

Occurrence and intensity of wild boar disturbances, effects on the physical and chemical soil properties of alpine grasslands

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Abstract

Background and aims Physical and chemical soil properties determine local plant conditions and resources, affecting plants' ability to respond to disturbances. In alpine grasslands, wild boar disturbances occur at different intensities, what may affect differently their soil properties. Alpine soils from five contrasted plant communities were explored within and outside disturbances, accounting for an overall and community scale effect. Additionally, we analysed the effect of disturbance intensity on soil NO_3^- -N and NH_4^+ -N.

Methods Soils were analyzed for physical (bulk density, moisture content and electrical conductivity), and chemical

properties (pH, total N and C, oxidizable C, C:N ratio, available K, P, Ca^{2+} , Na^+ and Mg^{2+}). Resin bags were used to compare the effect of the disturbance occurrence and intensity on soil NO_3^- -N and NH_4^+ -N.

Results Bulk density, total N and NO_3^- -N concentration were significantly higher in disturbed areas, while soil moisture, C:N, NH_4^+ -N, Na^+ , Mg^{2+} and Ca^{2+} concentrations were significantly lower. However, low disturbance intensity reduced NO_3^- -N and increased NH_4^+ -N concentrations.

Conclusions Wild boar occurrence and intensity strongly alter physical and chemical conditions of alpine soils, increasing soil compaction, and altering the availability

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of N forms. These changes may affect most plant species, thus affecting the structure and dynamics of alpine plant communities.

Keywords Soil disturbance · Mineral nitrogen · Ammonium · Nitrate · Wild boar rooting · Pyrenean alpine grasslands

Introduction

Soils are essential parts of terrestrial ecosystems, as they physically support primary producers and decomposers, maintain biotic communities and determine key processes such as nutrient cycling or material-energy flows throughout the system (Brady and Well 2002; Lavelle et al. 1997). At the ecosystem and community levels, soils determine the structure and dynamics of communities through their response to environmental fluctuations and disturbances (Pickett and White 1985). The effects of soil disturbance to ecosystem functioning, will depend on ecosystem structure and the processes affected by the disturbance (Pickett and White 1985). For instance, sensitivity to soil disturbance may be exacerbated in alpine ecosystems, because most plant biomass is within the first few cm of the soil and its response is limited by a relatively short growing season (García González 2008; Körner 1999).

Wild boars are one of the most widely distributed mammals worldwide (Olivier and Reeder 2008), being one of the main agents causing soil disturbance in the alpine habitats they inhabit (Bueno et al. 2009; Massei and Genov 2004; Olivier and Reeder 2008). The primary means by which wild boars disturb soils is by turning over the soil looking for underground feeding resources (hereafter ‘rooting’), which include nutritive plant and animal foods, such as rhizomes, bulbs, fungi, earthworms, insect larvae, and even small underground vertebrates (Schley and Roper 2003). Although rooting can cause extensive disturbance to soils, affecting up to hundreds of hectares (Bueno et al. 2009; Massei and Genov 2004; Welander 2000), it is unclear if rooting activities may enhance or degrade soil conditions for plants. In fact, few studies have investigated the effects of wild boar disturbances to soils, relative to the great diversity of ecosystems wild boars inhabit (Barrios-García and Ballari 2012).

Soil disruption by wild boars may affect physical, and chemical soil properties (Barrios-García and Ballari

2012; Brady and Well 2002), where some of them, such as bulk density, can be largely affected by rooting, whereas others like soil moisture may remain unaltered (Barrios-García and Ballari 2012). Singer et al. (1984) found a decrease in bulk density of rooted soils in beech forests of Tennessee, related with the mixing of the organic matter and mineral horizons. In turn, soil moisture did not change after rooting, neither in costal grasslands and oak forests of California (Cushman et al. 2004; Moody and Jones 2000), nor in Mabi forests of Queensland, Australia (Mitchell et al. 2007), but see Wirther et al. (2011). Broadly, soil chemical properties, can be divided in two groups regarding their response to rooting: one group has a positive or neutral response, with an increase or no change in its concentration following disturbance, and the other with decreasing or neutral concentration values. Specifically, N and its mineral compounds, NO_3^- -N and NH_4^+ -N, belong to the first group. Changes in N have led to arguments on a neutral (Bruinderink and Hazebroek 1996; Cushman et al. 2004; Moody and Jones 2000; Tierney and Cushman 2006) or a positive effect of rooting (Siemann et al. 2009; Sims 2005; Singer et al. 1984) through the increase in soil nutrients. On the other hand, C, P and exchangeable cations, Ca^{2+} , Na^+ , K^+ , and Mg^{2+} , belong to the second group, where neutral or negative effects on plants, have been argued through a potential nutrient loss by leaching (Lacki and Lancia 1983; Mohr et al. 2005; Moody and Jones 2000; Singer et al. 1984).

No study has covered the effect of wild boar rooting on the properties of alpine soils, where the high recurrence of rooting activities (Bueno et al. 2009; Welander 2000) may enhance their positive or negative effects, or both. Soil disturbances caused by other mammals, such as pocket gophers (*Thomomys talpoides*) (Laycock and Richardson 1975; Litaor et al. 1996; Sherrod and Seastedt 2001), moles (*Talpa europaea*) (Canals and Sebastiá 2000) or grizzly bears (*Ursus arctos horribilis*) (Tardiff and Stanford 1998) affect alpine soils. However, these disturbances differ in their frequency, extent and effects on soil properties, particularly in the way each mammal disturbs soil, i.e. burial, excavation or rooting (Hole 1981; Kotanen 1997). Even the effect of a given mammal species can differ among habitats and soils (Canals and Sebastiá 2000), so the effects of wild boar rooting on alpine soils cannot be directly inferred from disturbances caused by other mammals.

