Livestock grazing activities and wild boar rooting affect alpine earthworm communities in the Central Pyrenees (Spain)

Bueno, C.G.[a,b,*] & Jiménez, J.J.[b]

[a] *Department of Biological Sciences, University of Alberta, CW 405, Biological Sciences Bldg., Edmonton, T6G 2E9, Alberta, Canada*

[b] *Pyrenean Institute of Ecology (IPE-CSIC), Avda. Llano de la Victoria 12, Jaca 22700, Huesca, Spain*

* Corresponding author (Address during the study):

Pyrenean Institute of Ecology (IPE-CSIC),
Avda. Llano de la Victoria 12,
Jaca 22700, Huesca,
Spain.
Email: cgbuenog@gmail.com

Present address:

Department of Biological Sciences,
University of Alberta,
CW 405,
Biological Sciences Bldg.,
Edmonton, T6G 2E9,
Alberta,
Canada
Email: cgbuenog@gmail.com

Abstract

In alpine areas, shifts in traditional grazing activities are globally affecting ecosystem properties and rural livelihoods. The ongoing decrease in extensive husbandry, with a decline in sheep numbers and a relative increase in cattle stocking rates, has resulted in the abandonment of large alpine grazing areas. This pastoral change has been recently associated with increased disturbances of wild boar (Sus scrofa), mainly within cattle–stocked ranges. In turn, cattle areas favour earthworm communities, a preferred trophic resource for wild boars in mountain environments. However, it is unknown whether wild boar disturbances, together with grazing activities, can affect earthworm communities. Our aim is to analyze the abundance, richness and ecological categories of earthworms and soil parameters (soil C and N concentrations, moisture, and C:N ratio) in relation to the occurrence of wild boar disturbances and grazing activities at different stocking pressures. We sampled two different grazing scenarios differing in the distribution of cattle along a grazing gradient, which was represented by three levels of stocking pressure (high, intermediate and low). Our results showed a complex effect of grazing activities and disturbances on the abundance and richness of earthworms, along with variations in C:N ratio and soil moisture, especially with increasing cattle presence. At high–stocking pressures differences in earthworm abundance and richness between disturbed and undisturbed areas were limited, whereas at intermediate–stocking pressures earthworms were favored by wild boar disturbances. Ecological categories of earthworms responded differently; endogeic species were the most affected by grazing pressures and wild boar rooting, with highest occurrence at high–stocking pressures and within boar disturbed areas. In sum, pastoral use and soil disturbances affected earthworm community structure and composition in complex ways. These results indicate an interaction of processes that is relevant to understand current changes in alpine ecosystems.

Key-words: alpine grasslands, soil fauna, *Sus scrofa*, soil disturbance, cattle grazing, earthworm diversity.

1. Introduction

Alpine ecosystems are of high natural value and one of the areas with the highest conservation priority in Europe (92/43/EEC, of 21 May 1992). These habitats also have a high socio-economic value; traditional use of these areas for extensive husbandry during the last centuries has supported local economies, preserving cultural values and generating high quality products (Luick, 1998). In the last 100 years, land use changes have had a significant impact on the structure and use of alpine ecosystems. The abandonment of extensive husbandry, with a sharp decline of sheep herding and a relative increase of less-demanding cattle herds (Gartzia et al., In rev.; Lasanta-Martínez et al., 2005), together with extensive reforestation policies since the 1950s, have led to a gradual increase in forested areas (Boix-Fayos et al., 2007; Mather, 2001). The increase of forest cover has resulted in the expansion of the potential habitat for the wild boar (Sus scrofa L.). This circumstance, along with the gradual decline of the boar's large predators (bears and wolves), have led to a substantial increase of European populations of wild boar in the last decades (Apollonio et al., 2010; Barrios-García and Ballari, 2012).

Wild boars' omnivorous diet and their enormous adaptability are key factors to their population success (Barrios-García and Ballari, 2012). As they search for belowground feeding resources, such as plant rhizomes, bulbs and earthworms, wild boars may turn over hundred of hectares locally, generating extensive disturbances to crops, forests and natural grasslands worldwide (Apollonio et al., 2010; Barrios-García and Ballari, 2012; Bueno et al., 2009; Massei and Genov, 2004). These disturbances are of particular concern when they affect human activities. For example, in the Central Pyrenees (Spain), wild boar disturbances can affect up to 20% of alpine and subalpine grasslands used by domestic cattle, and are perceived by ranchers as a threat to their livelihoods (Bueno, 2011; Bueno et al., 2010).

