Universidad Zaragoza
1542

Tesis Doctoral

Las perturbaciones de jabalí en los pastos alpinos del Pirineo Central: una aproximación multiescalar

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2011

Repositorio de la Universidad de Zaragoza – Zaguan http://zaguan.unizar.es

TESIS DOCTORAL

LAS PERTURBACIONES DE JABALÍ EN LOS PASTOS ALPINOS DEL PIRINEO CENTRAL: UNA APROXIMACIÓN MULTIESCALAR

Memoria presentada por **Guillermo Bueno González** para optar al grado de Doctor en Veterinaria por la Universidad de Zaragoza

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Esta tesis, de acuerdo con el informe correspondiente, autorizado por los directores de la tesis y el Órgano Responsable del Programa de Doctorado, se presenta en formato de **compendio de publicaciones científicas**.

Los siguientes trabajos integrantes de esta memoria de tesis doctoral han sido publicados o aceptados para su publicación en revistas científicas:

- **BUENO, C. G.**; BARRIO, I.C.; GARCIA-GONZÁLEZ, R; GÓMEZ-GARCIA, D. , ALADOS, C.L. Assessment of wild boar rooting in Pyrenean alpine grasslands from pastoral and ecological points of view. Pirineos (in press; fecha de aceptación: 16-Noviembre-2010)

- **BUENO, C. G.**; REINÉ, R.; ALADOS, C.L.; GÓMEZ-GARCIA, D. Effects of large disturbances on alpine soil seed banks in Pyrenean grasslands. *Basic and Applied Ecology* (in press; fecha de aceptación: 16-Diciembre-2011)

- **BUENO, C.G.**; BARRIO, I.C.; GARCIA-GONZÁLEZ, R; ALADOS, C.L. & GÓMEZ-GARCIA, D. (2010). Does wild boar rooting affect livestock grazing areas in alpine grasslands? European Journal of Wildlife Research. 56(5): 765-770.

- **BUENO, C.G.**; ALADOS, C.L.; GÓMEZ-GARCIA, D., BARRIO, I.C. & GARCIA-GONZÁLEZ, R. (2009). Understanding the main factors in the extent and distribution of wild boar rooting on alpine grasslands. *Journal of Zoology* 279(2) 195:202.

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Resumen

Las poblaciones de jabalí han ido en aumento desde los años sesenta en casi todo su rango de distribución, lo que ha conllevado un incremento a su vez de sus perturbaciones. La principal perturbación que el suido ocasiona son las hozaduras, que consisten en voltear la cobertura vegetal de los pastos en busca de recursos alimenticios subterráneos. A pesar de su potencial incidencia, poco se conoce sobre su impacto en algunos hábitats sensibles a remociones en el suelo, tales como los pastos alpinos y subalpinos. En este trabajo doctoral se analizan los efectos principales de las hozaduras de jabalí en la estructura del paisaje vegetal y su uso ganadero, así como su efecto a nivel de comunidad, en las propiedades edáficas, los bancos de semillas y la flora. Finalmente se evalúa su efecto en términos de valores ecológicos y pastorales de los pastos alpinos pirenaicos a los niveles de organización estudiados: paisaje, comunidad y especies-grupos funcionales.

A escala de paisaje se cartografiaron las hozaduras en tres zonas de estudio representativas del Pirineo Central: Puerto de Aisa, Montaña de Sesa y Góriz (Góriz bajo y la Estiva), con una extensión total de 5103 hectáreas. Cerca de un 7% de los pastos alpinos estudiados resultaron estar perturbados. Además el análisis multivariante de las variables ambientales en relación al sitio de hozadura, sugiere que la selección del jabalí está determinada por tres factores de importancia decreciente: el hábitat de alimentación, las condiciones del suelo para ser *hozado* (grado de humedad) y la gestión humana, en términos de manejo pastoral.

Además se cuantificó la extensión afectada a las áreas de pastoreo estival, comparando las áreas de pastoreo vacuno y ovino con la cartografía de perturbaciones. El área de pastoreo afectada fue de un 16%, afectando más al ganado vacuno (20%) que al ovino (13%) centrándose las perturbaciones principalmente en intensidades intermedias de pastoreo. Dicho resultado sugiere un efecto negativo potencial a las economías locales basadas en parte en la ganadería extensiva, actualmente en declive.

A nivel de comunidad vegetal y de especies-grupos funcionales, se analizaron las propiedades del suelo, los bancos de semillas y la composición florística de las cinco comunidades más perturbadas por las hozaduras, comparando zonas perturbadas con zonas no perturbadas. El suelo dentro de las hozaduras mostró comparativamente mayores tasas de nitrógeno total y nitrato, y densidad aparente mostrando a su vez una disminución en la concentración de cationes (Ca^{+2}, Na^{+} y Mg^{+2}) y fósforo. Dichos resultados sugieren un aumento temporal de fertilidad y un posible lavado rápido de los cationes liberados en el suelo lo que puede explicar dichas diferencias. Por su parte, los bancos de semillas que se obtuvieron mostraron una densidad muy baja de semillas en general, donde los bancos de semillas persistentes a largo plazo, fueron los más abundantes. El efecto de volteado del suelo de la actividad hozadora transformó dichos bancos en bancos de semillas persistentes a corto plazo o temporales. Dicho cambio ubica un mayor número de semillas en superficie lo que estimula su germinación. Finalmente en la parte de la afección a la flora y su composición, se utilizó una aproximación multi-escalar para evaluar los cambios de los patrones de diversidad a tres escalas: la diversidad dentro de las comunidades (alfa), y la diversidad entre puntos de muestreo (beta-1) y entre comunidades (beta-2). Además se analizaron los cambios de diversos parámetros de diversidad dentro y fuera de las hozaduras paralelamente en cada comunidad. Finalmente se analizó el efecto de la perturbación en la abundancia de cada especie y grupo funcional. Las hozaduras produjeron una homogenización de la diversidad entre comunidades, incrementando a menor escala la heterogeneidad entre puntos de muestreo dentro de cada comunidad. Por otro lado, todas las comunidades sufrieron una disminución de su diversidad en términos de abundancia, riqueza, diversidad de Shannon, equitatividad y un aumento de dominancia, excepto las comunidades dominadas por gramíneas del género *Festuca* de gran porte: *F. eskia* y *F. paniculata.* Ambas comunidades mostraron propiedades resilientes ante la perturbación en términos de diversidad y dominancia. En cuanto a las especies y grupos cabe destacar un aumento en dicotiledóneas dentro de las hozaduras y un descenso en especies monocotiledóneas graminoides (en especial las gramíneas dominantes).

Por último se evaluó en términos de valor ecológico y pastoral el efecto de las hozaduras en los niveles de organización anteriormente estudiados. Las hozaduras afectaron más seriamente a valores pastorales medios y altos afectando menormente a valores ecológicos. Los grupos funcionales que resultaron más afectados en cuanto a su valor ecológico y pastoral coinciden con los mencionados anteriormente, con una reducción en especies monocotiledóneas graminoides y aumento de especies dicotiledóneas perennes, aunque estas últimas mostraron un aumento menor del valor pastoral en comparación con el aumento en su abundancia indicando el escaso valor pastoral de estas especies propias de la regeneración de las perturbaciones.

En conclusión, las hozaduras de jabalí afectan profundamente a los pastos alpinos pirenaicos, en su extensión y estructura, produciendo un aumento de fertilidad temporal, estimulando los bancos de semillas existentes, y favoreciendo un incremento de la diversidad de grupos funcionales lo que provoca en último término, una alteración de los patrones de diversidad variable a distintas escalas. Desde un punto de vista de la gestión y conservación de estos ambientes, en su mayoría protegidos, las hozaduras no parecen por el momento, tener un grave impacto en los valores ecológicos, pudiendo comprometer quizá los valores pastorales en un futuro cercano.

Summary

Wild boar populations have increased in numbers since the 60s in most of their distribution range, which has as well raised the impact of their disturbances. The most typical disturbance caused by wild boars is rooting, which consists in turning over the soil in search of underground feeding resources. Despite their potential impact on sensitive habitats such as alpine and subalpine grasslands, little is known about the ecological consequences of wild boar rooting. This PhD analyses the main effects of wild boar rooting at the landscape level and at the community level, on soils, soil seed banks and flora. Finally, their impact is evaluated across all scales from an ecological and pastoral point of view.

At the landscape level, wild boar rootings were mapped in three study areas representative of the Spanish Central Pyrenees: Puerto de Aisa, Montaña de Sesa and Góriz (5103 ha in total). Nearly 7% of the studied area was affected by wild boar disturbances. Rooting selection seems to be determined by a hierarchical suite of factors: the feeding habitat, soil conditions to be rooted (soil moisture) and human management in terms of livestock management. In addition, the grazing area affected *by wild boar rooting was estimated to be around 16%, affecting more cattle (20%) than sheep (13%) grazing areas, in sites with intermediate stocking rates. This result suggests a potential negative impact of wild boars on the already declining extensive livestock husbandry.*

At the community and species-functional group level, soil properties, soil seed banks and floristic composition of the five most disturbed grasslands were compared within and outside disturbances. Soils within disturbances had more nitrate and total nitrogen content, a higher bulk density and lower cation (Ca^{+2}, Na^{+} y Mg^{+2}) and phosphorus concentrations. These results suggest a temporal increase in fertility and a quick leaching of cations. Overall, soil seed banks were poor, being long term persistent the most abundant type. Wild boar rooting, by turning over soil turfs, exposed more seeds from these seed banks to germination conditions. Regarding floristic composition, changes in diversity were analyzed at three levels: within communities (alpha), among sampling sites (beta-1) and among communities (beta-2). Other diversity measures were compared within and outside disturbances in each community, and the effects of disturbance on each species and functional group were assessed. Wild boar rooting homogenized diversity among communities and increased heterogeneity among samples within each community. Disturbances reduced species abundance, richness, Shannon's diversity and evenness, and increased dominance, except in tall-tussock fescue communities, which were more resilient to disturbances. With regards to species, dicots increased within wild boar rooting and graminoids decreased, particularly the dominant grasses of each community.

Finally, wild boar rooting affected more moderate-to-high pastoral values and lower ecological values. Functional groups contributing to ecological and pastoral values followed the same trends as above, indicating a low pastoral value of the species involved in wild boar rooting regeneration.

In conclusion, wild boar rooting affects alpine grasslands in their extent and structure, temporarily increasing fertility, stimulating soil seed banks and favouring an increase in functional group diversity. From a management and conservation point of view, wild boar rooting does not seem to be a current threat for ecological values in these grasslands, but it may compromise grazing activities in the near future.

Capítulo 0. Introducción general

Los pastos alpinos

Definiciones

Dada la gran variedad de usos humanos que han configurado los actuales ambientes supraforestales, dichos ambientes han recibido varias denominaciones. Éstas a su vez se han aplicado de forma diferente en distintos sistemas montañosos, lo que ha conformado una enorme diversidad de términos que puede llevar a equívocos, siendo difícil de abordar sin previa aclaración. Empezamos pues este trabajo definiendo los conceptos de: "pasto" y "alpino", algunos conceptos relacionados, y presentando un esquema conceptual equivalente en lengua inglesa (Tabla 1).

¿Qué son los pastos?

Según la Sociedad Española para el Estudio de los Pastos (SEEP), por pasto debiéramos entender "cualquier recurso vegetal que sirve de alimento al ganado, bien en pastoreo o bien como forraje" (Ferrer et al 2001). Los pastos serían por tanto extensiones que contienen recursos vegetales nutricios para el ganado. Los pastos serían naturales si no han sido sembrados por el hombre, es decir si están formados por una flora espontánea, aunque en la práctica suelen requerir una actuación más o menos intensa por parte del hombre (San Miguel 2001). Para el caso de los ambientes supraforestales, la SEEP además define los pastos de puerto como "cualquier recurso de verano que se aprovecha por pastoreo extensivo. Se ubica en los pisos alpino y subalpino (incluso en el montano) y en los supra-, oro- y crioro-mediterráneo. Generalmente son pastos con relativa humedad y elevada densidad, que reciben ganado trashumante o transterminante" (Ferrer et al 2001).

¿Qué es alpino?

La definición de alpino ha sido y es también muy discutida, ya que su aplicación ha recaído en muy diferentes zonas montañosas del planeta. Para este estudio hemos seguido las recomendaciones de Körner (1999), adoptadas y ampliadas por Grabherr et al. (2003) y Nagy et al. (2009). En dichas obras se establece la zona alpina con la "línea de árboles" (*treeline*) como límite inferior y único. La línea de árboles es definida como aquella zona, entre el borde superior del bosque denso y los últimos individuos de árboles en los gradientes de altitud. Los mencionados autores desaconsejan además el uso del término "subalpino". Por un lado entienden que dicha zona correspondería a la transición o ecotono entre el bosque montano superior y la zona alpina, y no a una banda de vegetación característica en la amplitud de todos los sistemas de montaña. Además dicho término ha resultado muy ambiguo en su aplicación, no siendo ampliamente utilizado fuera del continente Europeo (Körner 1999b; Grabherr 2003; Nagy and Grabherr 2009b). En cambio, proponen la distinción de dos zonas alpinas: la superior, referida a la dominada por comunidades herbáceas permanentes de especies graminoides, y la inferior, dominada por arbustos enanos (Grabherr 2003; Nagy and Grabherr 2009b).

Término en inglés	Definición	Término en castellano
forage	cualquier recurso vegetal que sirve de alimento al ganado, bien en pastoreo o bien como forraje	forraje
meadow	comunidad vegetal espontánea densa y húmeda, siempre verde, producida por el hombre o la acción del pastoreo	prado
pastureland	cultivo forrajero constituido fundamentalmente por dos o más especies de gramíneas y leguminosas, que puede ser aprovechado por siega o pastoreo de forma indistinta	pradera de siega
prairie	comunidad natural dominada por especies herbáceas que, por efecto del clima, se secan o agostan en verano. Término francés para “pasto”, que se aplica a las Grandes Praderas de Norte América	pastizal
rangeland	comunidad natural dominada por especies herbáceas que, por efecto del clima, se secan o agostan en verano. Su densidad es variable y frecuentemente está salpicado de especies leñosas. Se aprovecha mediante pastoreo extensivo. Término americano.	pasto o pastizal

Tabla 1. Equivalencias entre términos en inglés y términos en castellano. Modificado de Ferrer et al (2001) para los términos en castellano, y Forage and Grazing Terminology Committe (1992) para los términos ingleses.

En la práctica, los pastos alpinos del Pirineo son los situados por encima de la línea de árboles, siendo la banda alpina superior las comunidades herbáceas permanentes naturales (pastos de alta-montaña) y la alpina inferior comunidades secundarias de origen forestal o arbustivo (pastos mesofíticos; San Miguel 2001). La banda inferior habría sido progresivamente ganada al bosque o al estrato arbustivo extendiendo los pastos herbáceos mediante actividades pastorales desde la Edad Media (Fillat 2008). En las últimas décadas, el abrupto abandono pastoral está produciendo procesos de matorralización y regeneración forestal que serán comentados a continuación.

Origen e historia de los pastos alpinos

Dos aspectos son fundamentales a la hora de describir la conformación actual de los pastos alpinos. Por un lado, hay que considerar el propio origen de la flora alpina: cómo y en qué condiciones ambientales se han originado y han llegado hasta su distribución actual los elementos florísticos. Y por otro lado, y no menos importante, es necesario considerar la historia de la interacción entre el pasto alpino y los animales herbívoros, modulada por el manejo humano que ha configurado el mosaico actual de comunidades alpinas.

Origen de la flora alpina

Dejando a un lado la compleja historia geológica que desembocó en la emergencia de los actuales Pirineos y la larga evolución de las plantas vasculares que dominan hoy las zonas de estudio, cabe mencionar las glaciaciones cuaternarias, la última (Würm) terminada hace unos 10.000 años, como el evento más influyente en la configuración de los pastos alpinos. Las glaciaciones no eliminaban totalmente la flora, pero sí la restringían a refugios micro-climáticos (*nunataks*) desde donde volvía a colonizar el territorio en los periodos interglaciares. Así, se formaban corredores de migración que permitieron el flujo de plantas, principalmente desde las regiones más septentrionales y las cordilleras montañosas de mayor tamaño hacia los nuevos territorios conquistados periódicamente por el hielo. Estos fenómenos de migración de especies, se muestran en la distribución actual de algunos grupos como el género asiático *Leontopodium* que alcanzó los Alpes y Pirineos desde los Himalayas (Körner 1999a), mostrando un lógico empobrecimiento de especies a lo largo de la ruta de migración. A su vez, estos procesos desencadenaron la especialización de plantas muy adaptadas localmente a los espacios disponibles, lo que dio origen al elemento endémico, que poseen todas las floras alpinas (Körner 1999a), y que en los Pirineos está muy bien representado en algunos géneros de preferencia saxícola, como *Saxifraga* y *Androsace* (Gómez-García et al 2005).

Por su situación geográfica, en los Pirineos confluyeron dos grandes "grupos corológicos" de flora: el Mediterráneo, desarrollado desde el Terciario y dominante en gran parte de la Península Ibérica, y el Euroasiático o eurosiberiano, que incluye los elementos boreo-alpinos (provenientes de la Península de Escandinavia), atlánticos (de la costa atlántica y las islas británicas) y eurosiberianos (de las estepas y montañas centroeuropeas y asiáticas; Gómez 2008a).

En los Pirineos, así como en el resto de cordilleras alpinas, conforme ascendemos en altitud disminuyen las plantas mediterráneas y aumentan las eurosiberianas; por encima de los 2000 m, las de origen boreo-alpino y los orófitos centroeuropeos cobran ya gran importancia y dominan totalmente por encima de los 2500 m (García and Gómez 2007). El número de especies, al igual que en el resto de las cordilleras mencionadas, muestra su máximo en niveles altitudinales intermedios (1000-1500 m) y disminuye hacia arriba y hacia abajo. No obstante lo anterior, por encima de 2000 m todavía encontramos un número apreciable de especies (Gómez et al 2003a) que todavía cobra mayor relevancia si consideramos la diversidad por unidad de superficie.

Historia de los pastos alpinos

La historia de los pastos alpinos se remonta a los herbívoros salvajes, extintos casi todos ellos en la actualidad, y cuya presencia queda avalada por los restos fósiles pertenecientes a bóvidos y équidos de los últimos miles de años (Sommer and Nadachowski 2006). Cabe suponer que muchas de las especies vegetales que conforman los pastos coevolucionaron con estos herbívoros en los claros de bosque, producidos tras catástrofes naturales (incendios, avalanchas) y mantenidos el por pastoreo durante miles de años. La presencia del hombre en el territorio de estudio se remonta al Paleolítico medio (Bahn 1983), aunque no es hasta finales del Neolítico (3300 a 2500 a.C.), coincidiendo con una época climática calurosa y seca, donde parece generalizado el cuidado y el seguimiento en altura del ganado en el Pirineo (Fillat 2008). Sin embargo, el cambio más notable sucede en la Edad Media (siglos IX-XI), donde la explotación agro-ganadera del territorio se desarrolla en todo su esplendor, cultivando principalmente los fondos de valle y pastoreando las laderas a lo largo de gran parte del año, gracias al gradiente fenológico consecuencia del altitudinal (Gómez 2008a). Este régimen de pastoreo reserva por cuestiones evidentes los pastos alpinos a la época estival. Esta doble utilización del territorio ocasionó una reducción del bosque, principalmente del subalpino pero también del montano, y una expansión de las formaciones herbáceas y arbustivas favorecidas por el fuego y la propia acción de los herbívoros. Desde entonces y a lo largo de los últimos mil años la presencia abundante de ganado doméstico estivante ha sido una constante en todo el Pirineo (Fillat 2008). La ampliación de los pastos y reducción del bosque todavía será más notable en los siglos XVIII y XIX con el incremento de población y la dominación de los usos forestales y agro-ganaderos (Villar 1975). Por el contrario, los cambios más recientes se han manifestado vinculados a un fuerte descenso de la carga ganadera, y a modificaciones de los tipos de gestión, sobre todo en el tipo de ganado estivante, que muestra un descenso del ovino y un aumento del vacuno (García Ruiz and Lasanta Martínez 1990).

A grandes rasgos, los usos del territorio que encontramos en los pastos alpinos del Pirineo son comunes a los que ocurren en otros sistemas montañosos humanizados (Nagy and Grabherr 2009b). Dichos usos históricos han desencadenado procesos de adaptación múltiple en la interacción pasto-herbívoro (Figura 1), y constituyen actualmente uno de los factores principales en la dinámica de pastos, como veremos en los siguientes apartados.

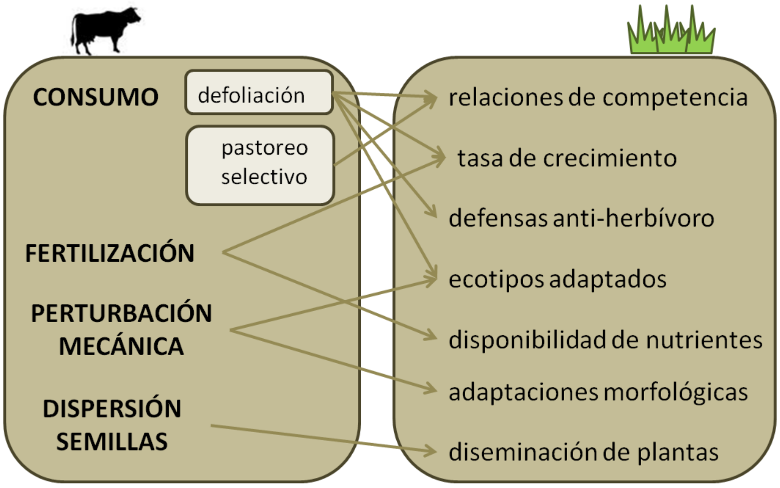

Figura 1. Resumen de las acciones y efectos de los herbívoros sobre el pasto (adaptado de García-González, 2008).

Distribución y composición de los pastos alpinos

Los factores que diferencian los pastos en cuanto a su distribución y composición florística son los que reflejan las necesidades y adaptaciones fisiológicas de cada especie o grupo de especies (disponibilidad y requerimientos de luz, agua, nutrientes, etc). Dada la dificultad de una medición directa de esos factores, se recurre en muchas ocasiones a medidas indirectas a partir de las características del ambiente o "factores abióticos" (principalmente los relacionados con la litología, el suelo, la topografía y el clima), más los que promueven la interacción de especies (facilitación y competencia) y los antrópicos, que reflejan la historia del uso pastoral (Fillat et al 2008; Franklin 2009). La dependencia de la escala espacial de muchos de estos factores ha promovido repetidamente su jerarquización (Tabla 2). Con todo, la complejidad que añaden las posibles interacciones entre los aspectos mencionados, la aparición de procesos estocásticos y su posible actuación a varias escalas, complica extraordinariamente la interpretación de las distribuciones de especies y por tanto de su modelización (Franklin 2009; Nagy and Grabherr 2009a).

Además teniendo en cuenta que los pastos alpinos son un conjunto de comunidades vegetales formadas con un bagaje evolutivo e histórico-adaptativo, el entendimiento en su composición para el Pirineo no sería posible sin distinguir los pastos situados en la zona alpina superior que se ubica, por término medio, sobre los 2300 m y los situados por debajo de dicha altitud, en la zona alpina inferior (Gómez et al 2003a). Los primeros consisten en comunidades naturales y permanentes, es decir sin posibilidad de sucesión en las actuales condiciones climáticas hacia formaciones arbustivas y arbóreas. Las segundas, por el contrario, son comunidades secundarias y, por tanto, con tendencia natural a su colonización arbustiva y arbórea tras la disminución o cese de la actividad ganadera.

	Escala (ámbito de acción)						
Factor causal ambiental	Global (>10000km)	Continental (2000-10000km)	Regional (200-2000km)	Paisaje (10-200km)	Local (1-10km)	Sitio (10-1000m)	Micrositio (<10m)
Clima	X	X	X				
Topografía			X	X	X		
Uso del suelo				X	X	X	
Tipo de suelo					X	X	
Interacciones bióticas					X	X	X

Tabla 2. Esquema jerárquico de los factores que afectan a la distribución de especies en el espacio, y su ámbito de acción (escala). Adaptado de Franklin (2009) y Pearson and Dawson (2003).

La distinción anterior atañe pues al origen y vocación evolutiva de los pastos y resulta trascendental en el estudio de las perturbaciones, al enmarcar de manera diferencial la dinámica posterior a la afección al suelo y las comunidades vegetales. Además, hay que considerar que con la altitud, aumenta la influencia de los factores abióticos (principalmente el clima y la topografía) a la par que disminuye la de los herbívoros y se ralentizan los procesos de colonización vegetal y en general los cambios en la estructura de las comunidades, por lo que la incidencia de las perturbaciones perdura más allá de lo que sucede a menor altitud (Gómez 2008a).

Manejo y conservación de pastos alpinos

El manejo y la conservación de los pastos, como de cualquier elemento natural, debe ir precedido por la definición de los elementos que se quiere conservar y del tipo de manejo más adecuado para ello (Sutherland and Hill 1995). A este respecto las evaluaciones ecológicas y económicas de los ecosistemas nos dan una referencia de los valores de las comunidades para la sociedad, a través de los bienes y servicios que nos proporcionan (Carpenter et al 2006). Desde un punto de vista ecológico las valoraciones (por ejemplo las evaluaciones de impacto ambiental) tienen que sopesar las actuaciones antrópicas y sus influencias indirectas sobre el equilibrio dinámico de los sistemas. Así, resulta de gran interés prever las modificaciones de los ecosistemas que acarreen procesos irreversibles en su organización, para poder evitar su degradación y, por ende, seguir disfrutando de los bienes y servicios que nos proporcionan (Carpenter et al 2006). El ecosistema de los pastos alpinos provee, entre otros bienes y servicios, calidad y pureza del agua, calidad de productos derivados de la ganadería extensiva y unos sistemas de manejo adaptados al medio, que además constituyen vehículos de trasmisión cultural. Además, el paisaje resultante tiene un valor añadido inherente de carácter lúdico, estético y espiritual (Margules and User 1981; Millennium Ecosystem Assessment Board 2005).

El manejo de los pastos en las montañas alpinas aprovecha la amplitud fenológica que promueve el marcado gradiente altitudinal de más de 2000 m y que se traduce en un largo periodo de aprovechamiento que incluye el verano y gran parte de la primavera y el otoño. Paralelo al gradiente de altitud puede reconocerse el de “intensidad de utilización”, que disminuye de abajo hacia arriba por la mayor severidad del clima y la topografía y el aumento de la distancia a las zonas habitadas (García-González et al 1990). Así, la media montaña presenta una mayor antropización que la alta, y en ésta, el nivel inferior se ha modificado más profundamente que el más elevado. La principal afección humana para el aprovechamiento ganadero se ha producido mediante la corta, la quema y el propio pastoreo. En todos los sistemas pastorales humanizados, tanto la corta como la quema han sido actividades de refuerzo al pastoreo (Ausden and Treweek 1995) con el fin de frenar la invasión de arbustos y árboles impuesta por la sucesión natural.

Respecto al efecto del pastoreo sobre el pasto, hay que señalar que tanto o más importante que el propio consumo vegetal (*grazing*) es el aporte de fertilidad a través de los excrementos y el pisoteo; los tres factores se ejercen de manera diferencial sobre las comunidades vegetales y, junto a la topografía, dan lugar a una marcada heterogeneidad a escala de paisaje. El tipo de gestión pastoral se ha ajustado a lo largo de la historia a las características particulares de los territorios y zonas pastorales, combinando las capacidades y necesidades de los gestores con las potencialidades productivas de los pastos y procurando siempre, por imperativo socioeconómico, un marco de sostenibilidad, mucho antes de que dicho concepto se convirtiera en lugar común (Ausden and Treweek 1995; Fillat et al 2008). Tanto infra-pastoreo como sobrepastoreo acarrean serios problemas de manejo y conservación (San Miguel 2001) y la carga adecuada muestra, por depender de ellas, tanta variabilidad como las variables topográficas, climáticas o de la vegetación.

El periodo vegetativo constituye un límite para el aprovechamiento de la vegetación y es particularmente estricto en las zonas alpinas; los pastos de este nivel sólo son aprovechables en la época libre de cobertura nival, que por ejemplo en el Parque Nacional de Ordesa a 2000 m de altitud, tiene en promedio 120 días (Del Barrio et al 1990). Por otra parte, la estructura y dinámica de los pastos queda determinada por el tipo de pastoreo y, en concreto, por el de los herbívoros que lo practican. No viene aquí al caso hacer mención de los distintos regímenes de pastoreo manifestados por el ganado lanar, caballar o vacuno, relacionado tanto por sus características morfo-fisiológicas como comportamentales, pero sí que es importante señalar el impacto sobre la vegetación que, al margen de su consumo, ocasionan. Por ejemplo, los grandes herbívoros (caballos y vacas) provocan huecos o agujeros (*gaps*) por pisoteo que pueden promover la expansión de determinadas especies. Esto se ha descrito en pastos británicos, para algunos cardos (*Cirsium sp.*) y otras especies tolerantes al pisoteo que aparecen en mayor número en las áreas de influencia del ganado (Ausden and Treweek 1995). Por su parte, el ganado ovino tiene un menor impacto en su pisada, pero su agrupamiento por manejo o comportamiento en majadas, acaloraderos, abrevaderos, etc. provoca una importante remoción del suelo y la vegetación que a veces se resuelve en cambios drásticos, dando lugar a las denominadas “comunidades nitrófilas”.

El objetivo actual de manejo de los pastos debería perseguir, por tanto, ajustar los requerimientos nutricionales del ganado con la oferta vegetal amplia y heterogénea que ofrece la montaña, tratando de conservar en la gestión los mecanismos y automatismos fruto de un ajuste secular (Montserrat 1964). Dicho objetivo requiere la estima de la capacidad de carga de los distintos territorios, teniendo en cuenta la productividad y calidad forrajera de cada tipo de pasto. A su vez es necesario añadir una valoración ecológica para medir el impacto en el funcionamiento del sistema evaluando los cambios en la diversidad y estructura de los pastos. En este último sentido es muy reseñable el método de evaluación desarrollado en Instituto Pirenaico de Ecología (Fillat et al 2008), con potencial uso en gestión del territorio y en la demarcación de lugares tanto ecológicamente como pastoralmente estratégicos para la conservación de los ecosistemas y sus usos (San Miguel 2001).

Dinámica de los pastos: el papel de la perturbación

La dinámica de los pastos estudia los cambios de la estructura de las comunidades que los conforman a lo largo del tiempo, en relación con los factores ambientales (Whittaker 1972). Ya se han comentado algunos de los factores que influyen en la distribución de las especies, siendo a su vez la variación en uno o varios de ellos lo que determina ciertos cambios en la estructura de los pastos. Dejando a un lado la influencia de las variaciones del clima a largo plazo que han promovido las grandes migraciones de la flora, los cambios más relevantes que promueven la dinámica de la vegetación son los cambios de gestión del pastoreo que comentaremos a continuación, y las perturbaciones, objeto central de la presente memoria doctoral.

El pastoreo produce en sus dos extremos cambios radicales. Por un lado el exceso de carga (sobrepastoreo) ocasiona una sobre-fertilización por el aporte excesivo de materia orgánica, con una alta acumulación de nutrientes (N, P, K, etc) que son tóxicas para muchas plantas a partir de determinadas concentraciones (Montserrat 1964). Como consecuencia, se produce una sustitución de las plantas y comunidades originales por otras resistentes tanto al incremento en nutrientes como al pisoteo que lo acompaña. En el otro extremo, el descenso o la desaparición del ganado, acarrea la disminución de la fertilidad y provoca un cambio en la estructura de los pastos, al ser favorecidas especies más resistentes al estrés ambiental y menos competitivas por los recursos (Montserrat 1964; Grime 1979). En las zonas de potencial forestal, la disminución de la presión de herbivoría favorece una lignificación progresiva por aumento de la cubierta de matorral en primer término y de la recolonización del bosque, procesos que se ven alentados o retardados, una vez más, por las condiciones edáficas y las características climáticas y topográficas, tal como ha sido recientemente estudiado en el P.N. de Ordesa-Monte Perdido (Komac 2010). Cabe recordar que la topografía juega también un importante papel en la montaña a mediana y pequeña escala al condicionar las características del suelo y del clima, dando lugar a variantes más o menos locales (topoclimas, microclimas) que en pocos metros o incluso centímetros de distancia, pueden mostrar características muy diferentes en fertilidad, capacidad de retención hídrica, período de innivación, de sequía, régimen de temperaturas, etc. La topografía se torna más intrincada con el aumento de la altitud, lo que se traduce en un aumento de la heterogeneidad vegetal que queda reflejado en un complejo mosaico de comunidades vegetales que cede su dominio a las formaciones rocosas (gleras, cantiles) sobre los 2300-2500 m de altitud.

Por último, las perturbaciones ocasionan el mayor impacto sobre la vegetación si tenemos a la vez en cuenta su carácter drástico y concentrado en el tiempo. En el caso de los pastos alpinos las perturbaciones que conlleven modificaciones en la estructura del suelo (*soil disturbances*) son verdaderamente destacables para la conservación (García-González 2008). La lenta velocidad de respuesta de las plantas, limitadas por su corto periodo vegetativo, hace que los nutrientes del suelo puedan perderse o degradarse, bien por lixiviación o bien por alteraciones de su estructura física y biótica (Vitousek 1985; Körner 1999b). Dicha degradación es debida a la pérdida de protección y tampón térmico que supone la cobertura vegetal para el suelo. De cualquier forma, como sucede en otros sistemas, la gravedad de la perturbación queda definida por su extensión y otras propiedades que, como contaremos a continuación, son de gran relevancia para conocer y evaluar su impacto.

Perturbación en pastos alpinos

Definición y tipos de perturbación

El concepto de perturbación ha sido abordado para su definición desde dos enfoques bien diferentes: uno, centrado en la planta y que podría calificarse de reduccionista, define como perturbación "cualquier mecanismo que limita la biomasa vegetal causando su muerte total o parcial" (Grime 1979). El otro punto de vista, holístico al centrarse en la población, la comunidad o el ecosistema (Pickett and White 1985), contempla la perturbación como "cualquier evento discreto en el tiempo que altera y afecta la estructura de la población, comunidad, o ecosistema, y cambia sus recursos, la disponibilidad de substrato o su ambiente físico". Siguiendo esta definición, la perturbación ha de ser entendida siempre relacionada con un particular y definida claramente a escala de organización vegetal, ya sea de individuo, población, ecosistema o paisaje (Pickett et al 1989), lo que requiere que su estudio la afronte como un proceso multiescalar en el tiempo y en el espacio (Laska 2001).

La clasificación y el estudio de las perturbaciones se basa principalmente en las siguientes características propias de la perturbación (Tabla 3): su distribución, frecuencia, periodo, predictibilidad, extensión, intensidad, severidad y la posible existencia de sinergias entre ellas (Pickett and White 1985). Sin embargo, hasta la fecha no hay una clasificación general aceptada de las perturbaciones y las distinciones más clásicas entre "endógenas" y "exógenas" según si el factor causal pertenece o no al sistema, han sido muy discutidas (Pickett and White 1985). La única propuesta general encontrada es la de Laska (2001) que diferencia las perturbaciones, según su origen, en "naturales" (bióticas y abióticas) y "antropogénicas" y, según su efecto en la dinámica de la vegetación, en "regresivas", "sucesionales" o "degenerativas".

Característica de la perturbación	Definición
Distribución	Distribución espacial en función de los gradientes geográficos, topográficos, ambientales y bióticos considerados.
Frecuencia	Número medio de eventos de perturbación por unidad de tiempo.
Periodo	Tiempo medio transcurrido entre dos perturbaciones.
Predictibilidad	Inverso a la variabilidad en el tiempo transcurrido entre eventos.
Extensión	Área afectada por la perturbación.
Intensidad	Fuerza de la perturbación por unidad de tiempo. La cantidad de biomasa destrozada o el grado de afección del sustrato pueden utilizarse como estimas de la intensidad de perturbación.
Severidad	Efecto biológico sobre la biocenosis.
Sinergia	Potencial efecto sobre la aparición de otro tipo de perturbaciones.

Tabla 3. Características de las perturbaciones. Modificado de Laska (2001) y Pickett y White (1985).

Siguiendo esta clasificación, las perturbaciones causadas por jabalí (hozaduras) en pastos son perturbaciones naturales bióticas, pudiendo ser tanto sucesionales como regresivas o degenerativas según el caso.

Al margen de las definiciones, las perturbaciones constituyen un tema central de la Ecología, ya que son una causa fundamental de la dinámica de las comunidades vegetales, de su estructura y diversidad y de la recuperación de los sistemas (resiliencia). El papel central de las perturbaciones en el rejuvenecimiento de los ecosistemas a muy largo plazo ha sido recientemente analizado y revisado a partir de largas series temporales, como se explica en el siguiente cuadro:

Retrogresión ecológica: En escalas temporales de miles de millones de años, y en ausencia del efecto rejuvenecedor de las perturbaciones naturales que inician la sucesión secundaria, primaria o temprana, las características del ecosistema (por ejemplo la productividad primaria neta, la descomposición y las tasas de reciclaje de nutrientes) experimentan disminuciones sustanciales, lo que se conoce como *regresión* del ecosistema. La regresión del ecosistema ha sido descrita por ecólogos, biogeoquímicos, geólogos y pedólogos, dentro de marcos conceptuales independientes. Así, se sabe que los cambios pedogenéticos a largo plazo impulsan los procesos biológicos a corto plazo, así como las consecuencias de estos cambios para el desarrollo del ecosistema, y que los fenómenos de regresión son comunes a muy distintos ecosistemas. Las perturbaciones contribuyen a rejuvenecer el ecosistema, y por tanto a su retrogresión ecológica (Peltzer et al 2010).

Las perturbaciones causadas por el jabalí

Aunque el comportamiento del jabalí es complejo y variable según el hábitat, el periodo del año y sus necesidades fisiológicas (Rosell et al 2001), podemos decir que los principales indicios de presencia de este suido son fundamentalmente: las bañeras, camas y parideras, hozaduras, rascaduras y colmilladas en árboles, corredores y pequeños rastros como huellas, heces, mascaduras o pelos (Tabla 4). De todos estos indicios, la perturbación principal y el indicador más preciso de su presencia son las hozaduras, dado que comprometen una extensa modificación de la estructura de la vegetación y las propiedades del suelo siendo a su vez uno de los signos más perdurables en el tiempo (Hone 1988; Herrero 2001; Rosell et al 2001; Massei and Genov 2004).

