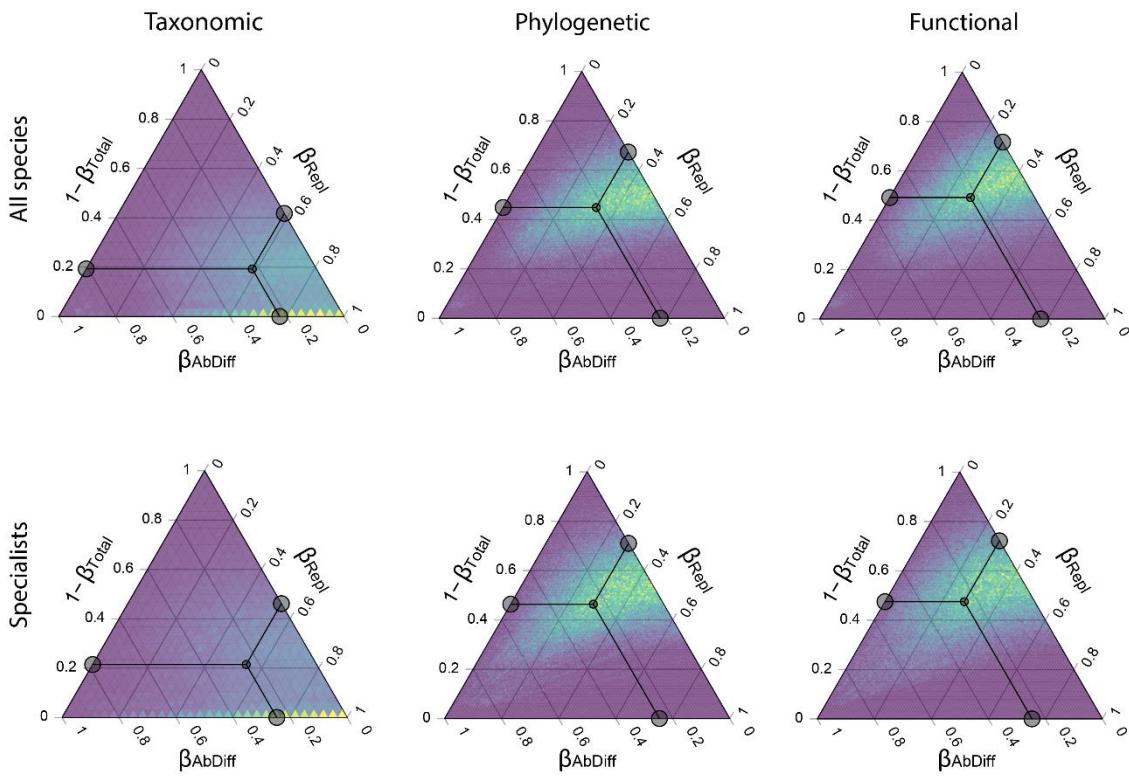
Fig. 4.2. Ternary plots illustrating beta diversity structure based on three components that up to 1. Above, beta diversity accounting for all vascular plant species in each plot; below, beta diversity accounting for specialist species in each plot. Circles represent the mean for each component (see Table 4.2) and colour scale represents the density of dots in the graph (dark purple – low density; yellow – high density).

Discussion

Environmental filtering and habitat heterogeneity in mires

We found a noticeable high plant richness in mires (254 species), although plant communities were not especially rich at plot scale (14.83 species/plot). Accordingly, we found high rates of beta diversity, reached mostly through species replacement, whereas community complexity was roughly similar between plots. Beta diversity was high at regional scale, and it held true for local scale. That is, we obtained high beta diversity figures even within mire systems. Interestingly, alpine mire micro-topographical heterogeneity leads to the formation of intricate mosaics (Pérez-Haase & Ninot, 2017) with high plant beta diversity and promotes biodiversity shifts (Bragazza et al., 2005). Habitat arrangement along environmental gradients can be both gradual or abrupt in wetlands (Larkin, 2016), but it always affects beta diversity patterns at detail scales (Brose, 2001; Hájek et al., 2009; Shi et al., 2010). Thus, environmental variables at local scale (pH, depth of the water table, hydrology) accounted for the 10.43 % of the variance in TβD and 14.44 % in FβD. These results agree with our hypotheses, and indicate that functional alpha diversity would change notably following these gradients in a more marked way than taxonomic diversity. According to these results, mires have a noticeable gamma
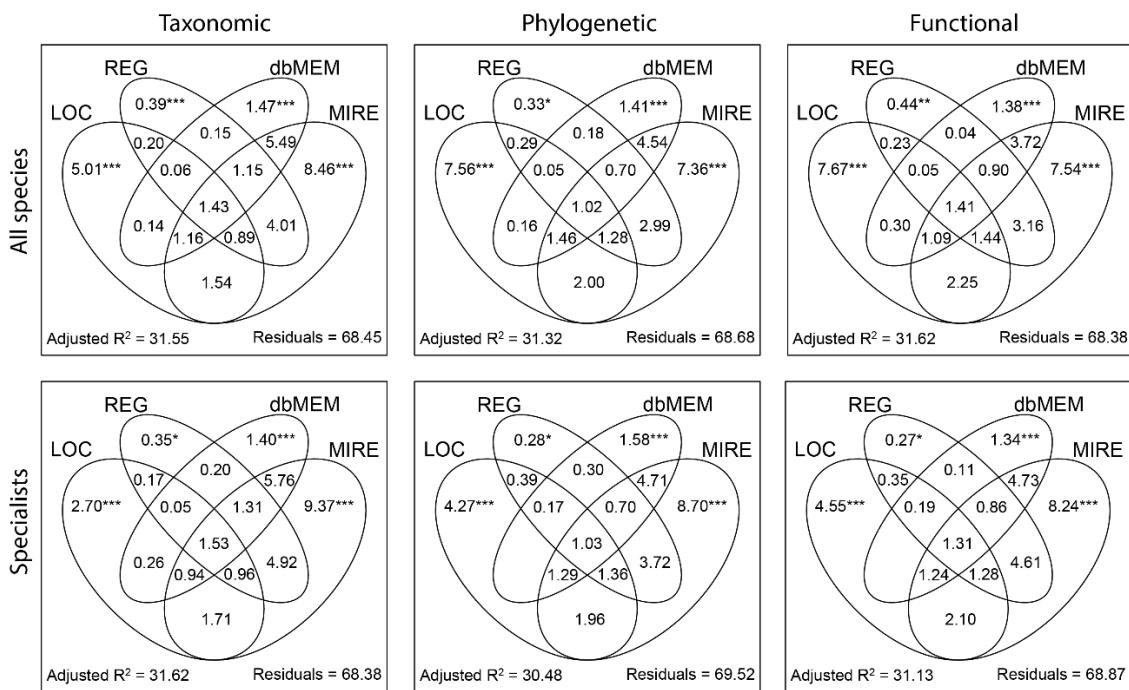
Fig. 4.3. Variance partitioning of beta diversity indices showing the contributions of different explanatory variable groups and their combinations expressed as percentages of total variation (based on Adjusted R^2). Above, beta diversity accounting for all vascular plant species in each plot; below, beta diversity accounting for specialist species in each plot. The unique fractions significance is indicated (*, $p<0.05$; **, $p<0.01$; ***, $p<0.001$). See Table 4.3 of the Supplementary Material for the results on the significance tests. We do not illustrate negative contributions. LOC = local scale environmental variables; REG = regional scale environmental variables; dbMEM = spatial variation; MIRE = mire system dummy variable.

diversity by the accumulation of relatively poor plant communities at plot scale (as found in springs by Sekulová et al., 2012). Also, since many of mire plant species only grow under mire stressing waterlogging conditions and are unable to thrive elsewhere, they notably contribute to gamma diversity in the region (Hájek et al., 2007; Horsáková et al., 2018; Pérez-Haase et al., 2019). The high differences on community composition both in short and long distances added to geographical fragmentation contribute to increase the heritage value of the Pyrenean mires (Astorga et al., 2014; Erdős et al., 2018).

The beta diversity rates for only mire specialists were strongly consistent with those for all plants. In fact, specialist species averaged the 77.4% of the species cover per plot although only represented the 40.5% of taxa in the whole dataset. These results denoted that beta diversity patterns correspond to those showed by specialist species, and so generalist species would play a secondary role. Importantly, some of these species are considered as threatened in the Iberian Peninsula or have few populations in the South of Europe, where they are regionally rare (Aymerich & Sáez, 2021).Horsáková et al. (2018) find contrasting factors driving specialist *versus* generalist species richness in European fens. They conclude that specialist species are mainly driven by geographical location of sites, which is consistent with our results. Thus, specialists' biodiversity varied at inter-mire level and beta diversity was lower within a mire than between different mires. In

fact, some rare specialist species in the Catalan Pyrenees such as *Carex diandra, C. lasiocarpa, Drosera longifolia, Juncus triglumis* are locally abundant (Escolà et al., 2022; Pérez-Haase & Ninot, 2017). The northern slopes of the Pyrenees are more influenced by Atlantic climate, foggier and rainier than the southern ones, under Mediterranean influence. These bioclimatic differences affect species richness at all habitats and in different elevation ranges (Ninot et al., 2013). In the north-west limit of our study area, Atlantic influence favours the formation of a great number of mires in the Aran valley, with highl natural values both for their extension and accumulation of rare species (Pérez-Haase et al., 2010).