One of the main attractants for wild boar rooting activity, especially in alpine environments, is the abundance of a valuable food item: earthworms (Baubet et al., 2004; Baubet et al., 2003; Edwards, 1994). For example in the French Alps, the frequency of earthworm occurrence in wild boar diet is around 92 % (Baubet et al., 2003). Earthworm abundance is positively related to the presence of livestock, because of the increased fertilization through dung deposition (Mijangos et al., 2006; Paoletti, 1999; Smith et al., 2008). However, at high stocking pressures, cattle trampling may negatively affect earthworm abundance (Cluzeau et al., 1992; Ligthart, 1997); therefore, earthworm abundance can be expected to be highest at intermediate stocking pressures. Similarly, the occurrence of wild boar disturbances is highest at intermediate stocking pressures (Bueno et al., 2010), which suggests that the occurrence of these disturbances might be linked to the abundance of earthworms. In any case, our knowledge of earthworm communities in alpine and subalpine environments is still limited.

In turn, wild boar disturbances modify physical and chemical properties of soils (Bueno et al., 2013; Lacki and Lancia, 1983) and, together with grazing management practices, could affect earthworm communities, altering habitat suitability for earthworms. Recent changes in alpine habitats (i.e. an abandonment of extensive grazing areas together with an increment of wild boar disturbances) could lead to changes in the functional composition of earthworms, because different species and ecological categories (sensu Bouché 1977) are known to respond differently to disturbances (Curry, 1998; Lavelle, 1988). Epigeic species, small superficial earthworms with exclusive litter diet, are very sensitive to the treading under high stocking rates. In contrast, the same scenario could be favorable to anecic species, which live in deep burrows and are able to escape easily by retreating into their burrows (Schon et al., 2011). However, wild boar disturbances may instead disrupt these burrows, having a negative impact on anecic species. On the other end, endogeic species, which live deeper in the soil and feed mainly on mineral soil particules, might be the most favoured by wild boar disturbances. Boars' disturbances allow more nutrients to reach deeper in the soil, where endogeic species are safer from wild boar foraging. In fact, endogeic earthworms are the only ecological category not found in boar's diet so far (Schley and Roper, 2003). In any case, the effects of wild boar disturbances and grazing management on earthworm communities are still unknown in alpine environments. Studies addressing the separate and combined effects of these concurrent changes are critical for understanding grazing abandonment processes in mountain ecosystems.

This paper aims to analyze the effect of livestock grazing activities and wild boar disturbances in the abundance, richness, ecological categories of earthworms, and soil properties, in two representative scenarios of extensive husbandry in the Pyrenees. In addition, this paper will contribute to the knowledge of earthworm community composition in relation to human management of alpine grasslands of the Central Pyrenees. This will help to cover the important knowledge gaps on the biogeographic distribution of these organisms (Decaëns, 2010). In turn, the ecological role of earthworms might be relevant in key soil processes for the functioning of the entire system (Edwards, 1994; Knight et al., 1992; Lawton, 1994; Paoletti, 1999). Earthworms are known to affect soil properties, through increasing soil porosity, aeration and water dynamics, and mineralization and humification of organic matter, especially increasing nitrogen availability for plants (Lavelle, 1988; Parmelee et al., 1998). Based on previous knowledge of soil disturbance and cattle grazing, we would expect two contrasting results. First, wild boar disturbances may negatively affect the abundance and richness of earthworms. Boars' disturbances increase soil compaction, through the removal of plant roots and the collapse of the soil gaps occupied by those roots, what is exacerbated by livestock treading (Bueno et al., 2013). This would degrade earthworm habitats and homogenize the diversity of niches, already limited in harsh environments (Decaëns, 2010). Another negative effect would also be expected, because wild boars feed on earthworms (Baubet et al., 2004). Secondly, if fertilization by livestock has a stronger or combined effect with wild boar disturbances on earthworm habitats, new niches with high nutrient availability for earthworms may be created. In this case, an enhancement of their abundance and richness could be expected.

2. Materials and methods

2.1. Study area and wild boar rooting

The study was conducted in two grazing areas of subalpine grasslands in the Spanish Central Pyrenees, Góriz, in Ordesa and Monte Perdido National Park (OMPNP; 42º36´N, 0º01´E), and Aisa, located on top of Aisa Valley (42º44´N, 0º35´W). The climate is alpine, with annual average temperature and precipitation of 5 ºC and 1720 mm respectively (García-González et al., 2007). Lithology comprised mainly calcareous substrates such as limestone, sandstone and flysch (an overlaying complex of marlstone and sandstones) (Badía et al., 2002). Grazing activities in the Pyrenees have shifted from sheep to cattle ranching and extensive husbandry has declined in the last decades (Gartzia et al., In prep.; Lasanta-Martínez et al., 2005).