Desde una perspectiva aplicada, hay que contemplar los problemas derivados de la actividad del jabalí, acentuados en las últimas décadas por el incremento de sus poblaciones y su gran ubicuidad (Massei and Genov 2004; Geisser and Reyer 2005; Cahill et al 2010). Las preocupaciones principales de gestores, conservacionistas y cazadores, se han centrado en los daños a la agricultura (Mackin 1970; Herrero 2001; Wilson 2004), a la regeneración y diversidad del bosque (Lacki and Lancia 1986; Groot Bruinderink and Hazebroek 1996; Gómez et al 2003b; Ickes et al 2003; Siemann et al 2009), y en menor proporción a la ganadería extensiva (Tisdell 1982; Kuiters et al 2005), su posible papel como reservorio de enfermedades transmisibles a los animales domésticos o incluso al hombre (Pérez-Martín et al 2000; Vicente et al 2006; Ruiz-Fons et al 2008; Van Hooft 2010), la depredación sobre puestas de aves terrícolas sensibles (Purger and Meszaros 2006) o de interés cinegético (Calderón 1977), la competencia alimentaria con otras especies (Focardi et al 2000), y el impacto edáfico que aumenta la erosión (Browning 2008; Figura 2). Aunque por otro lado se ha incrementado su interés en estudios sobre los efectos indirectos de las perturbaciones y su papel en procesos ecológicos como los patrones de diversidad y dinámica sucesional (Welander 2000a; Kotanen 2004), ciclo de nutrientes (Lacki and Lancia 1983; Singer et al 1984; Mohr et al 2005), facilitación de plantas invasoras (Cushman et al 2004; Tierney and Cushman 2006), pocos estudios cubren su afección a distintas partes del ecosistema y sus interrelaciones (Massei and Genov 2004), donde todavía el alcance de sus perturbaciones está lejos de ser delimitado.

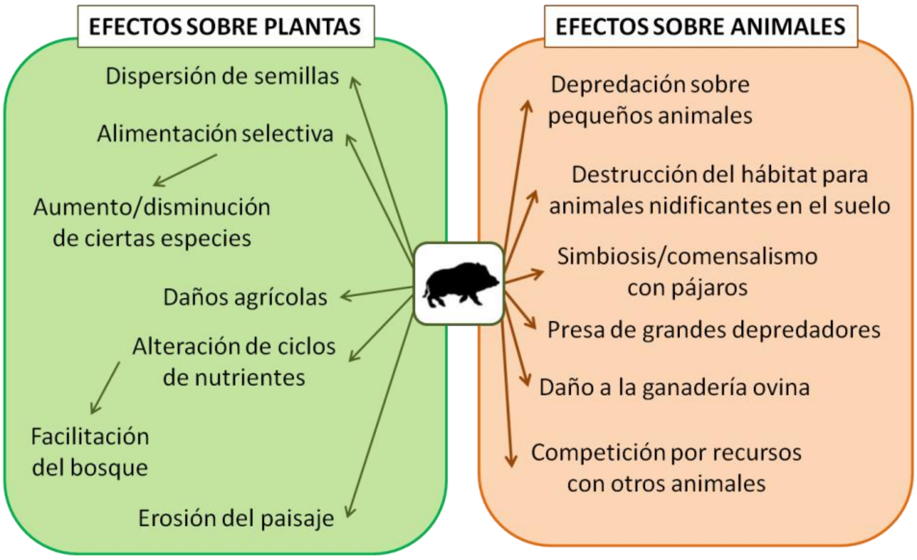

Figura 2. Potenciales efectos del jabalí sobre las plantas y los animales. Adaptado de Massei y Genov (2004)

De igual forma en los pastos alpinos, la principal perturbación creada por el jabalí, hozadura, consiste en el volteado de la cubierta vegetal con una profundidad de 10 cm y en extensiones que varían desde decímetros cuadrados a centenares de hectáreas (capítulo 1a; Figura 3). Esta afección a áreas pastorales es percibida por los ganaderos como una amenaza para las actividades tradicionales de ganadería extensiva y genera conflictos entre manejo y conservación (capítulo 1b).

Indicios de la presencia de jabalí	
Bañeras	Las bañeras o *bañas* son zonas a las que los jabalíes acuden a impregnarse el pelaje de barro, y que se reconocen por la impresión del cuerpo del animal y de su pelaje, que acostumbran a quedar claramente marcados. Se considera que estos “baños” tienen como finalidad la eliminación de ectoparásitos, aunque también se le atribuyen funciones de termorregulación o incluso sexuales.
Camas	Las camas de uso diario son pequeñas depresiones o rascaduras en el terreno. Pueden aparecer sobre un lecho de ramas y hojas si han sido utilizadas por grupos de hembras con crías. Las *parideras* pueden ser más elaboradas.
Hozaduras	Se trata de suelos removidos por el jabalí mediante la jeta, utilizando el disco nasal como palanca, con la finalidad de extraer alimentos hipogeos (larvas de insectos, raíces, bulbos, etc).
Marcas en árboles y arbustos	Los troncos de árboles y arbustos pueden mostrar dos tipos de indicios: *frotaderos*, marcas realizadas por el cuerpo del animal al rascarse que dejan una fina capa de barro y pelo sobre la corteza del tronco, y *colmilladas*, incisiones realizadas con los caninos como mensajes de carácter sexual, territorial o jerárquico.
Corredores	Zonas de paso entre la hierba o arbustos, que quedan marcadas por la rotura de tallos y ramas.
Huellas	Sobre sustrato blando son inconfundibles, ya que marcan los cascos de los dedos medios y los laterales. En sustratos duros pueden no dejar marca de los laterales.
Excrementos	De forma esférica o cilíndrica de color oscuro, de composición y tamaño variable, olor característico y escasa fragmentación vegetal, lo que permite identificar en ocasiones los alimentos no digeridos.
Mascaduras	Al mascar raíces o espigas, a veces los jabalíes escupen la parte fibrosa que no consumen, en forma de madeja deshilachada.
Pelo	Los restos de pelo en mallas cinegéticas, especialmente por la frecuencia de uso de determinados pasos, es un indicador fiable del uso del terreno que hacen los jabalíes.

Tabla 4. Indicios de presencia de jabalí. Modificado de Herrero 2001 y Rossell et al 2001.

Por otro lado, las hozaduras pueden ocasionar distintas respuestas en la estructura de la vegetación; así, en pastos del sur de Suecia dichas perturbaciones promueven el aumento de diversidad al levantar con un gran índice de reincidencia comunidades de especies dominantes, liberando recursos para otras especies menos competitivas, y también aumentando la heterogeneidad ambiental y dispersando especies por epizoocoria (Welander 2000a). En otras zonas montañosas, y especialmente donde el jabalí ha sido introducido, como Australia o EEUU (Bratton 1974; Hone 2002), las hozaduras provocan una disminución de la diversidad, lo que ha sido argumentado por una falta de especies adaptadas a dicha perturbación (Bratton 1975), lo que potencialmente incrementa el riesgo de extinción para una parte de la flora afectada (Bratton 1974). En este sentido no hay un papel único del jabalí, incluso en hábitats similares, siendo la variabilidad de su respuesta probablemente dependiente de complejos factores ambientales externos, adaptativos y relacionales (Massei and Genov 2004).

Figura 3. Hozadura de jabalí en el Parque Nacional de Ordesa y Monte Perdido (Foto: C.G. Bueno)

Jabalí: el visitante nocturno

Un animal con éxito (distribución y biología)

El jabalí (*Sus scrofa* L.) es un ungulado artiodáctilo de la familia de los suidos, ancestro del cerdo doméstico, distribuido por la práctica totalidad de Asia, norte de África y Europa, a excepción de las áreas más septentrionales con clima continental (Figura 4), resultando una especie tremendamente cosmopolita (Oliver and Leus 2008). Además ha sido introducida en América, Australia, Nueva Zelanda y diversas Islas del Pacífico configurando una de las distribuciones más extensas entre los mamíferos (Oliver and Leus 2008). En España está ausente en los archipiélagos de Baleares y Canarias, pero es abundante en la práctica totalidad del territorio peninsular (Sáez-Royuela and Tellería 1987; Rosell et al 2001). Su hábitat potencial cubre la totalidad de hábitats templados y tropicales y sólo excluye los desiertos y la estepa fría (Oliver and Leus 2008). En Europa prefiere los bosques, tanto de hoja caduca (hayedos y robledales) como perenne de tipo esclerófilo (encinares y alcornocales) y aciculifolio (pinares, abetales), aunque también ha sido encontrado en zonas más abiertas, como monte bajo mediterráneo, estepas, marismas y agrosistemas (Spitz 1999; Rosell et al 2001). En el Pirineo ocupa las zonas de bosque donde realiza la mayor parte de sus actividades (Herrero 2001).

Desde los años 60 las poblaciones de jabalí en España y Europa han sufrido un notable incremento (Saez-Royuela and Tellería 1986). Recientemente se ha comprobado esta tendencia también en zonas pirenaicas (Giménez-Anaya et al 2010). El abandono masivo de las zonas agrarias como consecuencia de la emigración hacia los centros industriales, trajo consigo la pérdida de cultivos marginales, la disminución de la cabaña ganadera extensiva y el abandono de la leña como combustible doméstico, lo que ha dado lugar a un aumento de superficies forestales, explotables por el jabalí (Gortázar et al 2000; Acevedo et al 2006). Estos cambios, unidos a las características biológicas del jabalí y la práctica desaparición de sus depredadores naturales (lobo y oso) han favorecido este aumento demográfico y, lo que es más importante, han modificado los factores limitantes de sus poblaciones (Sáez-Royuela 1989).

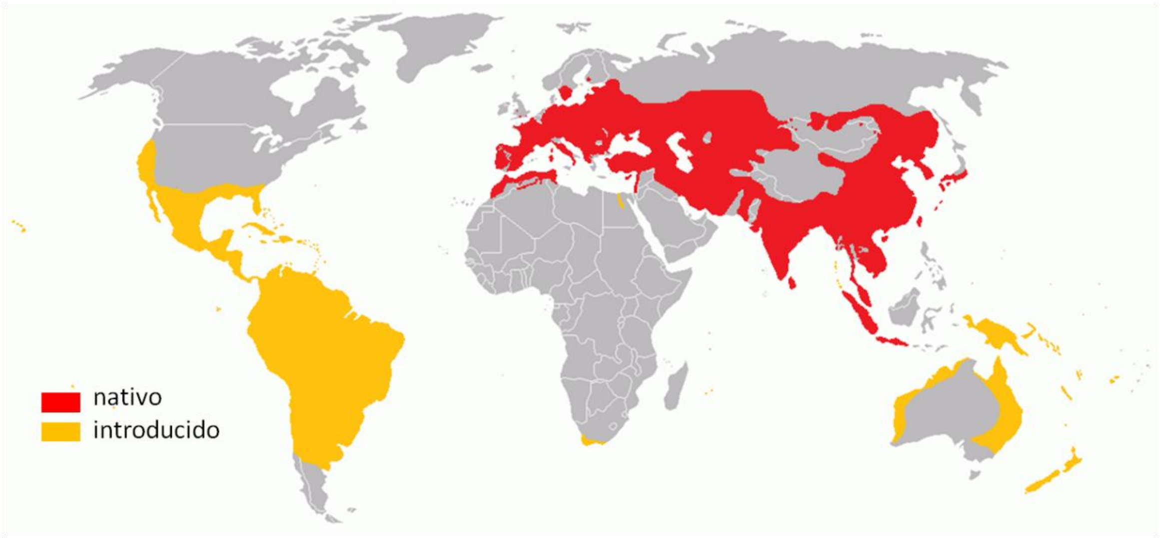

Figura 4. Distribución mundial del jabalí (*Sus scrofa* L.) reflejando su área de distribución original (en rojo) y las zonas donde ha sido introducido (en amarillo). Modificado de Oliver y Leus (2008) y Herrero (2001).

A este respecto las características biológicas que hacen del suido un animal tan adaptable son fundamentalmente tres: su flexibilidad en la reproducción, su variada alimentación y su gran capacidad para buscar alimento debajo del suelo (Fernández-Llario 2006). La reproducción es altamente prolífica y adaptable básicamente por la precocidad en alcanzar la madurez sexual, su gestación relativamente corta y la elevada media de crías por camada, en el Pirineo el número de fetos por camada es superior a 3 (Herrero 2001). Su alimentación es omnívora y consume una gran variedad de alimentos dependiendo de su disponibilidad estacional (Genov 1981; Dardaillon 1987; Schley and Roper 2003) aunque está basada fundamentalmente en un gran porcentaje de vegetales (90-95%) y una pequeña (pero constante) proporción de materia animal (5%; Schley and Roper 2003). Además ha sido señalada cierta tendencia a la estenofagia, a alimentarse en cada periodo, de pocos alimentos muy abundantes y nutritivos (Herrero 2001). El hocico de jabalí, estrecho, largo y recto, está diseñado para la búsqueda de alimento levantando las capas superficiales del suelo, aunque también muestra otras conductas en la búsqueda de alimento que incluyen el consumo de órganos aéreos de las plantas, cortezas de árboles, y frutos (Rosell et al 2001). Es además reseñable la flexibilidad de su área de campeo donde de unos pocos centenares de hectáreas puede llegar a varios miles, en función básicamente del número y género de los jabalíes, los recursos o las perturbaciones como la caza (Janeau and Spitz 1984; Spitz and Jeneau 1990; Santos 2002).

Los pastos alpinos ¿un recurso alternativo?

Diversos estudios realizados en los Alpes, muestran que la dieta del jabalí puede presentar enormes variaciones estacionales (Durio et al 1995; Baubet et al 2003; Schley and Roper 2003; Baubet et al 2004). En estas zonas desde finales de primavera hasta principios de invierno, el jabalí sube a alimentarse parcial o totalmente a los pastos de puerto, cuando los recursos en el bosque escasean (Baubet 1998; Herrero 2001). En los Alpes, la proporción total de materia vegetal encontrada en la dieta es mayor que la antes señalada, alrededor de 99 %, principalmente basada en partes aéreas vegetales, raíces y bulbos mientras que es reducida pero constante la alimentación de origen animal, fundamentalmente lombrices de tierra (Baubet et al 2004). Además la proporción de partes subterráneas en el grueso de la alimentación se incrementa con la altitud (Baubet 1998). Aunque el conocimiento de la dieta de los jabalíes es fundamental para entender su influencia ecológica en ambientes con elevado nivel de perturbación (Chimera et al 1995), en los Pirineos no hay información de la dieta del jabalí fuera de la temporada de caza (de Septiembre a Febrero aproximadamente; Herrero et al 2005), cuando más suben a puerto y realizan el grueso de las perturbaciones. De cualquier forma su dieta otoñal e invernal señala también una gran predilección por las partes vegetales (95%), especialmente las aéreas (71%) con una composición fundamentalmente basada en frutos secos (62%) como hayucos o bellotas de encina o quejigo. Otras fracciones como las partes vegetales subterráneas (23.8 %: raíces, rizomas o bulbos), o restos animales (3.8%) contribuyen en menor medida a la dieta del jabalí (Herrero et al 2005).

Y entonces… ¿esta tesis?

Justificación

Ya han sido mencionados los problemas que causa la presencia de jabalí en muchos de los hábitats que ocupa y la sensibilidad de los ambientes alpinos a ese tipo de perturbaciones. Además, la tendencia constatada al aumento de sus poblaciones, (Geisser and Reyer 2005) permite pronosticar un aumento de sus perturbaciones. La afección a grandes superficies de montaña podría comprometer las prácticas ganaderas tradicionales que, a su vez, son fundamentales para el mantenimiento de los pastos. Por ello, se hace necesario delimitar las zonas afectadas, definir sus patrones de distribución espacial y valorar el impacto sobre las actividades ganaderas (capítulo 1).

Por otra parte, se desconocen los efectos de la actividad del jabalí en los ecosistemas de alta montaña, pero estudios realizados en otros ecosistemas han puesto de manifiesto una gran complejidad de los mecanismos y procesos ligados a esta perturbación (Lacki and Lancia, 1986; Genard et al., 1988; Welander, 2000). Lo anterior, concede especial relevancia a dilucidar el impacto de estas perturbaciones en zonas alpinas, sobre la vegetación establecida (capítulo 2a), el banco de semillas del suelo (capítulo 2b), y sobre los parámetros edáficos (capítulo 2c) que, a su vez, determinarán el nicho para la regeneración de la vegetación.

Zona de estudio

Situación geográfica

El trabajo de campo de esta tesis doctoral se ha llevado a cabo en dos zonas disyuntas representativas del Pirineo Central, en la provincia de Huesca (Figura 5): Aisa y el Parque Nacional de Ordesa y Monte Perdido (PNOMP). La elección de las dos zonas de estudio se hizo en base al conocimiento previo de estas zonas en cuanto a su vegetación, geología, clima, etc., y al hecho de ser representativas del Pirineo Central y Occidental. Además, estas zonas presentan distinto grado de protección, una medianamente protegida por la figura de Parque Natural y otra bajo la máxima figura de protección, el Parque Nacional, y que esto podía ser un factor clave en la abundancia de jabalí, y por tanto del grado de afección de sus perturbaciones. Ambas zonas fueron consideradas para el estudio a escala de paisaje (ver siguiente apartado); sin embargo, los trabajos a una escala menor, dado el enorme esfuerzo de muestreo y las limitaciones de tiempo y financiación, se restringieron al Parque Nacional de Ordesa y Monte Perdido, ya que las perturbaciones de jabalí eran más abundantes en esta zona.

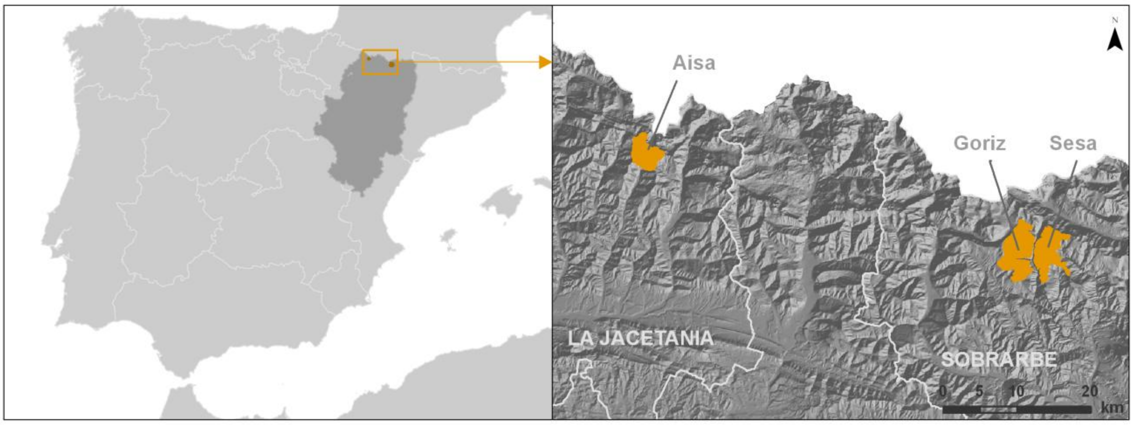

Figura 5. Localización de las zonas de estudio en el Pirineo Central

La primera de estas zonas, el puerto de Aisa, se ubica en la Comarca de la Jacetania, en el noroeste de la provincia de Huesca. El valle de Aisa muestra una orientación N-S, que comprende la vertiente meridional de los picos de Aspe, la divisoria occidental que componen los picos de Sombrero, Lecherines y Mallos de Lecherín y la parte oriental de la divisoria de aguas con el valle de Aratorés, justo antes del Pico Mesola (Figura 5a). La red hidrográfica se articula en los Barrancos de Igüer y Riguelo que, tras un corto recorrido confluyen para dar lugar al río Estarrún que vertebra ya la totalidad del valle de Aisa hasta tributar en el Aragón. El primero de los barrancos mencionados recoge también el agua de la “foya” de Aragüés, pequeño valle colgado entre 2100 y 2300 m.s.n.m., situado a septentrión entre los picos de Ruabe de Bernera y Llena del Bozo. En conjunto, toda esta cabecera del río Estarrún, se denomina el puerto de Aisa, que con una superficie de 1241 ha, alberga el ganado estivante de los municipios de Aisa, Esposa, Sinués y Borau. El territorio está incluido en el Parque Natural de Los Valles Occidentales, aunque el estudio en esa zona se realizó antes de dicha declaración (Diciembre de 2006).

La segunda zona de estudio se encuentra dentro del Parque Nacional de Ordesa y Monte Perdido, ubicado en la Comarca del Sobrarbe, en el nordeste de la provincia de Huesca, haciendo frontera con Francia. Los límites de esta zona corresponden aproximadamente con los puertos estivales de Góriz bajo y la Estiva (Figura 5b) y la Montaña de Sesa y Escuaín (Figura 5c), divididos en un eje norte-sur por el Cañón de Añisclo. En total esta zona de muestreo se extiende por 3863 ha, de un total de 15608 ha que posee el Parque y que representan el 35% de la superficie de pastos supraforestales del Parque.

Clima

El clima de ambas zonas de estudio se corresponde con el denominado “clima de montaña” (Creus 1983), con dos tipos fundamentales de influencias: por un lado la mediterránea continental en las vertientes sur, caracterizada por escasas precipitaciones, elevado déficit hídrico estival y gran oscilación de la temperatura, y por otro lado, una influencia atlántica montana, más acusada hacia el oeste, caracterizada a su vez por lluvias abundantes, ligera o nula sequía estival y oscilaciones térmicas moderadas (Creus 1983). En el Puerto de Aisa la influencia oceánica es más marcada, por su localización más próxima al Océano Atlántico.

Las precipitaciones muestran una variación anual, altitudinal y latitudinal que, en conjunto, puede cifrarse entre 1600 y 2000 mm anuales, con máximos de otoño y primavera (Badía et al 2008). Durante los meses de invierno predomina la nieve sobre los 1700 m donde puede llegar a formar un manto continuo de diciembre a marzo (Del Barrio et al 1990); en el resto de meses otoñales y primaverales, la cubierta de nieve muestra una gran heterogeneidad relacionada con la topografía, con una marcada impronta en la distribución de la vegetación. La temperatura media anual en el Parque Nacional de Ordesa es de alrededor de 5ºC (Estación de Góriz 2200 m, promedio de 29 años). En Aisa, la estación meteorológica más cercana al puerto se encuentra en el pueblo de Aisa (1043m), y la temperatura media anual es de 10,2º C. El periodo vegetativo (definido para las especies arbóreas como aquel con temperatura media superior a 7ºC) se reduce en altitud a razón de 11 días cada 100 m aproximadamente (Del Barrio et al 1990) para el periodo comprendido entre 1982 y 2006, el periodo vegetativo en la zona de estudio duró en promedio 120 días, entre finales de Mayo y finales de Septiembre (Komac 2010). Antes y después de este periodo vegetativo hay dos periodos (aproximadamente 68 días en total) libres de hielo, lo que puede alargar el periodo vegetativo de algunas plantas y comunidades hasta casi seis meses (Benito 2006).

Sustrato geológico

Tradicionalmente se han distinguido dos unidades geológicas y geomorfológicas en el Pirineo: la *Zona Axial Pirenaica* formada por materiales del ciclo hercínico (principalmente sedimentos paleozoicos y plutones graníticos) y el *Prepirineo* constituido por sedimentos deformados durante el ciclo alpino con predominio de materiales calcáreos. Este último consta a su vez de tres partes: las Sierras Interiores, las Depresiones Intermedias y las Sierras Exteriores (Soler and Puigdefábregas 1970; Soler and Puigdefábregas 1972). Ambas zonas de estudio se encuentran ubicadas en las Sierras Interiores Pirenaicas.

El sustrato geológico de las zonas de estudio está constituido fundamentalmente por sustratos calizos. En Aisa, predominan los materiales calcáreos mesozoicos y terciarios: calizas, margas y areniscas del Cretácico, y calizas del Paleoceno, con importantes fenómenos kársticos (García-Ruiz and Martí-Bono 2001). Hacia el sur, y delimitando la Depresión Intermedia, aparece el flysch eoceno, formado por areniscas y margas tableadas que aparecen muy plegadas (Soler and Puigdefábregas 1970; Soler and Puigdefábregas 1972). En el Parque Nacional de Ordesa, Góriz y La Estiva (en la margen izquierda del cañón de Añisclo aguas arriba) están dominados por sustratos calizos, dolomíticos y calizos margosos eocénicos (Riba 1980). Al otro lado del cañón, en la Montaña de Sesa, es más abundante el flysch Luteciense, resaltando en los bordes que lindan con Añisclo las calizas eocenas. En la zona más alta, la sierra de las Zucas, el material pasa a ser Cretácico dominado por calizas, dolomías y areniscas (Riba 1980).

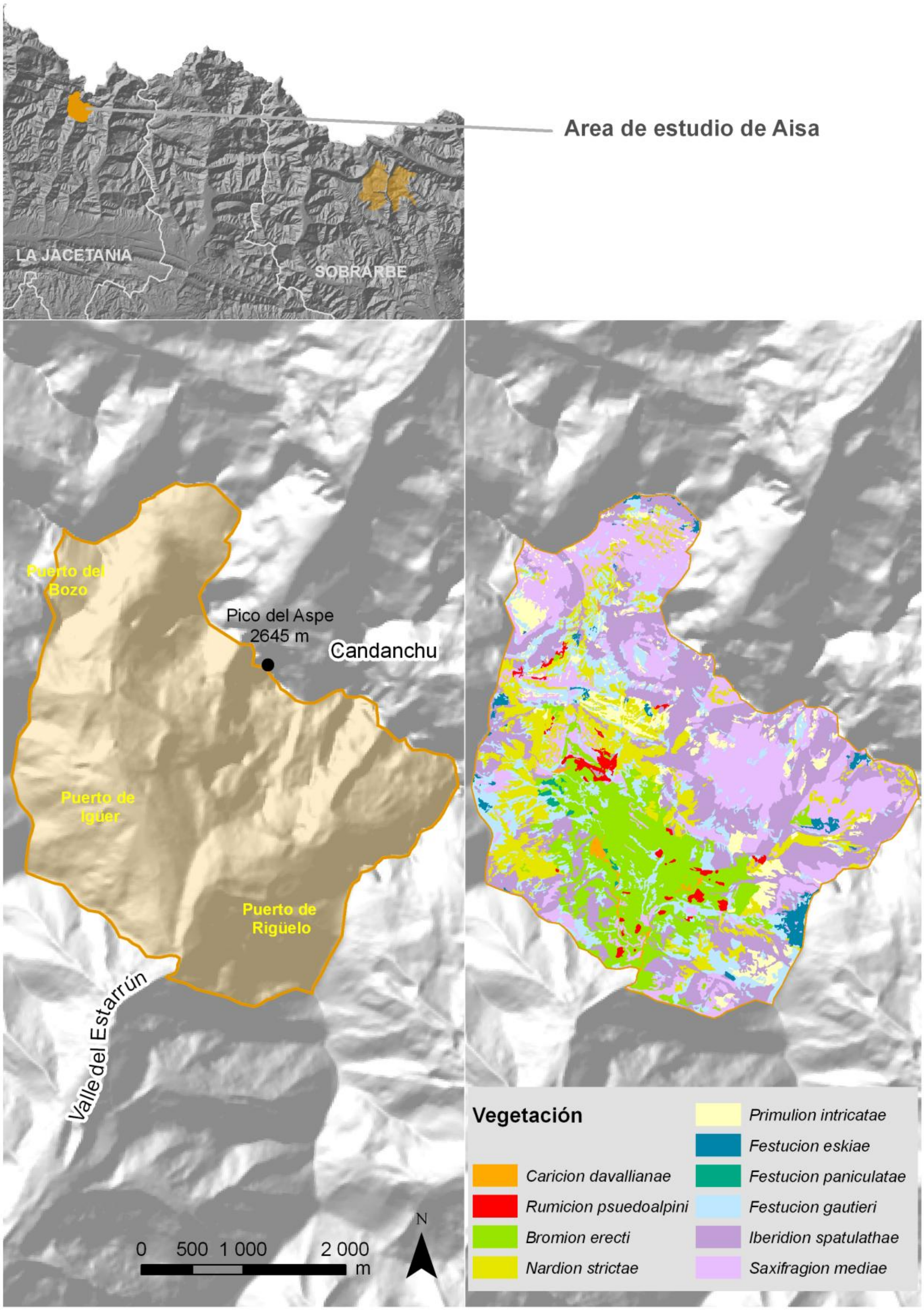

Figura 5a. Localización y mapa de vegetación del puerto de Aisa.

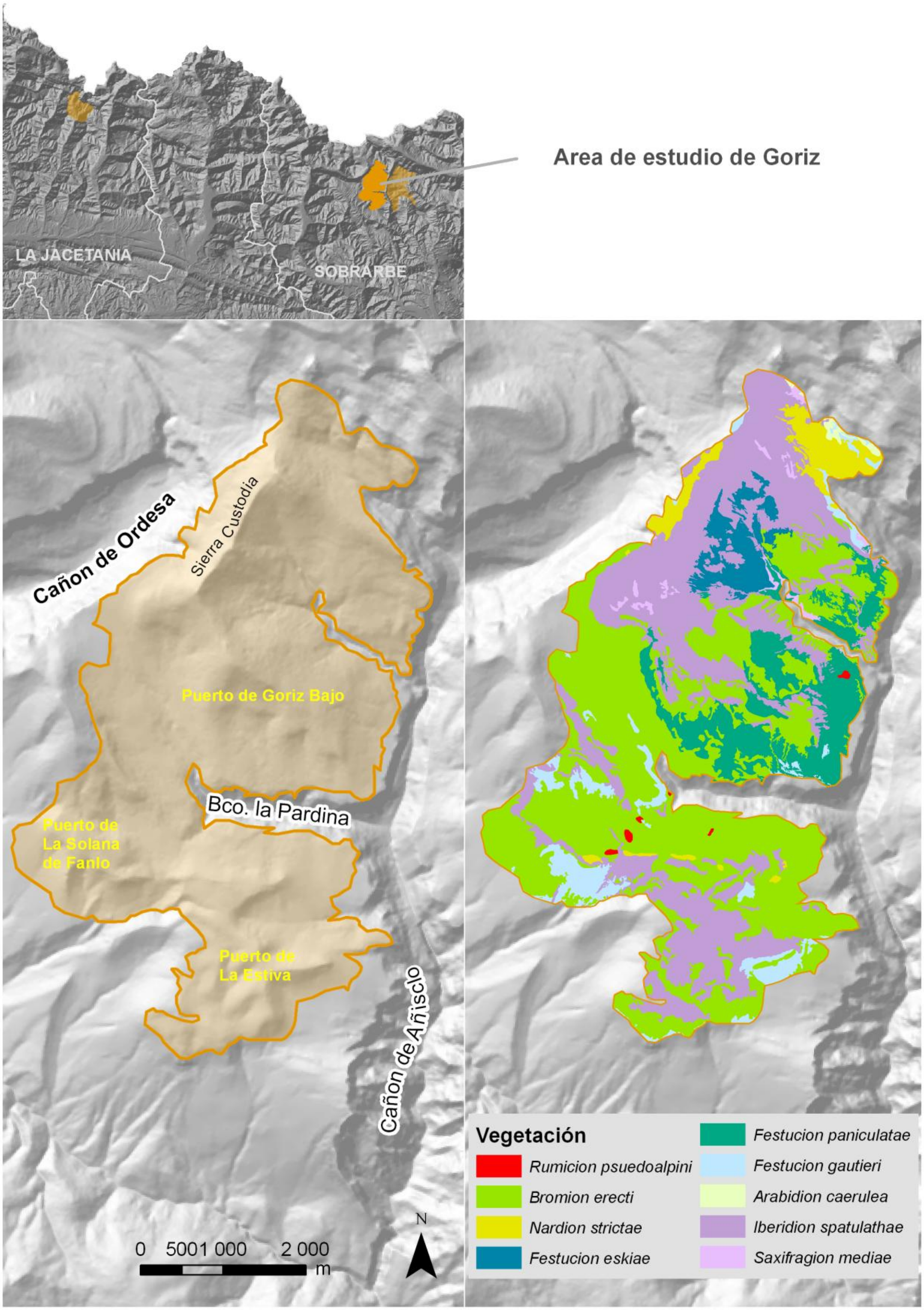

Figura 5b. Localización y mapa de vegetación de Góriz bajo y la Estiva.

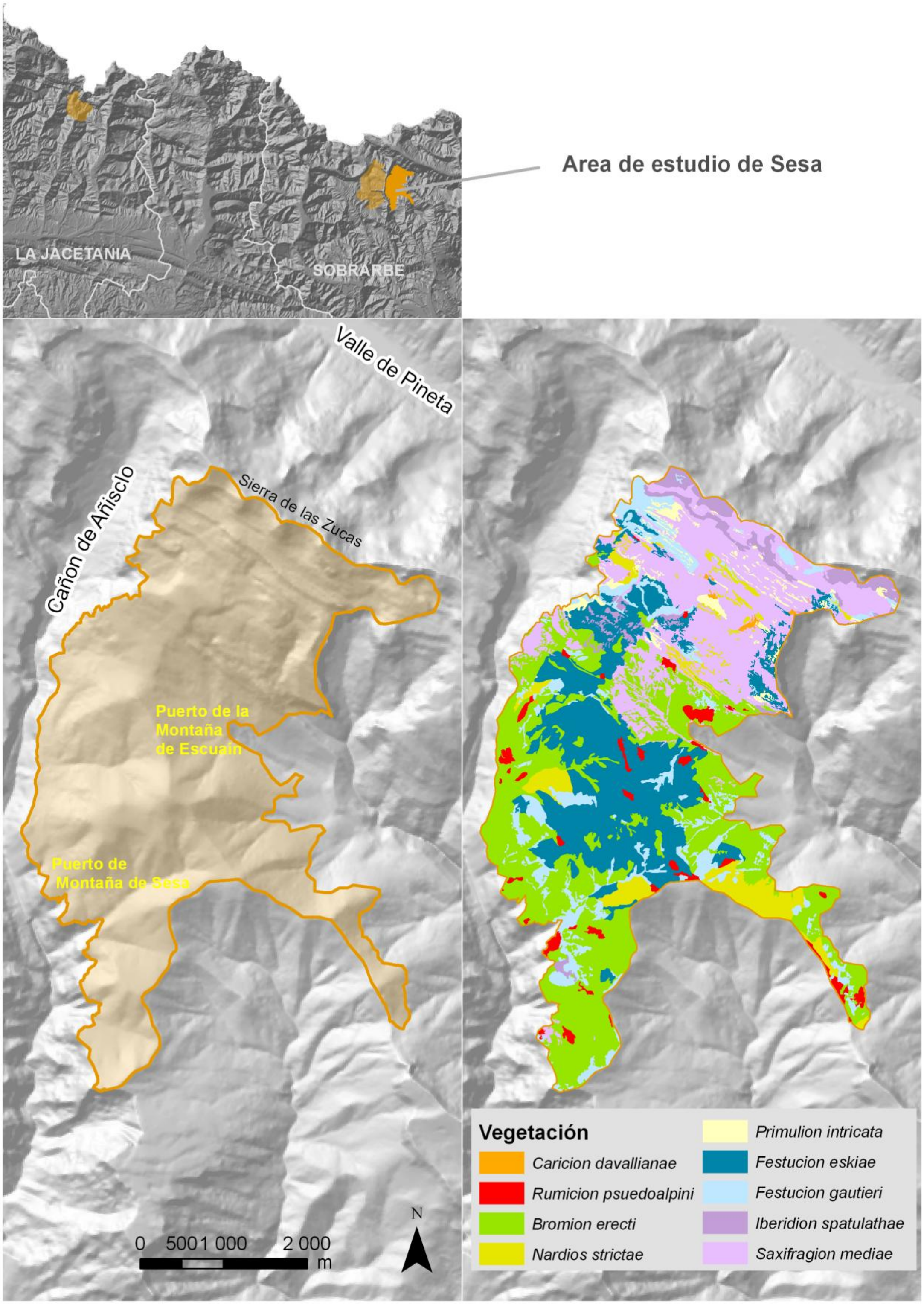

Figura 5b. Localización y mapa de vegetación de la Montaña de Sesa y Escuaín.

Topografía

Ambas zonas pueden considerarse muy representativas de la media y alta montaña pirenaica y, por tanto, están caracterizadas por un relieve muy intrincado con marcado desnivel altitudinal. La zona de estudio dentro del Parque Nacional de Ordesa tiene un desnivel altitudinal de unos 1300 m desde 1509 a 2787 m. Por su parte, la zona de estudio en el valle de Aisa tiene un desnivel de unos 1200 m, desde 1500 a 2680 m.

Uso de los pastos

La ganadería del Valle de Aisa es fundamentalmente ovina y vacuna. El pastoreo se reduce al período estival, entre Julio y Octubre, aunque las fechas de entrada y salida del ganado se han modificado en las últimas décadas por cambios de gestión y de requerimiento de pastos. El aprovechamiento pastoral se remonta de forma documentada a la Edad Media, aunque es muy probable el uso anterior y, como en el resto de la cadena montañosa, ha modificado radicalmente el paisaje a consecuencia de la deforestación y quema antrópica, lo que ha fomentado la expansión de algunas comunidades de pastos (majadales) y, en general, modificado la distribución de otras (Fillat et al 2005; Fillat 2008).

En el Parque Nacional de Ordesa, la principal actividad económica de la zona es el turismo, habiendo quedado la agricultura y la ganadería extensiva relegados a un segundo plano. Aún así se conoce moderadamente bien el aprovechamiento ganadero de los pastos del PNOMP gracias a varios trabajos detallados sobre el pastoreo en el Parque (Aldezabal et al 1992; Aldezabal 2001). En dicha zona el uso es fundamentalmente ovino y vacuno, aunque existen pequeños rebaños de caballos y cabras cada vez menos numerosos. Además se conoce detalladamente el tránsito de los animales en la periferia utilizando los llamados pasto de tránsito, que al estar a una menor elevación presentaban un óptimo aprovechamiento mucho antes de la subida a los puertos y en la bajada que corresponde para el puerto de Góriz desde el 1 de Agosto hasta el 10 de Octubre aproximadamente. Cabe añadir que actualmente se están produciendo dos cambios simultáneos en el pastoreo que alteran las dinámicas de los pastos alpinos pirenaicos: por un lado un descenso generalizado de la ganadería extensiva y por otro un paulatino cambio de ganado ovino por ganado vacuno (Lasanta-Martínez et al 2005).