Moreover, results indicate that matrix-derived and generalist species (i.e., non-specialists) play a secondary role on diversity patterns, since they showed lower abundance values together with a higher replacement between plots. Horsáková et al. (2018) find that the richness of matrix-derived species mainly depends on local conditions as pH or the depth to the water table, which determines the degree of habitat contrast against the surrounding matrix. Thus, generalist species must display low fitness in wet habitats and respond to an opportunistic role, so their presence must depend on belonging to the species-pool, on environmental local factors, and on their ecological tolerance (Miller et al., 2021).

As for functional diversity, the majority of traits were related to competitive ability and persistence *in situ* once established. Most dominant plants were perennial hemicriptophyte graminoids, with epigeogenous stems (as rhizomes), a clonal spread of few centimetres per year, and a multiplication rate of 1-10 clones per year. Focusing on the similitude between different facets of beta diversity, phylogenetic and functional ones were highly correlated. According to this, similar functional traits are phylogenetically close, i.e. traits exhibit a phylogenetic signal and related species tend to be ecologically similar, as analysed by Carvalho et al. (2020). In that sense, habitat filtering at long-term scales favoured some taxonomic groups to be adapted at mire specific

Table 4.3. Sum of the adjusted R^2 from the different compartments that belong to each of the four variable groups in the variance partitioning (i.e., percentage of total variance explained by each group of variables). All adj R^2 are significant (p<0.001).

Variable group		TβD	PβD	FβD
All species				
	LOC	10.43	13.82	14.44
	REG	8.28	6.84	7.67
	bdMEM	11.05	9.52	8.89
	MIRE	24.13	21.35	21.51
Specialists				
	LOC	8.32	10.46	10.97
	REG	9.49	7.95	8.98
	bdMEM	11.45	9.77	9.73
	MIRE	26.50	23.47	24.37

environmental conditions, a pattern that has been widely studied in broad-scale biogeographic theories (Kraft & Ackerly, 2014). In the same way, at the regional scale of the present study, some clades were more dominant and ubiquitous than others (*Poaceae, Carex spp., Juncus spp.*), so functional similarities reflected phylogenetic proximities.

Vegetation dynamics in Alpine mires

In the Pyrenees and other Alpine mountains, mires are found in small, scattered areas heterogeneously connected within a patchy landscape (Ninot et al., 2017; Pérez-Haase, 2016), so they represent inland insular habitats with different site characteristics, surrounding habitats and relative isolation (Horsák et al., 2012; Hubáčková et al., 2016). Despite the high number of explanatory variables used to characterize each plot in the study (assembled in four explanatory groups), variance partitioning calculations explained only around 31.5% of beta diversity variance between plots. In light of the results on variance partitioning, the beta diversity between plant communities clearly depended on site dependent characteristics. According to that, each mire system holds a local biodiversity beyond environmental and geological characteristics. Considering mire uniqueness, a few plausible interpretations arise, and we discuss it below.

On the one hand, we suggest that inhibitory priority effects drive community assembly in mires at regional scale. So, the colonization and establishment of a species in a mire would prevent the establishment of other species with similar functional features and ecological requirements (Fukami, 2015). This interpretation points at competitive exclusion interactions in spatial dynamics and zonation (Keddy, 2010), and species-sorting patterns would be subordinated to niche occupancy. This interpretation matches with the fact that functional beta diversity was notably lower than taxonomic beta diversity between plots. Moreover, geographic distances were more important for taxonomic than for functional beta diversity, so nearby plots would be taxonomically similar thanks to nearby species colonizations, whereas they would be substituted by other taxa at distant plots. Thus, different taxa with similar functional attributes would take the same ecological role in similar communities at different mires (Graco-Roza et al., 2021).

On the other hand, observed communities may not belong to late stages of plant succession in mires, but to different mid (or early) stages. Thus, species with less dispersal capacities would be still infra-represented in the metacommunity, and whose niche would be occupied by ubiquitous species or species that had colonized the site previously –beyond their competitive ability. Multiple biogeographical processes support this ecological hypothesis.

First, each mire has a particular age since its formation, what turns into a specific time of successional processes on plant communities. Different studies on calcareous

fens from Western Carpathian Mountains (Hájek et al., 2011; Horsák et al., 2012; Peterka et al., 2022), demonstrate that some specialist plants have affinities for old sites, and that richness for specialist plants is positively correlated with habitat age. According to them, the likelihood for a specialist species to colonize a mire increases with the age of the site, but they do not find this relation neither for matrix-derived species –with wider suitability areas– nor for bryophytes –with higher dispersal abilities. In the present study, reduced areas and habitat isolation could entail dispersal limitations for many vascular plants, accentuated by low seed production or viability, high seed size and weight, transient seed-bank and high seedling mortality (Middleton et al., 2006; Thompson et al., 1997; Van den Broek & Beltman, 2006). Different taxa with different dispersal abilities could show contrasting metapopulation dynamics, thus contributing to taxonomic beta diversity between distant mire systems at regional scale. At shorter distances, source-sink relations among patches may take place (i.e. mass-effect paradigm; Leibold, 2009). These interpretations coincide with the importance of the spatial structure between sampled plots (geographic distances) in the variance partitioning analyses. They played a more important role in taxonomic than in functional beta diversity, and a slightly greater in specialists than for all species together.

Second, mires experience environmental changes over time (Braun-Blanquet, 1948). Climate changes in the European Alpine mountains after glaciations resulted in multiple vegetation changes, as it has been widely documented in the Pyrenees (Cunill et al., 2012; Garcés-Pastor et al., 2017; Pèlachs et al., 2011). At the same time, each mire may experience shifts in the hydrological regime and environmental characteristics along centuries or millennia, paludification and terrestrialization processes, changes in its area, changes in peat accumulations or in the watercourse, etc. Different stages in ecological succession in mires can be eventually modified due to disturbance events, changes in the water level, or climate shifts (Bauer et al., 2003; Keddy, 2010). Thus, community assembly at long-term scales is subject to climate changes. At shorter scales, specific characteristics from each site can affect community dynamics: neighbouring habitats will influence the species-pool; current and past anthropic land uses at different spatial and temporal scales (grazing, fire, forestry) may be important drivers of community dynamics and biotic interactions (Spitale, 2021); and anthropogenic hydrological changes promote vegetation shifts (Koch & Jurasinski, 2015; Mälson et al., 2008). Unlike climate changes, these characteristics are independent from one mire to another, and would play a key role on the importance of the mire itself for biodiversity and plant succession. Thus, heterogeneous historical changes in distinct mires contribute to the observed higher beta diversity between plots from different mires.

Altogether, vegetation changes along time often occur at low pace in mires, sometimes slower than environmental changes. Such biological *inertia* was described in mire vegetation as the ability to persist in unfavourable habitats after environmental changes (Gorham et al., 1984). All of these previous reasons are plausible explanations of the rather low variance explained by the explanatory variables of the different facets
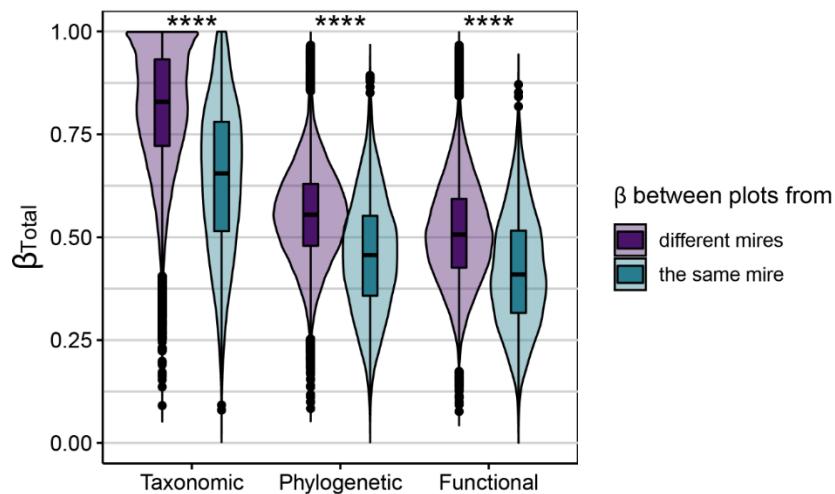
Fig. 4.4. Violin plots and boxplots of TβD$_{Total}$, PβD$_{Total}$ and FβD$_{Total}$ data aggregated according to the mire system origin from every pair of plots. In purple, pairwise comparisons between plots that belong to different mire systems, and in blue, pairwise comparisons between plots from the same mire system. Games-Howell post-hoc significant differences shown as **** (p<0.0001). See Table S4.3 of the Supplementary Material for mean and standard deviations of each group.

of beta diversity. Surely, biogeographic patterns in the Alpine mires result from the combination of multiple processes that take place at different temporal (from few decades to millennia) and spatial scales (from the micro-habitats in a mire to the species-pool at regional scales).