The aim of this study is to determine the effects of wild boar rooting on soils of alpine grasslands in the

Spanish Central Pyrenees, comparing soil physical (i.e. electrical conductivity, bulk density and moisture) and chemical (i.e. pH, C, N, P, and exchangeable cation content: Ca^{2+} , Na^+ , K^+ , and Mg^{2+}) properties, within and outside areas disturbed by wild boars. In addition, the study evaluates the potential effects of soil disturbances on the availability of nutrients; by examining the relationship between soil mineral N (i.e. NO_3^- -N and NH_4^+ -N) and the occurrence and intensity of wild boar disturbances. We expect wild boar rooting to have an effect on the physical and chemical soil properties of alpine grasslands, as this ecosystem functionally relies on belowground biomass located within the depth range of this disturbance. Specifically we hypothesized that: 1) wild boar rooting will decrease bulk density by mixing organic matter with mineral soil. 2) Wild boar rooting will simultaneously have positive effects, through increasing the availability of N forms, and negative effects to plants, through decreasing the availability of P and cations. 3) Rooting intensity (relative to occurrence) will increase the concentration of N mineral compounds up to a point, where the soil system might get exhausted. Determining how this extensive and recurrent disturbance affects alpine soil properties is critical for understanding how this disturbance might compromise the preservation of alpine soils and affect grassland dynamics.

Methods

Study area

The study was carried out in Ordesa and Monte Perdido National Park (OMPNP) (42° 36'N, 0° 00') in the Spanish Central Pyrenees. The study area comprises natural grasslands between 1,500 and 2,800 m a.s.l. with an average annual temperature of 5 °C and an average annual precipitation of 1,750 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. The soils are acidic, desaturated of bases, and have high organic matter content and structural stability in the A-horizon (umbric epipedon). Thus, the soil profiles are Humic Dystricrypts (Badía et al. 2008, 2002).

We selected the five grassland communities most extensively disturbed by wild boars, which are among the most widespread alpine grassland communities in

the Pyrenees (Bueno et al. 2009). The topography among those dense grasslands is smooth with slopes < 20° (Bueno et al. 2009). Three of the plant communities were each dominated by a single grass: *Festucion paniculatae* (FP, terms following phytosociological nomenclature) 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* (RP) by *Poa supina*, *Rumex pseudoalpinus*, *Chenopodium bonus-henricus*, etc. (Fillat et al. 2008).

Grazing activities in the area, mainly by sheep and cattle, date back to at least the Middle Ages (Montserrat and Fillat 1991) and differ in the abundance of livestock (Fillat et al. 2008). Average stocking rates for each community describe a grazing gradient, from the most grazed (RP: 0.50 SLU/ha) to the least (NS: 0.06 SLU/ha) specifically: RP>FP>BE>FE>NS (Bueno et al. 2011). These grazing activities should not be considered disturbances, as their historic use and prevalence are strongly linked with the origin and development of most Pyrenean alpine grasslands (Fillat et al. 2008; Montserrat and Fillat 1991).

The plant communities evaluated covered 54.3 % (2,773 ha) of the study area, but nearly 98 % of the wild boar disturbances occurred there (Bueno et al. 2009). The high recurrence of rooting, locally, made it very difficult to estimate the precise age of individual disturbances (Bueno et al. 2009; Welander 2000); therefore, we compared soils of areas where the vegetation was either disturbed or undisturbed, irrespective of age of disturbance. Disturbed patches had been rooted by wild boar, recently or within the previous 2 years and were identified by the presence of overturned pieces of turf, which differed from the signs of disturbance caused by other mammal species (Bueno et al. 2009). Undisturbed patches were completely covered by vegetation without any presence of overturned turf and forming a continuum with the surrounding grassland.

Sampling design

To quantify the effects of wild boar rooting on alpine grassland soils, we used a random stratified paired sampling design. In each one of the five plant communities, 20 sampling points were randomly distributed within, and 20 outside areas disturbed by wild boar in a pairwise

fashion (200 points in total). We used a previous disturbance map (Bueno et al. 2009) to randomly locate the points in the disturbed area using ArcGis 8.3 (ESRI). Then, in the field, we located the undisturbed areas, closest to the previous points. In 2006, 100 soil samples (20 per community, 10 outside and 10 within disturbed areas) were collected with a cylindrical metal core sampler that extracts a soil sample of 5 cm diameter and 10 cm deep. Disturbance depth relative to the surrounding soil level was assessed by taking 300 depth measures within wild boar disturbances and calculating the average disturbance depth (10.7 ± 0.3 cm, mean \pm standard error) in the study area. In August, 2007, at the peak of the growing season, 200 ion exchange resin bags were placed 10 cm below ground and left there for 45 days, for measuring the available mineral N content in the soils (NO_3^- -N and NH_4^+ -N). The geographical coordinates of each sampling point were recorded using a GPS (Garmin Etrex Venture, USA).

Disturbance intensity

Disturbance intensity was estimated by calculating the approximate volume (m^3) of soil that was overturned by wild boar rooting. At each sampling point within disturbed patches, two measures of disturbance depth and two orthogonal diameters of each disturbed patch were recorded. In addition, we approximated the shape of each disturbance (squared, rectangular, circular, ellipsoid or triangular). To calculate the volume of each disturbance, the average depth was multiplied by the area of the disturbance, which served as a proxy for disturbance intensity, based on the assumption that the more intensively wild boars disturb the larger the volume of soil that is overturned. Disturbance intensity differed among plant communities (highest in *FE* and lowest in *FP*), which indicated that wild boar rooting impacted alpine grasslands, differentially (Fig. 1).