Vegetación

La vegetación de las zonas de estudio es, como se ha descrito anteriormente, muy heterogénea con mezcla de especies y comunidades mediterráneas, submediterráneas, orófitos centroeuropeos, alpinos, etc. Los pastos herbáceos densos, es decir de alta cobertura vegetal, predominan en los terrenos más llanos y situados a menor altitud, mientras se enrarecen por encima de 2000 m (Remón and Gómez 1989). En el otro extremo, los pastos ralos o pedregosos, con cobertura vegetal inferior al 10%, ocupan las laderas más pronunciadas y ganan extensión conforme aumenta la altitud, de manera que son francamente predominantes por encima de los ya señalados 2000 m. En las crestas y otras zonas cacuminales, la exposición al viento puede provocar una temprana desaparición del manto nival y de su efecto protector; en esas circunstancias las fuertes oscilaciones térmicas diarias (que pueden superar los 30º) disparan fenómenos periglaciares, como la crioturbación, que ocasionan el ascenso de los materiales duros y una pedregosidad superficial en dichos terrenos que enmascara suelos bien desarrollados y muchas veces con alta fertilidad por la querencia del ganado en verano (Figura 5a, 5b y 5c - mapas de vegetación). Desde el punto de vista de la perturbación del jabalí hemos querido utilizar esta primera separación (pastos densos y ralos o pedregosos) asumiendo que el suido no tiene ni hay constancia de que haya tenido, interés alguno por pastos ralos o pedregosos dada su escasez de suelo donde le sería prácticamente imposible hozar. Aún así hemos distinguido en ambas, categorías siguiendo la información tanto fitosociológica disponible de la zona (Braun-Blanquet 1948; Villar 1982; Remón and Gómez 1989; Benito 2006) como desde un punto de vista pastoral (Aldezabal 2001; Fillat et al 2008) y productiva (Remón 1997).

Dentro de las comunidades de pasto denso, se pueden destacar los tipos de vegetación que señalamos a continuación:

Rumicion pseudoalpini: estas comunidades son conocidas como *majadales*, y son las que soportan un mayor uso pastoral: Normalmente se encuentran asociadas a cabañas –mallatas- de pastor, abrevaderos o puntos de sal. Es común la presencia de plantas, como *Chenopodium bonus-henricus, Rumex alpinus* o *Urtica dioica*, sin que ninguna domine de forma clara sobre las demás. Esta comunidad integra en nuestra clasificación al *Polygonion avicularis*, también con presencia intensa del ganado y que hemos agrupado para obtener una mayor entidad a escala del paisaje.

Bromion erecti: son pastos mesófilos muy abundantes en el dominio forestal y expandidos por el propio pastoreo hasta los 2000 m, por lo que tienen una marcada dependencia del incendio periódico. Muestran una notable diversidad de especies forrajeras, especialmente gramíneas: *F. rubra nigrescens, Agrostis capillaris, Poa pratensis, Briza media, Lotus corniculatus, Achillea millefolium, Galium verum*, ect.

Nardion strictae: incluye los pastos de carácter acidófilo localmente denominados *cervunales,* dominados por *Nardus stricta*. Son comunidades con una baja diversidad de especies y, en general, escaso valor pastoral, aunque ciertas variantes con buena representación de *Festuca nigrescens*, son frecuentados por el ganado. En las zonas que nos ocupan esta comunidad aparece muchas veces mezclada con la anterior.

Festucion spadiceae: corresponde a comunidades dominadas por *F. paniculata spadicea* que posee un porte muy alto (más de 1.5 m contando la espiga) y un rizoma muy denso, dando un aspecto reconocible a distancia. Son comunidades con baja diversidad específica y escaso valor pastoral. En este trabajo se ha denominado artificialmente *F. paniculatae* para englobar las comunidades dominadas por *F. paniculata fontqueri* del puerto de Aisa por presentar un misma estructura y respuesta a las perturbaciones.

Festucion eskiae: son los pastos dominados por *F. eskia*, gramínea alta y amacollada, situada en suelos de carácter ácido y muchas veces con pendientes moderadas o medias (hasta 30º). La gramínea dominante se diferencia de *F. paniculata spadicea* en el porte (más bajo) y la hoja (mucho más estrecha) y suele estar acompañada de *Trifolium alpinum.* Son igualmente comunidades con una baja diversidad de especies.

Primulion intricatae: es una comunidad que puede ser considerada vicariante en altitud de *Bromion erecti* por los ambientes que ocupa, aunque con una mayor innivación, y por su alta diversidad. Ocupa terrenos llanos o de escasa pendiente, situados por encima de 2000m y entre su flora característica cabe citar: Trifolium thalii, *F. rubra nigrescens, Plantago alpina, Lotus alpinus, Ranunculus montanus,* etc.

Entre las comunidades de pastos ralos destacamos:

Festucion gautieri (F. scopariae): corresponde a los pastos dominantes en las laderas pedregosas calizas de gran parte del Pirineo. Es una comunidad rala en sustratos con poco suelo y fuerte pendiente, que ocasiona inestabilidad y limita la presencia de muchas d elas plantas de los pastos densos. En consecuencia, presenta baja cobertura y aunque tiene una marcada dominancia de la gramínea pulvinular *Festuca gautieri*, tiene una diversidad elevada Es muy característica la fisonomía de eta comunidad por la forma de media luna tanto de la planta como de las guirnaldas que colonizan las laderas en bandas paralelas a las curvas de nivel, dependientes de la dirección de los vientos y la escorrentía.

Saxifragion mediae: corresponde a zonas de roquedo o cantil, con muy escasa vegetación en grietas y pequeñas repisas. No presenta gran número de especies pero sí una gran especialización a estos ambientes. Especies como *Potentilla alchemilloides, Lonicera pyrenaica* o *Erinus alpinus,* son comunes en esta alianza.

Iberidion spathulatae: se trata de comunidades de gleras (Iberidion spathulatae), adaptadas al continuo movimiento de las piedras, donde sobreviven pequeñas y dispersas manchas de vegetación, con ciertas especies como *F. glacialis, F. pyrenaica* o *Crepis pigmaea*.

Escalas: paisaje, comunidad y especie

Como se ha comentado anteriormente, el estudio de las perturbaciones ha de realizarse a distintas escalas, ya que sus impactos afectan con naturaleza diferente a distintos niveles de organización de los sistemas (Laska 2001). Además, y especialmente en lo que concierne a la flora resulta imprescindible el análisis a distintas escalas para evitar los sesgos observados cuando se toma una única escala en consideración (Crist et al 2003). Hemos considerado por tanto tres niveles: paisaje, comunidad vegetal y especie. El orden de realización de los trabajos con respecto a la escala espacial, fue necesariamente un orden decreciente en escala, ya que en los pastos alpinos pirenaicos y concretamente en las zonas de estudio no había ninguna cartografía ni estudio previo que identificase cuáles eran las zonas más removidas dentro de las unidades del paisaje y cuáles las comunidades afectadas. Después de dicha identificación, se siguió sistemáticamente la experimentación de hipótesis de trabajo a escalas más detalladas como se explicará en los siguientes apartados.

Objetivos y organización de la tesis

Esta tesis doctoral está estructurada en tres grandes capítulos que cubren las diferentes etapas y aspectos de esta investigación (Tabla 4).

Como punto de partida estudiamos la distribución espacial de las perturbaciones en tres zonas de estudio que representan los diferentes escenarios y comunidades vegetales de los pastos alpinos del Pirineo central: el Puerto de Aisa, Góriz bajo y la Estiva, y la montaña de Sesa (Figura 5), los dos últimos ubicados en el único Parque Nacional de Aragón, Ordesa y Monte Perdido (PNOMP). El propósito fue determinar qué variables ambientales definen mejor los daños causados por el jabalí a estos territorios de gran interés tanto ecológico como pastoral. Así, el primer apartado (capítulo 1a) describe las relaciones entre la extensión y distribución de las perturbaciones y las variables ambientales que mejor pueden definir esta distribución. De forma complementaria hemos afrontado el estudio de cómo dichas perturbaciones afectaban a las mejores zonas de pastoreo en el segundo apartado (capítulo 1b).

En un siguiente paso, a una escala espacial más fina, las perturbaciones suscitan diversas preguntas sobre su afección a los distintos componentes del los ecosistemas pastorales, tales como el suelo (capítulo 2a), el banco de semillas (capítulo 2b) y la vegetación y la flora (capítulo 2c), que nos daría información de la posible repercusión y procesos de regeneración de los pastos alpinos. Para este segundo capítulo escogimos las dos zonas dentro del PNOMP que aún a pesar de resultar más alejadas y con mayor dificultad de acceso y recorrido, mostraban un mayor impacto de superficie hozada, lo que nos facilitó la ubicación de las réplicas de este capítulo.

Una vez estudiadas las afecciones directas, quizás las más relevantes desde el punto de vista de la ecología vegetal (suelo, vegetación y banco de semillas), tratamos de definir los daños pastorales. Para dar este paso, aplicamos los criterios y métodos desarrollados por el grupo de trabajo del IPE (Gómez-García et al 2002; García-González et al 2003; Gartzia et al 2005; García-González et al 2007; Gómez 2008b) ya testados en otros territorios del resto del Pirineo y regiones vecinas.

Finalmente se discuten los resultados obtenidos (capítulo 4) dentro del marco de este trabajo, proponiendo algunas líneas futuras de investigación que han sugerido los mencionados resultados, y finalmente se exponen las principales conclusiones obtenidas.

Tabla 4. Resumen de los objetivos de cada uno de los capítulos y apartados.

CAPÍTULO 1	**ESCALA DE PAISAJE**
1a	¿Dónde y en relación a qué variables ambientales hozan los jabalíes?
1b	¿Cómo afectan las hozaduras al pastoreo extensivo?
CAPÍTULO 2	**ESCALAS DE COMUNIDAD Y ESPECIES**
2a	¿Cómo afectan las perturbaciones al suelo?
2b	¿Cómo afectan las perturbaciones al banco de semillas?
2c	¿Cómo afectan las perturbaciones a la flora y vegetación a distintas escalas?
CAPÍTULO 3	**VALORACIÓN ECO-PASTORAL DE LAS PERTURBACIONES**
3a	¿Cómo afectan las perturbaciones a valores ecológicos y pastorales?

Cada capítulo está precedido por una breve introducción, destacando la problemática que se aborda dentro del marco general de la tesis. La parte fundamental de cada capítulo está constituida por los artículos publicados en revistas científicas (capítulo 1a, 1b, 2b y 3) o bien en vías de publicación (capítulos 2a y 2c), por lo que quedan redactados en inglés. En algunos capítulos se añade información adicional, no incluida en el artículo publicado por limitaciones de espacio, pero que añaden datos y gráficos relevantes para la mejor comprensión de los temas estudiados y para abordar nuevas investigaciones.

Capítulo 1. Escala de paisaje

El estudio del paisaje ha emergido como una herramienta necesaria para evaluar el impacto de extensos y rápidos cambios en nuestro medio natural (Turner et al 2001). Esta nueva disciplina, la "ecología del paisaje" (*landscape ecology*) se centra fundamentalmente en la interacción entre los patrones espaciales y los procesos ecológicos, que son causa y consecuencia de la heterogeneidad ambiental. Uno de los procesos ecológicos fundamentales en la dinámica que genera y sustenta el mosaico de elementos paisajísticos, es la perturbación (Pickett and White 1985).

En el presente capítulo se estudia la distribución espacial de las hozaduras de jabalí y las variables ambientales relacionadas con su distribución y abundancia, con el fin de entender qué elementos paisajísticos y de manejo son atractivos o repulsivos para la actividad hozadora del suido (capítulo 1a). A su vez, en un segundo apartado (capítulo 1b), se profundiza en el efecto de las hozaduras para la actividad pastoral de la zona, motor tradicional de la economía local.

Understanding the main factors in the extent and distribution of wild boar rooting on alpine grasslands[♣]

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ABSTRACT

Wild boar (*Sus scrofa* L.) rooting is a large and frequent disturbance, very extended all over the world. However, its impact in some sensitive habitats, such as alpine and subalpine grasslands remains unknown. These grasslands are considered important sites for biological conservation and traditional grazing activities, and are frequently affected by wild boar rootings. In this study, we selected three study sites representing a range of scenarios in Pyrenean alpine and subalpine grasslands, with differing protection status and grazing management. We assessed the extent of wild boar rooting, and determined the main variables that influence their distribution, taking into account the interactions among them. Our results showed that wild boar rooting significantly affected alpine and subalpine grasslands in the Pyrenees especially in protected non-hunting areas (up to 12 % of the surface). The distribution of disturbed areas was influenced by a hierarchical suite of variables, among which vegetation, i.e. certain plant communities, was the most important. The apparent preference for dense grasslands might be associated with their soil depth, soil hardness, and diversity of feeding resources. The importance of other variables, such as topography, distance to primary resources, or grazing management, was site-dependent. A broad understanding of the effects of variables and their relationships provides insights into the actual factors affecting the rooting selection. We hypothesize that the selection of feeding habitat, followed by the conditions of the soil to be uprooted and human management, are the main underlying factors that shape the distribution of wild boar rooting in alpine and subalpine grasslands.

[♣] This chapter has been published in Journal of Zoology 279:195-202

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INTRODUCTION

Wild boar (*Sus scrofa* L.) rooting is a large and frequent disturbance that has become a recent concern (Massei and Genov 2004; Liddle et al 2006). Wild boars are worldwide distributed (Massei and Genov 2004), and their numbers have increased considerably from the sixties (Saez-Royuela and Tellería 1986), which has led to an expansion of their disturbances (Geisser and Reyer 2005). This widespread disturbance affects many of the habitats throughout its distribution range but studies have been focused mainly on forests (Welander 2000a; Gómez et al 2003b), crops (Herrero et al 2006a), and sites where wild boars have been introduced (Kotanen 1995; Hone 2002; Cushman et al 2004; Mitchell et al 2007). Among the activities of wild boar, rooting may have the most significant impact on soils, vegetation and ground-dwelling organisms (Massei and Genov 2004), and provides the most reliable evidence of its presence (Gallo Orsi et al 1995; Welander 2000a). While rooting, wild boars turn over the soil looking for food, i.e. bulbs, invertebrates or even small mammals, which can have an impact that varies from a few square centimetres to hundreds of hectares (Welander 2000a; Massei and Genov 2004).

These disturbances can be more concerning on certain ecosystems, such as alpine and subalpine grasslands, which are highly stable, but very sensitive to disturbance (Grabherr 2003). When any kind of disturbance occurs in these grasslands, i.e. an alteration of plant cover or a significant loss of soil, it is almost impossible to restore their original state (García-González 2008). Most of the Pyrenean grasslands are protected habitats and a major conservation priority (Benito 2006; García-González 2008; 92/43/EEC of 21 May 1992). They also have a high socio-economical value because of the traditional management of livestock, which reaches a balance between grassland production and biodiversity conservation (Olff and Ritchie 1998; García-González 2008). Thus, the extent of wild boar rooting and its impact on grasslands is a major challenge for ecologists, land managers, and land economists. On grasslands wild boar rooting reduces the amount of area available to grazing livestock, which might have an impact on traditional livestock management and the local economy (Gortázar et al 2000; Sibly et al 2005). In addition, it may affect soil structure, plant cover, and plant succession dynamics, as has been described for feral pig rootings (Kotanen 2004). Therefore, wild boar rooting can be considered a significant factor in the dynamics and conservation of alpine and subalpine grassland ecosystems.

To assess their extent, i.e. the amount of surface they affect, and to predict the likely impact of wild boar on an environment, rooting must be quantified and the variables that influence its distribution should be identified (Singer et al 1981). To our knowledge a precise assessment of their impact in sensitive ecosystems is lacking. In addition, references relate either to feral pigs or to wild boar, which can be misleading. It is known that feral pigs also root while looking for food, but caution should be made on the behavioural inferences that are driven from their populations, as they may not be comparable to those of wild boar. Topography, vegetation type, and distance to resources can influence the distribution of both wild boar and feral pig rooting (Hone 1988; Gallo Orsi et al 1995; Hone 1995). However, the relative importance of these variables remains unclear, which in turn compromises the sense and manner of future management actions. Moreover, the relationships among those variables have not been analysed, even though they can provide insights into the nature of their combined effects (Guisan et al 2002).

In the present study, we assessed the distribution and extent of wild boar rooting on alpine and subalpine grasslands in the Spanish Central Pyrenees, where it is native. We selected three study areas with differing stocking densities and protection status. Our objective was (1) to calculate the extent of those disturbances, as a measure of their impact, and (2) to identify the variables and their interactions, that influence the distribution of wild boar rooting in a range of alpine and subalpine grassland scenarios.

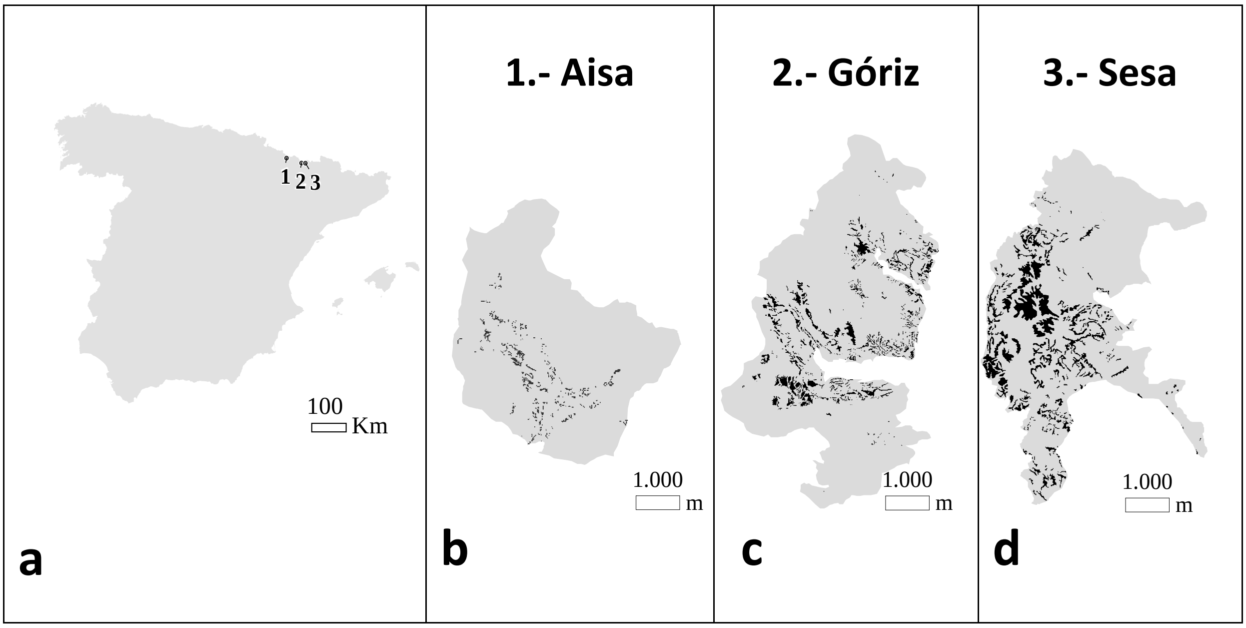

Figure 1. (a) Location of the study areas in Spain, which are indicated by dots and numbers (1-3). Wild boar disturbances are indicated in black: b) Aisa (1241.3 ha, 25.9 ha disturbed), c) Góriz (2189.3 ha, 128.6 ha disturbed) and d) Sesa (1673.7 ha, 192.9 ha disturbed).

METHODS

Study areas

The study was conducted in three areas of alpine and subalpine grasslands in the Spanish Central Pyrenees. We chose two sites, Sesa and Góriz, in Ordesa and Monte Perdido National Park (OMPNP; 42º 36’N, 0º 00’) and the other, Aisa, located on top of Aisa Valley (42º 40’N, 0º 34’W; Figure 1). Both are protected areas, but differ in their protection status: in OMPNP hunting is forbidden while in Aisa is allowed. In OMPNP, Sesa had intermediate-high stocking densities (0.6 SLU/ha, where SLU/ha are standard livestock units per hectare, and a livestock unit is equivalent to a 500-kg cow or six sheep) while Góriz had low-intermediate densities (0.4 SLU/ha); Aisa represented an intermediate situation (0.5 SLU/ha). Elevation ranged from 1500 to 2650 m a.s.l., and slopes were 0º-81.3º. The topography, lithography, climatic conditions, and vegetation of the sites were broadly representative of the Spanish

Central Pyrenees (Remón and Gómez 1989; Benito 2006). In the study areas, individual grasslands were classified based on previous botanic studies that used the phytosociological method, which is based on relative abundance and plant sociability (Braun-Blanquet 1948; Remón and Gómez 1989; Benito 2006). Further, the grasslands were assigned to one of two groups based on plant cover and soil depth. Grasslands were either sparse (cover <45% and soils <30-cm deep) or dense (cover >80% and soils >50-cm deep). All of the plant communities, except the Rumicion pseudoalpini, are identified by the European Union as “natural habitats of community interest”, and two of them (Nardion strictae and Caricion nigrae) are “priority habitats” (92/43/EEC of 21 May 1992). In this study we have considered alpine (natural communities) and subalpine (deforested areas for pastoral use) grasslands as the same general ecosystem, since both types, while having a different origin, represent a continuum in the three study areas.

Maps of disturbances

To determine the extent and distribution of wild boar rooting, we censused the study areas and elaborated three GIS maps (one per study area), during the summer 2005 (June to August). We distinguished wild boar rooting, from other soil disturbances, in the presence of pieces of turf completely overturned in different stages of erosion. Presence of wild boar footprints, and excrements corroborated wild boar activity in these areas. As we frequently found recurrent disturbances where fresh rooting overlaid older rooting, no age considerations could be made. To map the least accessible sites, from suitable viewing points we used binoculars (10x42) and a terrestrial telescope (20-60x65). The locations of all disturbances were drawn on ortho-rectified aerial photographs (1:3500) and georeferenced by >2300 GPS-derived coordinates. Drawings were digitalized in ArcMap 9.2 (ESRI software) and the extent of the disturbances was estimated using the ArcGIS extension, Hawth’s Analysis Tools 3.27. The accuracy of the maps was quantified by sampling 120 random points within each study area and calculating confusion matrices (Congalton 1991). In Aisa, Góriz, and Sesa, the accuracies were high (84.4%, 91.3%, and 90.0%, respectively).

Sampling design

Data were collected following a systematic sampling that took into account the spatial autocorrelation of wild boar rooting. We calculated the minimum distance at which sampling points were no longer spatially correlated and used that distance as a minimum threshold in selecting sampling points. To calculate that distance, we established six random 1025 m-long line transects in each area and, at 0.5-m intervals, the presence or absence of wild boar rooting was recorded, i.e. 2051 points per transect, 36918 in total (3 study areas, 6 transects by area). Transects were randomly generated with GIS using Hawth's Analysis Tools 3.27. For each transect, we generated a variogram function and calculated its range, i.e. the distance at which disturbances had no spatial dependency (Fortin et al 2002). Among the variograms, the average range was 35.15 m (95% confidence interval = 12.34-49.19 m) therefore, the threshold distance for the collection of data was 50 m. We selected points 50 m apart in our maps by GIS procedures, 4964 in Aisa, 8754 in Goriz and 6697 in Sesa, up to a total of 20414 points.

Variables examined

The study included four main variables that can influence the distribution of wild boar rooting: topography, distances to resources (water, forest, and livestock sites, i.e. areas where livestock regularly congregate), vegetation, and stocking density (Hone 1988; Gallo Orsi et al 1995). The topography, which included slope (degrees), aspect (degrees from north), and elevation (m a.s.l.), was derived from Digital Elevation Models (DEM) at a 10-m resolution, using GIS-based procedures. The root mean squared error (RMSE) of each DEM was 6.24 m and 6.36 m in Aisa and the OMPNP sites, respectively. To obtain North-South and East-West orientations, aspects were transformed to cosine and sine, respectively (Muñoz and Felicísimo 2004).

Distances to water, forests, and livestock sites were obtained by digitizing the locations of rivers, creeks, troughs, forests, and livestock concentration points from ortho-rectified 0.5 m-resolution aerial photographs and checked in the field.

For vegetation types, i.e. grassland communities, we elaborated two maps (1:5000), one for Aisa and one for OMPNP study sites (Góriz and Sesa). Polygons were drawn on aerial ortho-rectified photographs (1: 5000) in ArcMap 9.2, corrected using the results of field surveys, and categorized based on 11 phytosociological alliances. Accuracy was checked using the procedures applied to wild boar disturbances. The vegetation maps were highly accurate (76.2% for Aisa and 85.0% OMPNP vegetation map).

The stocking density map for Sesa and Góriz was developed using a previous stocking density map generated for OMPNP (Aldezabal et al 1992; García-González et al 2007). It included the numbers of head of cattle and sheep as of 2004 (data provided by the OMPNP) and were expressed in standard livestock units per hectare (SLU/ha).

Explanatory models

Data were analysed with two independent and complementary methods. One was based on generalized linear models (GLM), which focuses on the estimation of the weight of predictor variables that best explains the response variable, i.e. the presence of wild boar rooting. The other was based on classification and regression trees (CART), which complements the former by depicting the structure of the relationships among predictor variables (Hastie and Tibshirani 1990; Guisan et al 2002).

The GLM method was used to infer the effects, linear or otherwise, of each predictor on the response. Univariate GAM functions were used in the visual inspection of the relationships between each continuous predictor variable and the response (Nogués-Bravo 2006). Those functions improve the accuracy of GLM by fitting an appropriate polynomial approximation to each predictor variable (Guisan et al 2002). Quadratic approximations of all of the continuous variables that exhibited an inverted U shape in the GAM plots were tested, but the quadratic transformation of distance to livestock sites improved the GLM model in Sesa, only.

To assess the relative weight of each variable in the presence or absence of wild boar rooting, we performed a binomial GLM. Binomial GLM can be significantly biased by multicollinearity between predictor variables (Mac Nally 2002), which was assessed using the variance inflation factor (VIF) and Pearson correlation coefficients. To compensate for multicollinearity, each “problematic variable” was replaced by the studentized residuals from the linear regressions between the variables that were highly correlated, as predictors, and the “problematic variable” itself, as response variable (Graham 2003). Categorical predictors were transformed into dummy variables (Hair et al 2006).

In addition, to improve the understanding of each predictor separately and together, we evaluated the relationships among predictors using CART. CART is a non-probabilistic method that is based on an algorithm that recursively selects the best predictor, for the response variable, that separates the data into successive homogeneous groups. This iterative procedure generated a tree plot that relates predictors with the value where their response changes. The method is advantageous because of its relative robustness to multicollinearity, outliers, and non-normal distribution of variables, and its capacity to detect complex interactions among predictor variables without a priori specification (Breiman et al 1984; Karels et al 2004).

In both analyses, the overall fit was quantified by calculating the area under the curve (AUC) of the receiver operating characteristic (ROC) curve and overall accuracy was calculated using confusion matrices. Statistical analyses were performed using SPSS 15.0 (SPSS Inc.) and R 2.7.2 (R Development Core Team, 2008).

Table 1. Relative importance of the explanatory variables (absolute t value) obtained from the binomial GLMs of the three study areas in Spain, Aisa (a), Góriz (b), and Sesa (c). Negative t-values indicate a negative relationship with the presence of wild boar disturbances. Variables replaced by their residuals from a linear regression (variable vs. the other correlated variables) are indicated. The variable "Distance to livestock sites" in Sesa was square-transformed after checking GAM plots and best fit. Non-significant variables are not shown. B.= Coefficients; S.E.= Standard error ; Sig.= Significance

(a) Aisa **-2 log likelihood** **695.936**

Wild boar disturbances				
Presence (1)- Absence (0)				
Predictors	**B.**	**S.E.**	**t**	**Sig.**
Bromion erecti	3.899	0.341	130.842	0.000
Slope (Residual)	-1.073	0.142	-56.916	0.000
Distance to water (Residual)	-1.014	0.182	-31.137	0.000
Elevation (Residual)	-0.597	0.168	-12.691	0.000
Nardion strictae	1.126	0.338	11.114	0.001
Intercept	-4.152	0.628	-43.714	0.000

(b) Góriz **- 2 likelihood** **3073.659**

Wild boar disturbances				
Presence (1)- Absence (0)				
Predictors	**B.**	**S.E.**	**t**	**Sig.**
Festucion paniculatae	2.308	0.163	201.564	0.000
Bromion erecti (Residual)	4.457	0.357	155.497	0.000
Distance to livestock sites (Residual)	-5.349	0.445	-144.224	0.000
Festucion eskiae	2.806	0.251	124.729	0.000
Slope (Residual)	-6.756	0.662	-104.209	0.000
Stocking density	11.773	1.303	81.675	0.000
Distance to water	-3.676	0.438	-70.539	0.000
Distance to forest (Residual)	1.846	0.312	35.123	0.000
Elevation (Residual)	-1.774	0.350	-25.689	0.000
Intercept	-1.344	0.442	-9.260	0.002

(c) Sesa **- 2 likelihood** **3828.232**

Wild boar disturbances				
Presence (1)- Absence (0)				
Predictors	**B.**	**S.E.**	**t**	**Sig.**
Festucion eskiae	2.077	0.106	382.438	0.000
Distance to water (Residual)	-4.929	0.376	-172.107	0.000
Bromion erecti (Residual)	2.864	0.232	152.759	0.000
Distance to forest (Residual)	-3.338	0.297	-126.504	0.000
Distance to livestock sites (Residual)^2	-6.330	0.612	-106.984	0.000
Elevation (Residual)	-2.944	0.323	-83.310	0.000
Slope	-2.246	0.406	-32.617	0.000
Intercept	2.246	0.384	34.167	0.000

RESULTS

Extent of wild boar rooting

In the study areas in the Spanish Pyrenees, 7% of the 5104.3 ha area had been disturbed by wild boars. Sesa (11.5% of 1 673.7 ha) and Góriz (5.9% of 2 189.3 ha), were the most extensively affected areas, and Aisa was less affected (2.1% of the 1241.3 ha; Figure 1). The most affected grassland alliances were Festucion eskiae (22.5% of 476.8 ha), Festucion paniculatae (16.6% of 243.8 ha), Rumicion pseudoalpini (11.7% of 60.3 ha), and Bromion erecti (10.0% of 1652.9 ha), all in dense grasslands. Sparse grasslands contained few wild boar rooting.

Explanatory models

Binomial GLM

In the three study areas, the presence of four specific dense grasslands was the main explanatory variable followed by other variables, which differed among sites. In addition, in each area, distance to resources and topography variables, mainly slope or elevation, were negatively correlated. In Aisa, the main explanatory variable (largest absolute t value) was the presence of Bromion erecti community (Table 1a). In Góriz, Festucion paniculatae and Bromion erecti were the main variables (Table 1b). In Sesa, the main variables were Festucion eskiae and Bromion erecti (Table 1c). Model fitting and validation, and confusion matrices indicated that, in Aisa, Góriz, and Sesa, respectively: the AUC was 0.91, 0.81, and 0.79, and the corresponding accuracies were 84.1%, 73.4%, and 74.0%.

CART

CART indicated that dense grassland communities were the main predictor influencing, like in binomial GLM, the presence of disturbances in each study area (Figure 2). In Aisa, the algorithm selected first certain plant communities (Nardion, Bromion, and Rumicion) for the occurrence of wild boar rooting. Within those communities, rooting was mainly found in areas with gentler slopes (≤ 21º), or much closer to water (≤ 294 m) in steeper places (> 21º; Figure 2a). In Góriz, wild boar rooting also occurred within certain vegetal communities (F. eskiae, F. paniculatae, Bromion, and Rumicion). Within these and in areas close to livestock sites (≤ 1729 m), combination of gentler slopes (≤ 10º) with shorter distances to water (≤ 997 m), or higher slopes (> 10º) with certain vegetal communities (F. eskiae and F. paniculatae), were preferred for rooting (Figure 2b). In Sesa, again some plant communities (Primulion, F.eskiae, Rumicion, and Bromion) were the first splitting variable that accounted for the presence of wild boar rooting. In sites close to water (≤ 1444 m), disturbances were found in intermediate elevation ranges (1862-2284 m), or below if closer to water (≤ 448 m) (Figure 2c). In Aisa, Góriz, and Sesa, respectively, the AUC was 0.83, 0.82, and 0.80, and the corresponding accuracies were 88.5%, 79.8%, and 73.8%.

It is remarkable the influence of site-specific variables after certain plant communities have been taken into account. Thus, the combined effect of slope, elevation, and distances to water, seems to determine the occurrence of wild boar rooting in the three study areas, within those plant communities.

DISCUSSION

Our results showed that vegetation (i.e. some specific plant communities) was the main variable influencing the presence of wild boar rooting in Pyrenean grasslands. This has not been reported before for wild boar in natural habitats, but it has been shown for free-ranging pigs on mountain pastures (Vittoz and Hainard 2002). In mountain forests (Gallo Orsi et al 1995), vegetation has been cited as a determining variable in the occurrence of rooting, but not as the main one, probably because in those studies its relevance was hindered by other variables, such as elevation or management. Accounting for the complex interactions between variables may help disentangle the role of vegetation in these cases. In our study, the plant communities most commonly associated with wild boar rooting were certain types of dense grasslands, i.e. Festucion paniculatae, Festucion eskiae, and Bromion erecti, while sparse grasslands remained almost undisturbed. The preference of wild boars for dense grasslands can be related to their characteristic deep soils, which provide high quantity of foods, such as rhizomes, invertebrates, and small mammals or their hoards of bulbs (Kotanen 1995; Borghi and Giannoni 1997; Welander 2000a; Vittoz and Hainard 2002). Feeding requirements have been reported as a main factor determining the occurrence of rooting (Welander 2000a), to such an extent that supplementary feeding reduced 60 % of wild boar rooting damages to vineyards (Calenge et al 2004).

Within those preferred plant communities, the presence of wild boar rooting was influenced by a set of secondary variables that differed among sites. Those secondary variables reflected the particular characteristics of each site that locally constrained rooting by wild boar. In Aisa, where the slopes are steeper than in OMPNP, slope was the second most important variable, and wild boar rooting occurred on the gentler slopes. In Góriz and Sesa, their differences in the relative importance of distance to livestock sites to the occurrence of disturbances could be due to differences in the use of space by livestock. That parameter was more important in Góriz, where a few cattle flocks are concentrated in small, well-defined areas, than it was in Sesa, where a greater number of cattle and sheep are dispersed throughout the area. Wild boars might be attracted to areas used by livestock because of the fertilization effect of livestock in grassland communities, in which livestock-used grasslands are more productive and diverse than are the unused grasslands (Olff and Ritchie 1998). Evidently, wild boars follow a complex, but predictable, set of decisions when selecting where to root.

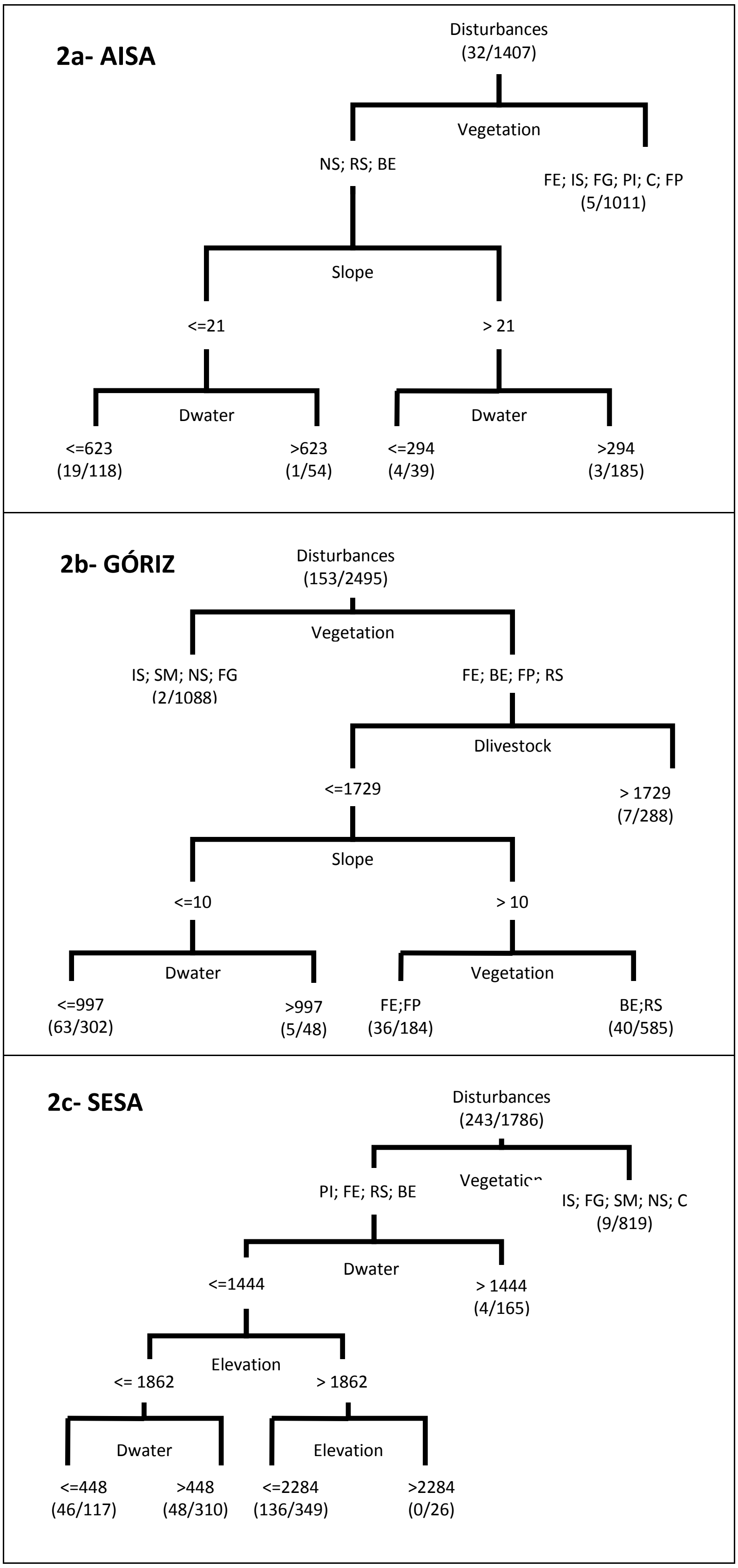

Figure 2. Tree plots with the hierarchical relationships among predictor variables derived from CART analysis in Aisa (2a), Góriz (2b), and Sesa (2c). In each step, the variable that best

split the data in two homogeneous groups of observations based on the presence or absence of wild boar disturbances was selected. The splitting value is shown, as well as the number of presences and absences (in parentheses separated by a bar), in each final node. BE = *Bromion erecti*, NS = *Nardion strictae*, RS = *Rumicion pseudoalpini*, FE = *Festucion eskiae*, FP = *Festucion paniculatae*, PI = *Primulion intricatae*, C = *Caricion nigrae* & *C. davallianae*, SM = *Saxifragion mediae*, IS = *Iberidion spathulatae*, FG = *Festucion gautieri*, DWater = Distance to water, and Dlivestock = Distance to livestock sites.