Conservation interest

Our results pointed out that the accumulation of plant communities from different mires –with their specific micro-habitats and site history– are key to understanding mire plant biodiversity in Alpine mountains. Thus, preserving only some locally interesting sites would be not sufficient to preserve mire biodiversity in a broad region. In that sense, conservation, restoration and management plans should not only be founded on species richness and species conservation status. Also, land managers must take beta diversity into consideration, since it provides significant insights to prioritization of conservation decisions (Bergamin et al., 2017; Legendre et al., 2005). At the same time, particularly rare plant communities are not specially species-rich (Illa et al., 2006). Environmental filtering in mires such as flooding or root-anoxia promote a decrease in species richness but an increase in rare specialist species (P. Keddy, 2005; Pérez-Haase & Ninot, 2017).

In the case of the present study area, most of the mires are located in protected areas (Fig 4.1), and two of the three areas with the highest protection level in the region belong to mires with great micro-habitat heterogeneity and great accumulation of rare species (Pérez-Haase & Ninot, 2017). However, these two areas do not include other mires from the same valleys that are necessarily connected in the metacommunity. More

importantly, many Pyrenean mires are situated in basins with hydroelectric regulations (dams, subterranean channels), where hydroelectric power stations caused severe disturbances. Still in protected areas, drastic changes in hydrological conditions occur and can affect plant communities (see Colomer et al. (2019)). Moreover, although most of the Pyrenean mires are located in protected areas, no species conservation plan for any threatened plant or bryophyte species has already been approved (GENCAT, 2021).

To sum up, here we demonstrated that Alpine mire plant diversity –taxonomic, phylogenetic and functional– vary first according to environmental conditions and to site-dependent characteristics, and second to spatial, climatic, and geologic factors. In line with Wintle et al. (2019), here we highlight the importance of preserving also small, isolated patches as they are likely to contribute to the regional gamma diversity with specialised biodiversity distributed along small terrestrial islands. Furthermore, along with the relevance of each mire system for specialists' biodiversity, we suggest that ancient mires may hold greater specialists richness (Peterka et al., 2022) and we advocate incorporating the age of each mire in future research and in conservation decision making in mountain mires. Prioritising ancient mires would guarantee the preservation of late succession stages in the community assembly of the mountain range mire metacommunity. The present work underscores the relevance of habitat-specific specialist species on beta diversity patterns, so we recommend checking for specialist species at each site to help decide site conservation prioritization.

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Supplementary Material from Chapter 4
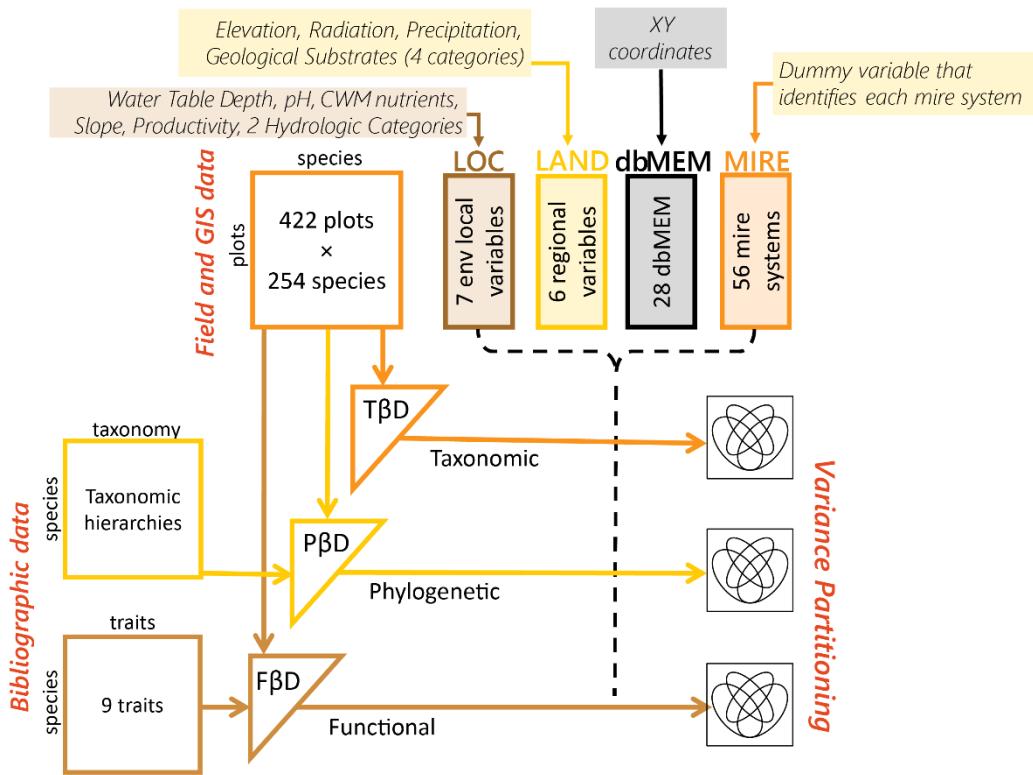
Fig. S4.1. Schematic flowchart of data analyses, from data collection (field and GIS data) to beta diversity calculations and variation partitioning results. We repeated the procedure considering only the 103 mire specialist species in the plots.
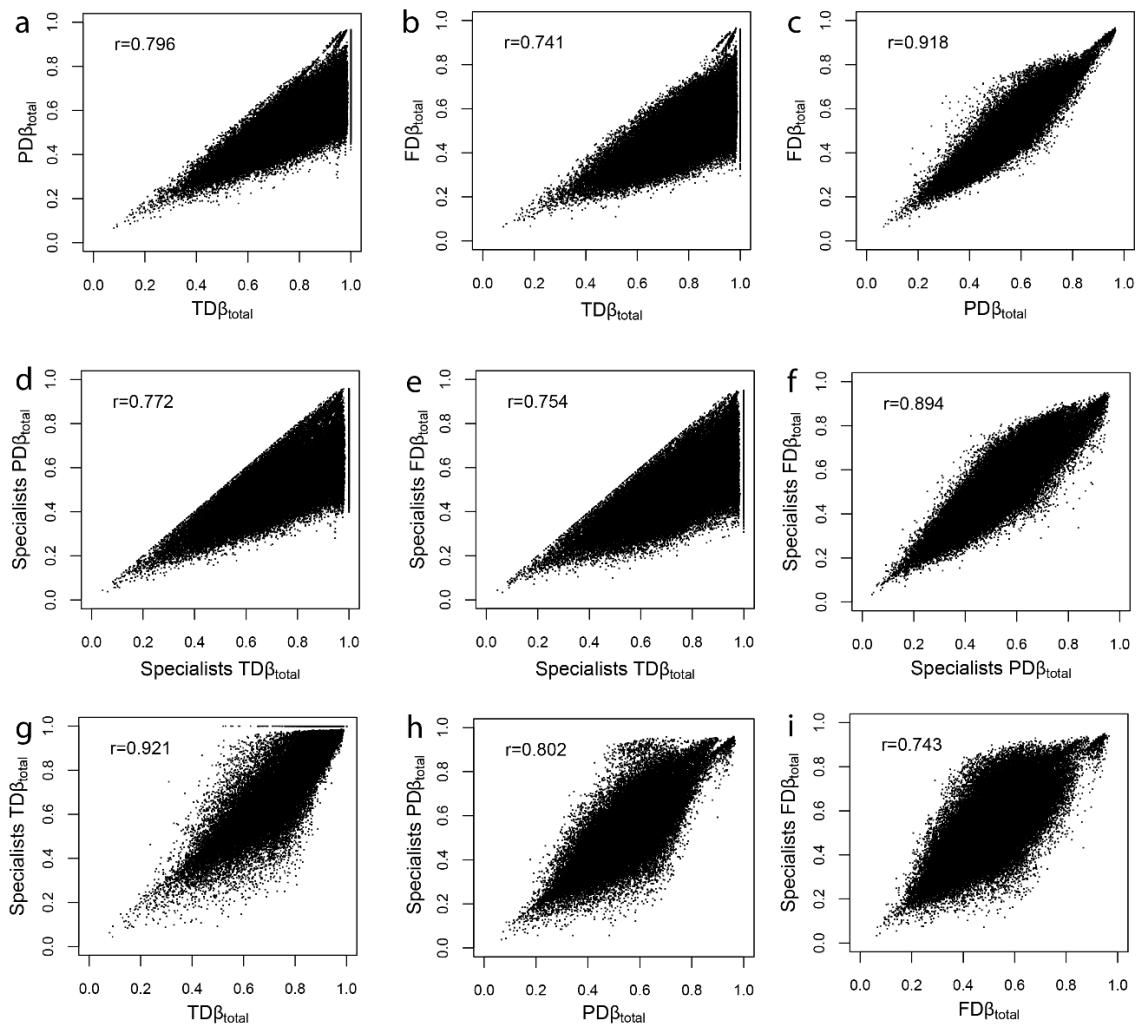
Fig. S4.2. Correlations between different beta diversity matrices (taxonomic, phylogenetic and functional for all species and for only specialists). Pearson correlation is indicated on each plot (r). From a to c, correlations between the three facets of beta diversity; from d to f, correlations between the three facets of beta diversity of specialist species; from g to i, correlations between the beta diversity of all species and of only specialists (taxonomic, phylogenetic and functional). All pairwise comparisons are significantly correlated according to Mantel tests ($p < 0.0001$).