Soil analyses

For all measurements except moisture content, samples were air-dried, sieved through a 2-mm mesh and ground finely. Moisture content was quantified by calculating the amount of mass lost by a 2-g soil sample after it was dried at 105°C for 24 h. Bulk density was calculated by dividing the mass of each soil core sample by its volume (Klute 1986). Soil pH was measured in a 1:5 soil water suspension after shaking for 2 h (Buurman et al. 1996).

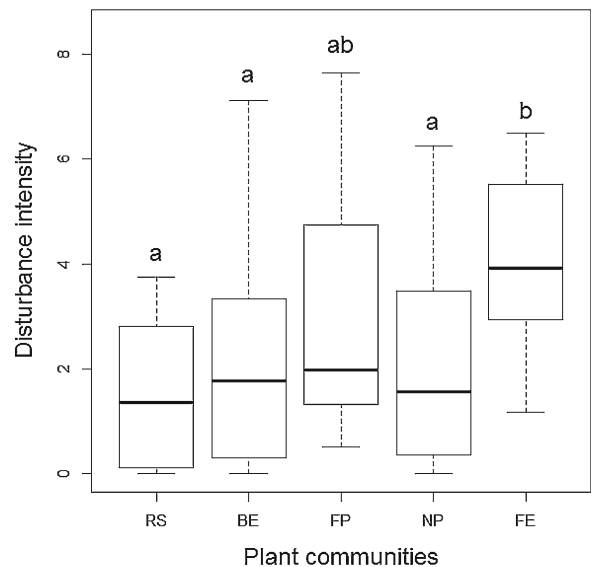


Fig. 1 Wild boar rooting intensity (log-transformed) in the five most extensively disturbed alpine grasslands in the Central Pyrenees, Spain. Lower-case letters indicate significant differences between plant communities based on a non-parametric multiple test at $\alpha < 0.05$. *BE* Bromion erecti; *FE* Festucion eskiae; *FP* Festucion paniculatae; *NS* Nardion strictae; *RP* Rumicion pseudoalpinii

Total C, oxidizable C, as well as total N were determined by an *Elementar Analysen Systeme GMBH* Autoanalyzer (Page 1982). To quantify organic matter, oxidizable C content was multiplied by the Van Bemmelen factor (1.724) (Heanes 1984). A 0.5-M sodium bicarbonate extraction at a nearly constant pH of 8.5 (Page 1982) quantified available P. To extract soil cations (Ca^{2+} , Mg^{2+} , Na^+ and K^+) 10-g sub-samples were shaken for 1 h in a 1 M ammonium-acetate solution at pH 7, and concentration was determined with ICP-OES (Thermo iCAP 6,000 series). The C:N ratio was calculated by dividing the proportion of oxidizable C by the proportion of total N of each sample.

To calculate the relative concentrations of soil mineral N (NH_4^+ -N and NO_3^- -N) ion exchange resin bags were used; specifically 8.5 g wet mass of cation and anion mixed bed ion exchange resin (J.T. Baker mixed-bed ion exchange resin, VWR Scientific Products) were placed in nylon stockings, thermo-sealed and cut (Binkley and Matson 1983; Page 1982). Resin bags were then buried at 10 cm for 45 days in the field. Once the resin bags were retrieved, they were air-dried for 2 days, before the cations were extracted using 100 ml of 1 M KCl (Tardiff and Standford 1998). NH_4^+ -N and NO_3^- -N 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 occurrence of wild boar disturbances, two complementary analyses were performed: a linear mixed model (LMM) and a Wilcoxon signed-rank test. The LMM was used to analyze the relative effect of disturbances in all the plant communities studied, where each soil property was the response variable for each model, and the presence/absence of disturbances, the plant communities (that were transformed into dummy variables) (Quinn and Keough 2002), and their interaction, were introduced as predictors. To account for a possible lack of independence between paired samples, mixed-effects models were used (Zuur et al. 2009). Specifically, a “pair” factor was added to the model as the random factor, which was estimated by assigning to each pair of observations ($n=100$; disturbed-undisturbed) a number from 1–50. Because of the lack of homogeneity in residuals spread across the different plant communities, we added an *identity* variance structure to the models that allows for different variances for each community. Three soil properties (electrical conductivity, P and K) were log-transformed to account for normality requirements in the residuals. To select the final model, likelihood ratio tests were used to compare the models with and without each predictor variable, non-significant terms were dropped from the final models (Zuur et al. 2009). A correlogram of the model residuals (Dormann 2007) did not reveal any significant spatial autocorrelation.

To evaluate the effects of wild boar rooting on each soil property within each plant community, *non-parametric* Wilcoxon Signed Rank tests were used because soil samples were paired and normality could not be assumed (Moore et al. 2008). These analyses complemented the LMM because they can identify the effects on soil properties that are specific to each plant community, which might go undetected in LMM.

Soil mineral N

To examine the relationship between available mineral N (NO_3^- -N and NH_4^+ -N) and the occurrence and intensity of disturbances in the soils from the five

grassland communities, two complementary analyses were performed, both attending to the occurrence and intensity of disturbances: LMMs and partial redundancy analyses (pRDA) (Legendre and Legendre 1998). LMMs captured the response of NH_4^+ -N and NO_3^- -N in all communities, while pRDA described how plant communities differed based on their soil concentration of NH_4^+ -N and NO_3^- -N. The LMMs with the occurrence of disturbance as predictor, were carried out in the same way as LMMs in the *Soil properties* section, but with NH_4^+ -N and NO_3^- -N as response variables. For the LMs taking into account the intensity of rooting, two aspects differentiated them from the previous LMMs: the data only contained samples within disturbances ($n=100$), so without the random factor, and the predictor *disturbance occurrence* was replaced by the *intensity of rooting*.