Understanding the complex interactions among explanatory variables can be a starting point to search for underlying factors not measured directly in the sampling design. For example, a smooth topography and proximity to certain resources can influence the occurrence and distribution of wild boar rooting (Hone 1988; Gallo Orsi et al 1995), but the manner and extent to which those variables interact is not well understood. In our study, we found that within some preferred plant communities, the distance to water at which wild boar disturbances are likely to be found can vary depending on the slope and elevation. Distance to water might reflect a gradient in the soil moisture that decreases as the distance from the water increases. Higher soil moisture would mean an easier soil to root for wild boars. In Aisa, rooting occurred at shorter distances to water on the steeper slopes and farther away where slopes were smoother. In Sesa, distance to water was not as important once a certain elevation threshold was surpassed. Soil moisture makes it easier for wild boars to root, as it has been reported in alpine grasslands (Gallo Orsi et al 1995) and forests (Welander 2000a). Typically, steeper areas retain less water and soil moisture decreases more dramatically away from the water source than do flatter sites (Hone 1995; Vittoz and Hainard 2002). In addition, soil has greater moisture content at higher elevations than it does at lower elevations and, thus, distance to water might be expected not to be a limiting factor above a certain elevation. In this sense, distance to water, elevations, and slope, are variables that indirectly reflect the underlying ecological factor of soil moisture, which in turn influences the hardness of the soil. This points out the need of including the structure of the relationships among explanatory variables in ecological models because most of the variables that are usually evaluated are indirect measures of the same underlying ecological factor (Guisan and Zimmermann 2000).

In our study areas, rooting affected up to 12% of the non-hunting area, which highlights the relevance of wild boar disturbances for the conservation of Pyrenean grasslands. Moreover, it is particularly worrisome because 97.6% of the disturbances occurred in designated "natural habitat types of community interest" (92/43/EEC of 21 May 1992). The proportion of total area that was affected is similar to other mountainous protected areas such as the Great Smoky Mountains National Park, U.S.A. (up to 15%; Bratton 1975) and Namadgi National Park, Australia (13.3%; Hone, 1988) but in these cases for feral pig (*Sus scrofa*) or wild boar crossed with feral pig. In our study, it is very likely that differences in the proportions of disturbed surface might have been due to differences in hunting management practices in the three areas. The proportion of disturbed area was lowest in Aisa, where wild boar hunting is allowed and, therefore, wild boar movements might be limited (Spitz and Jeneau 1990). Similarly, the proportion of disturbed areas is relatively low in some non-hunting areas, e.g. Sweden up to 6.28 % (Welander 2000a), and California, 7.5% for feral pigs (Kotanen 1995). In the OMPNP (Góriz and Sesa), hunting is forbidden, so wild boars can root with less concern about the need for shelter from hunters. Indeed, hunting pressure in neighbouring areas can increase the value of protected areas as refuges for wild boars (Acevedo et al 2006), which leads to an increase in the numbers of wild boars and their disturbances in these areas. The role of hunting management on the occurrence of wild boar disturbances warrants further study.

In conclusion, vegetation, as a measure of feeding habitat, was consistently the main variable determining the occurrence of wild boar rooting, in alpine and subalpine grasslands across the three study sites. The order of importance of subsequent variables closely related to wild boar rooting changed across sites. However, if the complex interactions among predictors are described, it is possible to grasp the underlying factors that are actually constraining the rooting activity of wild boars. In this sense, we found that after feeding preferences, the ability to root, as described by the interactions between elevation, slope and distances to water, and human management, i.e. hunting policy and grazing activities, might be the underlying factors behind most of wild boar rooting on alpine and subalpine grasslands.

ACKNOWLEDGEMENTS

We thank María Bueno, Ricardo Pineda, and Dorleta Jiménez for field assistance, Maite Gartzia for digitalizing and ground-truthing vegetation maps, and the staff of Ordesa and Monte Perdido National Park for the support and data provided. Earlier versions of the manuscript were considerably improved by R. Milla and S. Palacio. This research had financial support from the Spanish Ministries of Education and Science and Environment (MAM 2484/2002-059/2002 and PN-MEC CGL2005-01131/BOS) including an FPU grant to C.G. Bueno.

Does wild boar rooting affect livestock grazing areas in alpine grasslands?[♣]

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ABSTRACT

Interactions between traditional livestock management practices and wildlife activities are important in the conservation of many mountain ecosystems including the summer rangelands in the Spanish Central Pyrenees, where rooting by wild boar (*Sus scrofa*) is a large disturbance that can reduce the amount of area available to grazing livestock. This study explored the likely impact of wild boar rooting on Pyrenean grasslands. It quantified the extent of wild boar rooting in livestock grazing areas and determined whether wild boars selected or avoided areas depending on the type of livestock and stocking rates. Wild boar rooting affected 16% of livestock grazing area and occurred in sites that were grazed by cattle, rather than by sheep. In addition, a preference for areas that had intermediate stocking rates was found. The relationship between the increase in the number of wild boars and trends in livestock management suggests that the extent of wild boar rooting will increase especially in cattle grazing areas and therefore, the area available for cattle grazing in Pyrenean mountain rangelands would decrease significantly.

[♣] This chapter has been published in European Journal of Wildlife Research 56(5):765-770.

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INTRODUCTION

Mountain grasslands are mostly protected habitats and a major conservation priority in Europe (92/43/EEC of 21 May 1992). Those habitats have high socio-economic value because of the traditional livestock management practices, which sustain local economies, preserve cultural values, and produce high quality food (Luick 1998; Aldezabal 2001; Fillat et al 2008). Traditional European livestock management practices provide a balance between grassland production and conservation (Luick 1998; Olff and Ritchie 1998), maintain and enhance the structure and diversity of mountain grasslands (Dullinger 2003; Dennis 2008; Sebastià et al 2008), and prevent shrub encroachment (Pasche et al 2004).

In the last century, changes in land-use have had a significant impact on the structure and use of mountain ecosystems in Spain. Changes in grazing practices, i.e. a decrease in extensive livestock practices and a trend towards an increase in the number of cattle and a decrease in the number of sheep in extant herds because of the crisis in transhumance systems (Luick 1998; Lasanta-Martínez et al 2005), have led to the abandonment of grazing activities in some areas mostly used for sheep herding (Vicente-Serrano 2004). On the other hand, rural abandonment and an increase in forested areas (Lasanta-Martínez et al 2005) have indirectly increased wild boar populations because boars find more abundant and persistent shelters from hunting (Herrero et al 2008). Wild boar disturbances, i.e. rooting, have severely altered the structure and composition of grasslands in mountain ecosystems (Gallo Orsi et al 1995; Welander 2000b; Bueno et al 2009). In digging for food, wild boars turn over the soil, which can impact from a few square centimetres to hundreds of hectares (Gallo Orsi et al 1995; Massei and Genov 2004). Thus, they can disturb large areas, which can reduce the amount of area available to livestock (Tisdell 1982). Such a reduction can have an impact on traditional livestock management and local economies (Gortázar et al 2000). The need to quantify the extent of wild boar rooting in areas used by livestock is especially important in protected areas where livestock grazing is coupled with wildlife management and conservation (92/43/EEC of 21 May 1992). Several studies have contributed to the understanding of the main factors involved in the extent and distribution of wild boar rooting in mountain grasslands

(Gallo Orsi et al 1995; Welander 2000a; Bueno et al 2009), but there is little information about the interactions between wild boar rooting and traditional livestock management practices, especially in mountain environments. Livestock grazing appears to influence the occurrence of wild boar rooting in some areas (Bueno et al 2009), but most studies have focused on the impact of wild boar disturbances on crops, rather than livestock (Meriggi and Sacchi 1992; Calenge et al 2004; Wilson 2004; Herrero et al 2006a) and, to a lesser extent, on competition between wild boar and livestock for grazing areas (Kuiters et al 2005). The aim of this study is to explore the occurrence of wild boar rooting within livestock grazing areas in alpine grasslands, to determine its likely impact on livestock grazing activities. To address this objective, we quantify the extent of wild boar rooting in livestock grazing areas and evaluate the selection of wild boar rooting for areas used by cattle and/or sheep. We also evaluate if wild boar rooting occurs preferably at certain stocking rates, to infer to which extent grazing activities might be affected by wild boar rooting in the near future considering the current trends in livestock management.

METHODS

Study area

The study was conducted in Ordesa and Monte Perdido National Park (OMPNP) (42º 36’N, 0º 00’) in the Spanish Central Pyrenees. The study area comprised 3863 ha of natural grasslands between 1500 and 2800 m a.s.l, where the average annual temperature is 5 ºC and average annual precipitation is about 1720 mm, which is concentrated in spring and autumn (García-González et al 2007). The topography, lithography, and vegetation of the study area were broadly representative of the Spanish Central Pyrenees. Within the area, livestock management involves large herds of cattle and sheep, which use about 35% of the area during the grazing season (from July to October). In 2004, the numbers of cattle and sheep in the area were 1350 and 9580, respectively (data provided by the OMPNP). In the region, wild boars are abundant (~3.3 boars/km^2) despite being heavily hunted (Herrero et al 2005).

They inhabit nearby forests and frequently visit mountain grasslands to search for food, especially when food is scarce in the forests and grassland soils are friable (Welander 2000a; Herrero et al 2005). Hunting and providing supplementary feeding is not allowed within the National Park.

Wild boar rooting and stocking rate maps

To determine the extent and distribution of wild boar disturbances, the study area was mapped during summer 2005 (June-August). Disturbance patches were drawn on an aerial photograph (scale 1:3500), georeferenced by more than 1600 GPS point and incorporated into a GIS, generating a digital disturbance map (scale 1:5000). The minimum mapping unit was 5 m^2 and disturbances separated less than 1 meter were mapped jointly within the same disturbed patch. The accuracy of the map was 90.6 %, obtained by performing a confusion matrix (Congalton and Green 1999). 240 points were randomly located in the digital disturbance map, stratified between disturbed and undisturbed areas (120 points each), and checked in the field (for more details in this methodology see Bueno et al 2009). The map of the stocking rates was generated using a previous map for OMPNP based on an intensive monitoring of livestock movement during a whole grazing season in 1991 (Aldezabal et al 1992), and updating the numbers of cattle and sheep for 2004 (García-González et al 2007), which were expressed in standard livestock units (a 500-kg cow or six sheep) per hectare (SLU/ha) (for more details see García-González et al 2007). Shepherds and cowboys did not change from 1991 to 2004 (R. García-González pers. com.), so the same overall grazing areas used by livestock during the grazing season can be safely assumed (García-González et al 1990; García-González et al 2007; Fillat et al 2008).

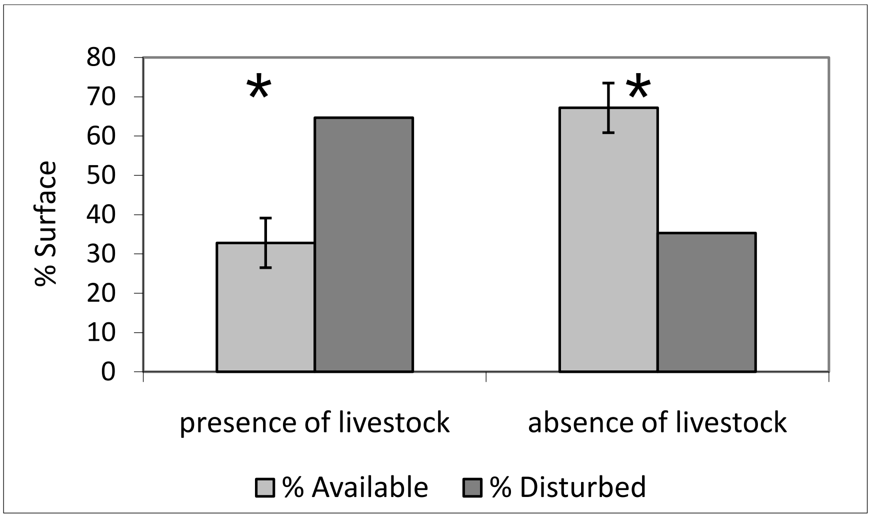
Resource Selection Analysis

To determine whether wild boar rooting was related to grazing areas, we performed a resource selection analysis comparing the rooted (ha) to the available (ha) surface, in which statistical inferences were based on the Chi-squared Test. The null hypothesis was that wild boars randomly selected areas used or not by livestock in proportion to availability (Manly et al 1993). When the observed and expected use of areas differed significantly from that based on availability, we used Bonferroni Confidence Intervals to detect significant selection or avoidance of areas by wild boar (Manly et al 1993; Alldredge and Griswold 2006). In addition, within livestock grazing areas, we distinguished between the areas used by cattle and those used by sheep. Areas used mutually (<18% of the area grazed) were categorized as cattle grazing or sheep grazing areas depending on their relative contributions (>50%) to the overall stocking rate. To extract data from the GIS maps, we used ArcGis 9.2.

Generalized Additive Models

To describe the relationships between the presence/absence of wild boar rooting and the stocking rates of cattle and sheep, we used univariate binomial Generalized Additive Models (GAM) with a logit link (Hastie and Tibshirani 1990; Nogués-Bravo 2006). To generate the response variable, i.e. occurrence of wild boar rooting, a sample of 1000 points was stratified into two classes based on the presence or absence of wild boar rooting (500 points inside and 500 points outside disturbed areas). To avoid spatial autocorrelation, points were chosen randomly, but were ≥50 m apart (Bueno et al 2009). Predictor variables for each model, i.e. sheep and cattle stocking rates respectively, were modelled using cubic regression splines, and the optimal amount of smoothing was estimated via cross-validation (Zuur et al 2009). To improve the fit of the model, stocking rates were log-transformed, which was appropriate because, within the study area, a few areas were used very intensively by livestock and most areas were used rarely or not at all (Aldezabal 2001). All statistical analyses were performed using R 2.7.2 (R Development Core Team 2008) and the *mcgv* package (Hector et al 1999).

a. Wild boar rooting in Ordesa and Monte Perdido National Park



b. Wild boar rooting within livestock-grazed areas

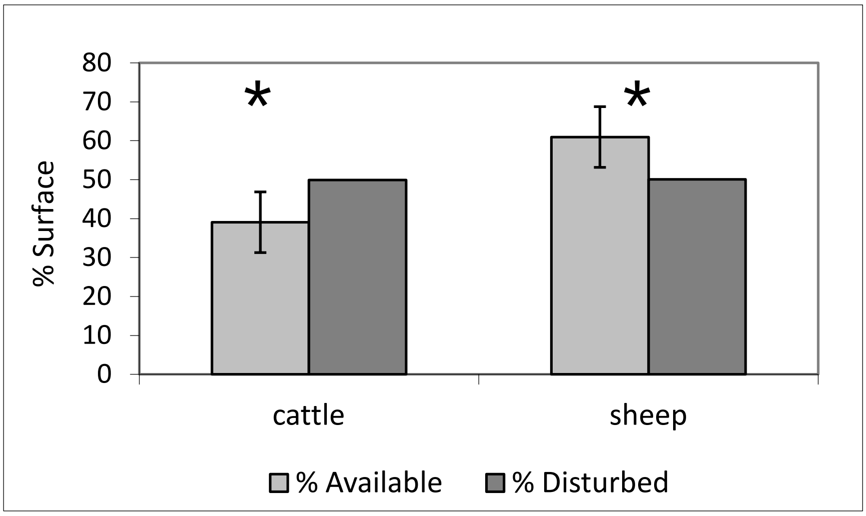


Figure 1. Wild boar rooting (a) in Ordesa and Monte Perdido National Park and (b) within livestock-grazed areas. Whiskers in the percentages of available surface (light grey bars) represent Bonferroni confidence intervals: non-random selection by wild boar occurred if these intervals are exceeded by the proportion of disturbed area (dark grey bars) while significant avoidance occurs when these intervals are not reached. Asterisks indicate significant cases ($p<0.05$).

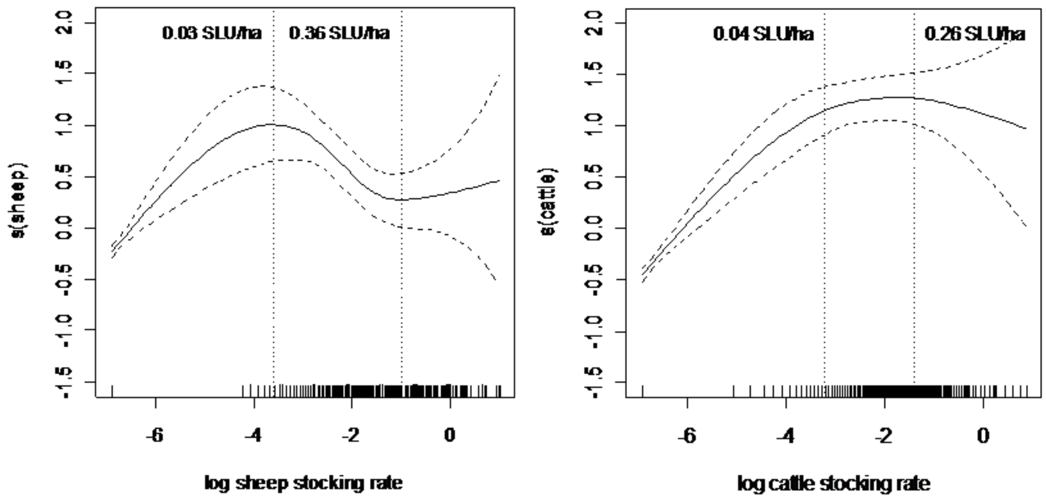
RESULTS

In OMPNP, rooting by wild boars was evident in 16.2% of the area used by livestock (206.6 ha out of 1268.2 ha); 20.8% of the areas used by cattle (103.01 ha out of 495.25 ha) and 13.4% of those used by sheep (103.58 ha out of 772.96 ha) were rooted. According to their availability within the total area studied in OMPNP, areas previously grazed by livestock were selected by wild boar for rooting and non-grazed areas were avoided (Figure 1a; Chi-squared= 146.85, p<0.001). Within grazed areas, those holding cattle were significantly selected whereas those used by sheep were avoided by foraging wild boars (Figure 1b; Chi-square = 10.29, p<0.05).

Both sheep and cattle stocking densities showed a non-linear pattern on the response. After cross-validation, the effective degrees of freedom were set to 3.272 and 2.198 for sheep and cattle respectively. Effective degrees of freedom reflect the ruggedness of the smoothing parameter, being values close to 1 straight lines and higher values indicating non-linearities. In both models, the smoothing term was highly significant (sheep: chi-squared=69.85, p=0.000; cattle: chi-squared=201.9, p=0.000). Areas grazed by cattle had a higher occurrence of wild boar rooting among a wider range of stocking rates compared to the areas grazed by sheep (Figure 2). The presence of wild boar rooting reached its maximum where the sheep stocking rate was 0.03 SLU/ha (Figure 2a). At higher stocking rates (up to 0.36 SLU/ha), this presence was reduced, and no response was shown further on. Wild boar rooting was largest at cattle stocking rates between 0.04 and 0.26 SLU/ha and, at higher rates, rooting affected a smaller extent (Figure 2b).

DISCUSSION

In the protected Pyrenean alpine grasslands of the OMPNP, Spain, wild boar rooting affected up to 16% of the area available to grazing livestock, which might represent a serious threat to the already declining livestock grazing activities. In addition, several factors suggest that the trend is worrisome. In recent decades, populations of wild boar have increased in Europe (Geisser and Reyer 2004; Acevedo et al 2006; Schley et al 2008). Larger populations might lead to an increase in wild boar disturbances, which has been observed in feral pig populations in other protected mountainous areas (Hone 2002). Furthermore, in the OMPNP, disturbances were not randomly distributed among livestock types and stocking rates. For foraging, wild boars appeared to prefer areas that had intermediate stocking rates and those grazed by cattle, and some of the areas grazed by sheep appeared to be avoided. Although the number of livestock in the area has decreased, sheep have been replaced by cattle because the latter are more profitable and less demanding; consequently, the relative number of cattle has increased in mountain ecosystems (Luick 1998; Lasanta-Martínez et al 2005). Given the relationships between wild boar rooting and the type of livestock and stocking rates, if current livestock management practices continue, wild boar rooting might expand in the near future.



a. sheep **b. cattle**

Figure 2. Estimated smoothing curves (cubic regression splines) and point-wise 95% confidence intervals for the Generalized Additive Models containing respectively the stocking rates of sheep (a) and cattle (b) as predictor variables, and the presence/absence of wild boar rooting as the response variable, in Ordesa and Monte Perdido National Park, Spanish Central Pyrenees. The horizontal axis shows the observed values of stocking rates (short vertical lines), and the vertical axis the contribution of the smoother to the fitted values. Critical values of untransformed stocking rates are indicated (vertical dashed lines).

Livestock activities influence the physical properties of soil and nutrient cycles (Bezkorowajnyj et al 1993; Mikola et al 2009), which might directly or indirectly influence the foraging behaviour of wild boars. The diet of wild boars in mountain ecosystems is not well studied, but the evidence suggests a clear relationship between rooting activity and the foraging for nutrient-rich foods such as animal proteins and plant storage structures (Baubet et al 1997; Schley and Roper 2003). Two of the local effects of grazing can explain the differences in wild boar rooting activities among stocking types and rates: faecal droppings differ between sheep and cattle because cattle produce larger scats and sheep disperse smaller pellets widely and in smaller quantities (Aldezabal et al 1993). Furthermore, cattle dung attracts more insects (Finn and Giller 2002), earthworms (Baubet et al 1997; Baubet et al 2003), and voles (Evans et al 2006) than does sheep dung, and wild boars actively seek these types of foods. In addition, trampling is more homogeneous and extensive in sheep grazing areas than in cattle grazing areas because sheep have a greater tendency to cluster (Albon et al 2007). Cattle trampling is heterogeneous and mostly limited to specific pathways, which leaves some patches untouched (Bezkorowajnyj et al 1993; Albon et al 2007). Areas that have high stocking rates might be less preferred by wild boar because of the soil compression caused by trampling (Kuiters et al 2005; Albon et al 2007), which makes the soil more difficult to dig (Bowman and McDonough 1991; Gallo Orsi et al 1995; Bueno et al 2009). Therefore, differences in the use of space by cattle and sheep might explain why cattle grazing areas were more strongly affected by rooting than were the areas grazed by sheep.

Given the current trends in livestock management in Spanish Pyrenees, i.e. an overall decline in the number of livestock and a trend towards cattle, rather than sheep, herding, and the increase in wild boar populations, the heterogeneous impact of wild boar rooting might increase in the near future. One result might be a significant reduction in the amount of area suitable for grazing cattle, which might have an adverse effect on the economy in the already depressed extensive livestock management systems in mountain summer rangelands in Spain.

ACKNOWLEDGEMENTS

We thank the staff of OMPNP for the support and data provided. This research was funded by the Spanish Ministry of Science and Innovation, and the Spanish Ministry of Environment (MAM 2484/2002-059/2002 and PN-MEC CGL2005-01131/BOS respectively), including a pre-doctoral fellowship to CGB. Earlier versions of the manuscript were considerably improved by S. Palacio, and B. MacWhirter improved the English version.

Capítulo 2. Escala de comunidad y especie

Una vez conocido la ubicación y extensión de las hozaduras de jabalí a una escala de paisaje, resulta fundamental comprender sus consecuencias a una escala más fina. Se ha señalado anteriormente el potencial impacto de este tipo de perturbaciones en zonas alpinas, que son particularmente sensibles a la remoción del suelo (García-González 2008). Estudios realizados en otros ecosistemas han puesto de manifiesto una gran complejidad de los mecanismos y procesos ligados a las perturbaciones de jabalí (Lacki and Lancia 1986; Genard et al., 1988; Welander 2000a), pero ninguno antes ha estudiado en detalle la afección a varios de los elementos del ecosistema. Es por ello que resulta fundamental estudiar el impacto de estas perturbaciones en zonas alpinas, sobre los parámetros edáficos (capítulo 2a), el banco de semillas del suelo (capítulo 2b), y sobre la vegetación establecida (capítulo 2c) que, a su vez, determinarán el nicho para la regeneración de la vegetación. Estos trabajos en su conjunto darán una información valiosa acerca de la posible repercusión de las hozaduras de jabalí y de los procesos de regeneración de los pastos alpinos.

Soil responses to large wild boar disturbances in Pyrenean alpine grasslands♣

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ABSTRACT

Wild boar is the most widespread ungulate in the world and its European populations are currently growing. The major impact of its presence is rooting, that consists of turning over the soil, removing plant cover and as a consequence, disturbing extensive areas in the whole range of habitats where it occurs. Some of these habitats, such as alpine grasslands, might be particularly sensitive to soil disturbances. Despite these disturbances may deeply alter the physic and chemical properties of soils and thereby affect the ecological baseline of ecosystems, the environmental consequences of wild boar rooting on soils have received little attention. Here, we analyze physical and chemical soil properties in the five most affected grasslands inside and outside disturbances in the Central Pyrenees, Spain. The main trend driven by disturbances was towards an increase in bulk densities and soil nitrate content, and a decrease in the concentration of some cations (Ca^{2+}, Na^{+}, Mg^{2+}) in all communities. Ammonium concentration was only altered in tall-tussock communities by the presence and intensity of disturbances. The consequences of these changes are a disruption in the soil structure that leads to a generalized soil compaction, and an increase of soil nitrate content within disturbances, differing with the intensity of disturbance. Understanding which soil properties are most affected by wild boar in the soils they root is a key step to disentangle the consequences to vegetation recovery and dynamics in sensitive habitats, as well as to provide insights to their impact on other habitats where wild boar rooting occurs.

♣ This chapter has not yet been published

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INTRODUCTION

Soils are essential parts of the ecosystems, as they physically support primary producers and decomposers, maintain biotic communities and determine main ecological processes such as nutrient cycling or material-energy flows throughout the system (Lavelle et al 1997; Brady and Well 2002). At the ecosystem and community levels, soils determine the structure, composition, and dynamics of communities through their response to environmental changes or to disturbances (Pickett and White 1985). Therefore, disturbances on soils are potential drivers of change, as they affect soil properties and indirectly most biotic communities and ecological processes that soils support. The severity of the impact depends on the target ecosystem and its resilience to different types of disturbances, with some habitats being particularly sensitive (Pickett and White 1985). Within mountain ecosystems, alpine habitats are likely to be very sensitive to such disturbances due to the reduced active growth period and their plant structure where most plant biomass is located in the first few cm belowground (Körner 1999b; García-González 2008).

Wild boar has been reported as one of the main agents causing soil disturbance in alpine habitats as well as in other ecosystems where it inhabits (Massei and Genov 2004; Bueno et al 2009; Oliver and Leus 2008). This suid has one of the widest distribution range of all terrestrial mammals and at the same time is one of the most widespread introduced vertebrate species worldwide (Oliver and Leus 2008). Its main disturbing activity consists on rooting up the soil looking for underground feeding resources (hereafter ‘rooting’). Despite being a widespread disturbance that can affect hundreds of hectares (Welander 2000a; Massei and Genov 2004; Bueno et al 2009), few studies have analyzed the effect of rooting on soil properties. Some studies relate to forest habitats (Lacki and Lancia 1983; Singer et al 1984; Groot Bruinderink and Hazebroek 1996; Moody and Jones 2000; Mohr et al 2005) and others to coastal grasslands (Kotanen 1994; Tierney and Cushman 2006) but none has focused on sensitive alpine grasslands. Other animal disturbances have been studied on alpine soils, such as those created by pocket gophers (*Thomomys talpoides*; Laycock and Richardson 1975; Litaor et al 1996; Sherrod and Seastedt 2001), moles (*Talpa europaea*; Canals and Sebastiá 2000) or even grizzly bears (*Ursus arctos* *horribilis*; Tardiff and Standford 1998). However, different animals can have varying effects on soil properties (Hole 1981), but even the same animal species may have different effects on different habitats or soils (Canals and Sebastiá 2000). In addition, the intensity of animal disturbance appears to be a fundamental disturbance property, since increasing intensities lead to increased degradation of plant communities and soils (Pickett and White 1985; Laska 2001).

The aim of the study is to determine the effects of wild boar rooting on soils in the five most disturbed alpine grassland communities in the Spanish Central Pyrenees. We suspect that a deep alteration of alpine soils, through modifying their structure or accelerating the leaching of nutrients, can compromise the preservation of alpine soils and may affect grassland dynamics. For a broad perspective we (1) first explored the main effects of wild boar rooting on soil properties, comparing soil parameters within and outside disturbances related to physical (i.e. electrical conductivity, bulk density and moisture) and chemical properties (i.e. pH, carbon, nitrogen, phosphorous, and cation content: Ca, Na, K, and Mg) of soils. Secondly, regarding the potential alteration in the availability of nutrients through soil disturbance, (2) we evaluated the relationship between soil mineral nitrogen (i.e. nitrate and ammonium), and the occurrence and intensity of wild boar disturbances. Comparing the effects of the occurrence and intensity of disturbance on soils may provide insights to its global effects taking into account the recurrent activity of rooting by wild boar that in turn is expected to generate greater soil alterations.

METHODS

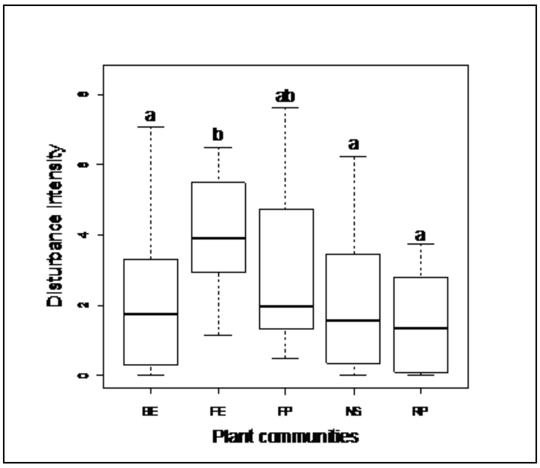
Study area

The study was carried out in Ordesa and Monte Perdido National Park (OMPNP) (42º 36’N, 0º 00’) in the Spanish Central Pyrenees. The study area comprises natural grasslands between 1500 and 2800 m a.s.l. with an average annual temperature of 5 ºC and an average annual precipitation of 1750 mm, most of which occurs in spring and autumn (García-González et al 2007). The geology is mainly limestone and calcareous sandstone, while the topsoil has a clay-loam texture, with illite as dominant clay type. Soils are acidic, desaturated in bases and with a high organic matter content and structural stability (umbric epipedon); with these properties, the soil profiles are classified as Humic Dystrocryepts (Badía et al 2002; Badía et al 2008). In the study area, we selected the five grassland communities most disturbed by wild boar, which are among the most extensive alpine grassland communities in the Pyrenees (Bueno et al 2009). The topography among these grasslands is smooth with slopes < 20º (Bueno et al 2009). These plant communities are dense grasslands, three of them being dominated by one grass species; Festucion paniculatae (FP) by *Festuca paniculata*, Festucion eskiae (FE) by *Festuca eskia* and Nardion strictae (NS) by *Nardus stricta*. The other two are co-dominated by more than three species; Briomion erecti (BE) by *Festuca gr. rubra*, *Agrostis capillaris*, *Lotus alpinus*, etc, and Rumicion pseudoalpini (RS) by *Poa supina*, *Rumex pseudoalpinus*, *Chenopodium bonus-henricus*, etc (Fillat et al 2008). Grazing activities, mainly by sheep and cattle, differ among plant communities from more intensively grazed with more presence of cattle to less grazed with less cattle, so the grazing gradient from the most grazed to the least is: RP>BE>FP>NS>FE. Livestock grazing determines the occurrence of RP while it determines the extent of BE (Fillat et al 2008). The selected plant communities cover an extent of 2773 ha (54.3 % of the whole study area) but receive close to 98% of the wild boar disturbances (Bueno et al 2009). The high recurrence of rooting makes its dating very difficult due to the continuous overlapping of successive rooting (Welander 2000a; Bueno et al 2009). Therefore in this study we consider two main states for vegetation, disturbed and undisturbed. Disturbed patches are those rooted up by wild boar recently or in the last two years, with the presence of some overturned pieces of turf that are a differential sign from other animal disturbance in the area (Bueno et al 2009). Undisturbed patches are those completely covered by vegetation without any presence of overturned turf and forming a continuum with the surrounding grassland.

Sampling design

A random stratified paired sampling design was applied in the study area. In each one of the five plant communities, sampling points were randomly set within and outside disturbances in a paired fashion. In 2006, 100 soil samples (20 per community, 10 outside and 10 within disturbance) were collected with a cylindrical metal core sampler that extracts a soil cylinder of 5 cm diameter and 10 cm depth. Geographical coordinates of each sampling point were recorded with GPS. Disturbance depth was measured relative to the surrounding soil level, by taking 300 depth measures within wild boar disturbances in the study area. Average disturbance depth was 10.7 ± 0.3 cm (mean ± standard error). In 2007, 200 ion exchange resin bags were placed 10 cm deep underground during 45 days in mid-August, during the peak of the growing season. Half of the resin bags (100) were placed in the same sampling points as the previous design, and the other half in new sampling points following the same sampling procedure.

Figure 1. Differences in disturbance intensity, in squared meters of removed volume of soil, among plant communities in the five most disturbed alpine grasslands in Central Pyrenees, Spain. Small-case letters represent significantly different groups among plant communities, tested with a non-parametrical multiple test procedure at alpha < 0.05 between all possible pairs of communities. BE=*Bromion erecti*; FE=*Festucion eskiae*; FP=*Festucion paniculatae*; NS=*Nardion strictae*; RP=*Rumicion pseudoalpini*.



Disturbance intensity

Disturbance intensity was estimated by calculating the approximate volume of soil in cubic meters which was overturned by wild boar rooting activity. For this calculus, in each sampling point within disturbances, two measures of disturbance depth and the two main diameters of each disturbed patch, as well as the approximate shape of each disturbance (i.e. squared, rectangular, circular, ellipsoid or triangular) were taken. Then the volume of each disturbance was calculated (the area of the disturbance multiplied by its average soil depth). This measure was used as a proxy for disturbance intensity, assuming that the more intense wild boar disturbs the more soil volume is overturned. Disturbance intensity differed among plant communities indicating a heterogeneous impact on alpine grasslands, being higher in FE and to a lesser extent in FP (Figure 1).

Soil analysis

Soil samples were air-dried, sieved at a mesh size of 2 mm and grinded for all soil analysis except for moisture content, which was determined by mass difference after drying 2 g of soil at 105 ºC during 24 hours, and bulk density, which was determined dividing the weight of each soil core sampled by its volume (Klute 1986). Soil pH was measured in a 1:5 soil water suspension after shaking for 2 hours (Buurman et al 1996). Total and oxidizable carbon, as well as total nitrogen, were determined by an Elementar Analysensysteme GMBH Autoanalicer (Page 1982). Organic matter was calculated from oxidizable carbon multiplied by Van Bemmelen factor (1.724; Heanes 1984). Available phosphorous was determined by 0.5 M sodium bicarbonate extraction at a nearly constant pH of 8.5 (Page 1982). Soil cations (Ca^{2+}, Mg^{2+}, Na^{+} and K^{+}) were extracted from 10g of soil, shaking 1 hour in 1M ammonium-acetate solution at pH 7, and their concentration was determined with ICP-OES (Thermo iCAP 6000 series). C:N ratio was calculated by dividing the percentage of oxidizable carbon and of total nitrogen.

Ion exchange resin bags were used to determine relative concentrations of soil mineral nitrogen (NH^{4+}-N and NO^{3-}-N). Resin bags were prepared according to Tardiff and Stanford (1998) with 8.5 g wet mass of cation plus anion mixed-bed ion exchange resin (J. T. Baker mixed-bed ion exchange resin, VWR Scientific Products) placed in nylon stockings (Page 1982; Binkley and Matson 1983). Resin bags were then buried at 10 cm for 45 days in the field. After that, they were retrieved and allowed to air-dry for two days, and then extracted with 100 ml of 1M KCl (Tardiff and Standford 1998). Ammonium and nitrate concentrations were determined colorimetrically (Maynard and Kalra 1993; Tardiff and Standford 1998).

Statistical analyses

Soil properties

To determine which soil properties were significantly altered by the presence of wild boar disturbances, two complementary analyses were used; binomial generalized linear mixed models (GLMM) and Wilcoxon signed rank tests. A binomial GLMM was used to analyze the relative effect of disturbances on soil parameters. For the binomial GLMM, the presence / absence of wild boar disturbances was used as the response variable, and all soil parameters and plant community categories, transformed into dummy variables, were introduced as predictors (Quinn and Keough 2002). Mixed effects models were used to account for the potential lack of independence in the paired observations due to the sampling design (Zuur et al 2009). Therefore a “pair” factor was introduced into the model as the random factor. This “pair” factor was calculated assigning, to each pair of observations (disturbed-undisturbed) a number from 1 to 50 (n=100). Linearity between pairs predictor-response variables was checked with univariate GAM plots (Zuur et al 2009), where all variables showed an approximate linear relationship with the response. Multicollinearity was evaluated based on Variance Inflation Factors (VIF) and Pearson correlation tests. Highly correlated variables (organic Carbon, total Carbon and organic matter) were not included in further analyses because they were strongly correlated (≥ 0.8) with "total nitrogen". In the final model all variables showed VIF <3 and Pearson correlations <0.5 (Graham 2003; Zuur et al 2009). To select the final model, backward and forward stepwise model selection procedures based on AIC were used (Zuur et al 2009). Spatial autocorrelation among observations was checked in the residuals using a residual correlogram and no significant spatial dependency was detected (Dormann 2007).

Wilcoxon Signed Rank tests were used to evaluate the effects of wild boar rooting on each soil parameter within each plant community, since samples were pair-matched and normality could not be assumed (Moore et al 2008). This analysis complements the former by focussing on each soil parameter within each plant community, which can be relevant for specific plant community effects that could be diluted by the GLMM.