Table S4.1. dbRDA variable selection through forward selection to beta diversity (TβD$_{Total}$, PβD$_{Total}$ and FβD$_{Total}$). We list the variables selected and indicate their adjusted R^2 (Adj R^2) and cumulative adjusted R^2 (Cum R^2). In bold, cumulative variation explained by each explanatory variable group.

Taxonomic beta diversity			Phylogenetic beta diversity			Functional beta diversity		
Variable	Cum R^2	Adj R^2	Variable	Cum R^2	Adj R^2	Variable	Cum R^2	Adj R^2
Local env		**0.104**			**0.138**			**0.144**
pH	0.029	0.029	Productivity	0.044	0.044	Productivity	0.055	0.055
Water table depth	0.05	0.021	Hummock hydr.	0.077	0.033	Hummock hydr.	0.086	0.031
CWM nutrients	0.07	0.02	CWM nutrients	0.1	0.023	CWM nutrients	0.109	0.023
Productivity	0.081	0.012	Cation contents	0.115	0.015	Cation contents	0.123	0.014
Cation contents	0.092	0.01	Water table depth	0.129	0.014	Water table depth	0.136	0.013
Hummock hydr.	0.1	0.009	pH	0.135	0.006	pH	0.141	0.005
Slope	0.104	0.004	Slope	0.138	0.003	Slope	0.144	0.003
Regional env		**0.083**			**0.068**			**0.077**
Elevation	0.037	0.037	Elevation	0.033	0.033	Elevation	0.042	0.042
Geo. acid granites	0.059	0.021	Geo. acid granites	0.049	0.016	Geo. acid granites	0.056	0.014
Precipitation	0.069	0.01	Precipitation	0.057	0.008	Precipitation	0.066	0.01
Geo. acid lutites	0.077	0.008	Geo. acid lutites	0.063	0.006	Geo. acid lutites	0.072	0.006
Geo. basic lutites	0.081	0.004	Geo. basic lutites	0.067	0.004	Geo. basic lutites	0.075	0.003
Radiation	0.083	0.002	Radiation	0.068	0.002	Radiation	0.077	0.002
bdMEM		**0.111**			**0.095**			**0.091**
MEM-1	0.014	0.014	MEM-1	0.012	0.012	MEM-1	0.011	0.011
MEM-4	0.026	0.012	MEM-4	0.022	0.01	MEM-4	0.021	0.01
MEM-7	0.036	0.009	MEM-7	0.03	0.008	MEM-7	0.03	0.009
MEM-6	0.043	0.007	MEM-10	0.037	0.007	MEM-10	0.037	0.007
MEM-10	0.05	0.007	MEM-2	0.042	0.006	MEM-9	0.042	0.005
MEM-9	0.057	0.006	MEM-6	0.048	0.006	MEM-2	0.047	0.005
MEM-2	0.062	0.006	MEM-9	0.053	0.005	MEM-5	0.052	0.005
MEM-5	0.068	0.005	MEM-5	0.058	0.005	MEM-3	0.056	0.005
MEM-11	0.072	0.005	MEM-3	0.063	0.004	MEM-11	0.06	0.004
MEM-22	0.077	0.004	MEM-14	0.066	0.003	MEM-14	0.064	0.004
MEM-3	0.081	0.004	MEM-11	0.069	0.003	MEM-6	0.067	0.004
MEM-14	0.084	0.004	MEM-18	0.072	0.003	MEM-8	0.07	0.003
MEM-8	0.088	0.004	MEM-22	0.075	0.003	MEM-18	0.073	0.003
MEM-13	0.091	0.003	MEM-25	0.078	0.003	MEM-25	0.075	0.003
MEM-12	0.093	0.002	MEM-13	0.081	0.003	MEM-13	0.078	0.003
MEM-25	0.096	0.002	MEM-8	0.083	0.003	MEM-22	0.081	0.003
MEM-18	0.098	0.002	MEM-23	0.085	0.002	MEM-17	0.083	0.002
MEM-15	0.1	0.002	MEM-12	0.087	0.002	MEM-23	0.084	0.002
MEM-17	0.102	0.002	MEM-15	0.089	0.002	MEM-12	0.086	0.002
MEM-23	0.104	0.002	MEM-17	0.09	0.002	MEM-15	0.087	0.002
MEM-20	0.106	0.002	MEM-19	0.092	0.001	MEM-24	0.089	0.001
MEM-24	0.108	0.002	MEM-24	0.093	0.001			
MEM-19	0.109	0.002	MEM-20	0.094	0.001			
MEM-16	0.11	0.001	MEM-16	0.095	0.001			

Table S4.2. dbRDA variable selection through forward selection to beta diversity for specialist species ($T\beta D_{Total}$, $P\beta D_{Total}$ and $F\beta D_{Total}$). We list the variables selected and indicate their adjusted R^2 (Adj R^2) and cumulative adjusted R^2 (Cum R^2). In bold, cumulative variation explained by each explanatory variable group.

Taxonomic beta diversity			Phylogenetic beta diversity			Functional beta diversity		
Variable	Cum R^2	Adj R^2	Variable	Cum R^2	Adj R^2	Variable	Cum R^2	Adj R^2
Local env		**0.087**			**0.109**			**0.114**
Cation contents	0.03	0.03	Productivity	0.033	0.033	Productivity	0.038	0.038
CWM nutrients	0.048	0.018	pH	0.055	0.022	Water table depth	0.06	0.022
Productivity	0.059	0.011	CWM nutrients	0.076	0.021	CWM nutrients	0.079	0.019
pH	0.07	0.011	Water table depth	0.091	0.015	Cation contents	0.098	0.019
Water table depth	0.079	0.008	Cation contents	0.099	0.008	pH	0.105	0.007
Slope	0.083	0.005	Hummock hydr.	0.105	0.006	Hummock hydr.	0.11	0.004
Regional env		**0.095**			**0.082**			**0.092**
Elevation	0.044	0.044	Elevation	0.043	0.043	Elevation	0.052	0.052
Geo. acid granites	0.067	0.024	Geo. acid granites	0.06	0.017	Geo. acid granites	0.065	0.013
Precipitation	0.08	0.012	Precipitation	0.069	0.009	Precipitation	0.078	0.013
Geo. acid lutites	0.089	0.009	Geo. acid lutites	0.076	0.008	Geo. acid lutites	0.086	0.007
Geo. basic lutites	0.092	0.003	Geo. basic lutites	0.08	0.003	Geo. basic lutites	0.09	0.004
Radiation	0.095	0.003						
dbMEM		**0.116**			**0.098**			**0.101**
MEM-1	0.015	0.015	MEM-1	0.012	0.012	MEM-1	0.012	0.012
MEM-4	0.027	0.011	MEM-4	0.022	0.009	MEM-7	0.022	0.01
MEM-7	0.037	0.01	MEM-10	0.03	0.008	MEM-4	0.031	0.009
MEM-10	0.046	0.009	MEM-7	0.038	0.008	MEM-11	0.041	0.01
MEM-6	0.054	0.008	MEM-11	0.045	0.007	MEM-10	0.048	0.007
MEM-9	0.061	0.007	MEM-6	0.051	0.006	MEM-5	0.055	0.006
MEM-11	0.067	0.006	MEM-9	0.056	0.005	MEM-6	0.06	0.005
MEM-5	0.072	0.006	MEM-5	0.061	0.005	MEM-9	0.064	0.004
MEM-22	0.077	0.005	MEM-2	0.065	0.004	MEM-22	0.067	0.003
MEM-2	0.081	0.004	MEM-14	0.068	0.004	MEM-18	0.07	0.003
MEM-8	0.085	0.004	MEM-18	0.072	0.003	MEM-3	0.073	0.003
MEM-3	0.089	0.004	MEM-22	0.075	0.003	MEM-17	0.076	0.003
MEM-14	0.092	0.003	MEM-3	0.078	0.003	MEM-12	0.079	0.003
MEM-17	0.095	0.003	MEM-15	0.08	0.002	MEM-14	0.082	0.003
MEM-13	0.098	0.003	MEM-17	0.082	0.002	MEM-2	0.084	0.003
MEM-25	0.1	0.003	MEM-25	0.085	0.002	MEM-25	0.087	0.002
MEM-18	0.103	0.002	MEM-8	0.087	0.002	MEM-15	0.089	0.002
MEM-12	0.105	0.002	MEM-13	0.089	0.002	MEM-8	0.091	0.002
MEM-24	0.107	0.002	MEM-12	0.091	0.002	MEM-13	0.094	0.002
MEM-20	0.109	0.002	MEM-24	0.093	0.002	MEM-24	0.096	0.002
MEM-15	0.111	0.002	MEM-20	0.094	0.001	MEM-20	0.097	0.002
MEM-23	0.113	0.002	MEM-16	0.096	0.001			
MEM-19	0.115	0.002	MEM-23	0.097	0.001			
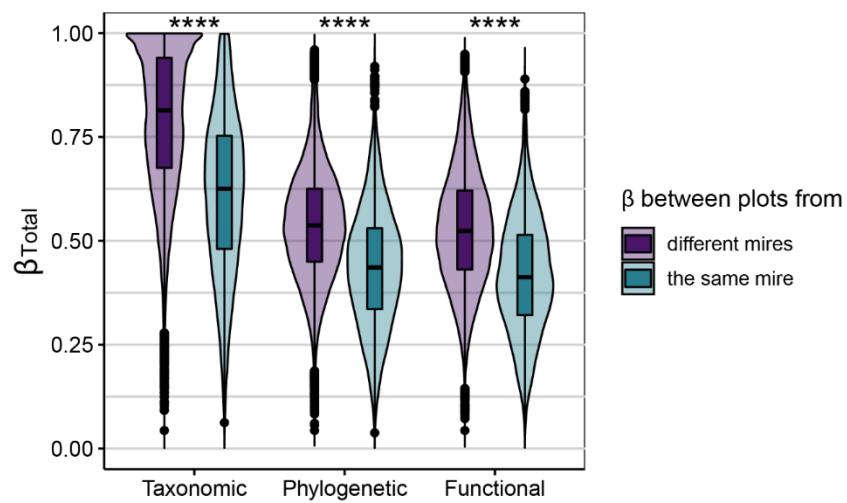
Fig. S4.3. Violin plots and boxplots of TDβ$_{Total}$, PDβ$_{Total}$ and FDβ$_{Total}$ of specialist species and according to the mire system origin from every pair of plots. In purple, pairwise comparisons between plots that belong to different mire systems, and in blue, pairwise comparisons between plots from the same mire system. Games-Howell post-hoc significant differences shown as **** (p<0.0001).