Wild boar rooting is a large soil disturbance with highly variable extent but a relatively homogeneous depth (10 cm depth, on average in these grasslands) (Bueno et al., 2013; Groot Bruinderink and Hazebroek, 1996; Kotanen, 1994; Tierney and Cushman, 2006). This disturbance is created when wild boars search for a variety of belowground feeding resources. One particularly appreciated food item, especially in mountain areas, are earthworms (Baubet et al., 2004). Wild boar rooting occurs especially in dense alpine grasslands and is directly related to cattle grazing activities (Bueno et al., 2009); rooting can affect more than 20% of cattle stocking areas (Bueno et al., 2010), significantly reducing the pastoral values of these grasslands (Bueno et al., 2011).

2.2. Stocking pressures and grazing gradient scenarios

In this study, we analyzed a grazing gradient, from high– to low–stocking pressures, commonly described in different alpine and subalpine areas of Europe (Badía et al., 2008; Common et al., 1998). High–stocking pressure sites were represented by areas within livestock resting places and around shepherd´s huts. These areas are normally dominated by tall, nitrophilous plants of the phytosociological alliance Rumicion pseudoapini (Table 1). Intermediate–stocking pressure sites were chosen in adjacent areas, with some evidence of livestock use (e.g., presence of cattle dung). These areas are commonly dominated by a highly diverse suite of species within the Alliance Bromion erecti (Table 1). Finally, the areas with low–stocking pressure were located where livestock, particularly cattle, does not graze often. These areas are dominated by Nardus stricta, a species not very palatable for livestock (Chadwick, 1960) but edible for earthworms (Knapp et al., 2012), within the Alliance Nardion strictae (Table 1). High– and intermediate–stocking pressure areas are spatially distributed at the valley bottoms, where livestock moves without difficulties and plant productivity is higher. Low–stocking pressure areas were located at slightly higher elevation, what usually entails steeper slopes and lower plant productivity (Garcia–Gonzalez et al., 1990). Two different grazing scenarios, but with similar stocking pressures, 0.5 Standard Livestock Units (SLU) ha^{-1} and 0.4 SLU ha^{-1} for Aisa and Goriz, respectively (Bueno et al., 2009) were chosen. The first one has a sharp grazing gradients (Aisa), where steeper slopes restrict cattle movements to the high–and intermediate stocking pressure areas (Garcia–Gonzalez et al., 1990). The second scenario (Goriz) is characterized by a smooth grazing gradient, where gentler slopes allow cattle to move with less restrictions (Aldezabal et al., 1999).

2.3. Sampling design, earthworm collection and soil analysis

We collected soil and earthworm samples following a previous detailed cartography of vegetation, with indication of the livestock resting place, shepherd´s huts, and wild boar rooting in both grazing scenarios (Bueno, 2011; Bueno et al., 2009). 30 paired samples were collected following a stratified design at each level of stocking pressure and in five different wild boar disturbances per scenario (total number of samples = 60). Each sampling unit was composed by two samples, one within and one outside wild boar disturbances. Samples within each level of stocking pressure were at least 50 m apart. Sampling was carried out from late spring till summer 2011, on the second day after a heavy rainfall to increase the chances for the earthworms to be within the soil depth range covered in this study (0–30 cm depth).

We applied a combination of formalin in one square meter (Bouché and Gardner, 1984) and extracted a soil monolith of 40x40x30 cm in the center of the each sampling point. Soil monoliths were carefully hand–sorted and inspected for earthworms. Soil samples were collected from the pit to homogeneously represent the whole horizon explored (0–30 cm). Earthworms were taken to the laboratory, where they were washed and preserved in 10% formaldehyde. Species were identified following available keys (Alvarez, 1971; Bouché, 1972), and the main ecological categories identified, i.e. anecic, epigeic, and endogeic (Bouché 1972).

Soil samples were air–dried and 10 g of soil were ground in a mortar and pestle for C and N determinations using a Variomax CN Analyzer (Elementar Analysesnsysteme, Hanau, Germany). A small amount (5 g) was used to estimate moisture content by weighing the sample after oven–drying at 60ºC for 48 h; soil moisture is expressed relative to the water percentage of the dried soil (v/v).