Binomial GLMM Response: Presence / Absence of disturbances Random Factor = Pair			
	B (± SE)	**z**	**p value**
(Intercept)	-19.86 ± 4.386	-4.528	0.000
BD	12.000 ± 2.517	4.768	0.000
Ca	-0.002 ± 0.001	-2.998	0.003
Na	-0.207 ± 0.084	-2.467	0.014
EC	0.007 ± 0.003	2.698	0.007
tN	8.208 ± 3.116	2.634	0.008
P	-0.001 ± 0.000	-2.427	0.015

Table 1. Soil parameters significantly modified by wild boar rooting on Pyrenean alpine grasslands, from a binomial Generalized Linear Mixed Model. B (± SE) = coefficient values ± Standard error; BD=Bulk density; Ca=Calcium; Na=Sodium; EC = Electric conductivity; tN=total nitrogen; P=Phosphorous.

Soil mineral nitrogen

To analyze the relationship between soil available mineral nitrogen (nitrate and ammonium) and the occurrence and intensity of disturbances among the five grassland communities, two partial redundancy analysis (pRDA) (Legendre and

Legendre 1998) were carried out. To relate mineral nitrogen with the occurrence (presence and absence) of disturbances, the response matrix of the pRDA was composed by 200 observations (rows) and 10 binary vectors (columns), 5 representing the presence (‘1’) and absence (‘0’) of plant communities within disturbances and 5 outside disturbances. The environmental matrix was composed by two vectors; the concentration of nitrate and ammonium in each of the sampling points (n=200). To relate the concentration of soil mineral nitrogen compounds with disturbance intensity, the response matrix was conformed by 100 observations (retaining only the observations within disturbances) and the environmental matrix was composed by five vectors representing the disturbance intensity in each one of the five plant communities. In both cases, multicollinearity among predictors was checked with VIF and Pearson correlation tests, and all predictors had values <0.3 and <0.5 respectively. Spatial autocorrelation was taken into account in the model by incorporating the axis obtained after applying spatial eigenvector maps (SEVM) from the distance matrix of the geographical coordinates of the observations (Dormann 2007). SEVM procedure extracts the potential spatial component of the model in orthogonal vectors that can be later included in regression or ordination models to account for spatial dependencies at different scales (Dray et al 2006; Griffith and Peres-Neto 2006). A forward selection of spatial predictors was carried out (Griffith and Peres-Neto 2006; Blanchet et al 2008) before SEVM axis were incorporated into pRDAs. Spatial autocorrelation was checked calculating the Mantel correlogram of the residuals (Legendre and Legendre 1998) and a global test of spatial autocorrelation using Moran’s Index (Dormann 2007). Autocorrelation was significantly reduced with the incorporation of selected SEVM predictors into the partial RDAs and no spatial dependencies were found.

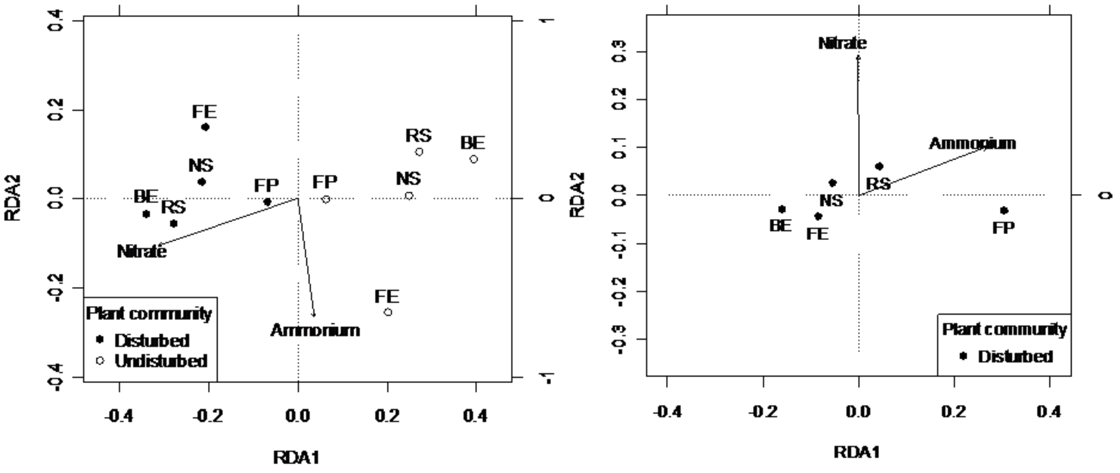
Again, Wilcoxon Singed Rank Tests were used to evaluate the differences in soil nitrate and ammonium concentrations between outside and within disturbances for each plant community.

All statistical analysis were performed with R 2.10.1 (R Development Core Team 2009) and the packages used were: *npmc* for non-parametric multiple comparisons, *glmmML* for binomial GLMM, *ncf* for correlograms, *car* for VIF, *mgcv* for univariate

GAM plots, *vegan* for pRDA, *packfor* for forward selection of spatial predictors, and *spdep* and *spacemakeR* for SEVM.

Figure 2. Relationships of nitrogen mineral compounds (nitrate and ammonium) with (a) the presence and absence of disturbances, and (b) disturbance intensity among the five most disturbed plant communities by wild boar, as modelled with partial RDA. Arrows show axes that were significant ($p < 0.05$) after a permutation test with 1000 permutations, except for *Nitrate* axis in (b). BE=*Bromion erecti*; NS=*Nardion strictae*; RP=*Rumicion pseudoalpini*; FE=*Festucion eskiae*; FP=*Festucion paniculatae*.

a) presence/absence of disturbances **b) disturbance intensity**



RESULTS

Relative effects on soil parameters

Taking all soil samples together and analyzing the effect of wild boar disturbance on the soil properties of Pyrenean grasslands, the factor “plant community” was not significant in the model (Table 1), so the global effects follow the same trend for all communities. The main soil property changed was bulk density, which had higher values in the presence of disturbances (positive Z value) (Table 1). This trend was consistent across communities with the exception of FP (Table 2). In the concentration of Ca, Na and P the trend was a decrease within disturbances coupled to a global increase in electrical conductivity (EC) (Table 1). In all communities the general trend was the same for the aforementioned elements, except for Ca that showed contrasting community-dependent results; for example, it increased in BE, while decreased in FP within disturbances (Table 2). Total nitrogen was significantly higher within disturbances, when taking all plant communities together (Table 1), but a subtle non-significant increase was found when studying each community separately (table 2). This reflects a global trend in all communities and a constant but subtle effect in each community.

Differences among communities, taking within and outside disturbance separately, showed that for FE soil pH in undisturbed areas had the lowest values among all undisturbed plant communities (Table 3). Regarding CN ratio among undisturbed communities, it differed among communities being higher at those dominated by a single grass species (FE, NS & FP; Table 3). For FP, the most productive in terms of biomass, CN ratio decreased in disturbed areas (Table 2) probably indicating a high decomposition rate of organic matter, as its content of soil organic matter was the highest in disturbed areas (Table 3). For FE, both outside and within disturbance, Ca soil concentration was lower than in the others communities (Table 3), probably due to its acidic nature and its scarce use by livestock.

Table 2. Soil parameters (median ± median absolute deviation) in each disturbed and undisturbed plant community. Significant differences between disturbed-undisturbed pairs tested with a *Wilcoxon Signed Rank test*. Significant differences at p values: '*' 0.05, '**' 0.01, '***' 0.001 are in bold. Plant communities order follows the grazing gradient form more grazed (left) to less. EC=Electrical conductivity; Ox.C=Oxidizable organic Carbon; tC=total Carbon; tN=total nitrogen; C/N=Carbon nitrogen ratio; OM= Organic matter; Moisture=Moisture content; BD=bulk density; P= phosphorous; Ca=Calcium; Mg=Magnesium; Na=sodium; K= potassium. *BE= Bromion ercti; NS=Nardion strictae; RP=Rumicion pseudoalpini; FE=Festucion eskiae; FP= Festucion paniculatae; Undist=Undisturbed areas; Dist=disturbed areas.*

Soil parameters	***RP***			***BE***			***FP***			***NS***			***FE***		
	Undist	**Dist**		**Undist**	**Dist**		**Undist**	**Dist**		**Undist**	**Dist**		**Undist**	**Dist**	
EC (mS/cm)	0.25±0.11	0.19±0.07		0.26±0.04	0.35±0.20		0.31±0.10	0.25±0.09		0.24±0.07	0.20±0.10		0.18±0.04	0.19±0.08	
pH (1:5)	4.52±0.76	4.87±1.00		5.42±0.22	5.75±0.74		5.34±0.53	5.26±0.40		4.83±0.36	4.71±0.55		4.01±0.36	4.01±0.39	
ox. C (%)	3.76±0.91	3.97±0.35		3.34±0.86	3.54±0.74		5.06±1.23	4.9±0.49		4.24±0.76	4.42±0.67		4.14±1.09	4.36±0.68	
tC (%)	4.51±0.97	4.74±0.54		4.21±1.04	4.73±0.81		6.33±2.02	6.18±0.50		5.09±1.16	5.69±0.97		5.61±1.43	5.8±1.77	
tN (%)	0.49±0.08	0.51±0.03		0.46±0.06	0.51±0.07		0.61±0.10	0.61±0.08		0.48±0.12	0.54±0.09		0.52±0.09	0.62±0.13	
C/N	9.28±0.67	9.1±0.78		8.82±0.43	9.17±0.70		**10.97±1.7**	**10.58±1.64**	*	10.79±0.96	10.26±1.43		10.72±0.58	10.05±0.88	
OM (%)	6.54 ± 1.58	6.91 ± 0.61		5.81 ± 1.50	6.16 ± 1.29		8.80 ± 2.14	8.53 ± 0.85		7.38 ± 1.32	7.69 ± 1.17		7.20 ± 1.90	7.59 ± 1.18	
Moisture (%)	7.53±3.03	9.7±0.69		7.27±2.58	9.22±1.74		10.61±2.61	9.88±1.59		8.22±3.18	10.72±1.53		8.67±3.85	11.33±3.15	
BD (g/cm^3)	**1.46±0.27**	**1.68±0.15**	**	**1.43±0.14**	**1.66±0.13**	**	1.44±0.25	1.45±0.11		**1.34±0.31**	**1.67±0.15**	* *	**1.18±0.10**	**1.5±0.05**	* *
P (Kg/ha)x10^{-3}	0.30±0.22	0.39±0.33		0.13±0.03	0.14±0.06		**0.37±0.08**	**0.30±0.15**	*	0.10±0.07	0.11±0.09		0.09±0.06	0.15±0.10	
Ca (Kg/ha)x10^{-3}	1.65±1.01	1.51±0.82		**1.47±0.65**	**1.98±1.07**	*	**1.37±0.58**	**1.08±0.36**	*	1.01±0.38	1.29±0.48		0.3±0.15	0.27±0.12	
Mg (Kg/ha)	21.12±8.55	19.71±9.51		20.81±5.50	18.58±3.95		14.27±5.32	13.05±1.77		14.57±4.89	14.67±5.56		**9.75±1.49**	**7.62±3.42**	*
Na (Kg/ha)	**7.24±2.61**	**4.04±1.35**	**	**10.44±1.45**	**7.64±1.72**	*	6.74±2.50	6.15±0.69		5.40±2.87	5.22±2.72		8.04±2.27	8.07±2.51	
K (Kg/ha)	99.72±78.88	105.32±40.66		44.00±15.10	50.99±18.80		55.46±15.12	48.45±25.06		40.15±13.41	60.61±23.35		39.79±11.35	45.54±18.29	

Soil mineral nitrogen

The amount of nitrate and ammonium in soils was clearly modified by the occurrence and intensity of wild boar disturbances in the alpine grasslands. In general we observed that the presence of disturbance significantly increased mineralization rates of nitrogen in terms of nitrate concentration in all communities (all cases $p<0.01$; Figure 2a). The effect in ammonium concentration was only found for tall-tussock grass dominated communities, FE and FP, being in FE significantly increased ($p<0.05$) by the presence of disturbances (Figure 2a) and FP by disturbance intensity (Figure 2b). These results would indicate the incidence of the occurrence and intensity of disturbances in the mineralization rate of nitrogen especially in those alpine plant communities, dominated by tall-tussock grass communities and scarcely grazed.

DISCUSSION

Wild boar rooting is a large soil disturbance that mainly affects the first ten cm of soil at Pyrenees grasslands. This has been also described in other ecosystems where wild boar or feral pig occur (Kotanen 1994; Groot Bruinderink and Hazebroek 1996; Tierney and Cushman 2006). Within this soil depth wild boars may find highly diverse food sources such as invertebrates and small vertebrates, as well as nutrient-rich bulbs and rhizomes (Singer 1981; Herrero et al 2005). In their foraging activity wild boars alter most biotic communities responsible for most of the nutrient cycling processes in soils (Lacki and Lancia 1983; Singer et al 1984). For instance, in the Pyrenean alpine grasslands the occurrence of wild boar rooting increased the availability of soil nitrate irrespective to plant community type, while soil ammonium remained unaltered. Soil nitrate concentration is the result of a complex trade-off; on one hand the nitrate 'input' corresponds to the nitrogen decomposition and mineralization rate, while the 'output' depends on plant N uptake, N immobilization by decomposers, leaching or run-off and denitrification rates (Vitousek 1985). Wild boar rooting may denude and disrupt the physical structure of the soil, altering soil properties such as aeration, soil temperature and soil moisture contents that in turn alter the trade-off between nitrate 'outputs' and 'inputs' processes (Groot Bruinderink and Hazebroek 1996; Moody and Jones 2000). The differences found in other areas disturbed by wild boar or feral pig in terms of nitrate soil content, range from consistent with ours, in mountain forest soils of Tennessee (Singer et al 1984) and Hawaii (Vitousek 1986), to contrasting results from simulated feral pig disturbances in coastal grasslands of California that found increasing ammonium availability only (Kotanen 1997a) or no significant change at all (Cushman et al 2004). This variety of responses from different habitats to a similar kind of disturbance may indicate that the alteration of nitrate trade-off may be different in each site. We can consider that in general the reduction of plant cover by rooting may reduce nitrate plant uptake, may accelerate the mineralization processes due to the aeration of the soil and may reduce N immobilization by decomposers (bacteria) as it has been described for pocket gopher soil disturbances (Canals et al 2003). Decomposers seem to be very affected by enhanced aeration, soil moisture decrease, and the increase of soil temperature, since the soil is exposed to direct solar radiation (Brady and Well 2002). Therefore the run-off, leaching and denitrifying processes, all directly dependent on climate, appear to be key processes that may potentially explain the different results found in different areas. In addition, we found that in one community (FE grasslands, the most intensively disturbed) an increase in nitrate is related with a decrease in ammonium soil availability. A possible explanation that might be added to the previous scheme can be based on the aeration effect of disturbances in the nitrification process of ammonium. An increased availability of oxygen, provided by the more intense disturbance, would facilitate nitrification of ammonium and the subsequent increase in nitrate, following the formula: NH_4+ + 1/2 0_2 --> NO_2^- +$2H^+$+H_2O --> NO_2 + 1/2 O_2--> NO_3. However, we detected no significant decrease of pH from the nitrification process in this community due to disturbances, which probably indicates that enough oxygen was introduced to the soil system by disturbances, allowing a quick conversion from nitrite to nitrate forms.

On the other hand, the impact of wild boar disturbances on the relative importance of each N-form may depend on the intensity of disturbance and the environmental constraints of each community. For instance, only FP grasslands showed a significant increase in ammonium content linked to increased disturbance intensities. FP is the most xeric community of the five selected (Benito 2006; Fillat et al 2008), and when compared to the other grasslands studied, it shows the highest organic matter content in disturbed areas and the highest C and N content in undisturbed areas. FP main dominant species is *Festuca paniculata* that has one of the highest rates of biomass productivity in these grasslands (Fillat et al 2008). Intense soil disturbances can lead to a continuous increase of oxygen but a decrease in water content due to the loss of plant cover that prevents direct soil water evaporation. Enhanced oxygen availability may increase the ammonification process from organic nitrogen forms to ammonium (Brady and Well 2002) that would be more slowly moved to nitrate probably because of the decrease in water soil content due to the higher intensity of soil disturbance and the more xeric conditions of this community (Benito 2006; Fillat et al 2008).

Table 3. Soil parameters' differences among plant communities derived from a multiple non-parametric test comparisons (p values<0.05), (a) in disturbed and (b) undisturbed areas. Different letters correspond to differences among communities. Plant communities order follows the grazing gradient form more grazed (left) to less. EC=Electrical conductivity; Ox.C=Oxidizable organic Carbon; tC=total Carbon; tN=total nitrogen; C/N=Carbon nitrogen ratio; OM= Organic matter; Moisture=Moisture content; BD=bulk density; P= phosphorous; Ca=Calcium; Mg=Magnesium; Na=sodium; K= potassium; *BE= Bromion ercti; NS=Nardion strictae; RS=Rumicion pseudoalpini; FE=Festucion eskiae; FP= Festucion paniculatae.*

	(a) disturbed					(b) undisturbed				
Parameters (units)	RP	BE	FP	NS	FE	RP	BE	FP	NS	FE
EC (mS/cm)	a	a	a	a	a	a	ab	a	ab	b
pH (1:5)	abc	a	ab	b	c	abc	a	ab	b	c
ox. C (%)	a	a	b	ab	ab	ab	a	b	ab	ab
tC (%)	a	a	b	ab	ab	ab	a	b	ab	ab
tN (%)	a	a	a	a	a	ab	a	b	ab	ab
C/N	a	a	a	a	a	ab	a	bc	bc	c
OM (%)	a	a	b	ab	ab	a	a	a	a	a
Moisture (%)	a	a	b	ab	ab	a	a	a	a	a
BD (g/cm^3)	a	ab	b	ab	b	ab	a	a	ab	b
P (Kg/ha)	b	a	ab	ab	ab	ab	a	b	ab	a
Ca (Kg/ha)	a	a	a	a	b	a	a	a	a	b
Mg (Kg/ha)	a	a	a	a	b	a	a	ab	ab	b
Na (Kg/ha)	b	a	a	ab	a	ab	a	b	ab	ab
K (Kg/ha)	b	ab	a	ab	a	a	a	a	a	a

Regarding the effect of rooting in other soil properties, the most remarkable change was an increase in bulk density for all communities except FP. Wild boars turn over the soil, so an immediate consequence might be a decrease in bulk density in disturbed areas. However, rooting also removes the plant cover together with the root fraction that provides a robust structure to alpine soils (Pohl et al 2009). Without the structural support provided by the roots, the effect of livestock trampling in summer and snow weight in winter may easily compact the disturbed soil. In this sense, in absence of factors leading to soil compaction, e.g. in absence of livestock trampling, disturbed soils would reduce their bulk density as it happens in North American mountain forests of Tennessee (USA; Lacki and Lancia 1983; Singer et al 1984). On the contrary, presence of sheep increased bulk density in soils disturbed by pocket gopher diggings in mountain rangelands of Oregon (USA; Laycock and Richardson 1975). The effect of plant cover removal on bulk densities is further evidenced by invariant bulk density values found when soil disturbances do not remove plant cover, such as those created by vehicle tracks in Alaska (Chapin III and Shaver 1981). In the case of FP grasslands, a great amount of litter from *F. paniculata* is mixed with the soil within disturbed areas, so that soil compaction rates might be buffered in this community, as it was also found in Tennessee where greater amount of organic matter within feral pig disturbance reduced the bulk density of disturbed areas (Lacki and Lancia 1983).

Wild boar disturbances also reduced the availability of nutrients such as Ca, Na and P, maybe through the disruption of soil structure (Lacki and Lancia 1983). As it has been exposed above, soil disturbances may break up stable aggregates of soil particles, increasing their mineralization (Malizia et al 2000), and decay in microorganism immobilization with the subsequent release of available cations and nutrients (Canals et al 2003). This release of nutrients can be partly absorbed by plants if disturbances are small and do not remove completely the root systems. Nutrients can be also partly stored as available forms in the soil, increasing their availability in disturbed areas, as has been reported for pocket gopher disturbances in Utah (Laycock and Richardson 1975) or Tuco-tuco (*Ctenomys talarum*) in Argentina (Malizia et al 2000). However, if disturbances are large enough, such as those created by wild boar, these nutrients are easily leached by rainfalls or snow melting (Lacki and Lancia 1983; Singer et al 1984) thereby reducing their soil content within disturbances.

In sum, we found that wild boar rooting deeply affects soil properties as it breaks up their structure, compacting the soil and altering its composition and stability. This affection is different and deeper as the intensity of disturbance increases, in terms of faster mineralization rates leading to deeper changes in soil properties. On the one hand, nutrients such as nitrate or mineral P are released and available because of the removal of plants, that can no longer uptake those nutrients, and to decomposers that also immobilize them. On the other hand, those nutrients are available as long as they are not leached by rainfalls or snow-melting processes what suggests a temporal availability that may indirectly increase the diversity of the overall communities whenever rooting is not excessively intense.

AKNOWLEDGEMENTS

We gratefully acknowledge the support of the Spanish Science and Innovation Ministry (PN-MICINN) (CGL2008-00655/BOS) and the Spanish Environmental Ministry (MMAMRM, Organismo Autónomo de Parques Nacionales 002/2007). The Ordesa and Monte Perdido National Park (OMPNP) provided logistic infrastructures and free access to the National Park. We also want to thank Sergio (Burgos) and Silvia Chueca for field assistance, Isabel C. Barrio, Maria Bueno and Paula (Fañanas) for lab assistance and Santiago Pérez, Melchor Maestro and Ramón Galindo for soil analysis in the lab.

Effects of large wild boar disturbances on alpine soil seed banks[♣]

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ABSTRACT

Wild boar rooting is considered one of the main large soil disturbances affecting the structure and composition of plant communities in alpine grasslands. While direct consequences on plant community have been widely studied, their effects on soil seed banks have received little attention although rooting is assumed to determine the successional processes and ultimately the ecological recovery of the communities. The aim of this study is to assess the effect of wild boar rooting on species and community soil seed banks. The rooting effect was studied in terms of seed abundance and diversity in the most disturbed plant communities by wild boar in Pyrenean alpine grasslands. Two hundred soil core samples were collected at two depths to account for (short/long term) persistent and transient seed banks within and outside wild boar rooting in those grasslands. The 'seedling emergence method' was used to identify and quantify seeds from the germinable seed bank. The soil seed bank found within disturbances was smaller than expected. At the species level, the main type of seed bank represented in these grasslands was long-term persistent, comprising 75 % of the seeds found. Rooting turned long-term persistent seed bank into short-term persistent and transient, by exposing seeds from the deepest part of the soil to germination conditions at the surface of disturbed areas. At the community level we found that rooting homogenized soil seed banks by increasing seed abundance and species richness in species-poor communities, while decreasing seed species dominance in nitrophilous communities. These results suggest a deep alteration of the structure of seed banks by wild boar rooting, which in turn, may not represent a real chance for colonization from soil seed banks.

[♣] This chapter has been published in Basic and Applied Ecology (accepted 16 December 2010)

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INTRODUCTION

Soil seed banks are main constituents of ecosystems (Harper 1977) because they strongly influence the resilience (Van Andel and Grootjans 2005) and restorability of plant communities (Bekker et al 1997; Klimkowska et al 2009). Furthermore, they determine essential ecological processes by maintaining species diversity (Díaz-Villa et al 2003) and composition (Fenner and Thompson 2005), and the regeneration of damaged or lost plant species and assemblages in some communities (Bekker et al 1997; Kalamees and Zobel 2002; Bossuyt and Honnay 2008).

Despite the importance of soil seed banks in ecosystems, their role in some sensitive habitats such as alpine grasslands (sensu Körner 1999), is not fully understood (Funes et al 2003). In alpine grasslands, clonal strategies prevail among the dominant grass species (Gómez-García et al 1995; Körner 1999b), which limits seedling establishment to severe disturbance events, which modify the dominant plant cover (Thomsen et al 2006). In addition, it is known that the dominant recovery processes and the relative contribution of seeds (Bullock 2000) is determined by the frequency and extent of disturbances (Turner et al 1998). Small gaps created by voles (Gómez-García et al 1999; Sebastià and Puig 2008), moles (Schiffers et al 2010), pocket gophers (Forbis et al 2004), and livestock trampling (Kohler et al 2006) are often re-colonized by the lateral expansion of dominant grasses with little contribution from soil seed banks (Kotanen 1997b; Gómez-García et al 1999). In contrast, in large disturbances, where the lateral expansion of dominant grasses is insufficient to recover bare ground efficiently (Kotanen 1997b), soil seed banks seem to play a more determinant role (Thompson et al 1998). Therefore, understanding regeneration processes in alpine grasslands after large disturbances requires knowledge of the structure and composition of soil seed banks.

Rooting by wild boars or feral pigs is a large soil disturbance, which affects alpine grasslands worldwide (Massei and Genov 2004; Bueno et al 2009). Despite the potential impacts of rooting (Massei and Genov 2004; Bueno et al 2010), little is known about the effects of rooting on soil seed banks in alpine grasslands. Large disturbances caused by wild boar range from several square meters to several hectares in extent, with an average depth around 10 cm (Welander 2000a; Bueno et al 2009). As a result of the rooting activity, soil seed banks can be altered in two main ways; by changing the occurrence of some sensitive species or by modifying the relative distribution of seeds within soil layers. These changes in the soil seed banks may affect subsequent successional processes and the recovery ability of the plant communities involved. In this study we evaluated the effects of wild boar rooting on the species- and community-level soil seed banks of the most disturbed plant communities in Pyrenean alpine grasslands. Our aims were (1) to understand the distribution and persistence of seed species within and outside disturbances in five grassland communities, (2) to analyze the direction of changes in seed diversity, and (3) to infer potential changes in the stability of the seed communities within and outside disturbances. A deep alteration in the structure of seed banks can be expected as a result of disturbances, as well as an increase in the number of seeds in the seed banks due to a reduction in plant competition and an increase in available space for seed germination and seedling establishment. This effect might be greater in grassland communities highly used by livestock because of their role as seed vectors. The results of this study will provide some insight into the importance of the role of seeds in grassland recovery from large animal disturbances.

METHODS

Study area

The study was conducted in Ordesa and Monte Perdido National Park (OMPNP) (42º 36’N, 0º 00’) in the Spanish Central Pyrenees. The study area covered 3863 ha of semi-natural alpine and subalpine grasslands (hereafter ‘alpine’ following Körner 1999) between 1500 and 2800 m a.s.l.. Climatically, this area has an average annual temperature and precipitation of 5 ºC and 1750 mm respectively. Geologically the area is mainly limestone, although soils are constantly washed and acidified, due to high annual precipitations (Fillat et al 2008). Within the study area we focused on the five grassland communities most disturbed by wild boar (2309.4 ha in total), which are among the most extensive alpine grasslands in the Pyrenees (Bueno et al 2009).

The area is grazed by sheep and cattle herds, which progressively move towards higher elevations throughout the summer period (Fillat et al 2008). The studied grassland communities are permanent dense alpine grasslands differing in plant structure and dynamics (Table 1). These differences are determined both by abiotic (i.e. topography) and biotic factors (grazing and soil disturbance by animals; Table 1). Among animal disturbances wild boar rooting is the most important one in Pyrenean alpine grasslands (Bueno et al 2009). These grasslands carry different stocking rates and grazing animals, varying from communities where cattle and sheep gather separately to rest or water, RP (Table 1), to communities scarcely grazed by cattle and temporarily used by sheep, NS and FE (Table 1). Three grasslands (NS, FE & FP; Table 1) are dominated by one grass species, whereas the other two grasslands, BE and RP (Table 1), are co-dominated by more than 5 species (Table 1). Within grasslands dominated by one grass, higher stocking rates locally increase their plant diversity reducing plant domination (Fillat et al 2008). The botanical nomenclature used was according to Gómez-García, Mateo, Mercadal, Montserrat and Sesé (2005).

Sampling design and seed bank analyses

200 soil core samples were collected in spring (May-June) 2006 as suggested by Thompson, Bakker & Bekker (1997). We followed a random stratified sampling design where 10 sampling units were randomly located within wild boar disturbances in each plant community (50 sampling units in total). As a result, units were at least 15 m apart. Each sampling unit consisted of two square frames of 0.5 m^2 with one randomly located within disturbance and the other close to the disturbance. In each square, two soil cores (10 cm depth and 2.5 cm radius) were taken, one in the upper left and the other in the bottom right corner. To account for transient and persistent species' seed banks, which occur at different depths (Thompson et al 1997), each core was divided longitudinally into two sections (0-5 cm and 5-10 cm). From each square the upper and lower halves of the two soil cores were pooled separately, thus obtaining one sample per square and soil depth.

Table 1. Characteristics of grassland communities in the study area; elevation (m), slope (º), stocking rates (Standard Livestock Units per hectare (SLU/ha)), extent (ha), percentage area affected by wild boar disturbances, plant richness and dominant plant species. Plant richness was 'low' (<20 plant species), 'medium' (15-25 species) or 'high' (>30 species). Mean values are given ±1SD except those for which other measure is indicated. Data based on previous studies (Aldezabal 2001; Benito 2006; Fillat et al 2008; Bueno et al 2009). Botanical nomenclature according to Gómez-García et al (2005).

Characteristics	*Bromion erecti (BE)*	*Nardion strictae (NS)*	*Rumicion pseudoalpini (RP)*	*Festucion eskiae (FE)*	*Festucion paniculatae (FP)*
Type	Mesic-calcareous	Mesic-acidic	Nitrophilous	Mesic-acidic	Xero-mesic calcareous
Elevation	1901.4±134.9	2057.0±245.0	1814.8±126.7	2023.6±162.3	1918.8±92.6
Slope	15.9±8.0	23.3±8.5	15.2±8.2	22.6±7.4	14.6±6.4
Dominant aspect	SW	NW	SW	SW	S
Stocking Rate	0.12±0.28	0.06±0.10	0.50±0.66	0.08±0.16	0.26±0.33
Total extent	1385.3	180.6	44.8	458.3	240.5
% disturbed	10.8	2.7	11.4	23.3	16.8
Plant richness	high	low	medium	low	low
Dominant plant species	*Festuca rubra,* *Agrostis capillaris,* *Briza media,* *Trifolium pratense,* *Lotus corniculatus*	*Nardus stricta*	*Chenopodium bonus-henricus,* *Taraxacum officinale,* *Trifolium repens,* *Urtica dioica,* *Poa supina*	*Festuca eskiae,* *Trifolium alpinum*	*Festuca paniculata*

To analyse soil seed banks the 'seedling emergence method' was used (Ter Heerdt et al 1996). Soil samples were washed over a 0.2-mm mesh sieve and the resulting concentrated samples were spread evenly on sterilized potting compost (Ter Heerdt et al 1996). To avoid seed burying and germination from the compost, a thin nylon net (0.1 mm mesh width) between samples and compost was set. Samples were kept in a germination chamber for four months under controlled cycles of night (10 h at 15 ºC) and day (14 h at 25 ºC; 5-8 Klux). Each emerged seedling was identified and removed from the trays (Bekker et al 1997). Samples were watered twice a week and, in the final month, 1g/l of gibberellic acid (GA_3) was added to the irrigation water to interrupt the dormancy of seeds and induce germination (Ikuma and Thimann 1960; Evans et al 1996).

Data analyses

Species' seed banks

The soil seed bank of each plant species was assigned to one of three persistence categories based on its relative abundance in different soil depths (following Thompson et al. 1997): Long-term persistent (LTP); seeds are most abundant in the deep samples (5-10 cm). Short-term persistent (STP); seeds are equally or most abundant in the upper layer (0-5 cm). Transient (T); seeds occurred only in the upper layer (0-5 cm). Seed abundance of each species within each soil depth in disturbed and undisturbed areas were compared using Wilcoxon Signed Rank Test for paired designs, because samples were pair-matched and normality could not be assumed (Moore et al 2008).

Community seed banks

To quantify the changes caused by wild boar disturbances in abundance and diversity in community seed banks, the number of seeds was counted in each sample and four complementary diversity indices were calculated: Shannon Diversity, Pielou Evenness, Simpson Dominance, and Species richness (Kindt and Coe 2005). To select the most appropriate indices to assess the effects of wild boar disturbances on soil seed banks, while avoiding problems due to collinearity, a binomial hierarchical partitioning (HP) analysis was performed (Mac Nally 2000). The presence or absence of disturbance was taken as the binary response variable, and the independent contribution of each diversity measure was evaluated. After HP a permutation test (500 permutations) was conducted to assess significance of each contribution. Only Simpson dominance, abundance and richness, had p-values <0.05 and were therefore the only indices included in further analyses.

To evaluate the changes in abundance and diversity associated with wild boar disturbances in plant communities, Generalized Linear Models (GLM) were used. For each sampling site, we defined a differential vector as the value of each measure in the disturbed area minus the corresponding value in the undisturbed area (Moore et al 2008). Differential vectors reflect the effects of disturbance on each selected measure of diversity, and were taken as the dependent variables while plant community was the independent variable. In each GLM, the intercept was removed and the dependent variable was centred by its mean, to assess the effect of disturbances in all community seed banks (Gelman and Hill 2007). All modelling assumptions were met, including spatial independence of model residuals and the absence of strong multicollinearity, that were checked using correlograms and Variance Inflation Factors (VIF), respectively (Dormann 2007).

Finally, to analyze the effect of disturbances on the stability of soil seed banks in grassland communities, we compared the variability of diversity measures in disturbed vs. undisturbed areas, as an inverse proxy of stability, using the coefficient of variation. Statistical analyses were performed in R 2.9.0 (R Development Core Team 2009) using the package *BiodiversityR* for diversity and abundance indices calculations, *car* for Variance Inflation Factor (VIF) calculations, *ncf* for residual correlograms, and *hier.part* for Hierarchical Partitioning analysis.

RESULTS

Species' seed banks

From the soil core samples collected in alpine grasslands, 351 seeds from 19 species germinated (Table 2; Table 3[♦]). The average seed density obtained was 894 seeds/m^2 (15 seed/kg of soil), but it ranged from 255 seeds/m^2 in NS to 2686 seeds/m^2 in RP (Table 3). Almost half of the seeds were *Poa supina* and almost 90% belonged to the six most abundant species (*P. supina*, *Festuca gr. rubra*, *Agrostis capillaris*, *Urtica dioica*, *Trifolium repens*, and *Thymus praecox*; Table 2). The number of *Poa supina* seeds was higher in undisturbed sites in both soil layers (Table 2). For *Festuca gr. rubra* and *Agrostis capillaris*, the number of seeds was higher in the top layer in disturbed sites. For *Urtica dioica*, in undisturbed sites the number of seeds was higher in the bottom layer, while the opposite occurred in disturbed sites. For the rest of species, no significant differences were found (Table 2).

[♦] This table was included as an appendix in the published version.

Table 2. Distribution of the emerged seedlings of different species in disturbed and undisturbed areas and the effect of wild boar disturbances on each type of soil seed bank (I, 0-5 cm & II, 5-10 cm). 'Effect' details the total number of seeds and the corresponding percentage from the total number of seeds collected. 'Strategy' details the CSR functional strategy; competitive (C), stress-tolerant (S), ruderal (R) or a combination of them, following Grime (1988). No available data were found for the Cantabric-Pyrenean endemic *Iris latifolia*. SB: type of soil seed bank. LTP: Long-term persistent. STP: Short-term persistent. T: Transient. '*' $p < 0.05$, for *Wilcoxon signed rank paired test* for data between disturbed and undisturbed soil seed banks at each soil depth.

		Undisturbed			**Disturbed**				
Species	**Strategy**	**I**	**II**	**SB**	**I**	**II**	**SB**	**Total**	**Effect**
Poa supina	*R*	49*	97*	LTP	11	11	STP	**168**	LTP to STP/T 263 seeds 75%
Festuca rubra	*CSR*	7*	11	LTP	21	17	STP	**56**	
Agrostis capillaris	*CSR*	3*	6	LTP	7	6	STP	**22**	
Urtica dioica	*C*	0*	8*	LTP	9	0	T	**17**	
Trifolium repens	*CR*	8	4	STP	6	6	STP	**24**	No change 50 seeds 14%
Thymus praecox	*S*	8	2	STP	6	3	STP	**19**	
Stellaria media	*R*	0	3	LTP	0	4	LTP	**7**	
Ranunculus gouanii	*CSR*	0	0		3	7	LTP	**10**	Fugitive spp. 18 seeds 5%
Ranunculus bulbosus	*RS*	0	0		2	2	STP	**4**	
Scleranthus uncinatus	*R*	0	0		2	2	STP	**4**	
Ranunculus acris	*CSR*	3	0	T	1	1		**5**	Unclassified 20 seeds 6%
Trifolium pratense	*CSR*	3	1	STP	1	0		**5**	
Taraxacum officinale	*R*	1	1		0	0		**2**	
Nardus stricta	*CS*	0	0		0	2		**2**	
Capsella bursa-pastoris	*R*	0	2		0	0		**2**	
Galium verum	*CSR*	0	0		0	1		**1**	
Iris latifolia	---	0	1		0	0		**1**	
Pilosella officinarum	*CSR*	0	0		0	1		**1**	
Potentilla erecta	*CSR*	1	0		0	0		**1**	
Total		83	136		69	63		351	100%

The most important effect of wild boar disturbances on species' seed banks was a change in the type of soil seed bank from LTP to STP or T, which comprised the most abundant species in the seed banks: *Poa supina*, *Festuca gr. rubra*, *Agrostis capillaris*, and *Urtica dioica*, that represent 75% of the total amount of seeds emerged (Table 2). In some other species (*Trifolium repens*, *Thymus praecox* and *Stellaria media*, representing 14% of seeds), no remarkable differences were found. Finally, three species (*Ranunculus gouanii*, *R. bulbosus*, and *Scleranthus uncinatus*, representing 5% of seeds) were fugitive species because they occurred in disturbed sites, only (Table 2).

Community seed banks

Seed density was highest in RP (2686 seeds/m^2) and BE (828 seeds/m^2; Table 3), which are species-rich communities, with intermediate wild boar disturbances and high stocking rates (Table 1). The grassland communities exposed to the lowest stocking rates, NS and FE, had the lowest seed densities (Table 1; Table 3), despite being least and most affected by wild boar rooting. FP represented an intermediate situation, with intermediate-high stocking rates and high incidence of boar rooting (Table 1). Wild boar rooting increased seed abundance in FE and FP, while seed richness was only promoted by disturbances in FP (Table 4). Seed dominance and richness also increased in FP (Table 4), probably related to greater seed abundance within disturbances as some of these new species in the seed bank become dominant, such as *Festuca gr. rubra* (Table 3). For RP a clear decrease in seed dominance was found, driven by the limited occurrence of *Poa supina* within disturbances in RP seed banks.

Table 3. Seed densities (seeds/m^2) of the species present in the soil seed bank of the five grassland communities studied between disturbed by wild boar and undisturbed communities.