To quantify the relationship between soil NH_4^+ -N and NO_3^- -N content, and the occurrence (presence and absence) and intensity of wild boar disturbances pRDAs were used. For rooting occurrence, the response matrix was composed by 200 observations (rows) and 10 binary vectors (columns), of which five represented the presence (‘1’) or absence (‘0’) of plant communities within disturbed soils and five represented undisturbed soils. The environmental matrix comprised two columns: the concentrations of NO_3^- -N and NH_4^+ -N in each of the sampling points ($n=200$). To quantify the relationship between the concentrations of mineral N compounds in the soil and the intensity of disturbances, the response matrix contained 100 observations (the samples from disturbed soils, only), and the five vectors that represented the disturbance intensity in each of the five plant communities comprised the environmental matrix. To detect multicollinearity among predictors VIF and Pearson correlation tests were used, and all of the predictors had values <0.3 and <0.5 respectively. By incorporating the axis obtained after applying spatial eigenvector maps (SEVM) from the distance matrix of the geographical coordinates on the observations (Dormann 2007), spatial autocorrelation in the data was taken into account in the model.

The SEVM procedure extracts the potential spatial component of the model in orthogonal vectors, which can be 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 performed (Blanchet et al. 2008; Griffith and Peres-Neto 2006)

before SEVM axes were incorporated into pRDAs. To test for spatial autocorrelation, the Mantel correlogram of the residuals (Legendre and Legendre 1998) and a global test of spatial autocorrelation using Moran's Index (Dormann 2007) was calculated. Spatial dependencies were not detected with the incorporation of selected SEVM predictors into the pRDAs.

All of the statistical analyses were performed with R 2.13.0 (R Development Core Team 2009); specifically *npmc* for non-parametric multiple comparisons, *lme* for LMM, *ncf* for correlograms, *vegan* for pRDA, *packfor* for forward selection of spatial predictors, and *spdep* and *spacemakeR* for SEVM.

Results

Effects of wild boar rooting on soil properties

Wild boar rooting had a significant effect on all properties measured, in all or some of the plant communities studied, with the exception of pH, K concentrations and the properties based on C such as total C, oxidizable C and organic matter (Tables 1, 2 and 3).

Regarding the physical properties, in all plant communities except FP, the bulk density and moisture content of soils was higher in disturbed patches than in undisturbed ones (Table 1; Fig. 2), being significant for each community in the case of the bulk density (Table 3; Fig. 2). Among chemical properties the concentrations of N were significantly higher in disturbed than in undisturbed patches (Table 1; Fig. 2), while the concentration of Mg^{2+} , Na^+ and C:N ratio tended to be lower within disturbed areas than in undisturbed areas (Table 1; Fig. 2). Finally the responses of P and Ca were community-dependent, where Ca concentrations increased in RP and BE communities, while both decreased in FP community within disturbed areas (Table 3).

Among communities, in undisturbed areas soil pH was lowest in the FE community (Table 4), and C:N ratios were highest in the three communities with a single dominant grass species (FE, NS & FP; Table 4). In FP, the most productive community in terms of biomass, C:N ratio was lowest in disturbed areas (Table 3), which probably reflected a high decomposition rate of organic matter because the amount of soil organic matter was highest in disturbed areas (Table 3). Both in disturbed and undisturbed sites, Ca

soil concentrations were lowest in the FE community (Table 3), probably because the soils were acidic and received limited input of Ca from livestock.

Soil mineral N

The amount of NO_3^- -N and NH_4^+ -N in alpine soils was strongly influenced by the occurrence and intensity of wild boar disturbances (Table 2; Fig. 3a and b). In all five plant communities, wild boar rooting significantly increased the mineralization rate of N as reflected by soil NO_3^- -N concentrations (Table 2; Fig. 3a and 4a). In the communities dominated only by tall-tussock grass (FP and FE), disturbances have a significant ($p < 0.05$) effect on the NH_4^+ -N concentration in soils (Fig. 3b and b). Specifically, soil NO_3^- -N concentrations were negatively correlated with the presence of wild boar rooting in FE communities (Fig. 4a) and positively correlated with disturbance intensity in FP communities (Fig. 4b). The trend in soil NO_3^- -N and NH_4^+ -N concentrations changed when disturbance intensity reached a value around $5 m^3$, indicating a clear intensity threshold for soil mineral processes in these grasslands (Fig. 3c and b).

Discussion

In the alpine grasslands of the Spanish Pyrenees, wild boar rooting causes large disturbances to both physical and chemical soil properties, affecting on average the upper 10 cm of the soil, where wild boars may find most of their food (Herrero et al. 2005; Singer 1981). This is the first reference to the effect of wild boars rooting on soils in alpine habitats, although such effects have been observed in other ecosystems worldwide (Barrios-Garcia and Ballari 2012; Groot Bruinderink and Hazebroek 1996; Kotanen 1994; Tierney and Cushman 2006).