Discussió general

Estany de Mollàs. Fotografia d'Eulàlia Pladevall.

Discussió general

En els quatre capítols precedents analitzem la naturalesa de les comunitats de plantes de les molleres alpines i la dinàmica de la vegetació que hi té lloc. Procurem entendre quins patrons ecològics determinen la construcció de comunitats, i quina sensibilitat tenen aquests hàbitats a canvis en les condicions abiòtiques o en els usos del sòl. Ho fem a diferents escales d'espai i temps, destriant així alguns processos que ocorren a la vegada però a diferents nivells en l'estructura de la vegetació. La fisiografia abrupta de les muntanyes alpines causa variació en les condicions ambientals i en la biodiversitat de les comunitats de mollera. Els estudis que conformen el treball se centren en les molleres dels Pirineus centrals, i els seus resultats poden ser de gran interès per fonamentar una gestió conservativa d'uns espais amb un alt valor patrimonial.

Gradients ambientals i interaccions biòtiques

És ben sabut que un dels principals gradients ambientals que determina la variació florística a les molleres alpines és la profunditat de l'aigua freàtica (Bragazza et al., 2005; Bragazza & Gerdol, 1999; Marini et al., 2008). A més a més, la composició de la vegetació en molleres d'alta muntanya s'ha relacionat amb la variació del nivell freàtic al llarg del temps (Hájková et al., 2004; Pérez-Haase, 2016). Aquests fets reflecteixen la capacitat de les plantes vasculars per prosperar en sòls saturats d'aigua durant períodes més o menys llargs de temps, i representa, per tant, un factor abiòtic clau en la construcció de les comunitats de mollera. Al capítol 1 hem observat diferències clares en el desenvolupament de plantes especialistes d'hàbitats de mollera en funció del règim hidrològic al que les hem sotmès. Sobre sòls inundats, *Carex rostrata* i *C. nigra* van desenvolupar estructures fotosintètiques més vigoroses i una inversió més gran en expansió lateral dels individus. De fet, plantes amb una mida del clon més gran toleren millor els períodes d'inundació i produeixen més brots vegetatius (Deng et al., 2016). Fraaije et al. (2015) i Malkinson & Tielbörger (2010) ja apuntaven que els requeriments abiòtics de les espècies poden variar al llarg del desenvolupament dels individus. En concordança, nosaltres hem observat que les preferències hídriques de *C. nigra* són ben diferents per al reclutament de plàntules que per a l'expansió lateral dels individus adults.

Altres gradients ambientals que dirigeixen la composició florística dels hàbitats de mollera són la fertilitat, el tipus hidrològic (molleres ombrogèniques o minerogèniques), o l'acidesa i les característiques químiques de l'aigua, entre d'altres (Glaser et al., 1981; Malmer, 1986; Rydin & Jeglum, 2013; Wheeler & Proctor, 2000). Malgrat això, al capítol 4 –estudi de la importància dels patrons ecològics i geogràfics sobre la variació de la

biodiversitat a les molleres pirinenques– hem demostrat que només una petita part de la diversitat beta entre comunitats de mollera s'explica exclusivament pel conjunt de variables ambientals que caracteritzen cada lloc. Així, si no tenim en compte la seva disposició en l'espai, expliquen com a molt 1/5 part de la variació total de la diversitat beta. Aquest paper, força modest, dels gradients ecològics, posa de relleu la multiplicitat d'altres factors que contribueixen en la construcció de les comunitats de mollera.

Altres treballs han estudiat les relacions entre variables ambientals i biodiversitat en molleres alpines a altres massissos europeus, com als Carpats i als Alps. Sekulová et al. (2013) suggereixen que el *pool* d'espècies en hàbitats disposats en illes terrestres no depèn de l'àrea total del sistema muntanyós. Paral·lelament, segons Sekulová et al. (2012), la diversitat alfa de les comunitats de molleres de muntanya no canvia malgrat canvis en la mida del pool d'espècies regional. Consideren que això es podria explicar per l'exclusió competitiva entre espècies dins les comunitats, que limitaria la seva riquesa. Tant els resultats del capítol 4 com els del capítol 1 d'aquesta memòria apunten també que l'exclusió competitiva entre plantes tindria rellevància en la zonació de les plantes especialistes de mollera. Tot i així, l'exclusió competitiva és generalment molt baixa en molleres amb limitació pels nutrients (Rydin & Barber, 2001), ja que les plantes perennes acostumen a coexistir durant períodes de temps prolongats malgrat tenir habilitats competitives diferents (Rebele, 2000). En els nostres treballs no hem constatat el desplaçament total d'una espècie degut a la competència interespecífica d'altres tàxons. Per exemple, al capítol 1, malgrat detectar diferències competitives entre espècies, totes les plantes van créixer notablement. Els resultats d'aquesta memòria suggereixen que les diferències en la capacitat competitiva de tàxons amb nínxols encavallats expliquen una part de les diferències en les abundàncies relatives de les espècies.

Dispersió i colonització de plantes vasculars al paisatge alpí

Les molleres alpines són topogràficament complexes, el que comporta una elevada heterogeneïtat de condicions ambientals en distàncies curtes, que alhora condueix a una alta diversitat de comunitats vegetals dins una mateixa mollera (Colomer et al., 2019; Miserere et al., 2003; Pérez-Haase & Ninot, 2017). Bona part d'aquesta variabilitat ha estat descrita en forma d'associacions fitosociològiques, però múltiples combinacions locals d'espècies escapen del mètode sigmatista (Braun-Blanquet, 1948; Casanovas, 1991; Pérez-Haase et al., 2010). En relació amb això, al capítol 4 hem registrat valors de diversitat beta alts dins de cada sistema de molleres. Aquests resultats van en la mateixa línia que els de Pérez-Haase & Ninot (2017), que identifiquen l'antiguitat de la mollera i la longitud de gradients ambientals com dos determinants de la variació de la composició de les comunitats vegetals i de la riquesa total de la localitat (vegeu també Hájek et al., 2011; Horsák et al., 2012).

A una escala més àmplia, la dispersió i l'establiment tant de briòfits com de plantes vasculars afecten la composició de les comunitats vegetals i la riquesa dels hàbitats (Kraft & Ackerly, 2014). Mitjançant complexes xarxes de metacomunitats, les diferents molleres estan o han estat interrelacionades per la dispersió de les plantes, fet que ha estat poc estudiat, però del què tenim evidències a partir dels macroinvertebrats en sistemes muntanyosos (Jiang et al., 2021; Z. Li et al., 2021) o dels macròfits aquàtics en xarxes hidrogràfiques (García-Girón et al., 2019). De fet, el grau de semblança florística entre molleres depèn de la distància que les separa, i són més semblants com més a prop es troben (Graco-Roza et al., 2021). L'estudi de la composició florística de les molleres d'alta muntanya del capítol 4 mostra que cada sistema de molleres té una signatura original pel que fa el conjunt florístic local (vegeu també Pérez-Haase et al., 2019). A més a més, les condicions ecològiques locals afecten més la diversitat funcional de les comunitats vegetals que la taxonòmica, com també s'ha observat en aiguamolls d'altres regions (Morandeira & Kandus, 2017; Robroek et al., 2017). És a dir, les comunitats properes –en molleres properes o dins una mateixa mollera– tendiran a ser força semblants taxonòmicament gràcies a colonitzacions d'espècies a distàncies curtes, però espècies diferents amb atributs funcionals similars ocuparan el mateix nínxol ecològic en comunitats distanciades dins la metacomunitat (Graco-Roza et al., 2021).