Community	Species	Undisturbed	Disturbed	Total
Bromion erecti	*Agrostis capillaris*	127	0	64
	Festuca rubra	331	662	497
	Pilosella officinarum	0	25	13
	Ranunculus acris	76	51	64
	Ranunculus bulbosus	0	25	13
	Scleranthus uncinatus	0	25	13
	Stellaria media	25	0	13
	Thymus praecox	229	0	115
	Urtica dioca	0	76	38
	Total	**789**	**866**	**828**
Nardion strictae	*Agrostis capillaris*	102	51	761
	Capsella bursa-pastoris	25	0	13
	Festuca rubra	102	76	89
	Nardus stricta	0	51	25
	Poa supina	25	0	13
	Potentilla erecta	25	0	13
	Scleranthus uncinatus	0	51	25
	Stellaria media	51	0	25
	Total	**331**	**229**	**280**
Rumicion pseudoalpini	*Agrostis capillaris*	0	25	13
	Capsella bursa-pastoris	25	0	13
	Poa supina	3692	560	2126
	Ranunculus bulbosus	0	25	13
	Taraxacum officinale	51	0	25
	Thymus praecox	0	102	51
	Trifolium pratense	51	0	25
	Trifolium repens	306	306	306
	Urtica dioca	204	25	115
	Total	**4329**	**1044**	**2687**
Festucion eskiae	*Agrostis capillaris*	0	229	115
	Festuca rubra	25	0	13
	Iris latifolia	25	0	13
	Ranunculus bulbosus	0	51	25
	Scleranthus uncinatus	0	25	13
	Stellaria media	0	102	51
	Thymus praecox	0	25	13
	Urtica dioca	0	25	13
	Total	**51**	**458**	**255**
Festucion paniculatae	*Agrostis capillaris*	0	25	13
	Festuca rubra	0	229	115
	Galium verum	0	25	13
	Ranunculus gouanii	0	255	127
	Thymus praecox	25	102	64
	Trifolium pratense	51	25	38
	Urtica dioca	0	102	51
	Total	**76**	**764**	**420**
Total density of the area sampled		**1115**	**672**	**894**

Regarding changes in the variability of community seed banks, disturbances reduced variation in seed abundance and species richness in FE and FP, which were the most variable in undisturbed areas, whereas the variability in BE and NS remained almost unchanged with or without disturbance. For RP, wild boar disturbances reduced the variability in seed abundance but variability in species richness was not affected (Figure 1). Regarding dominance, an increase in variability was found for FE, FP and NS, and a reduction for RP (Figure 1). Overall, wild boar disturbance seem to have a homogenizing effect on the community seed banks.

DISCUSSION

We found a low number of seeds in the community seed bank (894 seeds/m^2), with two grassland communities (BE and RP) accounting for more than 88% of all the seeds found. The overall number of seeds was surprisingly low when compared to other regions (Funes et al 2003; Bossuyt et al 2007), but is in accordance with previous studies in many grasslands (Thompson et al 1997; Gómez-García et al 1999). Indeed, this seems to be a characteristic of alpine environments, in which less reliance on seed banks for reproduction (in favour of clonal strategies) can be related to the short vegetative period (Körner 1999b). Contrary to what was expected, in the present study lower quantities of seeds were found in disturbed areas relative to undisturbed ones. For most species large disturbances may not represent a real chance for colonization from seed banks, probably because grassland plant species do not produce many seeds (Bossuyt and Honnay 2008) and its relatively short-distance seed dispersal (Körner 1999b). Therefore, the role of seeds in the recovery process from large disturbances in alpine grasslands might be only secondary with the exception of some dynamic grassland communities (Bossuyt and Honnay 2008), such as RP for which seed densities found were highest, where grazing activities may drive plant and seed bank structure.

Table 3. Changes in seed diversity, abundance and dominance indices, induced by wild boar disturbance in the study area, modelled using GLM, where centred diversity measures were the dependent variables and plant community the independent variable. Significant values are in bold.

	Abundance		Richness		Dominance	
	t	**p-value**	**t**	**p-value**	**t**	**p-value**
Bromion erecti	**2.63**	**0.012**	-0.60	0.549	-1.51	0.137
Nardion strictae	**2.11**	**0.041**	-1.61	0.115	0.50	0.621
Rumicion pseudoalpini	-1.13	0.265	-1.60	0.114	**-2.99**	**0.005**
Festucion eskiae	**5.26**	**0.000**	1.40	0.166	1.22	0.229
Festucion paniculatae	**5.09**	**0.000**	**2.41**	**0.020**	**2.78**	**0.008**

Species' seed banks

In the alpine grasslands of the Spanish Pyrenees, the most significant effect of disturbances caused by wild boar rooting was to convert long-term persistent seed banks, which are the primary type of seed bank in these alpine grasslands, into short-term persistent or transient seed banks. That is, the condition shifted from one in which most seeds occurred in the deep section of the soil to one in which seeds occurred primarily or exclusively in the upper horizon. Wild boar overturns turf and soil, which brings most of the seeds of most species closer to the surface. In that way, seeds receive more light stimuli and are exposed to reduced above- and below-ground competition (Bullock 2000), which increases the probabilities of seed emergence and seedling establishment (Fenner 2000).

Similar patterns have been described for small gaps, created by small animals such as voles (Gómez-García et al 1999), pocket gophers (Forbis et al 2004), or ants (Dauber et al 2006). These small disturbances cause the movement of seeds in grassland soils from the deeper parts to the surface and vice versa, which changes the composition and abundance of seeds in the horizons of the soil (Gómez-García et al 1999; Forbis et al 2004; Dauber et al 2006; Sebastià and Puig 2008). Unlike extensive wild boar rooting, these animals create localized disturbances in which a small area of the soil and a small number of seeds are affected.

In the alpine grasslands of OMPNP, Spain, seed species were not more abundant in areas disturbed by wild boar rooting than in undisturbed areas, as would be expected in a new colonization gap. For *Poa supina*, the most common species, more seeds occurred in undisturbed areas. This ruderal species is closely related to *Poa annua*, and is specialized in environments highly-disturbed by livestock, where higher concentrations of organic matter, soil moisture content and bulk densities, are likely to reduce competition (Kohler et al 2006). In this sense, dominance of *Poa supina* appears to be broken by large wild boar disturbances, as they may alter its establishment. The opposite strategy can be found in fugitive species, which only persist in gaps created by disturbances. *Scleranthus uncinatus* is an annual ruderal species, which is adapted to soil removal and frequently found on wild boar disturbances (Benito 2006). However, the most effective seed response to wild boar disturbance was found in *Agrostis capillaris* and *Festuca gr. rubra*, which can be considered as polyvalent in terms of the functional strategy they adopt, since they can behave as competitors, stress-tolerant or ruderal depending on environmental conditions (Grime et al 1988). Thereby the seeds of these species can withstand both, grazing and soil disturbances, through seed production adopting a ruderal strategy (Klimkowska et al 2009), being favoured (or less disfavoured) by certain combinations of them.

Community seed banks

In the alpine grasslands of the Spanish Pyrenees, the changes in the soil seed banks of the plant communities caused by wild boar rooting affected most grassland communities. In FE and FP, wild boar rooting increased the abundance and richness of seeds in their seed banks. These communities are dominated by one competitive grass species that relies most often on vegetative reproduction and forms very stable communities lightly used by livestock. Here, wild boars create large gaps that are suitable for seed colonization, which increases community heterogeneity and maintains high levels of plant diversity (Bekker et al 1997; Kalamees and Zobel 2002; Bossuyt and Honnay 2008). Wild boar rooting reduced species dominance in RP, particularly *P. supina*, which led to an increase in seed abundance and richness in the seed banks. By contrast, species-rich communities (BE and RP) experienced moderate or high rates of grazing and wild boar rooting did not influence significantly the abundance or richness of seed species. In addition, the high number of species that use a dual strategy (stress-tolerant and ruderal) in those communities, e.g. *A. capillaris* and *F. gr. rubra* might help to explain the lessened impact of soil disturbance on moderately or highly grazed grasslands. Moderate grazing activities might increase the resilience of alpine grasslands to soil disturbances, whereas low grazing or very intensive grazing might lead to increased instability in the structure and dynamics of grasslands.

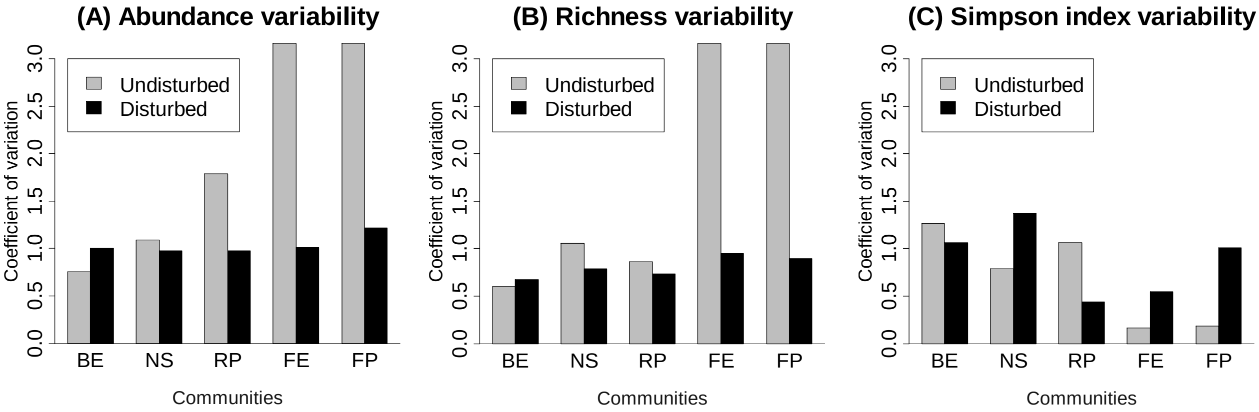

Figure 1. Variability in seed abundance (A), species richness (B) and Simpson Dominance indices (C), based on the coefficient of variation of the community seed banks in undisturbed (grey bars) and disturbed (black bars) areas in the five studied plant communities. BE=*Bromion erecti*; NS=*Nardion strictae*; RP=*Rumicion pseudoalpini*; FE=*Festucion eskiae*; FP=*Festucion paniculatae*.

Wild boar rooting affected the variability in seed diversity among grassland communities, particularly in terms of species seed abundance and richness (Figure 1). As a consequence, disturbed community seed banks became more homogeneous. In addition, disturbances caused by wild boar appeared to be interconnected through the action of animal vectors such as livestock and the wild boar itself (Heinken et al

2006), which can be an important source of propagules (Welander 2000a). Interconnected disturbed areas can ensure that a regeneration niche is readily available, which might be fundamental to the maintenance of biodiversity (Bekker et al 1997; Fenner 2000; Kalamees and Zobel 2002; Bossuyt and Honnay 2008).

In sum, large disturbances, such as those caused by wild boar rooting, may not represent a real chance for seed colonization despite they can significantly alter the structure and composition of species and community seed banks in alpine grasslands. Disturbances changed the nature of the species' seed banks from long-term persistent to short-term persistent or transient seed banks, which increased the number of seeds exposed to germination conditions. In turn, wild boar disturbances increased the relative abundance and richness of most of the seed species in alpine grasslands, except those restricted to heavily grazed environments. The homogenizing effect of disturbances among alpine plant communities might ensure the persistence of regeneration niches. However, the immediate effect of large disturbances on grasslands leads to rapid changes, probably followed by a slow regeneration process dominated by lateral expansion instead of seed banks.

ACKNOWLEDGEMENTS

We thank Silvia Chueca and Sergio (Burgos) for field assistance, Paula (Pueyo de Fañanas), and Maria Bueno for lab assistance. Special thanks to Isabel C. Barrio for encouragement and helpful suggestions that improved the manuscript and to three anonymous reviewers and the editor (Klaus Hövemeyer) for their valuable comments. English was reviewed and improved by B. MacWhirter. Financial support was provided by the Spanish Ministries of Science and Innovation, and Environment (MAM 2484/2002-059/2002, PN-MEC CGL2005-01131/BOS, PN-MCI CGL2008-00655/BOS), including an FPU grant to C.G. Bueno.

Effects of large soil disturbance on the diversity and structure of Pyrenean alpine grasslands[♣]

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ABSTRACT

Alpine environments have low resilience to soil disturbances, such as wild boar rooting that in turn, might be the most frequent and extensive soil disturbance in some alpine areas. A direct consequence of rooting is a reduction in plant cover, which may drastically modify the structure, composition and diversity of plant communities. Despite the potential role of wild boar as an ecosystem engineer, little is known about its direct effects to these habitats. Here, we analyze the plant species composition within and outside wild boar disturbances in the five most disturbed grasslands in the Spanish Central Pyrenees, taking four hundred point quadrats. Firstly, we evaluated the effect of rooting to species diversity at different scales. Secondly we analyzed the effect of wild boar rooting on the main constraints of diversity, i.e. spatial and environmental drivers. Thirdly the effect of wild boar rooting was evaluated on each plant community using plant abundance, richness, diversity (Shannon) and dominance (Simpson) indices. Finally, favoured and disfavoured plant species and functional groups were determined by their relative frequencies within and outside disturbances. Rooting affected the Shannon species diversity depending on the scale, increasing the diversity among samples while reducing diversity among plant communities. In turn, the effect of rooting in each plant community was a reduction in plant abundance, richness and diversity, and an increase in dominance. However, in communities dominated by tall-tussock *fescue* species (*Festuca eskia* and *F. paniculata*) the effect on diversity and dominance was not evident. Regarding species and functional groups, dicots seem to have some advantage over most dominant perennial graminoids in disturbed areas, being the latter clearly disfavoured. In sum, wild boar disturbances promoted a deep alteration of the diversity and structure of alpine plant communities and their diversity constraints, differing with the scale of study and with the presence of tall-tussock fescue species.

[♣] This chapter has not yet been published

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INTRODUCTION

Disturbance has been considered part of natural ecosystems and has been deemed responsible for vegetation structure, dynamics and diversity (Pickett and White 1985; Hobbs and Huenneke 1992). In any system, resilience to disturbances is strongly determined by the structural characteristics of the system itself, and the history and characteristics of disturbances (Hobbs and Huenneke 1992; Kotanen 1995; Laska 2001). Understanding the nature of the disturbance agent and its circumstance in each system, is therefore one of the first tenets in the study of disturbances (Pickett and White 1985; Laska 2001). In some systems the main disturbances might be provoked by a single agent (Laska 2001). If this agent is an organism capable of altering structural parts of ecosystems that in turn provokes a cascade of interactions and dependencies among biotic and abiotic elements of the ecosystem, then this agent can be considered an ecological engineer (Jones et al 2010). As these agents usually affect different ecological processes and diversity spatial patterns, the measure of the consequences of their activities should be considered in a range of different spatial scales (Turner et al 2001; Willis and Whittaker 2002), directly related with the nature of the agent and its activities (Laska 2001).

Wild boar is probably the most widespread distributed mammal in the world attending to its native and introduced distribution range (Massei and Genov 2004; Oliver and Leus 2008). It has been considered as an ecosystem engineer in some habitats where it has been introduced, due to its disruptive direct effects (through rooting) on the structural parts of soil and plant communities (Welander 2000b; Cuevas et al 2010). Rooting is a large soil disturbance, extensively present wherever wild boar inhabits (Massei and Genov 2004; Oliver and Leus 2008). It occurs when wild boars turn over the soil looking for underground feeding resources. A direct consequence of this foraging activity is the extensive removal of plant cover (Massei and Genov 2004). The extent of rooted areas varies from squared cm to hundreds of hectares, representing in most cases considerable proportions of landscape units affected (Bueno et al 2009). Despite these considerations, few studies have covered the effects of wild boar rooting on plant communities quantitatively (Massei and

Genov 2004) and most of them relate to areas where wild boars are an introduced species (Bratton 1974; Howe et al 1981; Kotanen 1995; Hone 2002; Cushman et al 2004; Cuevas et al 2010).

On the other side, the potential affection caused by a certain disturbance to a particular system, is closely determined by the characteristics of each system in relation to the nature of each disturbance (Hobbs and Huenneke 1992). In this sense, it would be straightforward to focus the study of the effects of each disturbance on habitats sensitive to this disturbance, in order to manage and control the major inconvenient effects for these habitats (Hobbs and Huenneke 1992; Hiddink et al 2007). One example are large soil disturbances in alpine areas, an ecosystem that is particularly sensitive to extensive modification of its soil-plant structure, since its regeneration processes are extremely slow (Körner 1999b). In these systems wild boars are presumed to act as ecosystem engineers because they modify plant cover extensively (Bueno et al 2009), although a quantification of their effects at different scales on diversity and structure is still lacking.

The aim of this study is to evaluate the effects of wild boar rooting on plant composition, structure and diversity of alpine grasslands in the Spanish Central Pyrenees at different scales. Firstly, we wanted to evaluate the role of these disturbances in driving the diversity of plant communities at different scales, and to assess the contribution of the main external factors (i.e. spatial and environmental constraints) in determining the variation of community composition (beta diversity) among sites in both disturbed and undisturbed areas. Secondly, we wanted to investigate the role of wild boar disturbances at a local scale in determining plant abundance, richness, diversity (Shannon) and dominance (Pielou) at the community level and assess which plant species and functional groups are favoured and disfavoured by these disturbances.

METHODS

Study area and sampling design

The study was conducted in Ordesa and Monte Perdido National Park (OMPNP) (42º 36’N, 0º 00’) in the Spanish Central Pyrenees. The study area covers 3863 ha of natural grasslands between 1500 and 2800 m a.s.l. Annual average precipitation in the area is 1750 mm with an annual average temperature of 5ºC. The geology corresponds mainly to limestone, calcareous sandstones and marlstones. Within the study area we focused on the five natural grasslands most disturbed by wild boar (2309.4 ha in total), which are among the most extensive alpine grasslands in the Pyrenees (Bueno et al 2009): Bromion erecti (BE), Naridon strictae (NS), Rumicion pseudoalpini (RP), Festucion eskiae (FE) and Festucion paniculatae (FP). All these plant communities are dense grasslands, being three of them (NS, FE and FP) dominated by one grass species (*Nardus stricta*, *Festuca eskia* and *F. paniculata* respectively), while the other two (BE and RP) are more diverse with several co-dominating species (see Bueno et al (in press) and Fillat et al (2008) for a detailed description of each plant community). Grazing activities in the area relate mainly to cattle and sheep herding, with a little contribution of horses.

Table 1. Observed and expected alpha-, beta- and gamma diversity in undisturbed and disturbed Pyrenean grasslands. H_1 were the expected values calculated from individual-based randomizations and H_2 shows the expected values from sampled-based randomizations. In parenthesis are the 95% confidence limits from both randomizations.

	Observed		**Expected (Undisturbed)**		**Expected (Disturbed)**	
	Undisturbed	Disturbed	H_1	H_2	H_1	H_2
α_1	2.267	2.455	2.400 (2.416, 2.385)	2.400 (2.416, 2.385)	2.477 (2.490, 2.463)	2.477 (2.490, 2.463)
β_1	0.370	0.747	0.852 (0.861, 0.843)	0.753 (0.760, 0.746)	1.059 (1.068, 1.051)	0.992 (1.000, 0.985)
β_2	0.795	0.620	0.180 (0.186, 0.174)	0.663 (0.679, 0.648)	0.287 (0.293, 0.282)	0.616 (0.624, 0.608)
γ	3.432	3.823	3.432	3.432	3.823	3.823

Using a previous map of wild boar disturbances in the area (Bueno et al 2009), a random stratified sampling design was carried out. 40 sampling units were randomly located within disturbed areas in each plant community and the same number of units were set in the nearest undisturbed area (400 sampling units in total). Each sampling unit consisted of two square frames of 25 x 25 cm, 5 cm grid. In each square, 25 point-intercept contacts were set in the bottom-left corner of each grid (50 point-intercept contacts per sampling unit, 20000 in total). To quantify the abundance of species, all individuals contacted by a 20 cm-long vertical nail at each point-intercept were identified (Goodall 1952).

Statistical analysis

Hierarchical components of diversity

To analyze the effect of wild boar rooting in plant diversity at different spatial scales, we followed the partitioning procedure proposed by Crist and co-authors (2003). Thereby, total diversity can be expressed as the proportional contribution of diversity at each level in a hierarchical design, accounting for the diversity within samples (alpha components) and among samples (beta components; Whittaker 1972; Wagner et al 2000). The highest diversity level, gamma, is partitioned into alpha and beta components: $\gamma = \alpha_1 + \sum_{i=1}^{m} \beta_i$, in the m levels of sampling (Lande 1996; Crist et al 2003). In our study we use Shannon Diversity Index as diversity measure with three levels of sampling. The first level was the sampling unit level, and its diversity (alpha 1) was calculated as the average diversity of all sampling units. The second level (alpha 2) was the community level, and its diversity was calculated as the average of samples within each community. Finally, the third level was the gamma diversity (alpha 3) that was the overall diversity of all samples. To calculate the beta components we subtracted the alpha component of a level to the alpha component of the following level: $\beta_i = \alpha_{i+1} - \alpha_i$ (Wagner et al 2000; Crist et al 2003; Gering et al 2003). In our case, as we had three levels (i.e. three alpha components) we could calculate two beta components only. Beta 1 accounts for the diversity among sampling units and beta 2 for the diversity among plant communities. No departures from independence of alpha and beta components that lead to important bias in the resulting diversity components are expectable here, since the stratified balanced design provided equal community weights, which are proved to validate their use with Shannon diversity index (Jost 2007).

Table 2. Relative importance of each environmental variable of the pure environment fraction in RDA, for undisturbed (a) and disturbed areas (b). p- values was calculated from ANOVA like permutation test with 999 permutations. The environmental variables that were non-significant are not shown. Sig.= Significance codes: '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1. BG = percentage of bare ground; DLRS = Distance to livestock resting sites.

a) Undisturbed

Variables	F	p-value	sig.
Elevation	81.457	0.001	***
Cattle	31.004	0.001	***
East	18.984	0.032	*
Southeast	15.853	0.074	.
Sheep	15.802	0.069	.

b) Disturbed

Variables	F	p-value	sig.
BG	294.943	0.001	***
DLRS	63.319	0.001	***
Cattle	59.079	0.001	***
Elevation	54.139	0.001	***
Sheep	32.426	0.001	***
Slope	27.696	0.001	***
Marls	21.233	0.014	*
West	19.847	0.021	*

Factors explaining beta diversity

Beta diversity has been defined as 'the variation of community composition among sites in a geographic area' (Whittaker 1972). To analyze the role of space and environment in explaining the spatial variation of community composition (beta diversity) within and outside disturbances we used canonical partitioning methods, also known as "raw-data approach" (Legendre et al 2005; Tuomisto and Ruokolainen 2006). These methods consist in separating the variance inherent to the community composition data into independent components. Through this partition it is possible to measure the independent contribution of each component that is expected to be influential in explaining the variance of community composition (Borcard 1992; Legendre and Legendre 1998). Two main components are normally distinguished for explaining the variation in the presence or abundance of the organisms; the spatial and environmental heterogeneity (Legendre and Fortin 1989). As both components interact, in practical terms their study leads to the study of four fractions; pure environmental, pure spatial, an indivisible mix of both, and the fraction that represents their unexplained contribution (Borcard 1992; Peres-Neto and Legendre 2010). In turn the environmental component can also be subsequently divided into minor ecologically meaningful portions if it is required (Peres-Neto and Legendre 2010). This spatial components can be calculated by eigenvalue decomposition of a weighted matrix of geographic similarities among sampled sites (Borcard and Legendre 2002; Dray et al 2006; Peres-Neto and Legendre 2010). This complex calculation is called Moran's eigenvectors maps (MEM), and requires a suitable selection of the spatial weighted matrix and the spatial components within each matrix, in each study case (Dray et al 2006). This spatial weighted matrix was selected based on Akaike's Information Criterion (AIC) values obtained running redundancy analysis (RDA) models with the response matrix and each one of the candidate spatial weighted matrices (Dray et al 2006). The spatial weighted matrices considered were among those connecting sample points at different distances, i.e. 100, 300, 1000, 3000 and 7000 m (6870 m was the maximum distance among sampling points in our study area), and among those connecting by the numbers of neighbours, i.e. 1, 2, 5, 10 or 20. In our case the best spatial weighted matrices were those connecting groups of the nearest five points for undisturbed areas and those connecting pairs of sampling points for disturbed areas. For the selection of the most suitable spatial vectors among the selected matrices we used a forward selection procedure (Blanchet et al 2008; Peres-Neto and Legendre 2010). Regarding the selection of the environmental variables, Variance Inflation Factor (VIF) and Pearson correlation tests were used taking as threshold values < 3 and < 0.5 respectively. Variables with higher values were removed from the analysis, to avoid collinearity problems (Zuur et al 2009). The environmental variables considered were geology, topography, grazing activities (stocking rates of cattle and sheep and distance to livestock resting sites) and the percentage of bare ground (including rock cover). Geological information was obtained from geological maps 1:50000 (Ríos-Aragüés et al 1980) and considered three categories; i.e. calcareous marlstone, sandstone and limestone. As for topographical variables we considered slope, eight aspect categories and elevation, which was obtained from an elevation model of the study area (grid 10 m^2 , RMSE= 6.26 m). Grazing information for cattle and sheep stocking rates was obtained from a previous intensive monitoring of livestock movements in the study area (Aldezabal et al 1992), after digitalisation and GIS treatments (García-González et al 2007; Bueno et al 2010).

Community, species and functional groups comparisons

In addition we compared diversity measures among the five most disturbed plant communities; abundance, richness, Shannon diversity, Simpson dominance and Pielou evenness indices (Kindt and Coe 2005), and between disturbed and undisturbed areas. For that purpose, paired t-tests or Wilcoxon paired rank tests were used depending on if normality could be assumed to fit the data; paired t-tests were used only for abundance and richness.

To determine which plant species are favoured and disfavoured by wild boar disturbances we compared abundance of each species within and outside disturbances using Wilcoxon paired rank tests on each plant communities and on the overall pool of species, since neither datasets fit normality assumptions.

All statistical analyses were performed with R 2.11 (R Development Core Team 2010), except for individual and sample-based randomization tests where Matlab 7.1 was used. In particular we used the following R packages; *vegan* and *BiodiversityR* for canonical partitioning, *packfor* for forward selection of variables and *SpacemakeR* for MEM.

Table 3. [next page] Species that significantly increased ('Favoured species') or decreased ('Disfavoured species') in abundance in areas disturbed by wild boar. Only species that showed significant changes within a plant community (BE: Bromion erecti, NS: Nardion strictae, RP: Rumicion pseudoalpini, FE: Festucion eskiae, FP: Festucion paniculatae) or for the pooled data ('all') from Wilcoxon paired rank tests are shown. Significance is indicated with asterisks: '*' p<0.05, '**' p<0.01, '***' p<0.001.

Favoured species	Functional group	Plant community
Cirsium acaule	perennial dicot	NS*
Barbarea intermedia	perennial dicot	all*
Sanguisorba minor	perennial dicot	NS*
Tragopogon lamottei	perennial dicot	BE*, all*
Polygonum aviculare	annual dicot	RP*, all**
Crocus nudiflorus	bulb	all*
Disfavoured species		
Agrostis capillaris	perennial graminoid	BE***, NS**, RP***, FP*
Carex caryophyllea	perennial graminoid	BE***, NS***, RP*, FE***, FP*
Deschampsia flexuosa	perennial graminoid	FE*, all**
Festuca eskia	perennial graminoid	FE***, all**
Festuca paniculata	perennial graminoid	FP***, all**
Festuca gr. rubra	perennial graminoid	BE***, NS***, RP***, FP***
Koeleria pyramidata	perennial graminoid	BE***, NS***, RP*, FP**
Lolium perenne	perennial graminoid	RP*
Nardus stricta	perennial graminoid	NS***, FE***
Poa alpina	perennial graminoid	FP**
Poa pratensis	perennial graminoid	RP*
Poa supina	annual graminoid	RP***, all*
Achillea millefolium	perennial dicot	BE***, RP***, all**
Alchemilla gr. colorata	perennial dicot	BE**, all**
Campanula scheuchzeri	perennial dicot	all*
Centaurea montana	perennial dicot	all*
Cruciata glabra	perennial dicot	all*
Galium pumilum	perennial dicot	NS**, FP*, all**
Galium verum	perennial dicot	BE*
Gentiana acaulis	perennial dicot	all*
Leontodon hispidus	perennial dicot	NS*, all**
Lotus corniculatus	perennial dicot	BE***, NS***, all**
Pilosella lactucella	perennial dicot	NS*, all*
Pilosella officinarum	perennial dicot	BE**, NS***, FP*
Plantago alpina	perennial dicot	BE**, NS**, all**
Plantago lanceolata	perennial dicot	BE**
Plantago media	perennial dicot	BE***, FP*, all***
Potentilla erecta	perennial dicot	NS***, all***
Potentilla neumanniana	perennial dicot	BE**, FP*, all**
Prunella vulgaris	perennial dicot	BE*, NS**, all**
Ranunculus bulbosus	perennial dicot	RP**, all*
Sanguisorba minor	perennial dicot	BE*
Thymus praecox	perennial dicot	BE*, NS**, all**
Trifolium alpinum	perennial dicot	NS***, FE***, all***
Trifolium pratense	perennial dicot	BE***, all**
Trifolium repens	perennial dicot	BE***, RP***, FP*
Vicia pyrenaica	perennial dicot	BE*, FP**, all*
Merendera montana	bulb	BE*, FP*, all**

RESULTS

Differences in species occurrence between disturbed and undisturbed areas were around 20% in total, 6% of the species present in disturbed areas were not found in undisturbed areas and 13 % of the species that were found in undisturbed areas were not found in disturbed areas.

Hierarchical components of diversity

The additive partitions of the Shannon diversity showed that α_1 explained 66.05% and 64.22% of the plant diversity in undisturbed and disturbed grasslands respectively, 10.78% and 19.59% among sampling units (β_1) and 23.16 % and 16.21 % among communities (β_2; Figure 1). The Shannon diversity indices in undisturbed compared to disturbed areas were lower among sampling units (β_1; t=10.18; p=0.00016; Figure 1), higher among grassland communities (β_2; t=-3.23; p=0.032; Figure 1) while they were not significantly different within samples (α_1).

Factors explaining beta diversity

The percentage of variance of community composition explained by environmental variables and space was 75.12 % for the undisturbed areas and 52.74 % for disturbed areas (Figure 2a). The main fractions involved for undisturbed areas were the pure spatial fraction and the shared fraction between environment and space, accounting for 48.63 and 22.42 % respectively (Figure 2a). For disturbed areas the main fractions were the pure spatial and the pure environmental ones, that accounted for 26.24 and 17.14 % respectively (Figure 2a). The variables involved in the pure environmental fraction differed as well within and outside disturbances. The main variables involved for undisturbed areas were topography (elevation and East aspect variables; Table 1a), and grazing (cattle grazing; Table 1a), that respectively explained 60.61 and 20.67 % of variance (Figure 2b). For disturbed areas those main factors were the percentage of bare ground, grazing (distance to livestock resting areas and cattle and sheep grazing; Table 1b), and to a lesser extent topography (elevation, slope and West aspect; Table 1b) with 44.36, 17.40 and 15.70 % of explained variance respectively (Figure 2b).

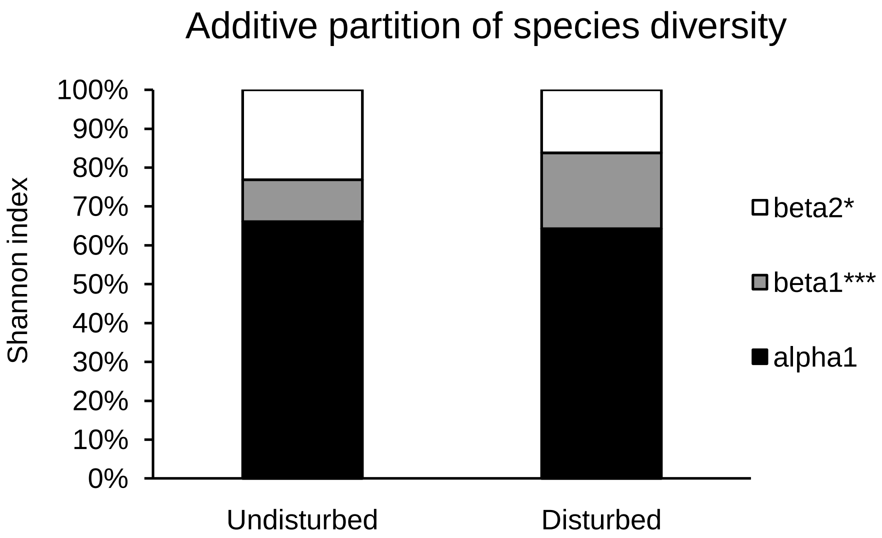


Figure 1. Contribution of the additive partitions of the overall Shannon diversity index explained by hierarchical level in undisturbed and disturbed areas by wild boar in Pyrenean grasslands within OMPNP. Alpha 1 (α_1) is within sampling unit diversity, beta 1 (β_1) in among sampling unit diversity and beta 2 (β_2) is among plant community diversity. '*' p<0.05, '***' p<0.0001 from Wilcoxon paired rank tests.

Community, species and functional groups comparisons

Abundance and species richness were higher in undisturbed areas for all communities except for richness in FE for which no significant differences were found (Figures 3a, b). Shannon's diversity index and Simpson dominance showed significant differences between disturbed and undisturbed areas, higher Shannon diversity and lower Simpson dominance values respectively, except for FE and FP (Figures 3c, d).

38 plant species were significantly disfavoured by wild boar rooting at least in any of the plant communities or in the pool of all communities studied (Table 3). All dominant species from communities dominated by few species were affected, such as *Festuca eskia* and *Trifolium alpinum* in FE, *F. paniculata* in FP, or *Nardus stricta* in NS (Table 3). In addition some of the main co-dominant species in communities not

dominated by a few species were also reduced in abundance, such as *Poa supina* or *Trifolium repens* in RP, *F. gr. rubra*, *Agrostis capillaris*, *T. pratense* or *Lotus corniculatus* in BE (Table 3). From the 6 species favoured species, 5 were dicots and 1 bulb, being none of them favoured in any of the two tall-tussock fescue communities (FE or FP) (Table 3). One species, *Sanguisorba minor*, was found to be both favoured in NS and disfavoured in BE (Table 3) what may indicate strong environmental differences between these communities.

Functional groups were modified by wild boar rooting, decreasing the percentage of abundance for perennial graminoids while increasing for perennial dicots, and marginally for annual graminoids and bulbs (Figure 4).

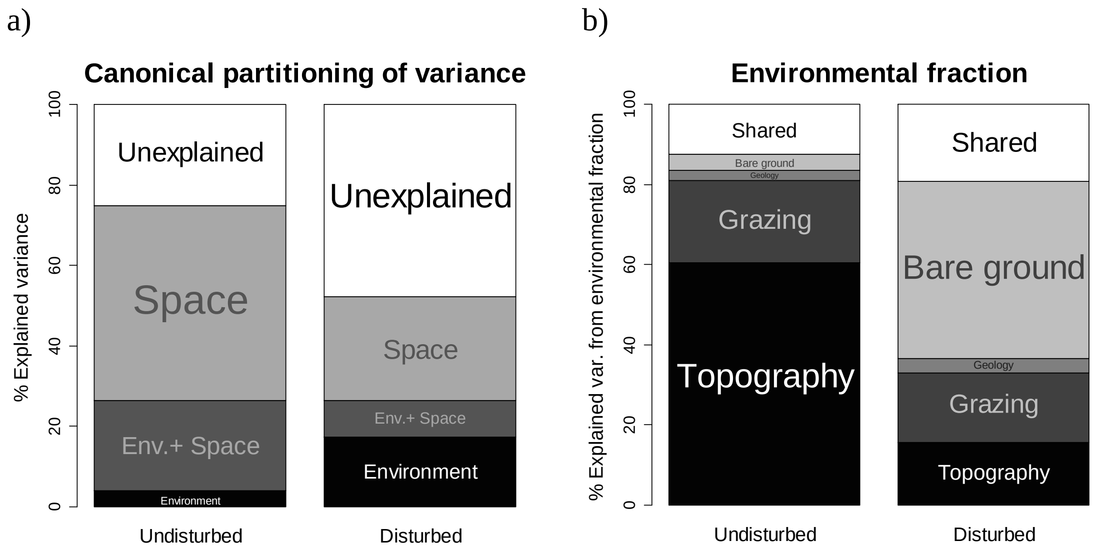


Figure 2. Percentages of variation of, community composition data explained by environment and space (a) and within 'pure' environmental fraction (b), for undisturbed and disturbed areas. All fractions were significant at p<0.001 using permutation tests with 999 permutations, except within environmental fraction, in undisturbed areas: grazing fraction (Pseudo-F=1.61; p=0.006), bare ground and geology fractions were non-significant while in disturbed areas, geology fraction (Pseudo-F=2.12 and p=0.014) were a bit less significant. The significance of the fractions of 'environment + space' and 'unexplained' in (a) and 'shared' in (b) cannot be calculated as stated by Legendre et al. (2005).

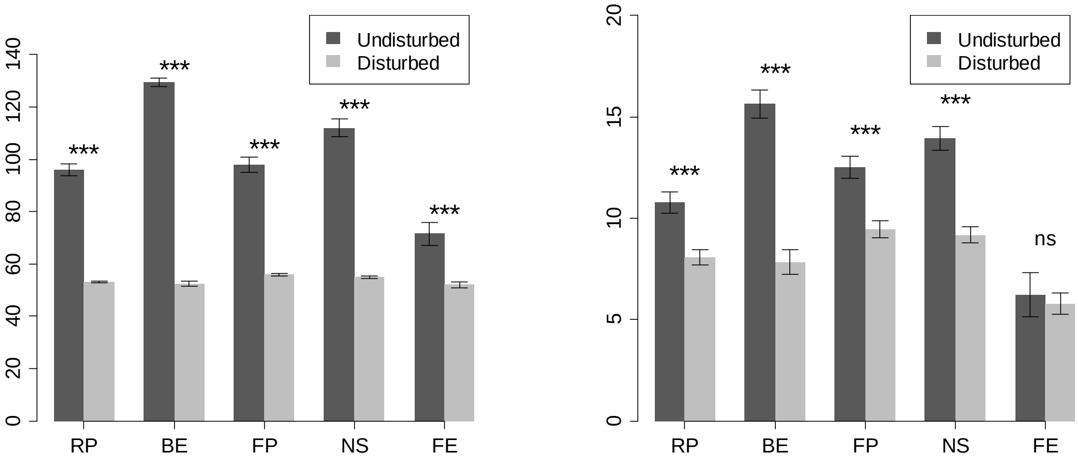
DISCUSSION

Effects of disturbance on diversity components at different scales

The components of plant diversity at different scales (α, β and γ) were analyzed and compared in areas with and without wild boar disturbances in Pyrenean alpine grasslands. Wild boar rooting strongly altered the plant diversity of these grasslands depending on the scale (i.e. each diversity component). The major contribution of diversity components in undisturbed sites was the α_1 component, i.e. within-samples diversity, followed by β_2, i.e. diversity among communities, and β_1 components, i.e. diversity among samples. The diversity among communities (β_2) is usually higher than the diversity among samples (β_1) since different communities have characteristic and differential plant compositions, while samples may not necessarily do. The dominance of the within-samples component (α_1) is related to the additive partition procedure using Shannon diversity index (Crist et al 2003). This index reflects the distribution-abundance relationship of species, having the most abundant species higher weights. Since individual plants of the same species are likely to be found at higher frequency at finer scales due to dispersal constraints, the Shannon diversity index is likely to be higher within samples than among them (Blackburn and Gaston 2000; Crist et al 2003).