Contrary to our expectations, wild boar rooting increased bulk density in alpine grasslands in all plant communities but FP, where values were similar within and outside disturbances. Wild boars turn over the soil, so an immediate effect might be a reduction in bulk density in disturbed areas; however, rooting removes the plant cover along with the root fraction, which provides a physical support 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 can easily compact the disturbed soils. In the

Table 1 Physical and chemical soil properties in relationship with the occurrence of wild boar rooting (disturbances), in the five most disturbed plant communities of the alpine grasslands in the Spanish Pyrenees, based on Linear Mixed Models

Response variable	Linear mixed models (<i>pair</i> as a random factor)						
	Dist.		Plant Com.		Dist. × Plant Com.		
	F	p value	F	p value	F	p value	
BD (g/cm ³)	66.172	0.000	4.559	0.004	3.878	0.009	Physical
Moisture (%)	13.643	0.001	1.964	0.116	2.373	0.068	
EC (μS/cm)*	0.833	0.366	2.770	0.039	2.596	0.049	Chemical
pH	0.211	0.648	23.492	0.000	–	–	
tN (%)	4.540	0.038	3.618	0.012	–	–	
tC (%)	0.231	0.633	5.648	0.000	–	–	
Ox.C (%)	0.139	0.711	6.729	0.000	–	–	
OM (%)	0.489	0.488	5.081	0.002	–	–	
C/N	5.027	0.030	7.203	0.000	–	–	
P (mg/kg)	1.255	0.269	7.238	0.000	2.673	0.044	
Ca (mg/kg)*	21.836	0.000	12.066	0.000	2.838	0.035	
Mg (mg/kg)	43.064	0.000	10.773	0.000	–	–	
Na (mg/kg)	30.026	0.000	2.160	0.089	–	–	
K (mg/kg)*	0.087	0.769	3.135	0.023	–	–	

Each soil property acts as a response variable while the predictors were: the presence/absence of disturbances (Dist.), the five plant communities (Plant Com.) and the interaction of both. The factor *pair*, which account for the paired design, acted as a random variable. F and p values are shown. ‘*’ indicates the element that was log-transformed to fit normality requirements. Significant p values (< 0.05) are in bold *BD* bulk density; *EC* electrical conductivity; *tN* total N; *tC* total C; *Ox.C* Oxidizable C; *OM* Organic matter; *C/N* CN ratio

absence of factors that compact soil, e.g. livestock trampling, disturbed soils can have reduced bulk density; for

instance in mountain forests of Tennessee, USA (Lacki and Lancia 1983; Singer et al. 1984). On the contrary, in

Table 2 The concentration of soil exchangeable NO₃⁻-N and NH₄⁺-N in relationship with the occurrence of wild boar disturbances (a) and disturbance intensity (b), in the five most

disturbed plant communities of the alpine grasslands in the Spanish Pyrenees, based on Linear Mixed Models and Linear Models, respectively

Response variable	Linear Mixed Models (<i>pair</i> as a random factor)					
	Dist.		Plant Com.		Dist. × Plant Com.	
	F	p value	F	p value	F	p value
a) Occurrence of disturbances						
NO ₃ ⁻ -N *	80.023	0.000	1.844	0.127	–	–
NH ₄ ⁺ -N *	7.796	0.006	92.531	0.000	–	–
Linear Models						
	Int. Dist.		Plant Com.		Int. Dist. × Plant Com.	
	F	p value	F	p value	F	p value
b) Intensity of disturbances						
NO ₃ ⁻ -N *	0.104	0.748	6.718	0.000	4.288	0.003
N- NH ₄ ⁺ -N *	0.062	0.804	36.462	0.000	–	–

The concentration of soil NO₃⁻-N and NH₄⁺-N acted as response variables, while the predictors were: the presence/absence of disturbances (*Dist.*), the five plant communities (*Plant Com.*) and the interaction of both (*Dist. x Plant Com.*) for (a) and the intensity of disturbance (*Int. Dist.*), *Com.* and the *Dist. x Plant Com.* for (b). In (a), the factor *pair* acted as a random variable to account for the paired design. F and p values are shown. ‘*’ indicates the element that was log-transformed to fit normality requirements. Significant p values (< 0.05) are in bold

Table 3 Physical and chemical soil properties (median±median absolute deviation) in areas disturbed and undisturbed by foraging wild boars in the five plant communities most disturbed in the Central Pyrenees, Spain

Properties (units)	p BE		p FP		p NS		p FE		p					
	Undist	Dist	Undist	Dist	Undist	Dist	Undist	Dist						
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	**
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	
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	
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	
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	
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	
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	
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		10.72±0.58	10.05±0.88	
P (Kg/ha)×10 ⁻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		0.09±0.06	0.15±0.10	
Ca (Kg/ha)×10 ⁻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		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	

Significant differences between disturbed-undisturbed pairs were tested using a *Wilcoxon Signed-Rank test*. Significant differences at p values (p): ** 0.05, *** 0.01, **** 0.001 are in bold

BD bulk density; EC electrical conductivity; tN total N; tC total C; Ox.C Oxidizable C; OM Organic matter; C:N C N ratio; BE Bromion ereti; NS Nardion strictae; RP Rumicion pseudoalpinii; FE Festucion eskiaae; FP Festucion paniculatae; Undist Undisturbed areas; Dist disturbed areas