Segons els nostres resultats, la persistència *in situ* de les espècies és encara més important que la distància entre comunitats Els nostres resultats encaixen amb un notable efecte prioritari inhibidor de les espècies (*priority effect*). És a dir, l'establiment d'una espècie en una comunitat local dificultaria l'establiment futur d'una altra espècie amb un nínxol ecològic similar. Aquests resultats concorden amb els de Robroek et al. (2017) als coixins d'esfagnes a escala Europea, on observen que la substitució d'espècies entre comunitats llunyanes ocorre sobretot entre espècies funcionalment similars. La fisiografia complexa dels Pirineus –com en altres muntanyes alpines– fa que la probabilitat de colonització de les espècies especialistes d'un hàbitat favorable quedi supeditada a la connectivitat entre les tesel·les similars en el mosaic complex del paisatge (Dullinger et al., 2011). De fet, els inventaris realitzats als capítols 2 i 4 mostren que les comunitats locals no són gaire riques en espècies, però en canvi el reemplaçament d'espècies entre punts de mostreig és molt elevat. També altres estudis demostren que els patrons de diversitat en comunitats fontinals al llarg dels gradients ambientals difereixen entre sistemes muntanyosos alpins diferents (Sekulová et al., 2012) i el mateix passa amb les molleres (Sekulová et al., 2013). Al capítol 4 hem estudiat una mostra prou representativa de la diversitat de comunitats de mollera als Pirineus, i d'acord amb el que discuteixen aquests autors (Sekulová et al., 2013), els resultats haurien de ser consistents per al conjunt de molleres dels Pirineus, mentre que podríem esperar partons lleugerament diferents en altres sistemes alpins (com Alps o Carpats).

En relació a la colonització de les comunitats de mollera per part de noves espècies, l'entrada de pins a les molleres és més probable com més superfície de pineda envolti les molleres, ja que això les fa més accessibles a la germinació i establiment de pinetons

(capítol 3). Encara que les llavors dels pins tinguin una bona vagilitat, la majoria no arriba gaire enllà (Anadon-Rosell et al., 2020). Tot plegat apunta a que el paper del conjunt d'espècies locals és fonamental en la composició específica de les molleres, en consonància amb que es tracta d'un conjunt d'illes humides en una matriu d'ambients més secs que provoquen el seu aïllament i dificulten l'arribada de noves espècies de més lluny (Deák et al., 2018; Dullinger et al., 2011; Horsáková et al., 2018). Per tant, cada mollera és singular perquè presenta una combinació d'espècies particular. Si estudiem aquests patrons a escales detallades de temps i espai observem quin paper juguen les espècies ja presents a prop del punt d'estudi. Així, en el cas de la colonització de sòl nu després de l'alteració per trepig, veiem com el creixement mitjançant òrgans d'expansió vegetativa de les espècies clonals ja establertes pren tanta o més rellevància que la dispersió per llavors (capítol 2).

Usos del sòl i dinàmica de la vegetació

El llegat d'usos del sòl d'una mollera i del seu entorn expliquen una part de la seva singularitat (Norstedt et al., 2021). Al capítol 3 hem pogut relacionar diverses variables a escala de paisatge –ambientals, climàtiques i d'usos del sòl– amb la probabilitat de les molleres de ser colonitzades per poblacions de pi negre (*Pinus uncinata*) en les properes dècades. Així, l'increment de pins a les molleres es preveu superior a altituds baixes (estatge subalpí) i en molleres properes a pinedes i que tenen un aprofitament ramader baix. És a dir, l'increment de la densitat de pins a les molleres va lligat amb els usos del sòl de les molleres i dels seus hàbitats limítrofs. Aquests resultats concorden amb els d'altres treballs realitzats als Pirineus a escala regional, que documenten un increment notable de la coberta de bosc (*encroachment*, embosquinament) i de la seva densificació (Améztegui et al., 2010), que ha provocat una homogeneïtzació notable del mosaic de vegetació del paisatge des de la segona meitat del segle XXè (Améztegui et al., 2021). A escala regional es relaciona aquest canvi amb la davallada de les activitats forestals i de la transhumància (García-Ruiz et al., 2020; Gracia et al., 2011), i no tant amb el canvi climàtic (Améztegui et al., 2016). En aquest sentit, els resultats a les molleres van en concordança amb la dinàmica forestal de la resta del paisatge, i malgrat que les preferències ecològiques del pi negre siguin lluny de les molleres, és previsible que aquesta tendència augmenti en un futur proper.

Com ja apuntàvem, els usos del sòl actuals i passats dins una mollera afecten la seva composició florística i les seves funcions i serveis ecosistèmics (Norstedt et al., 2021). Per exemple, s'ha demostrat que, als Alps, molleres més afectades per la pressió ramadera tenen menys diversitat de briòfits i menys briòfits rars (Spitale, 2021). També, un canvi brusc en la freqüentació ramadera deriva en canvis en les abundàncies relatives de les espècies de plantes vasculars a mitjà termini. Així ho demostren diversos estudis, que van observar com l'exclusió ramadera total fa disminuir la riquesa de les comunitats de mollera (Schultz et al., 2011; Shi et al., 2013) o provoca la homogeneïtzació de la

biodiversitat entre localitats diferents (Golodets et al., 2010). L'hervivorisme afecta la composició florística a escala de detall (rebrot de plantes veïnes, germinació i establiment de plançons, competència per la llum), i així ho hem constatat al capítol 2, en la mateixa línia que Kohler et al. (2006). La important davallada en la floració i la fructificació que l'herbivorisme indueix en les espècies de mollera, típicament representades per poblacions disperses, també ha de tenir importància en la seva genètica poblacional. En definitiva, la ramaderia impacta la composició de les comunitats de plantes de mollera a diferents escales temporals i espacials (vegeu també Mohandass, 2016). Per tant, la història de l'ús ramader de cada mollera és un factor determinant per entendre les diferències en les comunitats de molleres diferents (capítol 4).

Escales temporals i espacials en la dinàmica de la vegetació

Al capítol 1 hem constatat que les espècies són capaces de sobreviure i créixer en profunditats de nivell freàtic contrastades, malgrat que en condicions naturals es presenten en una variabilitat d'aquest factor més acotada, com passa amb *Carex rostrata* i *Juncus filiformis*. A més, les espècies de l'estudi van respondre poc a la competència interespecífica, i cap de les espècies va desplaçar les altres tot i tenir estratègies de creixement i mides prou contrastades. Aquests resultats indiquen que els processos que determinen la composició d'espècies a cada comunitat són subtils, i que possiblement operin lentament. En aquest sentit, les comunitats de mollera es veurien modificades lentament responent a un canvi en les condicions ecològiques, mostrant una notable inèrcia a persistir en condicions desfavorables durant èpoques prou extenses (Gorham et al., 1984).

L'escala de temps i d'espai a la que observem els diferents processos de dinàmica de la vegetació permet que els puguem detectar amb més o menys dificultat (Delcourt et al., 1982). Així, a escales de temps llargues, sabem que típicament les cubetes de sobre-excavació glacial passen lentament d'un estany, a un aiguamoll, i finalment a un mosaic de prats humits (Braun-Blanquet, 1948; Pérez-Haase & Ninot, 2017). Les evidències d'aquest procés no deriven tant d'observació directa, sinó més aviat d'observacions sincròniques –emprant espai per temps, en diferents localitats anàlogues– o a través de sondatges que permetin analitzar nivells estratigràfics diferents. En canvi, la resposta de la vegetació davant de fenòmens més bruscos, com la sobrepastura o la colonització de pins, és força més ràpida i permet ser abordada en el termini de pocs anys. Gràcies a l'estudi detallat de la resposta de la vegetació hem pogut observar com tant per l'entrada de llavors (de diverses espècies al capítol 2, de pins al capítol 3), com pel desenvolupament de rizomes i estolons (capítols 1 i 2) el paisatge de les molleres és dinàmic. La direcció d'aquests canvis és sovint poc clara, però apunta cap a la ràpida cicatrització dels sòls més alterats si minva la pressió dels grans herbívors (capítol 2) i cap a la progressiva reducció de la mida de les molleres obertes en benefici de les arbrades, per embosquinament (capítol 3). Es preveu que el canvi climàtic causi problemes en la

conservació de les molleres a escala global (Erwin, 2009; Minayeva & Sirin, 2012), com a mínim per l'increment segur de la temperatura i la conseqüent reducció de les reserves de neu a l'estiu (Dong & Menzel, 2020; Morán-Tejeda et al., 2017). En aquest sentit, l'estudi d'Essl et al. (2012) pronostica que el canvi climàtic posarà en risc la gran majoria de les molleres austríaques a finals del segle XXIè, incloent-hi les alpines. A escales de temps curtes, però, el que es nota més són les respostes als canvis d'usos del sòl. A l'alta muntanya, lliure en general de pertorbacions dràstiques com els drenatges i l'explotació de torba, el que afecta més la dinàmica de la vegetació són la intensificació ramadera o bé l'abandonament de la pastura (Garcia-Pausas et al., 2017).