The effect of large wild boar disturbances was detected mainly for beta components. For β_1 disturbed samples had higher values than undisturbed ones. Through reducing the abundance of dominant species, wild boar rooting may increase the local environmental heterogeneity and diversity among samples (Clark and Johnston 2011; Komac et al in press). Diversity among communities (β_2) was lower in disturbed areas, what indicates that disturbances homogenized the diversity of plants at the community level by bringing communities to early successional stages where few specialist species may be available (Denslow 1980; Kotanen 1996).

Figure 3. Abundance (a), richness (b), Shannon diversity (c), and Simpson dominance (d) indices in undisturbed and disturbed areas, for each of the five plant communities most disturbed by wild boar in alpine grasslands of OMPNP. Significance between disturbed and undisturbed areas were tested with paired t test. Significance codes: ‘***’ 0.001, ‘**’0.01, ‘ns’ non-significant. RP=*Rumicion psuedoalpini*; BE=*Bromion erecti*; FP=*Festucion paniculatae*; NS=*Nardion strictae*; FE=*Festucion eskiae*.

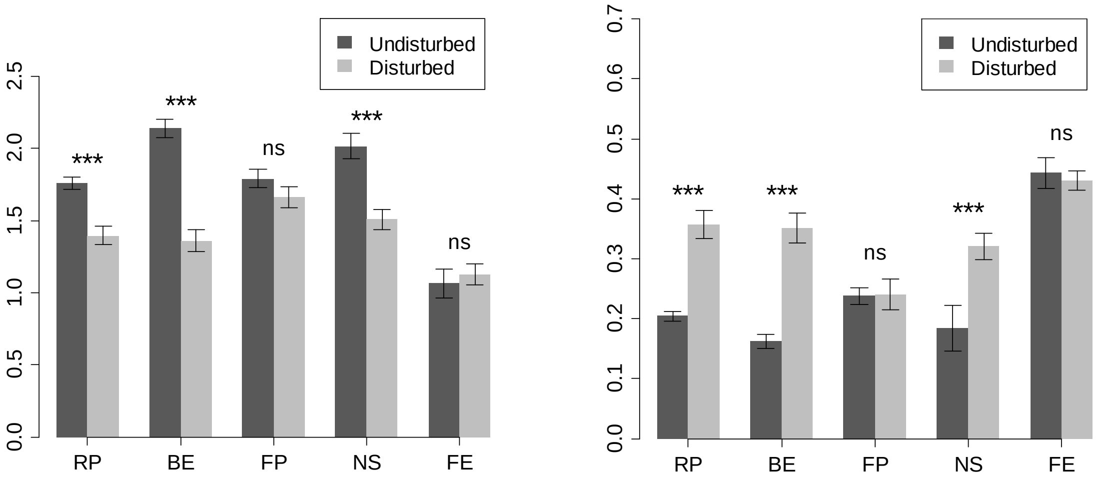


a) Abundance

b) Richness

c) Shannon diversity index

d) Simpson dominance index



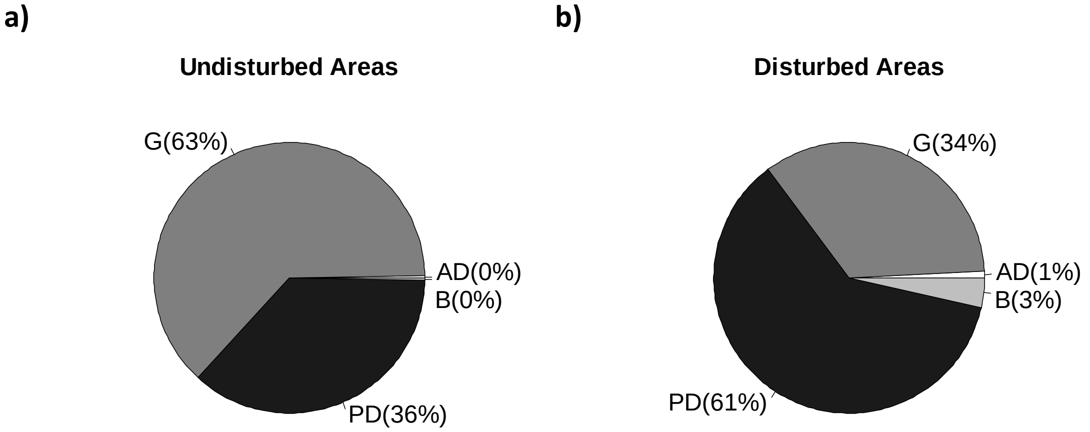
Environmental and spatial constraints of community composition

Wild boar rooting altered the relative contribution of environmental and spatial factors to the variation of plant community composition among sites. In undisturbed areas, variation of community composition was mainly explained by the spatial fraction, which involves both endogenous and exogenous processes that generate spatial autocorrelation structures (SAC; Franklin 2009). The mixed environmental and spatial fraction may represent exogenous SAC, since exogenous SAC is generated from environmental drivers that are spatially structured (Franklin 2009). On the other hand the pure spatial fraction can be considered as mostly generated by endogenous SAC, which arises from neutral processes (Bell 2001; Hubbell 2001), such as dispersion, reproductive strategies, facilitative or competitive interactions (Franklin 2009). These neutral processes are in turn related with self-organization patterns that are known to determine the structure of alpine plant communities (Alados et al 2007). Wild boar rooting seems to modify these endogenous processes and self organization patterns in plant communities as it drives communities to early successional stages, with higher extent of bare ground (Kotanen 1996; Kotanen 1997b). In these stages, plant interactions may be reduced and spatial-dependent resources released from dominant plant species (Suding and Goldberg 2001). This change is therefore less constrained by the species established and resource limitation, with a reduction of the pure spatial fraction and an increase of the unexplained fraction (Figure 2), probably indicating a higher participation of stochastic mechanisms in the structuring of the plant assemblage (Seabloom et al 2005).

Recently, some caution has been recommended for direct interpretation of endogenous SAC with neutral processes. Criticisms relate to the potential occurrence of unmeasured environmental variables and to the fact that environmental variables may mask some variance explained co-incidentally by neutral processes (Anderson et al 2010). Since in this study all environmental variables that theoretically explain vegetation variation have been taken into account (Franklin 2009) and the explained variance of endogenous and exogenous portions was separately and jointly calculated, significant biases are not expected.

Regarding the role of the pure environmental fraction, topography and grazing were the most relevant environmental factors in undisturbed areas. While the proportion explained by grazing did not change abruptly between undisturbed and disturbed sites, topography played a secondary role in disturbed areas, where the higher availability of resources (higher percentage of bare ground) might have been the main driving factor. In undisturbed areas resources are limited so the most competitive plants. In turn, these species are more sensitive to physiological stress (Grime 2001), that is shaped by topographic variability, since elevation, slope and aspect determine critical factors such as extreme values of solar radiation, temperature or water availability (Körner 1999b). On the contrary disturbances release main resources and reduce the amount of dominant plants, allowing them to be less stressed by topographical factors, allowing fugitive plants to establish (Platt and Weis 1985) or outcompete (Suding and Goldberg 2001) in gaps.

Figure 4. Percentage of abundance for the plant functional groups in (a) undisturbed and (b) disturbed areas at Pyrenean alpine grasslands (OMPNP). G = Graminoids; AD = Annual dicots; PD = Perennial dicots and B = Bulbs.



Effect of rooting on community diversity

Community diversity between disturbed and undisturbed areas was clearly reduced by wild boar rooting for Abundance, Richness (except in FE), Shannon Diversity and Simpson Dominance. In previous studies dealing with feral pig disturbances, Richness measures, yielded variable results; a reduction in Australian subalpine grasslands (Hone 2002) and an increase in Californian Mediterranean grasslands (Kotanen 1995). This contradictory result is explained mainly by the differential role of annuals in each area. While in Mediterranean grasslands annuals play a main role increasing the richness within disturbed areas (Lavorel et al 1994; Kotanen 1995), in Australian subalpine areas annuals were as scarce as in our study area yielding no compensation to the great plant cover removal, and thus having less number of species than in undisturbed areas (Hone 2002). For measures such as Shannon diversity and Simpson dominance, an exception was found in plant communities dominated by two tall-tussock *Festuca* species (*F. eskia* and *F. paniculata*). These grasslands seem to be resilient to disturbance regime in these terms, with the particularity of being both the most affected in extent (Bueno et al 2009) and intensity (chapter 2a) in the area. The almost complete dominance of these species in each community and their physical and chemical inhibitory effects to the surrounding species (Gonzalo-Turpin and Hazard 2009; Viard-Crétar et al 2009) yield lower values of Shannon diversity and higher values of Simpson Dominance in undisturbed areas. When disturbances bring affected patches to early successional stages, the dominance of few fugitive species may reach comparative values of the dominant tall-tussock fescue communities in undisturbed areas. As a result both communities showed a resilience effect to this disturbance in terms of diversity and dominance. Likewise, Kotanen (1995) found that one native bunchgrass species, *Danthonia californica*, was resilient to pig disturbances in Californian Coastal grasslands, and a possible co-evolution between disturbance and assemblage dynamics was hypothesized. In our case, community resilience might reflect some possible previous adaptation of these communities to this or any similar disturbance regime. Finally, the finding of one species (*Sanguisorba minor*) both favoured and disfavoured by wild boar rooting depending on two different plant communities, may indicate the complex and diverse circumstance of each species within different plant communities.

Effect of rooting on functional groups and species

Regarding community structure based on functional groups, rooting provoked a clear shift, where dicots dominated in disturbed areas and graminoids dominated in undisturbed areas. This result is in agreement with previous studies; in large disturbances from feral pig rooting (Kotanen 1997b; Cushman et al 2004) and in smaller soil disturbances in alpine grasslands (Gómez-García et al 1995; Sherrod et al 2005; Sebastià and Puig 2008), dicots have shown to be more easily adaptable to early succession stages after soil disturbances (Goldberg and Werner 1983; Kotanen 1997b). Annual species do not seem to have a clear role in the re-vegetation processes, as has been recently reported from soil seed bank analyses in these areas (Bueno et al in press). Contrary to these results, annuals have a higher contribution to re-vegetation processes at least temporarily in other Mediterranean grasslands (Lavorel et al 1994; Kotanen 1996; Tierney and Cushman 2006). However, in Pyrenean grasslands this might be directly related with the scarce proportion of annual propagule pools independent to grazing activities (Kotanen 1996; Sebastià et al 2008; Bueno et al in press). Bulbs as well do not seem to have a clear unique response to these disturbances in this habitat. Only two bulb species were found with significant contrasting abundance within and outside disturbances; *Crocus nudiflorus* and *Merendera montana*, being favoured and disfavoured by wild boar disturbances respectively (Table 3). This result contrasts with those found for mole-vole mound disturbance in the same habitat, where both bulb species were favoured by mole-vole disturbances (Gómez-García et al 1995). This might be explained by the role of small mammals as dispersers of some bulb species, such as *Merendera montana*. Voles create numerous hoards of bulbs that are frequently not completely consumed, thus favouring germination and establishment of these plant species (Borghi and Giannoni 1997; Gómez-García et al 2009). However the variation of the vulnerability of bulbs to soil disturbances is almost unknown. Only a few studies have dealt with the secondary succession processes after disturbance, mostly in relation with reproductive strategies of different bulb species (Bratton 1974; Howe et al 1981; Gómez-García et al 2004) or phenology (Kotanen 1996; Gómez-García et al 2009), which highlights the lack of studies covering this group of plants.

In sum, large disturbances by wild boar rooting in Pyrenean alpine grasslands strongly modify the structure and composition of plant diversity depending on the spatial scale considered and on the presence of tall-tussock fescue species. In turn, rooting influence the hierarchy of environmental constraints that may partly determine plant assemblage configuration and the direction of colonization processes.

ACKNOWLEDGEMENTS

We gratefully acknowledge the support of the Spanish Science and Innovation Ministry (PN-MICINN; CGL2008-00655/BOS) and the Spanish Ministry of the Environment (MMAMRM, Organismo Autónomo de Parques Nacionales 002/2007). The Ordesa-Monte Perdido National Park (OMPNP) provided logistic infrastructures and free access to the National Park.

Capítulo 3. Evaluación eco-pastoral a ambas escalas

Dada la tendencia actual al incremento de las poblaciones de jabalí (Massei and Genov 2004; Geisser and Reyer 2005; Cahill et al 2010), cabe esperar que la incidencia de sus perturbaciones también aumente en un futuro próximo. En las zonas alpinas de pastos supraforestales esta afección es percibida por los ganaderos como una amenaza para las actividades tradicionales de ganadería extensiva y genera conflictos entre manejo y conservación (Bueno et al 2010). Para evaluar los potenciales daños a las zonas pastorales, en este capítulo aplicamos los criterios y métodos desarrollados por el grupo de trabajo del Instituto Pirenaico de Ecología (Gómez-García et al 2002; García-González et al 2003; Gartzia et al 2005; García-González et al 2007; Gómez 2008b) ya testados en otros territorios del resto del Pirineo y regiones vecinas, para valorar de forma cuantitativa los pastos desde un punto de vista ecológico y pastoral.

Assessment of wild boar rooting on ecological and pastoral values of alpine Pyrenean grasslands[♣]

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ABSTRACT

Wild boar rooting is nowadays one of the main disturbances in Pyrenean alpine grasslands. Its consequences for the ecosystem are not perfectly understood yet despite alpine grasslands in the Pyrenees have an important economical role and a priority conservation interest. The ecosystem services of this habitat lay mainly on pastoral and ecological values that wild boar rooting seems to affect. In this study, we measured those ecological and pastoral values at different scales within and outside wild boar rooting to improve our understanding of the reach of these disturbances in this sensitive habitat. A preference for areas of high pastoral and intermediate ecological values was found for wild boar rooting at the regional level. However at the community level, disturbances notably reduced pastoral and ecological values in all communities. At the local level, the ecological value of bulbs and the pastoral value of annual dicots increased within disturbances, suggesting that disturbances may favour functional group diversity. In sum, wild boar rooting affects Pyrenean alpine grasslands moderately, with higher affection to pastoral than ecological values at all levels, what should be considered for the management and preservation of these habitats since these disturbances are likely to increase.

[♣] This chapter has been accepted for publication in Pirineos.

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INTRODUCTION

A crucial step to value an ecosystem is to accurately report how it may contribute to human wellbeing, through measuring what have been called 'ecosystem services'. This term includes both the naturally-occurring ecological processes and the benefits to humans that can be derived from them (Balmford et al 2008). However, we still lack the theoretical basis that links ecological diversity to ecosystem services underlying human wellbeing (Carpenter et al 2006). The need to develop indicators that synthesize and simplify the ecological complexity has been recently claimed, to aid monitoring biological, physical and social changes related to the ecosystem services (Carpenter et al 2006).

The main ecosystem services provided by mountainous areas are related to the provision of high quality water and food, control of climate and erosion, biodiversity and carbon storage, as well as recreation, aesthetic and spiritual values (Millennium Ecosystem Assessment Board 2005). The greatest historical environmental change in these areas has been the spread of grasslands through scrubland and forest reduction from the Middle Ages on (Fillat et al 2008). This progressive change due to livestock activities has developed a seminatural system with high ecological and pastoral values in a dynamic trade-off based on plant-herbivore interactions (Olff and Ritchie 1998; Austrheim and Eriksson 2001; Fillat et al 2008). More recently, livestock grazers have changed in European mountain systems from almost exclusive sheep herds to comparatively higher numbers of cattle heads (MacDonald et al 2000; Lasanta-Martínez et al 2005). Alongside with this trend, a sharp decline of extensive husbandry has occurred in the last decades in favour of more productive intensive farming systems (Luick 1998; Körner 1999b). In particular, this last trend has been related with drastic changes in the ecosystem structure, such as shrub encroachment and forest recolonization (Lasanta-Martínez et al 2005; Lasanta-Martínez et al 2006), what in turn may increase fire events (Carcaillet et al 2009), reduce biodiversity (Helm et al 2006), and boost some forest animal populations beyond an equilibrium threshold (Laiolo et al 2004).

Wild boar is a native forest species whose populations have been increasing from the sixties in their European distribution range (Saez-Royuela and Tellería 1986) being nowadays considered a pest in several areas within and outside its native distribution range (Oliver and Leus 2008). The main effect of its presence is an extensive disturbance that consists in turning over the soil while searching for underground feeding resources. These disturbances (hereafter 'rooting') affect directly some ecosystem elements, such as soils (Lacki and Lancia 1983; Bueno et al. unpublished) and vegetation (Bratton 1975; Bueno et al. unpublished), and may indirectly alter some ecosystem processes such as nutrient cycling and species turnover (Kotanen 1995; Bueno et al. unpublished). Rooting can be worrisome in some places, as it may affect habitats particularly sensitive to soil disturbances such as Pyrenean alpine grasslands (García-González 2008) with indirect consequences to traditional grazing activities that preserve the system and hold local economies (Bueno et al 2010). Therefore, evaluating the direct and main indirect implications of these disturbances is basic to guide adequate management actions and understand future consequences (Carpenter 2002). Despite its relevance for conservation and management, little attention has been given to the evaluation of alpine grasslands ecologically and in terms of forage quality (Gartzia et al 2005; García-González et al 2007) and even less the approaches that take into account the main disturbances that affect such sensitive areas (García-González et al 2003).

The main objective of the present study is to determine the effect of wild boar rooting in terms of pastoral and ecological values of Pyrenean alpine grasslands. We are especially interested in measuring its effect on ecological and pastoral attributes of grasslands at the regional (1), the plant community (2) and plant functional group (3) levels within and outside wild boar disturbances. The integration of these three levels may provide insights into the global assessment of this animal impact to a sensitive ecosystem within a protected area such as Ordesa and Monte Perdido National Park (OMPNP).

METHODS

Study area

The study was carried out in the alpine grasslands (above the present treeline; sensu Körner 1999) within Ordesa and Monte Perdido National Park (OMPNP; 42º 36’N, 0º 00’), located in the Spanish Central Pyrenees. The extent of the study area is 3.865 ha (~25% of the entire National Park), ranging from 1500 to 2800 m a.s.l. The climate in this area is a proper high-mountain climate with 5 ºC and 1720 mm of annual average temperature and precipitation respectively (García-González et al 2007). Lithology comprises mainly calcareous substrates such as limestone, sandstone and flysch (an overlaying complex of marlstone and sandstones). Pyrenean alpine communities within OMPNP can be structurally separated into sparse and dense grasslands depending on plant cover and soil depth (Bueno et al 2009). For community comparisons, we selected the five most disturbed plant communities, with a total extent of 2309.4 ha, close to 2/3 of the total surface, but receiving more than 96 % of wild boar disturbances in the study area (Bueno et al 2009). Plant communities were classified at alliance levels following phytosociological procedures (Braun-Blanquet 1979; Benito 2006). The selected communities are all dense grasslands located at sites with smooth topography and elevations lower than 2400 m a.s.l. Communities mainly differ in their diversity-dominance composition of species and their livestock use. Three of them are dominated by one grass species: Festucion eskiae (FE), Festucion paniculatae (FP) and Nardion strictae (NS) by *Festuca eskia*, *F. paniculata spadicea* and *Nardus stricta*, respectively. The other communities have tree or more co-dominant species: Bromion erecti (BE; *Festuca rubra nigrescens*, *Agrostis capillaris*, *Plantago media*, etc) and Rumicion pseudoalpini (RP; *Chenopodium bonus-henricus*, *Rumex alpinus*, *Poa supina*, etc; Fillat et al 2008). Among these plant communities a grazing gradient can be set, from the most to the least used by livestock: RP > BE > FP > NS > FE (Fillat et al 2008). Grazing use and plant diversity are intrinsically linked especially in RP and BE. The occurrence of RP is totally dependent on the high presence of livestock and the extent of BE depends partly on moderate intensities of grazing (Fillat et al 2008). Extensive husbandry is the main land use within OMPNP, mainly by cattle and sheep with little contribution of horses. Wild boar is relatively abundant in the surroundings of OMPNP with densities from 3.3 to 3.8 boars/km^2 (Herrero et al 2005; Giménez-Anaya et al 2010). It lives in the forest but visits alpine grasslands whenever forest feeding resources are scarce and soils are wet enough to be easily grubbed (Welander 2000a; Herrero et al 2005). Therefore wild boar disturbances occur mainly in late spring, with the snow-melting effect on soil, and early autumn, with higher rainfall events (García-González et al 2003). Also it has been suggested that protected areas where hunting activity is forbidden can act as refuges for wild boars (Acevedo et al 2006; Herrero et al 2006b) so higher wild boar disturbances within OMPNP can be expected (Bueno et al 2009).

Wild boar rooting, ecological and pastoral maps

Wild boar rooting in the study area was mapped during summer 2005 (June-August; for more details see Bueno et al. 2009). The whole study area was explored, and each disturbance patch over one squared meter was drawn over an aerial photograph (scale 1:3500). Most disturbance patches were also georeferenced by GPS (more than 1600 GPS data). Then the map was elaborated crossing both sources of information (drawings and GPS data) in a Geographic Information System (Bueno et al 2009). The accuracy of the map was also evaluated taking 120 random points clearly falling within disturbance patches and 120 outside those patches (i.e. clearly outside disturbances) and calculating the overall accuracy of the map through a confusion matrix (Congalton and Green 2009). The overall accuracy of the map was 90.6 % of correct classification (Bueno et al 2010).

For the ecological and pastoral maps we used a previous vegetation map of the area of a similar scale (1:5000; García-González et al. 2007). The extent of each plant community was replaced by the ecological and pastoral values of each community previously calculated for the Spanish Central Pyrenees (García-González et al 2007). Those values were categorized into three levels (Figure 1[♦]): low, medium and high, taking three equal intervals of the ecological and pastoral range values for the study area.

[♦] This figure was not included in the published version.

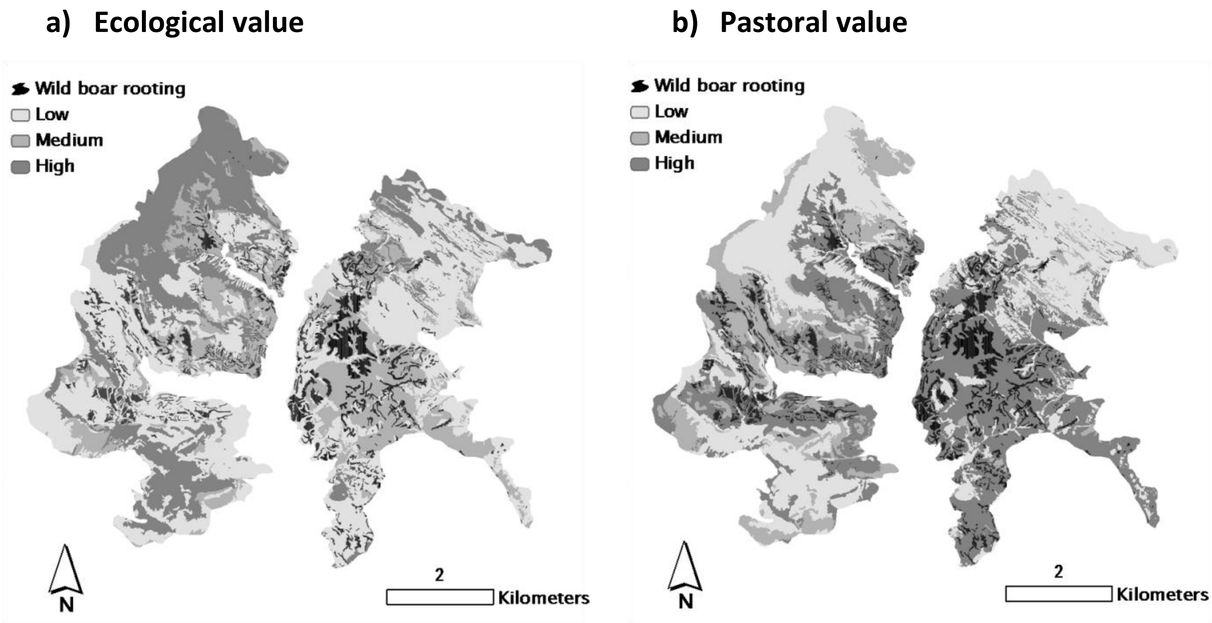


Figure 1. Maps of ecological (a) and pastoral (b) values in OMPNP. The map of wild boar disturbances is overlaid (black).

Sampling design and data collection

To determine the composition of species, and their relative abundance, comparatively within and outside disturbances a paired stratified sampling design was used. 40 sampling units were randomly located within disturbance patches in each community. For each sampling unit within disturbances another sampling unit outside disturbances was set the closest possible to the previous (400 sampling units in total). Therefore the design was stratified by plant communities and paired within/outside disturbances. The sampling unit was composed by two square frames of 0.25 m^2 of 5 cm grid. The size of the square frame was selected as a proxy of the minimum wild boar disturbance size (unit of disturbances) found in this habitat (CGB, pers.obs). In each square, 25 point-intercept contacts were set in the bottom-left corner of each grid (50 point-intercept contacts per sampling unit, 20,000 in total). To quantify the abundance of species, all individuals contacted by a vertical nail at each point-intercept were recorded (Goodall 1952). Among the species found, we distinguished four types of functional groups: annual and perennial dicots, graminoids (most of them perennial in the study area), and bulbs.

Ecological and pastoral values for community and plant functional groups

Community pastoral and ecological values were calculated as the average values obtained multiplying the frequency of the species for each sampling unit in each community within and outside disturbances (previously sampled, see data collection section) by the species ecological (EV) and pastoral values (PV; see below) previously calculated in this area (García-González et al 2007). We refer as pastoral value to what García-González (2007) referred as potential pastoral value, without considering the selection of the herbivore.

Ecological and pastoral values of plant functional groups were obtained from averaging the EV and PV of each species multiplied by its corresponding frequency in each sampling plot, for each plant functional group (i.e. annual dicots, bulbs, perennial dicots and graminoids) within and outside disturbances.

EV was estimated as the average of three ordinal components (values ranging from 0 to 5) related to plant species distribution in Europe, the Iberian Peninsula and the Spanish Pyrenees (Gómez-García et al 2002).

PV was calculated by dividing the quality of each species by a proper conversion factor to get comparable values to ecological values (in our study the conversion factor was equal to ten). Quality of each species is obtained by summing up the percentages of total plant nitrogen (N) and total plant phosphorous (P), multiplied by its digestibility (Dg), expressed as the percentage of dry matter; $Q=(N+P) \times Dg$ (Gómez-García et al 2002; García-González et al 2007; Fillat et al 2008). Pastoral values for the community level in this study, differed from Gomez-García et al. (2002) in that they were calculated taking into account the quality values of the most abundant species and their frequencies within communities, instead of analyzing the quality and production from community samples per se.

Statistical analyses

To determine whether the occurrence wild boar rooting on the OMPNP grasslands was related to areas comprising low, medium or high ecological and pastoral values, we used resource selection analysis (RSA) (Manly et al 1993). RSA compares the used area (disturbed by wild boar) to the available, where the null hypothesis is that wild boars root up the soil independently of its ecological and pastoral values, i.e. in proportion to their availability in the study area. RSA is based first on a Chi-squared Test, to test the null hypothesis and after rejection, Bonferroni confidence intervals are used to detect which level (low, medium or high) of ecological and pastoral values are (more or less) selected relative to their availability (Manly et al 1993; Alldredge and Griswold 2006).

To assess the differences between disturbed and undisturbed plant communities in ecological and pastoral values, we used paired t-tests owing to the pair-matched sampling design (disturbed-undisturbed). Ecological values were square root transformed to achieve normality.

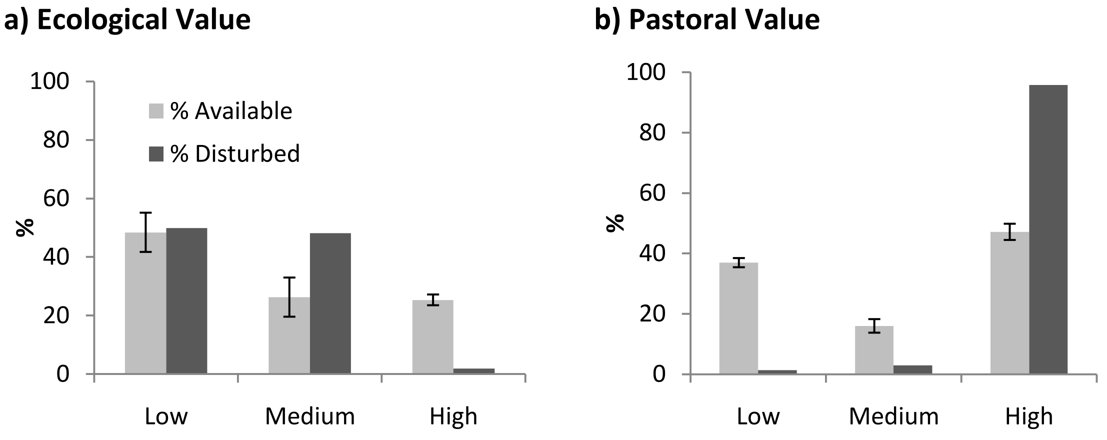
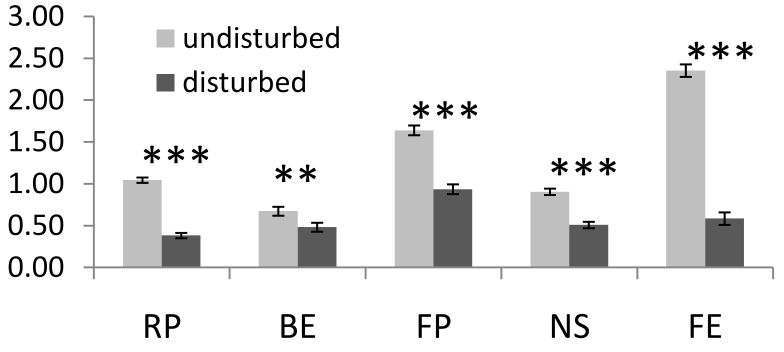


Figure 2. Percentage of disturbed areas by wild boar rooting in comparison to the percentage of available grasslands at low, medium and high ecological (a) and pastoral (b) values. Error bars represent *Bonferroni* confidence intervals (BCI). Percentages of disturbed areas higher or lower than BCI indicate selection or avoidance by rooting wild boars in each level respectively. All pairs of comparisons were significant at $p<0.001$ except low ecological values that were not significant.

a) Ecological value



b) Pastoral value

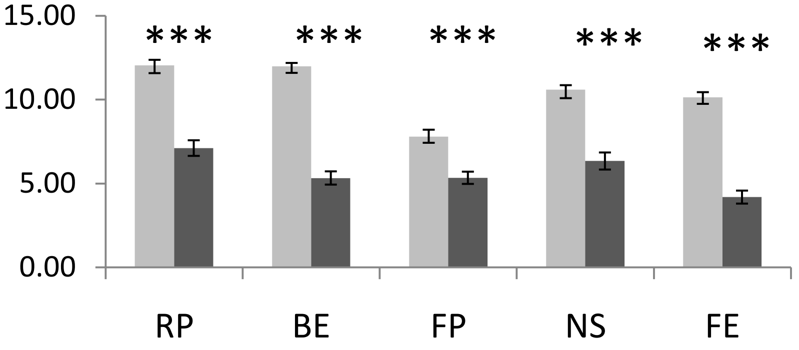


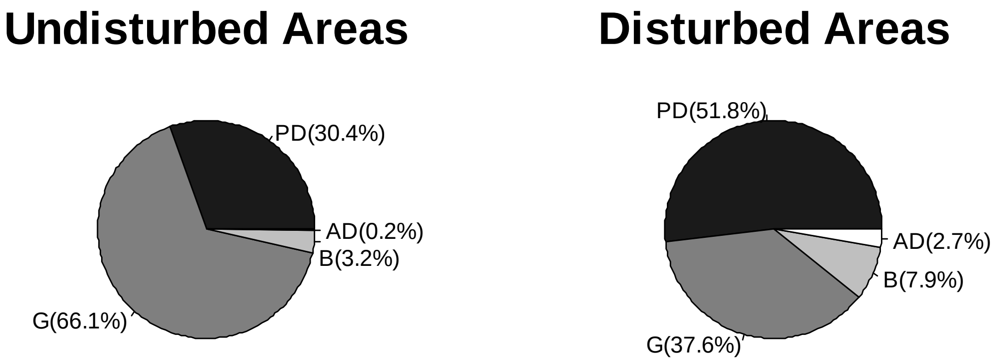
Figure 3. Ecological (a) and pastoral (b) values within and outside wild boar disturbances in the five grassland communities most affected by rooting. Mean values (±SE) are shown. Significance of comparisons between disturbed and undisturbed areas within each plant community was assessed using paired t-tests and is indicated by the asterisks. ‘**’ $p<0.01$, ‘***’ $p<0.001$

All statistical analyses were performed with R 2.10.1 (R Development Core Team 2010).

RESULTS

At the regional level, wild boar significantly selected areas with intermediate ecological values, avoiding those with high ecological values and used those with low ecological values in proportion to their availability (Figure 2a). On the contrary, areas with high pastoral values were actively selected by wild boar to root while low and intermediate values were significantly avoided (Figure 2b).

a) Ecological value



b) Pastoral value

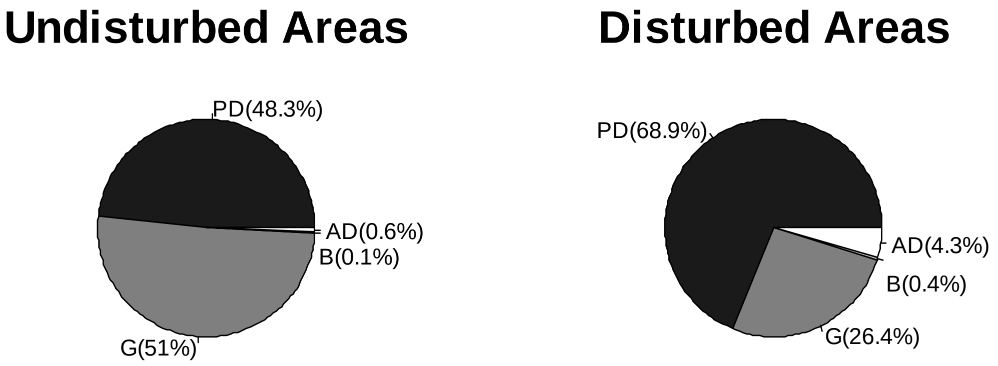


Figure 4. Ecological (a) and pastoral (b) values within and outside wild boar disturbances for plant functional groups. PD= perennial dicots, G= graminoids, AD= annual dicots, B= bulbs.

At the community scale, ecological values were higher in undisturbed areas than in disturbed ones when considering all plant communities together (t=-16.02; p=0.000). This trend was consistent within each plant community (Figure 3a). In relation to the pastoral value, a similar trend was detected towards a decrease in pastoral value within disturbances for all communities taken together (t=-20.04; p=0.000) and separately (Figure 3b).

For plant functional groups, both ecological and pastoral values outside disturbances were mainly due to graminoids and perennial dicots. Within disturbances the relative contribution changed, being perennial dicots the main group in determining both ecological and pastoral values. Interestingly, the ecological value of bulbs and the pastoral value of annual dicots increased within disturbances (Figure 4).

DISCUSSION

The multi-scale approach used in the present study has let us assess the effects of wild boar rooting on ecological and pastoral values of Pyrenean alpine grasslands. At a regional level, rooting affects mainly areas of high pastoral value, but it is least concerning from an ecological point of view. While searching for underground feeding resources rooting reduces plant cover at the community level, with the subsequent reduction in ecological and pastoral values. However, when detailed analyses are performed at the plant functional group level, responses differ within disturbances, even increasing the values for annual dicots and bulbs despite the reduction in plant cover.

At the regional level, we found that wild boars select those areas that have a great pastoral value, which directly affects traditional grazing activities. Areas with higher pastoral values are those that are more used by livestock (García-González et al 2007), hold the most nutrient-rich plants, and might be preferred by wild boars simply due to physiological constraints. Wild boars are monogastric animals, so that they cannot absorb nutrients from plant digestion as efficiently as do ruminants, which have a much longer and complex digestive system (Hofmann 1989). Therefore, wild boars may need to look actively for high-nutrient content foods, which they would more easily find in these highly-valuable pastoral areas, as plants in highly grazed areas are suggested to have higher nutrient content, both above and belowground (Bryant et al 1983; Gibson 2009). However, this feeding selection for nutrient-rich food items may in part not fit previous results showing a preference of wild boars to root in livestock grazing areas that withstand a moderate stocking pressure instead of areas with high stocking pressure (Bueno et al 2010). Assuming the most grazed areas i.e. areas with high stocking rate, have plants with higher nutrient content (Milchunas and Laurenroth 1993; Gibson 2009), why would wild boars not prefer intensively-stocked instead of intermediately grazed areas? There are at least two plausible explanations for this. The first one relates to the physical properties of soils under high livestock pressure, since heavily grazed areas are more soil-compacted due to livestock trampling (Van Haveren 1983; Albon et al 2007; Bueno et al unpublished), what would make it harder for wild boars to dig in them (Bueno et al 2009). A second explanation would be that intensively-grazed plant communities are dominated by herbivore-tolerant species (Ritchie et al 1998; Olofsson and Oksanen 2002). These plant species compensate the loss of biomass caused by herbivory through faster nutrient uptake rates that allow faster re-growth rates and the production of nutrient-rich tissues (Tilman 1988; Holland et al 1992). A key point here is where nutrient resources are allocated. In herbivore-tolerant species nutrient resources are mainly allocated aboveground, compensating for herbivory loss, while belowground biomass receives fewer nutrient resources (Holland and Detling 1990; Ritchie et al 1998). This may explain why these areas dominated by herbivore-tolerant species are of less interest to rooting wild boars that instead display a grazing behaviour in these sites (C.G. Bueno pers. obs.). On the contrary, for intermediate grazed areas with moderate-to-low herbivore densities a decelerating effect on nutrient cycling can be expected (Tilman 1988; Ritchie et al 1998). In these cases herbivores may be more selective and feed on nutrient-rich plant species, subsequently increasing the dominance of nutrient-poor species or plants with physical or chemical defences against herbivory (Pastor and Neiman 1992; Ritchie et al 1998; Hanley et al 2007). These species may in turn have more resources belowground as they invest more in rooting competence (Tilman 1988), being potentially more attractive to rooting wild boars.