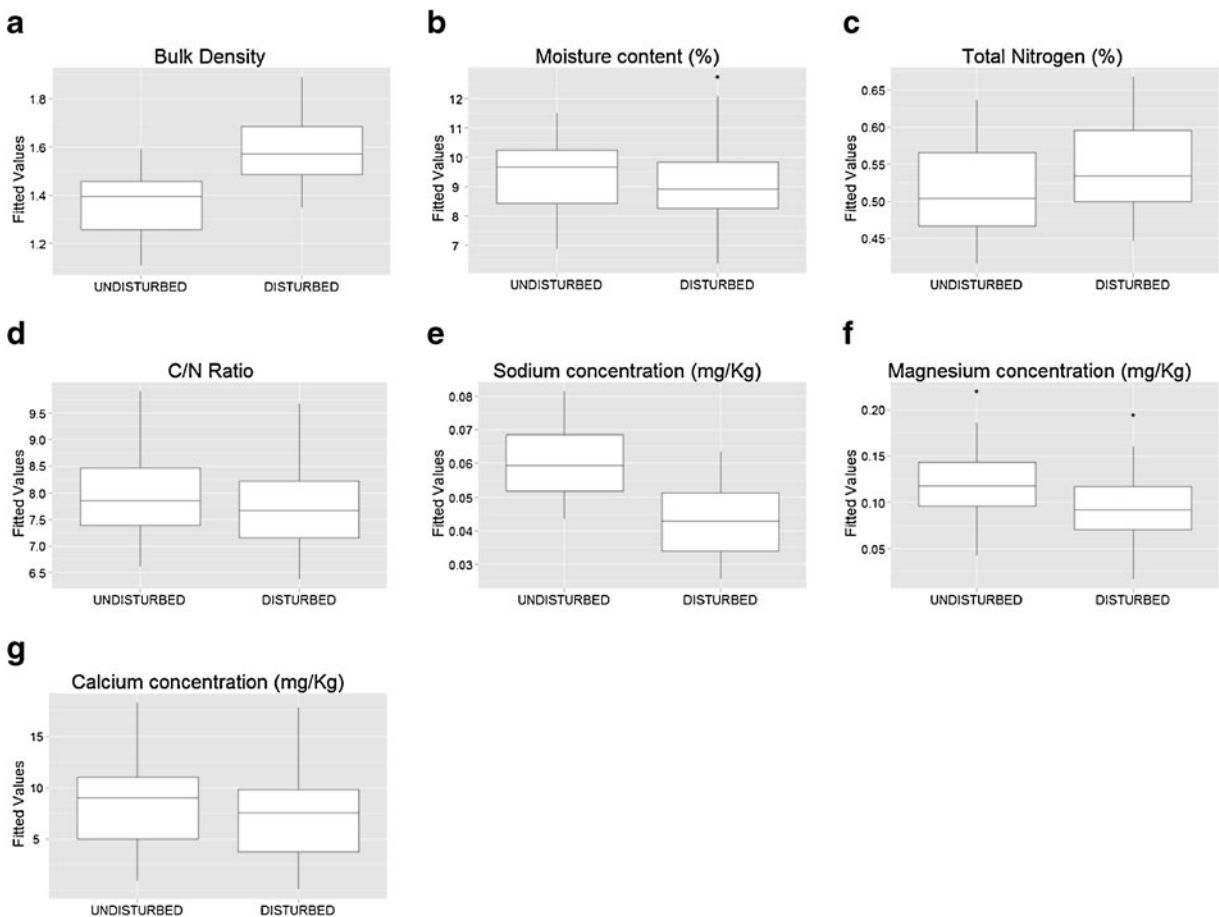


Fig. 2 Fitted values of the significant soil properties that differ in undisturbed and disturbed areas by wild boar rooting. Fitted values were obtained from the adjusted Linear Mixed Models (see Table 2 for

details) with respect to the occurrence of disturbances in the five most disturbed plant communities in the alpine grasslands of the Spanish Pyrenees, Spain. **a–b** Physical properties. **c–g** Chemical properties

mountain rangelands of Oregon, USA, the presence of sheep increased the bulk density of soils disturbed by pocket gopher digging (Laycock and Richardson 1975). The effect of plant cover removal on bulk densities is inferred by the invariance in the bulk densities of soils when disturbances do not remove plant cover; e.g., disturbances caused by a vehicle in Alaska (Chapin and Shaver 1981). Within disturbed areas in FP grasslands, a substantial amount of litter from *F. paniculata* is mixed with the soil, which might ameliorate soil compaction rates in this community. This was the case in Tennessee, where the relatively greater amounts of organic matter within areas disturbed by feral pigs reduced the bulk density of the soils in these locations (Lacki and Lancia 1983).

As expected, wild boars had a simultaneous positive and negative effect on nutrient concentrations. With

their rooting, wild boars may alter most of the biotic communities that are responsible for most of the nutrient cycling processes in soils (Lacki and Lancia 1983; Singer et al. 1984). In the Pyrenees, wild boar rooting, increased the availability of soil N and NO_3^- -N, decreased it for Mg^{2+} , and Na^+ but did not alter significantly the concentrations of soil NH_4^+ -N, nor K^+ . Disturbance can break up stable aggregates of soil particles, increase the mineralization of soil organic matter, with the subsequent release of available nutrients (Canals et al. 2003) The increase in the release of soil nutrients can be partly absorbed by plants if disturbances are small and they do not remove entire root systems. In addition, nutrients can be also stored in the soil in available forms, which increases their availability in disturbed areas e.g., disturbance to the soil by pocket gopher disturbances in Utah (Laycock and Richardson

Table 4 Physical and chemical soil properties differences among the five common plant communities most disturbed in the Central Pyrenees (Spain) derived from a multiple non-parametric test comparisons (p values<0.05), (a) in undisturbed and (b) in disturbed areas

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

Different letters indicate significant differences among communities

BD bulk density; EC electrical conductivity; tN total N; tC total C; Ox.C Oxidizable C; OM Organic matter; BE Bromion erecti; NS Nardion strictae; RS Rumicion pseudoalpini; FE Festucion eskiae; FP Festucion paniculatae

1975) and tuco-tuco (*Ctenomys talarum*) in Argentina (Malizia et al. 2000). However, if disturbances are large enough, such as those created by wild boars, plant roots can be dramatically affected and these nutrients are easily leached by rain or snowmelt (Lacki and Lancia 1983; Singer et al. 1984), which reduces their concentrations in disturbed soils.