Els patrons ecològics, per tant, es manifesten a diferents escales tant temporals com espacials (Fig. 8) i l'aproximació al seu estudi s'hi ha d'ajustar. Per exemple, el desenvolupament d'una planta perenne (*plant performance*: germinació, fenologia, rebrot...) és visible entre anys consecutius i fins i tot dins un mateix període de creixement. La dinàmica de tancament de petits espais nus de vegetació (*gaps*) va directament lligada al desenvolupament i reproducció de les plantes entre temporades de creixement consecutives. Tot i així, com més gran sigui l'àrea de mostreig, més temps es requerirà per observar canvis significatius en la colonització d'aquests espais (capítol 2). Hem registrat canvis en l'estructura de les comunitats, la successió vegetal i la dinàmica del paisatge gràcies als treballs dels capítols 2 i 3, amb escales de mostreig que van d'uns pocs centímetres a l'àrea que ocupa tota una mollera. De la mateixa manera, les escales temporals d'observació dels resultats van d'un any a unes quantes desenes d'anys. Finalment, escales de mostreig regional ens permeten interpretar, o inferir, els patrons de diversitat a una escala temporal molt més llarga (fins a desenes de milers d'anys). Amb tot plegat, poques aproximacions experimentals treballen a escales temporals curtes i espacials molt àmplies a la vegada, i viceversa. Una excepció en seria, per exemple, el seguiment fenològic repetitiu de píxels mitjançant sensors remots, ja que permet observar canvis molt ràpids en àrees molt àmplies (Reed et al., 2009). En contraposició, la paleoecologia estudia l'evolució del paisatge a escales temporals molt llargues a través de l'anàlisi de mostres en un punt de mostreig molt concret (Birks & Birks, 1980).
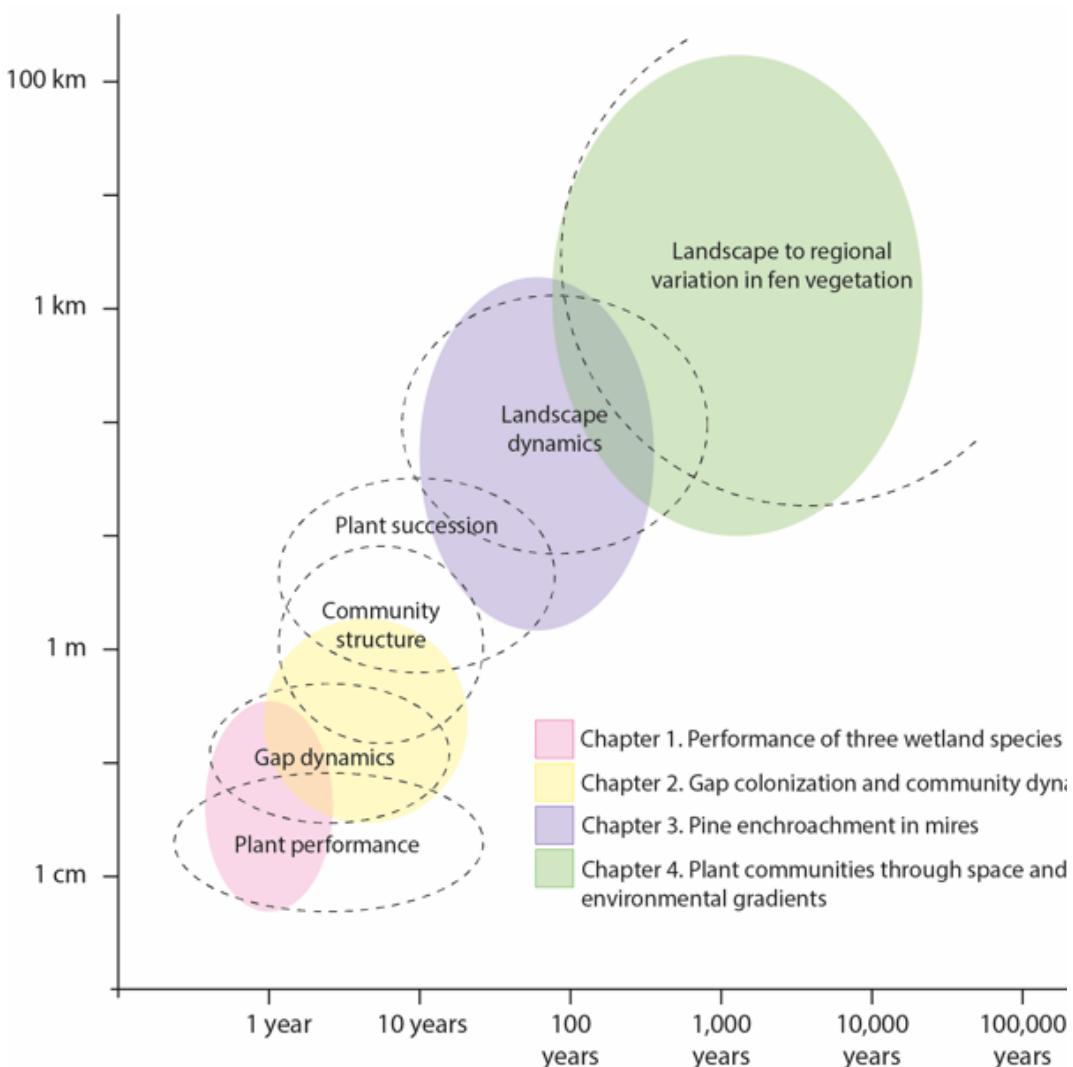
Fig. 8. Coordenades generals d'espai i temps en les que tenen lloc els diferents patrons ecològics (línies discontínues) als diferents capítols de la memòria (fons de color).

Gestió i conservació

Als paisatges de muntanya els ambients humits són escassos perquè hi ha poques àrees on es pugui acumular aigua. Els pocs indrets on això passa contenen una biodiversitat molt diferent de la dels hàbitats que els envolten (vegeu, per exemple, Tukiainen et al., 2019). Pel que fa a les plantes vasculars i als briòfits, la diversitat que contenen és elevada, però sobretot destaquen moltes espècies que no es troben enlloc més del paisatge (Horsáková et al., 2018; Jiménez-Alfaro et al., 2012) i que per tant enriqueixen de manera significativa la biodiversitat a escales de paisatge a regional. A més de la pròpia riquesa en espècies, les molleres de muntanya ofereixen diversos serveis ecosistèmics, que van des d'una certa regulació de la circulació de l'aigua, al manteniment d'altra biodiversitat associada, i als usos recreatius i estètics (Mitsch et al., 2015). Per tots aquests valors, els hàbitats humits són una prioritat de conservació (van Diggelen et al., 2006). Si, a més a més, tenim en compte que encaren amenaces diverses

(Joosten et al., 2017), com els canvis en els usos del sòl i la possible baixada dels nivells freàtics, i que es tracta d'ambients fràgils (Joosten et al., 2017), no és sorprenent que estiguin a l'agenda dels gestors del territori (LIFE+ LimnoPirineus, 2014; LIFE Tremedal, 2015).

D'altra banda, cal tenir en compte que a escala mundial, les torberes degradades emeten un 5% de les emissions de CO_2 d'origen antròpic (Bonn et al., 2016). A l'Europa temperada, la majoria de torberes han estat degradades degut a canvis d'usos del sòl en els darrers 150 anys (Tanneberger et al., 2021). La restauració de les molleres pot mitigar els efectes del canvi climàtic i contribuir a l'adaptació dels hàbitats de mollera a l'escalfament global. A més, fa disminuir la vulnerabilitat de les pròpies molleres a canvis ambientals. En aquest sentit, la restauració de les molleres és una bona solució basada en la natura (*nature-based solution*) per assegurar el manteniment dels serveis ecosistèmics a escala global (Bonn et al., 2016). A la vegada, els coneixements científics són claus per assegurar projectes de restauració exitosos (el que es coneix com a gestió basada en la ciència, o *science-based management*). Combinar projectes de restauració amb coneixements acadèmics i coneixements pràctics previs (*know-how*; Hulme, 2014) permetrà comprendre les trajectòries de canvi de la biodiversitat, i encaminarà la gestió ambiental existosa de les molleres més exitosa en el futur. La retroalimentació de les dues vessants ha de permetre una gestió dels hàbitats que pugui assegurar els serveis ecosistèmics i el valor intrínsec de les comunitats vegetals alhora (Bonn et al., 2016).

Als Pirineus, la majoria de les molleres d'alta muntanya es troben en zones protegides sota alguna figura de protecció, com la Xarxa Natura 2000, Parcs Naturals i Parcs Nacionals de les diferents administracions i països –encara que a altituds inferiors, molts aiguamolls propers a zones urbanes no tenen cap mesura de protecció. En general, l'aprofitament que se'n fa no va més enllà de la ramaderia extensiva i de l'ús lúdic d'excursionistes. Excepcions notables són la producció d'energia, la captació d'aigua i les pistes d'esquí alpí (Catalan et al., 1997; Joosten et al., 2017; Krautzer et al., 2012). De fet, només el 56% de les molleres de les muntanyes del centre i del sud d'Europa es troben en àrees amb algun tipus de protecció, i es calcula que el 32% estan degradades (Tanneberger et al., 2021). Aquest fet magnifica la importància de mantenir les molleres pirinenques en un bon estat de conservació i supervisades per òrgans gestors. En aquestes circumstàncies és prioritari assegurar el bon estat de conservació de les molleres poc alterades, no afectades per modificacions hidrològiques (drenatges, preses, aprofitament hidràulic) i sense sobre-freqüentació ramadera actual (com també reclama als Alps Spitale, 2021). A més, és important assegurar que un increment del pas d'excursionistes o corredors no malmeti la coberta vegetal d'hàbitats especialment sensibles (coixins i catifes d'esfagnes i comunitats amb un nivell freàtic molt alt).