On the other hand, wild boar rooting mainly affected areas with an intermediate ecological value. This might be related to the origin and dynamics of these grasslands in the Middle Ages, when lands were gained to the forest for grazing activities (Fillat et al 2008; Bueno et al 2010). The floristic composition of those communities might have changed from stress-tolerant species in the early stages, to grazing-tolerant species spread or even brought along from lowland areas by livestock (Austrheim et al 1999). These species introduced by livestock have a very wide distribution being some of them sub-cosmopolitan, leading thus to plant communities with lower ecological values. Currently, species and communities with higher ecological value would be more restricted to rocky or high elevation habitats, where livestock does not graze (García-González et al 2007; García and Gómez 2007) and wild boar does not root (Bueno et al 2009).

Regarding the effect of rooting in the ecological and pastoral value of plant communities, a decreasing trend was detected for all plant communities. Lower ecological and pastoral values within disturbed areas can be simply explained by a sharp decrease in plant cover, which would reduce the potential pastoral biomass together with the occurrence of ruderal or fugitive species within disturbances (Kotanen 1995; Bueno et al unpublished). When studying plant functional groups in more detail, the trend is similar for graminoids being the perennial dicots and to a lesser extent the bulbs and annual dicots, the groups that had notably increased their pastoral and ecological values within disturbances. This increase in the diversity of functional groups may suggest a slight increase in community dynamics and ecosystem processes (Tilman et al 1997). However, when comparing the abundance of these functional groups (chapter 2c; Figure 4) to their equivalents in ecological and pastoral values, the main difference was a decrease in the ecological value of perennial dicots (from 61% to 51.8% abundance), a decrease in the pastoral value of bulbs (from 3% to 0.4%) and an increase in ecological value of bulbs (from 3% to 7.9%) within disturbances in comparison to its raw percentage of abundance. This suggests that disturbances reduce the pastoral values of alpine grasslands through increasing the abundance of perennial dicots and bulbs, while increasing their ecological values through increasing the abundance of bulbs.

In conclusion, wild boar mainly affects to pastoral and, to a lesser extent, to ecological values of Pyrenean grasslands at the regional and community level. For ecological values, despite finding a clear trend of ecological degradation due to disturbances, areas of high ecological value remained unaffected. Therefore, notwithstanding the vast extent of wild boar rooting (321.5 ha in the study area; Bueno et al 2009) and the evident affection to grazing in this protected area (16.2 % of livestock grazing area affected by wild boar rooting; Bueno et. al. 2010), the impact of wild boar may be considered as moderate in terms of current conservation value. Nevertheless, the potentially increasing trend of this disturbance (Bueno et. al 2010) may lead to some concerns regarding the preservation of these habitats in the near future.

ACKNOWLEDGEMENTS

We would like to thank María Bueno, Ricardo Pineda and Dorleta Jiménez for field assistance, Maite Gartzia for digitalizing and ground-truthing vegetation maps and the staff of Ordesa and Monte Perdido National Park for the support and data provided. CGB was funded by a FPU fellowship from the Spanish Ministry of Education. Additional comments provided by two anonymous reviewers greatly improved earlier versions of this manuscript. We gratefully acknowledge the support of the Spanish Science and Innovation Ministry (PN-MCI) (CGL2008-00655/BOS), the Spanish Environmental Ministry, and the National Parks Network (MMAMRM 002/2007).

Capítulo 4. Discusión general y conclusiones

Resultados generales (qué hemos aprendido)

Efectos de las hozaduras en los pastos alpinos

Las hozaduras de jabalí, a escala de paisaje, afectan una extensión aproximada del 7% de la zona de estudio. En conjunto, esa superficie perturbada supera la que ocupan la mayor parte de las comunidades vegetales, exceptuando las más extendidas: los pastos mesófilos de *Bromion erecti* (30%), las gleras (21%), los cantiles (13%) y las comunidades dominadas por *Festuca eskia* (9%) y por *F. gautieri* (>7%; capítulo 1a).

Desde el punto de vista de la conservación del medio natural, es destacable el hecho de que dichas perturbaciones, u otras que afectan al suelo de forma similar, no siempre constituyen un fenómeno de aparición reciente en los ecosistemas pastorales de montaña (Canals 1997). Por el contrario, algunas de estas perturbaciones están posiblemente ligadas a actividades históricas (Aldezabal 2001) y pueden incluso formar parte de la dinámica natural de algunos tipos de pastos, como ha sido señalado en comunidades de *Festuca eskia* horadadas por micromamíferos (*Microtus spp*) cuyas galerías podrían mejorar las condiciones del suelo, aumentando su aireación y su capacidad de retención hídrica (Montserrat 2008). En lo que respecta al jabalí, se ha constatado un notable incremento de sus poblaciones y hozaduras en todo el Norte de la Península Ibérica durante los últimos 50 años (Nores et al 1995), al igual que ha sucedido en diversas partes de los Alpes desde los años 70-80, donde, además, se ha observado el establecimiento paulatino de poblaciones a mayor altitud (D'Andrea et al 1995; Moretti 1995; Baubet 1998).

Si analizamos el impacto sobre las diferentes unidades de pastoreo, las hozaduras de jabalí afectan fundamentalmente a los pastos utilizados por el ganado vacuno. En el Parque Nacional de Ordesa y Monte Perdido (PNOMP) la remoción del suelo se ha constatado en más de un 20% de la superficie pastada por las vacas (capitulo 1b). Queda así constatado el daño causado por el jabalí a la ganadería extensiva, ya de por sí actualmente deprimida (MacDonald et al 2000; Lasanta-Martínez et al 2005). Desde una perspectiva ecológica, que puede resultar prioritaria en territorios amparados por figuras legales de protección, las hozaduras no tienen por qué contemplarse necesariamente (siempre y en todo lugar) como un riesgo para los pastos de montaña, ni en cuanto al mantenimiento de la diversidad se refiere ni en la conservación de especies y poblaciones raras, endémicas o con otros valores de conservación (capítulo 3). A este respecto, cabe señalar que las hozaduras se ubican mayoritariamente en pastos densos (con suelos profundos y alta cobertura vegetal), cuya flora está principalmente constituida por plantas comunes, muchas con amplias áreas de distribución y sin amenazas para su persistencia, lo que otorga escaso valor ecológico a sus comunidades vegetales (capítulo 3; García-González et al 2007; Gómez 2008b). Por otro lado, se ha comprobado una relación inversa entre la superficie hozada y el tamaño de las hozaduras (Welander 2000a; García-González et al 2003). En zonas extensamente perturbadas, es frecuente encontrar numerosas hozaduras de tamaño pequeño (algunos cm) o mediano (algunos dm), formando islas. Esta particular disposición de las perturbaciones mostrando una fragmentación creciente conforme aumenta la extensión hozada salvaguarda la conservación de la riqueza florística, al preservar muchas zonas inalteradas que actúan como reservorios de la flora, y puntos de inicio de la recolonización vegetal, aún a pesar del descenso de diversidad encontrado en nuestras zonas de estudio (capítulo 2c). Así, las distintas áreas perturbadas constituyen un mosaico de zonas removidas e inalteradas donde las especies más sensibles a la remoción del suelo habrían desaparecido ya probablemente en los primeros estadios de perturbación (Kotanen 1994; Welander 2000a).

La tendencia a un descenso de la diversidad en zonas perturbadas que hemos encontrado en nuestras zonas de estudio (capítulo 2c) coincide con la encontrada en otros trabajos similares realizados en las montañas de Tennessee (EEUU) y en pastos subalpinos de Australia (Bratton 1975; Hone 2002). En sentido contrario, diversos estudios realizados en hábitats variados sometidos a la acción del jabalí o del cerdo salvaje (islas hawaianas, pastos costeros californianos, bosques atlánticos británicos o prados y pastos alpinos inferiores en la vertiente francesa de los Pirineos) han mostrado un notable incremento de la diversidad, al menos en los tres primeros años subsiguientes a la perturbación (Spatz and Mueller-Dombois 1975; Kotanen 1995; Welander 1995; Milton et al 1997; Welander 2000a; García-González et al 2003; Cushman et al 2004; Sims 2005; Tierney and Cushman 2006). Este aumento es frecuentemente argumentado como prueba de la “hipótesis de la perturbación intermedia”, según la cual niveles medios de perturbación maximizan la diversidad temporalmente (Connell 1978; Connell 1979).

No podemos concluir hasta la fecha, si nuestros resultados pueden constituir una excepción a la hipótesis señalada o bien indicar que el nivel de perturbación supera los que cabría considerar “medios”. Sea como fuere, queda constatado que, a pesar del aumento temporal de fertilidad (capítulo 2a) y la reducción de la competencia por los recursos que se produce al disminuir la cobertura vegetal (capítulo 2c), las hozaduras de jabalí ocasionan en nuestros ambientes pastorales de montaña una disminución de la diversidad, tanto en número de especies como en el reparto de sus frecuencias.

Por otra parte, hay que señalar el papel que en la recuperación de la diversidad juega el “fondo florístico” disponible para la recolonización, no sólo en la vegetación establecida sino también en el banco de semillas. En los pastos de los estudios mencionados de Australia y Tennessee la flora que recubría las hozaduras era la misma que la de los alrededores inalterados. La ausencia de una flora ruderal supone, en consecuencia, un límite a las posibilidades de revegetación que, en estas condiciones, dependerá exclusivamente de las capacidades colonizadoras de la flora preexistente (Bratton 1975).

En los ambientes donde se ha constatado un repunte de diversidad tras la perturbación, son las especies anuales las que dominan mayoritariamente los procesos de revegetación y las que contribuyen principalmente a ese aumento de diversidad, que puede resultar efímero si dichas especies son reemplazadas a corto plazo por las de la vegetación original establecida (Spatz and Mueller-Dombois 1975; Kotanen 1995; Welander 1995; Milton et al 1997; Welander 2000a; Cushman et al 2004; Sims 2005; Tierney and Cushman 2006).

En nuestras zonas de estudio el banco de semillas corresponde a un número muy reducido de especies, en gran proporción pocas especies de plantas anuales. Su papel en la revegetación se ha mostrado muy limitado espacial y temporalmente y parece ser muy dependiente de una actividad pastoral intensa (capítulo 2b), ya que el predominio en muchas comunidades de plantas con un alto grado cobertura, reproducción vegetativa y crecimiento clonal, restringe las oportunidades de germinación de las semillas a los huecos (*gap dynamics*) ocasionados por las pezuñas, boñigas, caída de piedras, toperas, etc. Aun así, cabe esperar posteriormente tasas minúsculas de reclutamiento (supervivencia de plántulas) frente a las vigorosas estrategias de expansión vegetativa de las especies dominantes (*Festuca*, *Nardus*, *Carex*, *Trifolium alpinum*). En estas condiciones, donde al rigor del clima y la topografía se añadiría a la ausencia de grandes perturbaciones persistentes en largos períodos de tiempo, el desarrollo y mantenimiento del banco de semillas habría sido inoperante. En este sentido, la aparición reciente de grandes superficies abiertas a la colonización, supondría una “nueva” oportunidad todavía no cubierta por las estrategias adaptativas desarrolladas en los largos períodos de coevolución pasto-herbívoro, es decir una escasez de propágulos disponibles para la colonización, ya señalada por Kotanen (1996). Lo anterior quedaría avalado por la escasísima representación que los terófitos muestran en los pastos de la alta montaña: apenas un 4% en el piso alpino, frente a un 22% en el conjunto de la cordillera (Villar et al 2001; capítulos 2c y 3).

Tomando en consideración aspectos metodológicos, es conocido el sesgo que existe en los estudios sobre las variaciones en la diversidad mediadas por hozaduras. Es difícil determinar la proporción de perturbaciones en distintos estadios de revegetación de un territorio en un momento determinado (Welander 2000a). La mayoría de los trabajos o bien estudian sólo un rango de perturbaciones según su edad, normalmente en perturbaciones de menos de 1 año de antigüedad (Welander 1995; Milton et al 1997; Arrington et al 1999), o bien siguen esas mismas perturbaciones en periodos que normalmente no superan los 3 años (Spatz and Mueller-Dombois 1975; Kotanen 1995; Welander 2000a; Cushman et al 2004; Sims 2005; Tierney and Cushman 2006). Para evitar ese sesgo y obtener una visión global del impacto, se realizó la cartografía de las hozaduras en las zonas de estudio (capítulo 1). Posteriormente se muestrearon de forma estratificada, las cinco comunidades más perturbadas por el jabalí que, en conjunto, albergaban el 98% del total de las perturbaciones cartografiadas. El muestreo se realizó al azar y con el mismo número de réplicas en cada comunidad, pero en diferente número para cada propiedad estudiada: 400 réplicas para la Flora (capítulo 2c) y 200 para suelos y semillas (capítulos 2a y 2b), lo que nos aseguró una representación real (una instantánea) de las hozaduras teniendo en cuenta la variedad de los estadios sucesivos que pueden coexistir en un momento determinado.

A escala de comunidad y especie, nuestros resultados señalan la afección directa de las hozaduras a las propiedades físico-químicas del suelo (capítulo 2a), a los limitados bancos de semillas (capítulo 2b) y a la vegetación y flora (capítulo 2c). En nuestras zonas perturbadas, el suelo dispone de nutrientes en su forma más asimilable para las plantas (inorgánica; capítulo 2a), con un efecto visible en los bordes de las hozaduras, donde la vegetación muestra un mayor vigor a juzgar por el crecimiento y color que muestra (C.G. Bueno, obs. pers.). Además, la remoción de la cubierta vegetal en las hozaduras y el volteo de la tierra, unido al aumento temporal de fertilidad, favorece la dispersión de las semillas (Welander 2000a; Heinken et al 2006) y su germinación (Fenner 2000; Sims 2005). A estas dinámicas cabe posiblemente atribuir la presencia de algunas plantas encontradas únicamente en las hozaduras un 6 % del total de esos ambientes (capítulo 2c).

Considerando el conjunto de acciones promovidas y desencadenadas por el jabalí, cabe definirlo como un decisivo agente que modifica el ambiente físico y modula la disponibilidad de recursos potenciales para otros organismos, alterando la estructura vegetal y, en concreto, la composición florística y la diversidad (Jones et al 1994; Wright and Jones 2004; Jones et al 2010). En suma, un “ingeniero de ecosistemas” (*ecosystem engineer*; Vitousek 1986; Hone 2002; Sims 2005; Cuevas et al 2010). O, más modestamente, por su potencial repercusión positiva en ciertos geófitos bulbosos apetecibles por el suido, como un “proto-agricultor” (García-González et al 2003). A la luz de los resultados del capítulo 2, hay que reconocer al jabalí también su papel como facilitador de la auto-regeneración de los pastos si la intensidad de perturbación presenta niveles bajos. Hay que señalar también las posibles sinergias con otras perturbaciones comunes en los pastos, como las originadas por el pisoteo del ganado o bien por la actividad de topos y topillos (Gómez-García et al 1995; Canals 1997; Gómez-García et al 1999; Gómez-García et al 2004; Kohler et al 2006; Sebastià and Puig 2008). A diferencia de éstas, las hozaduras de jabalí muestran una mayor persistencia (e impacto visual), que es resultado del período más largo requerido para su colonización, tanto más prolongado cuanto mayor es la altitud a la que se producen. La recolonización de suelos removidos por el jabalí en pastos montanos del Pirineo francés, situados sobre 1000 m de altitud, ha mostrado una velocidad de recolonización notablemente mayor que la que hemos observado en nuestras zonas de estudio (García-González et al 2003) ubicadas a mayor altitud. En este sentido la extensión de una hozadura constituiría una característica clave en procesos de degradación del suelo, a través del lavado de nutrientes y la compactación del suelo (Vitousek 1985; capítulo 2a). Una mayor extensión perturbada, implicaría un mayor período de tiempo para su revegetación, lo que aumentaría la probabilidad de su degradación (Welander 2000a). Además, las grandes extensiones hozadas están sometidas a una intensidad y frecuencia mayor de nueva actividad hozadora (Kotanen 1995; Welander 2000a; García-González et al 2003) lo que agrava las consecuencias de degradación y pérdida de suelo y disminuye la capacidad de respuesta del medio para su cicatrización (Pickett and White 1985; Vitousek 1985; Laska 2001; Mohr et al 2005).

En el presente trabajo, las hozaduras de jabalí afectaron de distinta forma a cada parte de los ecosistemas pastorales estudiados: suelo (capítulo 2a), banco de semillas (capítulo 2b) y vegetación (capítulo 2c), en los distintos niveles de organización contemplados (especies, comunidad y paisaje), alterando sus patrones espaciales y los procesos desencadenados, lo que cabe interpretar como una alteración de la resiliencia de los ecosistemas y por ende de su funcionalidad (Tilman et al 1997; Elmqvist et al 2003), y permite contemplar al jabalí como un verdadero ingeniero de ecosistemas (Jones et al 2010).

Beneficios y perjuicios de las hozaduras de jabalí

De los resultados de nuestro estudio y desde un análisis que no puede dejar al margen una visión antropocéntrica, y aún con el sesgo añadido de nuestro privilegiado entorno socio-económico, podemos catalogar las consecuencias de las perturbaciones como beneficiosas o perjudiciales para nuestros intereses:

Entre las consecuencias beneficiosas, podemos señalar: la dinamización de comunidades muy dominadas por ciertas gramíneas con crecimientos clonales, cuya rotura propicia el renuevo de la vegetación (capítulo 2c), un incremento temporal de fertilidad (capítulo 2a), la activación y renovación del banco de semillas (capítulo 2b) y el incremento local de la heterogeneidad y diversidad (capítulo 2c).

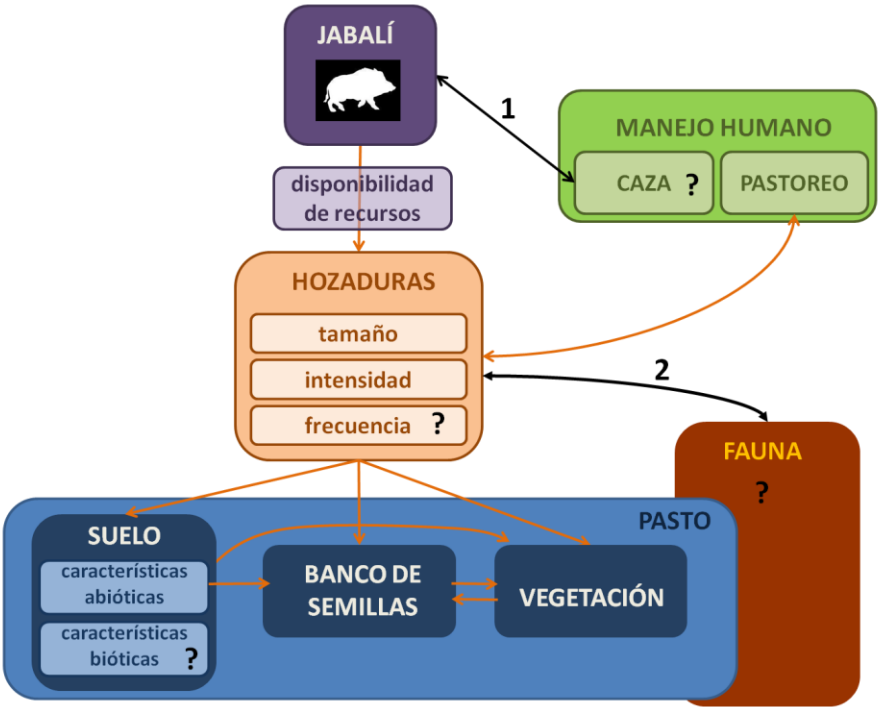
Entre las dañinas, cabe destacar: la afección o destrucción de pastos muy valorados para la ganadería extensiva (capítulo 1b), la homogenización de su diversidad entre comunidades (capítulo 2c), una posible pérdida de fertilidad a largo plazo a través del lavado de nutrientes (capítulo 2a), una larga exposición de los suelos desnudos en las grandes hozaduras que aumenta el riesgo de erosión (capítulo 2b) y una disminución, a escala local, del valor ecológico de la vegetación (capítulo 3).

A la luz de estas consecuencias, no es posible emitir un juicio global sobre la presencia del jabalí en nuestras montañas y, como sucede con otros fenómenos de la naturaleza, hay que analizar los diferentes contextos en que se producen, que incluyen las propias características ambientales, los modos de vida del territorio y la disponibilidad de recursos y las características y comportamiento de las poblaciones del jabalí; en concreto, señalamos los siguientes parámetros:

- Usos ganaderos del territorio, disponibilidad de pastos, evaluación de las afecciones (utilización, viabilidad y tendencia ganadera) (capítulo 1b).
- Patrones espaciales y temporales de las hozaduras (tamaño, recurrencia e intensidad de las mismas (capítulo 2c).
- Consecuencias en la estructura y dinámica de las comunidades afectadas (incluyendo bancos de semillas; capítulos 2b y 2c).

Algunos huecos por cubrir – sugerencias de investigación

Con el objetivo de avanzar en el conocimiento del papel de las hozaduras de jabalí en los pastos, comentamos algunas sugerencias para estudios complementarios a los que aportamos en la presente memoria doctoral. En el Esquema 1 se ofrece una panorámica general simplificada de las posibles variables que pueden jugar un papel decisivo en el impacto del jabalí en los pastos alpinos.



Esquema 1. Relaciones entre las hozaduras y diversos componentes del sistema. En naranja se indican las relaciones tratadas en esta tesis, y en negro las relaciones que se sugiere investigar.

Destacamos dos apartados en relación a su potencial interés de investigación:

1.- El primero con el fin de detallar las características de las poblaciones de jabalí en la zona de estudio y la influencia de la caza sobre las mismas e indirectamente sobre la extensión de hozaduras. Conocido el efecto de los incrementos de poblaciones en el aumento de hozaduras en zonas de montaña (Baubet et al 2004), su descenso provocaría una disminución de la competencia intraespecífica por los recursos alimenticios (Uzal and Nores 2004) y por ende una reducción de la actividad hozadora en pastos alpinos. En general es conocido el efecto renovador de las poblaciones de jabalí mediante la caza, llegando a porcentajes de renovación del 30-40%, siendo el principal factor de mortalidad en diversas poblaciones ibéricas (Rosell 1998) y francesas (Spitz et al 1984). Los únicos estudios publicados sobre la dinámica poblacional de los jabalíes en el Pirineo aragonés (Herrero 2001; Herrero et al 2008) señalan que la caza, dada la alta longevidad de los jabalíes cazados en el Pirineo, no constituye una causa de mortalidad demasiado importante. Alternativamente, la disponibilidad de alimento otoñal (bellotas y hayucos) aparece como el principal regulador poblacional (Herrero et al 2005). De cualquier manera dentro del PNOMP la caza está prohibida, pudiendo dicha zona ser utilizada como refugio (Acevedo et al 2006; Herrero et al 2006b) lo que aumentaría artificialmente su presencia y probablemente la extensión de sus hozaduras (capítulo 1a). Sería por tanto recomendable estudiar la densidad de población de jabalí en las zonas de estudio, en relación a su presión cinegética para determinar qué parámetros poblacionales, susceptibles de ser modelados mediante dicha presión, mantendrían un nivel aceptable de perturbaciones (Hone 1995).

2.- Por otra parte, el estudio del impacto de las hozaduras sobre la fauna, incluyendo comunidades de microorganismos del suelos, invertebrados y mamíferos, resulta fundamental para evaluar globalmente el impacto en el ecosistema (Canals et al 2003; Schley and Roper 2003; Massei and Genov 2004; Mohr et al 2005). En este sentido la abundancia por ejemplo de oligoquetos ha sido señalado como uno de los reclamos principales para el jabalí en su actividad hozadora en pastos alpinos de montaña en los Alpes, al formar allí parte de su dieta (Edward 1994; Baubet et al 2003; Baubet et al 2004). Además, se conoce que el papel de dichos oligoquetos en el ecosistema pastoral parece incrementar su relevancia cuanto más se investiga en la estabilidad, estructura y dinámica del suelo y la vegetación, ya que influyen directamente en la degradación y los ciclos de nutrientes, y afectan indirectamente al funcionamiento de todo el sistema (Knight et al 1992; Edward 1994; Lawton 1994; Paoletti 1999). El aumento de ganado vacuno, como es tendencia actual en el Pirineo, puede favorecer el aumento y la concentración de oligoquetos en majadales, abrevaderos, puntos de sal, etc (Popp 1997; Lavelle and Spain 2001; Bueno et al 2010). Por último, considerando una hipótesis complementaria, cabría analizar si el efecto de las tendencias actuales en el pastoreo y el manejo extensivo de ganado en los pastos pirenaicos, altera la cantidad y diversidad de oligoquetos en el suelo, lo que supondría un atractivo añadido para el jabalí y su actividad hozadora, junto a posibles consecuencias en el ciclo de nutrientes del suelo y la revegetación.

También faltan por completar los estudios de animales que parecen promover las hozaduras en los ambientes de montaña; en concreto, ciertos micromamíferos excavadores como topos, y distintas especies de topillos, que parecen ser directamente depredados por el suido (García-González et al 2003; Schley and Roper 2003) o damnificados por la búsqueda de sus almacenes subterráneos de bulbos y rizomas (Kotanen 1995; Borghi and Giannoni 1997; Focardi et al 2000; Welander 2000a).

Conclusiones / conclusions

1.- Las hozaduras afectan una superficie que hemos valorado entre el 2.1 y 11.5% de los pastos estudiados, lo que define al jabalí como el principal factor de remoción del suelo.

Wild boars root between 2.1 to 11.5% of the available surface of alpine grasslands, what makes them one of the main agents of disturbance in these areas.

Estos primeros datos de la extensión perturbada, podrán ser calculados y desglosados por épocas del año o estaciones, en las que la dieta del jabalí sea aproximadamente constante, para extender su comprensión y su posible evaluación en una dimensión temporal. En este sentido sería preciso usar herramientas de cartografiado como fotografías a alta resolución o imágenes de satélite para poder abarcar territorios comparables o superiores a este.

2.- Las preferencias en la selección de los lugares de hozadura parecen estar jerárquicamente relacionadas con tres grandes factores: sus preferencias de alimentación, la facilidad para hozar y el manejo humano.

Rooting selection seems to be hierarchically related to three main factors: feeding selection, the capacity of the soil to be dug and human management.

La vegetación de los pastos densos de *Rumicion pseudoalpini*, *Bromion erecti* y las comunidades dominadas por *Nardus stricta*, *Festuca eskia* y *F. paniculata*, y en menor medida *Primulion intricatae*, fueron las variables que más determinaron primeramente la selección del jabalí. Seguidamente, la humedad en el suelo que, potencialmente, determina la facilidad de hozar y asegura la presencia de fauna edáfica apetecible en los primeros centímetros del suelo. Por último, el manejo humano, en concreto el uso ganadero del territorio, afecta también esta elección. Queda por verificar la influencia de la caza en la selección de los lugares de hozadura.

3.- Las hozaduras afectan a un porcentaje considerable de las zonas de pastoreo de vacas y ovejas (16 %), especialmente en zonas de pastoreo vacuno con presiones intermedias de pastoreo

Rooting affects a wide proportion of the areas used by livestock (16%), especially those with intermediate cattle densities ("stocking rates").

Dada la potencial repercusión en las economías y cultura rural que parece tener las hozaduras, sería aconsejable extender el conocimiento de la influencia del jabalí a otras zonas de pastoreo con distinta composición de herbívoros y presión ganadera, para poder determinar y predecir su impacto sobre otras zonas de pastoreo extensivo de montaña.

4.- Las hozaduras afectan a la estructura y composición de los suelos, produciendo un aumento en su compactación y un aumento temporal de nutrientes (nitrógeno total y nitratos) disponibles para las plantas.

Rooting affects the structure and composition of soils, increasing soil compaction and a temporal rise in nutrient availability (nitrate and several cations) for plants.

Para completar el entendimiento de las consecuencias de estas perturbaciones, sería preciso realizar seguimientos a largo plazo en las propiedades físico-químicas del suelo, y extender dicho estudio a las comunidades bióticas del suelo (bioedafón) como bacterias, hongos (micorrizas), invertebrados y pequeños y medianos mamíferos excavadores.

5.- El papel del banco de semillas en la regeneración de las hozaduras es muy reducido debido a la baja densidad de semillas disponibles en los pastos alpinos. El principal efecto de las perturbaciones sobre el banco de semillas consiste en promover a la superficie las que son más abundantes (las persistentes a largo plazo), facilitando las condiciones para su germinación.

The role of soil seed banks in the revegetation of wild boar rooting is rather limited due to the paucity of seeds in alpine seed banks. The main effect of rooting is to expose long-term persistent seed banks to germination conditions.

Nuestros resultados apuntan a una gran variabilidad de los bancos de semillas debido al uso pastoral. Sería recomendable realizar estudios sobre la influencia del tipo y carga ganadera en la variabilidad de estos bancos de semillas para explorar su papel potencial como fijadores de nutrientes, evitando la degradación del suelo.

6.- Las hozaduras modifican la estructura y composición florística de los pastos , teniendo un efecto diferencial a diferentes escalas. Así, las hozaduras producen una homogenización de la diversidad entre comunidades, mientras que ocasionan un efecto contrario cuando la diversidad se mide a una escala menor.

Rooting affects the structure and composition of alpine grasslands, having a different effect depending on the scale. Overall, rooting homogenized diversity among communities, but this effect was reversed at smaller scales.

7.- Las comunidades dominadas por especies de Festuca que forman grandes macollas, Festuca eskia y F. paniculata, presentaron características resilientes a la perturbación en términos de diversidad y dominancia.

Plant communities dominated by tall-tussock fescues (Festuca eskia and F. paniculata) were more resilient under wild boar disturbances in terms of diversity and dominance.

Ciertas especies de gramíneas de características similares (*bunchgrass* o *tussock*) han sido citadas como núcleos de resistencia a las hozaduras muy importantes para la recolonización y recuperación de la estructura vegetal de los pastos así como controladoras de flora invasiva (Kotanen 1995; Kotanen 2004). Sería preciso un estudio detallado de las características funcionales de las especies con respecto a su respuesta específica a las hozaduras de jabalí para entender la respuesta de la vegetación a las hozaduras.

8.- Las hozaduras modifican los factores ambientales y los patrones espaciales que configuran los pastos, en especial el efecto de la topografía y las interacciones entre las plantas (reducción de la competencia por el espacio y sus recursos). En ese sentido, especies dicotiledóneas fueron favorecidas o menos perjudicadas que las gramíneas dominantes como *Nardus stricta*, *Festuca eskia* o *F. paniculata*.

Rooting modified the constraints imposed by environmental factors and spatial patterns in determining the structure and composition of alpine grasslands, particularly the effect of topography and of interactions among plants. In this sense, dicots were more favoured (or less disfavoured) than dominant graminoid species (Nardus stricta, Festuca eskia and F. paniculata).

Estos cambios en el micro-ambiente generados por las hozaduras, unidos a los cambios en las propiedades del suelo, aseguran la presencia de nichos de regeneración donde plantas eficaces para la cobertura vegetal de esas zonas están presentes y disponibles en los pastos, lo que acelera su regeneración y reduce su potencial degradación.

9.- Las hozaduras afectan significativamente a los valores ecológicos y pastorales de los pastos alpinos a escala de paisaje, comunidad y grupo funcional. Su incidencia es destacable para los valores pastorales a escala de paisaje, mientras que resulta moderada para los ecológicos.

Rooting significantly affects the ecological and pastoral values of alpine grasslands at various scales. Pastoral values were most affected, while affection to ecological values was moderate.

Dada la incidencia actual, es imprescindible al menos en lugares de declarado interés conservacionista (Parques Nacionales, Naturales, LICS, etc.) el desarrollo de seguimientos en la extensión de las hozaduras. Han sido varios los estudios (Acevedo et al 2006; Herrero et al 2006b) que apuntan a las zonas protegidas de la caza como lugares reserva para los jabalíes donde, de producirse un incremento en su número, sus consecuencias en el pasto serían potencialmente mayores.

10.- Evaluando globalmente la acción del jabalí en los pastos estudiados, hay que remarcar su papel como ingeniero de ecosistemas, especialmente en las comunidades con menor presión de pastoreo, donde las hozaduras incrementan la heterogeneidad ambiental y promueven su dinámica.

Wild boars can be regarded as ecosystem engineers in alpine grasslands, especially in areas with low grazing intensity, where wild boar rooting increases environmental heterogeneity and promotes grassland dynamics.

Agradecimientos

Quisiera empezar esta sección, quizá la más caótica de todas, pero sin duda la que no debe dejar indiferente a muchos... Voy a intentar seguir un hilo conductor que va a ser mi tesis en un gradiente temporal, para ir desenredando sentimientos de gratitud hacia la gente cercana que me ha hecho disfrutar este periodo a la vez muy especial y singular.

Agradecer a mis directores Daniel e Inma, motor y alma gestora de este proyecto, binomio singular (diferentes pero complementarios), siempre buscando soluciones creativas y positivas que han hecho posible que este trabajo tuviera un camino, siendo a la vez los guías y referentes del mismo.

A Ricardo García que sin muchos reparos podría considerarse casi un tercer referente en este trabajo donde participa activamente en varios de los apartados, aunque evidentemente su mérito para mí no es ese. Es sobre todo porque me ha atendido con mis dudas absurdas y coherentes, con una paciencia impagable.

Si Ricardo es un referente científico fundamental, Federico es un referente sin adjetivos, del buen ser, del saber mirar y entender, del saber tratar, del saber ser transparente y honesto, este sí que es un camino duro, cómo trabajar el egoísmo, la competitividad, aguantar los codazos y no perderse, no encerrarse, no aislarse..., pues lo puedo asegurar, él es la llamita de esperanza que resuelve la duda...

A Pepe y Santi por hacerme la vida de laboratorio y las sobremesas más humanas y divertidas, a Cristina trabajadora infatigable, por pelearse en conseguir buena parte de la bibliografía aquí citada, a Melchor y Ramón por los análisis de suelo, a Chan por darme esas clases magistrales de GIS "pa tontos", a Maite por toda la ayuda en cartografía, campo, críticas constructivas (y los estupendos mapas de las zonas de estudio), y por ser parte de un equipo en Jaca que somos ella y ...yo, vaya!... A todos los compañeros del IPE de Jaca que me han hecho la vida laboral mejor, especialmente a: Antonio Lanaspa, Álvaro, María Jesús y Miguel Ángel. A Luis Villar por todas las conversaciones interesante sobre flora y sus derivados y por invitarme reincidentemente al curso de Flora. A Gabriel Montserrat por todo el interés,

bibliografía y ánimo que me dio para estudiar las raíces en las zonas perturbadas y que pronto espero poder retomar. Al Profesor Montserrat por el espíritu y detenimiento con que me ha transmitido sus reflexiones sobre el jabalí.

A mis referentes prójimos, Sara de Ibort, y Ruben, por estar muy cerca aún estando a distancia. Sin olvidar a los otros referentes necesarios, Jose Luis Benito, Yolanda, David Nogües y Ana Marinas. A los coetáneos de ciencia, a Ben compañero en Ordesa, a David Moreno compañero de sobremesas y despacho y a Alvarito compañero de proyectos a medias. A las nuevas generaciones Palomilla, Hugo, Yacine, que dan ganas de volver a empezar (es un decir, claro...).

A todos los estudiantes de prácticas que me han ayudado en mis muestreos de campo y los han hecho muy especiales: Ricardo, Dorleta, Sergio, Silvia y Paula. Y en especial a una reincidente que es mi hermana pequeña.

Desde un punto de vista más alejado de la ciencia he de agradecer también a mis compañeros de piso en estos años, parte por tanto de una familia muy especial de gente: Sergio, Marcos, Edel, Albertico, Pirri, Vacilo, Gonzalitus, Popi, Chan, Nachete y Jara, Luismi y a otros casi compañeros de piso Emi, Isa (Sieso), Alex, Esther, Josete, Sara, Felipón, Darío...

A mis amigos de Madrid cercanos físicamente: David y Patxopa, y los que se quedaron en la urbe y me siguen contestando cuando los llamo, que dice mucho cuando llevas más de 5 fuera de un sitio: Chesca, Julito, Juan, Darío, Juanjo, Ester, Luis, Nuria, Sandra, Irene, David, Dani, Pablito, Amaya y Javi. A otros fundamentales, dispersos por Cáceres, Soria y Jaen: Ninón (gracias por esa experiencia del equipo pitufo en Ordesa) , María Polo, Perci, Sandrita y la familia Santamaría...

A mis amigos de adopción cordobesa, que me aceptaron sin condiciones, desde la UCO: Francis, Pablito, Pepe, Leire y Francesca, y fuera de la UCO: a Vico, Alejo, María (setas) y Bryant.

A Sieso de Jaca por su valentía y a Artaso por intentar el más difícil todavía...

A mi familia, en especial a mis padres y mis hermanas que me han apoyado y animado desde antes de empezar...

I also want to thank to Keith, Jerome, Bhushan and Tekki and all the staff of ISU GIS center for making me feel like at home in my first experience abroad. Thanks to Peter Banks that adopted me in his lab and let me collaborate within a really nice project in the middle of the Australian Mallee. Special gratitude is due to Johan Olofsson, who took care of me and Isa in one of my best experiences abroad, both scientifically and personally. Also to some really nice people at Umea: Jonas, Ed, Ola and Kristina that helped us enjoy the cold in October...

Y por último y por su infinita e impagable voluntad, ayuda y apoyo a Isa, por ser un estímulo constante y un proyecto de vida que sonríe a cada instante.

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