In Pyrenean alpine soils after wild boar rooting, N mineral forms (NO₃⁻-N & NH₄⁺-N) were altered by disturbance intensity until a value 5 m³ was reached. This value corresponds for example, to a square of 7 m side and 10 cm depth. Relatively larger or deeper disturbances, those with higher disturbance intensity, may not affect the mineralization processes for these soil N forms. In addition, and regarding the disturbance common size in the area, higher than the aforementioned size (C.G. Bueno pers. obs), we can expect that this mineralization saturation may be reached easily.

Soil NO₃⁻-N concentration is the result of a complex tradeoff; NO₃⁻-N 'input' that is the result N mineralization rates, while the 'output' depends on plant nitrogen uptake, nitrogen immobilization by decomposers, leaching or run-off and denitrification

rates (Vitousek 1985). In the soils of mountain forests of Tennessee (Singer et al. 1984) and Hawaii (Vitousek 1986) the effects of rooting by wild boar or feral pig on NO₃⁻-N concentrations were similar to those observed in the Pyrenees, but simulated feral pig disturbances in coastal grasslands of California either, increased NH₄⁺-N availability concentrations only (Kotanen 1997), or had no significant effect on either form of N (Cushman et al. 2004). The variation among habitats in their responses to similar types of disturbances suggests, perhaps, that the habitat differs in the composition of the NO₃⁻-N trade-off, in its sensitivity to disturbance or both.

In general, the reduction of plant cover by rooting might reduce plant NO₃⁻-N uptake, accelerate mineralization because of the soil aeration, and reduced nitrogen immobilization by decomposers (bacteria), which has been described for pocket gopher soil disturbances (Canals et al. 2003). In the FE grasslands of the Pyrenees, which was the community most intensively disturbed by wild boar rooting, the concentrations of NO₃⁻-N and NH₄⁺-N were inversely correlated. It is possible that the aeration effect of disturbances influenced the nitrification of NH₄⁺-N because if the

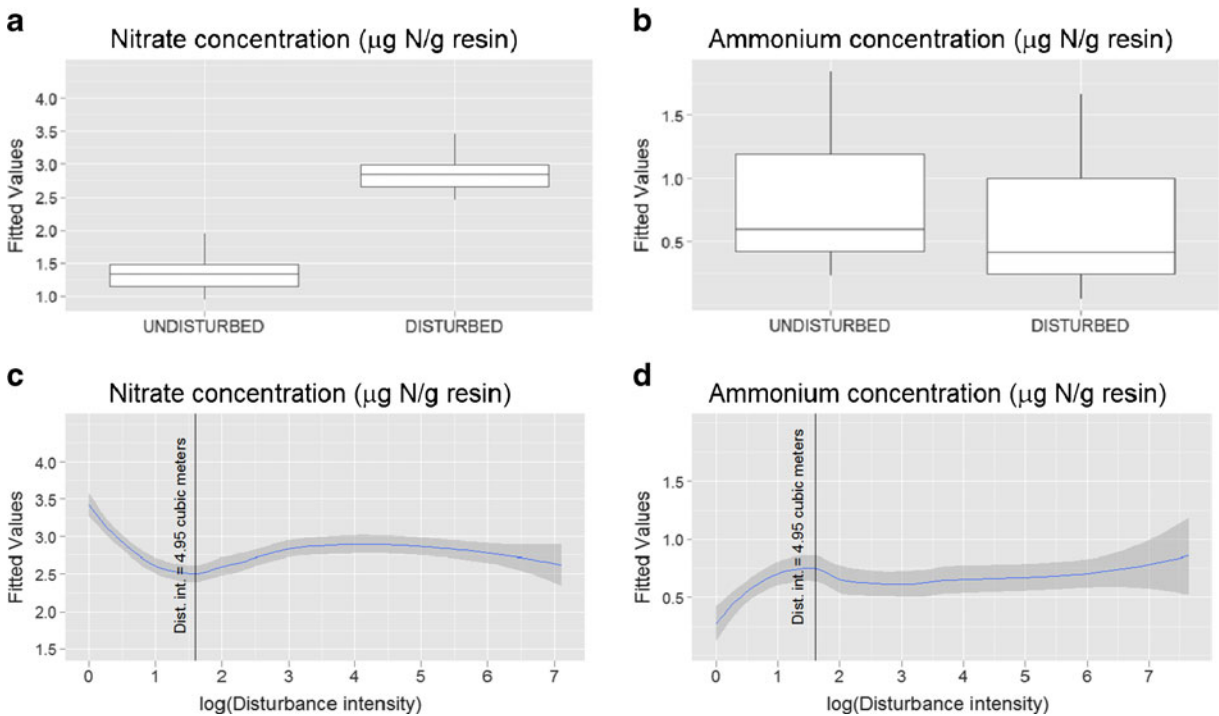


Fig. 3 Concentrations of soil NO₃⁻-N and NH₄⁺-N with respect to the occurrence of wild boar disturbances (**a-b**) and to the intensity of disturbances (**c-d**), in the alpine grasslands of the Spanish Pyrenees, Spain. Concentration values were previously fitted using Linear Mixed Models (see Table 2 for details). Disturbance intensity values were log-transformed for improving model fit. For detailed visualization of the relationship

between disturbance intensity and soil nitrate and ammonium concentrations, (**c**) and (**d**) plots respectively, an adjusted local smoothed regression line (blue) with its 95 % confident intervals (gray) was used. Black vertical lines indicate the level of disturbance intensity where the concentration trend of NO₃⁻-N and NH₄⁺-N started to change (at disturbance intensity of 4.95 m³ in both cases)

intensity of disturbances increased the availability of oxygen in the soil, it would facilitate the nitrification

of NH₄⁺-N and thereby, increase NO₃⁻-N concentrations (Brady and Well 2002), as follows:



Nevertheless, the impact of wild boar disturbances on the relative abundance of each N-form may depend on the intensity of disturbance and the environmental characteristics and dynamics of each community. For instance, in FP grasslands, only, disturbance intensity and NH₄⁺-N concentrations were positively correlated. FP is the most xeric of the five alpine communities studied (Benito 2006; Fillat et al. 2008), and the soils there had the highest organic matter content in disturbed areas and the highest concentrations of total C and N in undisturbed areas. The dominant species in FP community, *F.*

paniculata, has one of the highest rates of biomass productivity among the Pyrenean grasslands (Fillat et al. 2008). Intensive and frequent disturbances can cause a steady increase in the amount of oxygen in the soil, but in turn, reduce water soil content because of the loss of plant cover, which prevents the direct evaporation of soil water. An increase in the amount of oxygen in the soil can increase the ammonification of organic N to NH₄⁺-N (Brady and Well 2002). This would reduce the rate at which NO₃⁻-N is formed for FP community, probably because of the high intensity of soil disturbance and the

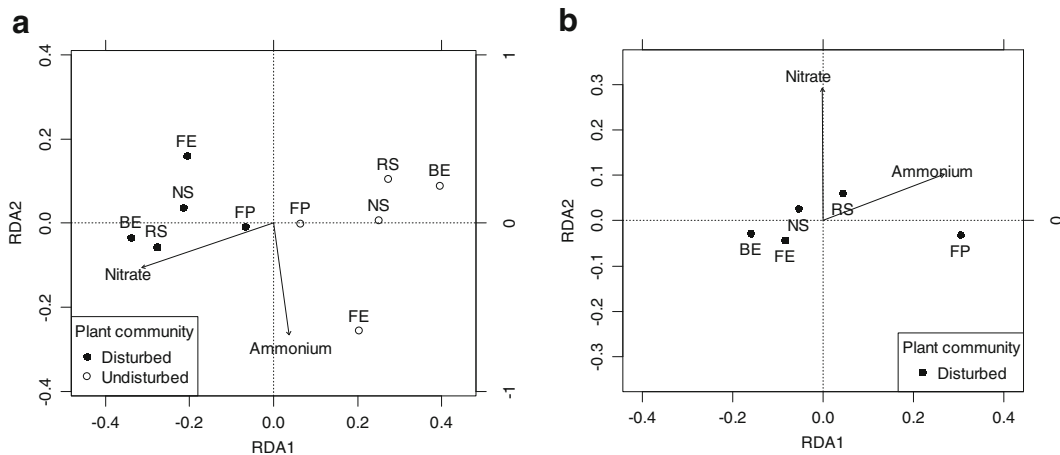


Fig. 4 Concentrations of the exchangeable soil NO_3^- -N and NH_4^+ -N in the occurrence of disturbances by wild boar (a) and with respect to disturbance intensity (b), among the five most disturbed plant communities in the alpine grasslands of the Central Pyrenees,

Spain, modelled with pRDA. Axes were significant ($p < 0.05$) based on a permutation test ($N = 1,000$ permutations), except for NO_3^- -N axis in (b). BE Bromion erecti; NS Nardion strictae; RP Rucicion pseudoalpini; FE Festucion eskiae; FP Festucion paniculatae

abovementioned xeric conditions of this community that would produce a reduction in the activity of nitrifying bacteria (Stark and Firestone 1995).

Our results pointed out a shift on soil conditions for plants, in particular an increase in soil compaction and availability of N forms. These effects, with an intrinsic reduction on plant competition, filter the species, which may reach these gaps, or survive rooting. In fact different plant compositions have been described for disturbed, when compared to closest undisturbed, vegetation patches (Barrios-Garcia and Ballari 2012). Species diversity within disturbed areas usually decreases (Barrios-Garcia and Ballari 2012; Kotanen 1994), but at the local scale; if disturbance recurrence holds populations of fugitive or disturbance-tolerant species, the overall species richness may increase (Welandar 1995). However, it is unclear if diversity at regional scales and among affected communities (beta diversity) may benefit from wild boar rooting. In any case, in the Pyrenean alpine grasslands, two plant functional groups have been pointed out to increase their abundance due to wild boar rooting: annuals and geophytes (Bueno 2011; Palacio et al. *in rev*). On one hand, annuals are enhanced by rooting through stimulation of their seed banks, although they are very scarce and highly dependent on livestock grazing activities (Bueno et al. 2011). On the contrary, geophyte communities seems to take advantage of the increase in the availability of N form after rooting, increasing their fit and, likely, their dynamics (Palacio et al. *in rev*).

Conclusion

In summary, in the Pyrenean grasslands, wild boar rooting deeply affects soil properties because it alters soil structure, compacts the soil and modifies its composition. The effect is different and more substantial as the intensity of disturbance increases; i.e., mineralization rates are higher until the saturation point is reached, which leads to deeper changes in soil properties. Nutrients such as NO_3^- -N or available P increase because rooting removes plants and might alter decomposer communities, which are no longer available to take up these nutrients and immobilize them. In addition, those nutrients may remain available to plants unless rain and snowmelt leach them, which suggest that differences in the availability of nutrients might contribute to an increase in the diversity of plant functional groups whenever rooting is not excessively intense.

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