Tenint en compte els resultats principals del capítol 2 d'aquesta memòria, l'exclusió ramadera durant tant sols una temporada de creixement ja és suficient perquè s'acceleri la colonització de les zones sense vegetació o amb l'estructura subterrània molt malmesa,

i per assegurar un desenvolupament major dels òrgans aeris de les plantes vasculars. En aquest sentit, l'estat de conservació de molleres molt freqüentades per bestiar domèstic podria millorar gràcies a la redirecció consensuada de ramats o al tancament temporal de zones concretes. Per exemple, evitar la pastura durant algunes setmanes claus afavoriria la reproducció sexual de les plantes (Fig. 9). També, evitar la pastura extensiva durant algunes temporades de creixement afavoriria la recuperació de la vegetació a les zones més malmeses. En cas de voler restaurar comunitats de mollera molt malmeses pel trepig (*pugging*), es pot facilitar la colonització de sòls remoguts mitjançant el trasplantament de graminoides rizomatoses amb segments internodals llargs i comunes; per exemple *Carex nigra* o *Agrostis stolonifera*. En canvi, la sembra de llavors seria una mesura indicada només en àrees danyades extenses i protegides del trepig.

Segons les conclusions del capítol 1, el transplantament de plantes rizomatoses és una mesura útil per la restauració de sorrals circumdants als estanys d'alta muntanya, després de l'eliminació o rebaixament d'una presa artificial. L'establiment ràpid de les plantes –trasplantades en estadi adult– assegura la fixació del sòl i l'inici de la successió vegetal. En aquest sentit, *Juncus filiformis* ha resultat ser una bona pionera, amb creixement ràpid si bé amb baixa habilitat competitiva, fet que assegura l'enriquiment espontani de les comunitats al llarg del temps.

Fig. 9. Les plantes de comunitats protegides de l'herviborisme tenen un èxit superior en la floració i fructificació, cosa que promou una major pluja de llavors i taxes més elevades de dispersió d'espècies de mollera. A la imatge, tancat d'exclusió ramadera a Bedet, juliol de 2019. Fotografia de Nil Escolà.

En relació a l'embosquinament, preveiem que continuï la colonització progressiva de pins a les molleres de muntanya (capítol 3). Per això és important estudiar quins efectes té l'entrada de pins sobre les comunitats de mollera, i així valorar l'amenaça real d'aquesta dinàmica per al seu estat de conservació. En aquest sentit, els resultats de treballs previs d'altres regions són poc clars (Frankl & Schmeidl, 2000; Ohlson et al., 2001; Woziwoda & Kopeć, 2014). De la mateixa manera, és important poder preveure quins efectes tindria l'eliminació brusca dels pins sobre la hidrologia i sobre la composició florística de les molleres, tant a curt com a mitjà termini. Davant la dinàmica paisatgística esperada, calen nous estudis per poder prendre decisions de conservació i gestió fonamentades.

Per a la conservació d'hàbitats o espècies amenaçades, és important prioritzar allò que és únic i allò que és fràgil a l'àrea biogeogràfica (Le Berre et al., 2019). En aquest sentit, és molt recomanable protegir poblacions d'espècies molt rares als Pirineus com ara *Carex lasiocarpa, Equisetum fluviatile* o *Sphagnum lindbergii*, entre d'altres. També, algunes molleres tenen un alt valor patrimonial per l'extensió i qualitat de conservació dels seus hàbitats, per la seva antiguitat i per les espècies que contenen (Pérez-Haase & Ninot, 2017). Tot i així, al capítol 4 hem constatat que la biodiversitat de les molleres alpines només s'explica gràcies a l'especificitat de cada mollera en concret, sumades al llarg de la metacomunitat. Per tant, conservar els hàbitats de mollera passa no només per preservar unes poques molleres intrínsecament interessants, sinó per protegir el conjunt de sistemes a una escala geogràfica més àmplia.

Conclusions

Catuarta. Fotografia d'Eulàlia Pladevall.

Conclusions

Als capítols precedents hem estudiat la dinàmica de la vegetació en molleres alpines a escales temporals i espacials contrastades. Els resultats obtinguts ajuden a entendre quines amenaces reals de conservació tenen aquests hàbitats als Pirineus, i com preservar la seva biodiversitat i les seves funcions ecosistèmiques a escales locals i regionals. Els estudis realitzats ajuden a preveure la resposta de les comunitats als canvis ambientals i d'usos del sòl. Seguidament enumerem les principals conclusions que s'extreuen dels experiments i estudis realitzats.

1. *Carex nigra, Carex rostrata* i *Juncus filiformis* tenen capacitats competitives lleugerament diferents, que no varien en funció del nivell freàtic al que se sotmeten. *J. filiformis* és una planta pionera indicada per iniciar la successió vegetal en la recreació de molleres, ja que té taxes de creixement elevades, però és poc competitiva. En canvi, *C. rostrata* és més competitiva i prefereix sòls inundats, on esdevé una bona colonitzadora per expansió lateral dels clons.

2. La restauració de comunitats utilitzant la sembra de llavors només és recomanable en àrees sense vegetació establerta i no subjectes a períodes d'inundació prolongats. La competència per la llum atura el desenvolupament de les plàntules de *C. nigra*, mentre que individus adults de la mateixa espècie s'estableixen exitosament a nivells freàtics contrastats i amb competència interespecífica. El desenvolupament d'òrgans de creixement clonal assegura l'expansió de la població a mitjà termini.

3. Les relacions interespecífiques entre plantes rizomatoses afecten proporcionalment tant el compartiment aeri com els òrgans de creixement clonal subterranis. Cal tenir en compte, però, que els experiments de pocs mesos de durada són insuficients per valorar la inversió de les plantes rizomatoses en el seu creixement clonal.

4. En terminis curts de temps, els claps sense vegetació produïts pel pas del bestiar domèstic es recuperen a velocitats similars, independentment de la pressió ramadera que suporti una mollera. Aquests claps promouen la dinàmica de la vegetació però no contribueixen significativament a la riquesa d'espècies de les molleres. La recuperació de la coberta vegetal està protagonitzada principalment per l'expansió lateral de plantes clonals i per briòfits, i no s'assoleix després de dos anys. Tot i així, l'exclusió ramadera evita la creació de nous claps.

5.   L'exclusió ramadera accelera la recuperació de la coberta vegetal (de plantes vasculars i briòfits) als sòls remoguts, que ocupen àrees àmplies a les molleres subalpines. A més, l'estructura de la vegetació de les comunitats denses canvia a curt termini, amb una alçada de la vegetació herbàcia i una acumulació de fullaraca molt superiors. Els canvis en la diversitat vegetal i en l'abundància de briòfits i herbes no són detectables després de dos anys d'exclusió ramadera.

6.   Des de la segona meitat dels segle XXè, el nombre de molleres dels Pirineus centrals que contenen pins (*Pinus uncinata*) ha incrementat un 136%, i la densitat de pins ha incrementat al 82% de molleres que ja en tenien. Tot i així, la majoria de molleres no contenen arbres. La taxa de creixement dels pins a les molleres canvia a distàncies molt curtes (pocs metres), però és menor que en altres hàbitats propers sota les mateixes condicions climàtiques.

7.   Tot i que el pi negre prefereix sòls ben drenats, esperem que l'establiment de pins incrementi a les molleres, com també ho fa a altres hàbitats pirinencs oberts. Les molleres susceptibles d'experimentar més increment de pins són aquelles que estan a l'estatge subalpí i envoltades de pinedes, i que tenen una pressió ramadera més baixa.

8.   Cada sistema de molleres té un *pool* florístic local particular, més enllà de les seves característiques ambientals i geològiques. Aquesta singularitat específica s'explica per múltiples factors històrics propis de cada mollera i geogràfics. A més, l'efecte prioritari inhibidor té un paper important en la construcció de les comunitats de mollera, ja que espècies diferents amb atributs funcionals similars es reemplacen entre comunitats diferents.

9.   La biodiversitat de les molleres alpines varia en primer lloc en funció del sistema de molleres on es trobi la comunitat i de les característiques ecològiques locals concretes; i en segon lloc, varia en funció dels factors geològics, espacials i climàtics. La diversitat beta taxonòmica, filogenètica i funcional és només parcialment congruent en una àrea determinada.

10.   Els patrons de biodiversitat de les molleres alpines són el resultat de la combinació de múltiples processos que ocorren a diferents escales temporals (des d'un any fins a mil·lennis) i espacials (des de centímetres fins a escales regionals, i des dels micro-hàbitats d'una mollera al *pool* d'espècies regional). Malgrat que els canvis en la vegetació de molleres alpines siguin lents, la dinàmica de la vegetació resulta molt aparent en períodes curts de temps quan s'observen els canvis a escales de detall.

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