2.3. Data analysis

To determine the effect of grazing activities and wild boar rooting on soil properties and on the abundance and richness of earthworm communities, a generalized linear model (GLM) approach was used. Response variables of these models were, for soil properties: concentration of N, C, C:N ratio and soil moisture; for earthworm community characterization, earthworm abundance and richness. In all cases, predictor variables were grazing scenario (sharp or smooth grazing gradients; see above), stocking pressure (high, intermediate and low) and wild boar disturbance. To account for the effect of wild boar disturbances, a binary variable representing the presence ("1") or absence ("0") of disturbances was included.

In all models, the three way interaction (grazing scenario, stocking pressure and wild boar disturbance) was included in the full model. This was carefully considered a priori, because the responses of soil properties or earthworm communities may vary depending on (and not independently of) the sharpness of the grazing gradient (grazing scenario), the stocking pressure or the presence/absence of wild boar disturbances. To obtain the final models, we followed a backward stepwise procedure, keeping only variables and interactions that significantly improved model fit (Zuur et al., 2009). Tables of deviance analysis, comparing the reduction in model deviance to the model residuals with and without each factor are reported here, as recommended when analyzing the effects of factors with more than two levels (Zuur et al., 2009).

All models **met residual's normality and homocedasticity** and all, but earthworm abundance, were fitted using a Gaussian distribution with a identity link function. Earthworm richness was previously log-transformed. For the abundance model, a Poisson distribution was used with a log link function. No significant spatial autocorrelation was found in the residuals of the final models, after visual inspection of correlograms (Dormann, 2007; Zuur et al., 2009). Multiple post-hoc comparisons using Tukey estimations were used to determine which groups were significantly different.

To analyze the effect of wild boar disturbances and grazing on the three ecological categories of earthworms, i.e. anecic, epigeic and endogeic, similar analyses and validation procedures with GLMs were carried out. The presence/absence of each ecological category was analyzed separately, and included in the model as a binary response variable, using a binomial distribution with a logit link function. Therefore the results for ecological categories of earthworms are to be interpreted as the effect on the presence/absence of each category instead of the effect on their abundance, as was the case for the previous analyses. The R statistical computing package (version 2.13) was used for all statistical analyses (R Development Core Team, 2011).

3. Results

149 earthworms were collected in the study, belonging to 6 different genera: *Aporrectodea*, *Allolobophora*, *Eisenia*, *Lumbricus*, *Octolasion* and *Prosellodrillus* (see Appendix 1).

3.1. Soil Properties

Soil concentrations of C and N (both highly correlated, r=0.97) were significantly affected by the two-way interactions between the stocking pressure with wild boar disturbance, and with the grazing scenario (Table 2). High-stocking pressures were related to higher concentrations of C and N within sites undisturbed by boars, but showed the opposite trend in disturbed sites (Figure 1a & 1c). Generally, an increase in N and C concentration along the grazing gradient was observed for both grazing scenarios, but in the smooth gradient this trend was distorted by highest concentrations of C and N at low-stocking pressures, probably responding to the higher presence of cattle (Figure 1b & 1d). Regarding the C:N ratio, the interaction between the stocking pressure and the grazing scenarios had a significant effect (Table 2). The smooth gradient scenario, with more presence of cattle along the grazing gradient, showed an homogeneous C:N ratio along the gradient. C:N ratios at low stocking pressures were higher in this case than in the sharp grazing scenario, where, in turn, C:N ratios were highest at high-stocking pressures (Figure 1e). Soil moisture was significantly higher in the smooth gradient compared to the sharp gradient scenario (Table 1; Figure 1f).

3.2. Earthworm abundance and diversity

The abundance of earthworms was significantly affected by the interaction of the three factors studied: the occurrence of wild boar disturbances, the stocking pressures and the grazing scenario (Table 3). The abundance of earthworms was higher at high-stocking pressures relative to low-stocking pressures, both in undisturbed and disturbed areas by wild boar (Fig. 2a & 2b). Following this trend, no differences in earthworm abundance were found in the sharp gradient scenario between disturbed and undisturbed sites by wild boar (Fig.2a). In the smooth gradient scenario abundance tended to be lower within disturbed sites (Fig.2b); the greatest earthworm abundance in this scenario was found in undisturbed sites at intermediate stocking pressure (Fig. 2b).

Earthworm species richness showed an interaction between the grazing scenario and the occurrence of wild boar rooting, along with a significant, independent effect of the stocking pressure (Table 3). Richness was higher at high–than at low stocking pressures (Fig. 2c). In the sharp grazing scenario, areas disturbed by wild boar showed higher earthworm richness than in undisturbed ones. No differences were found in the smooth grazing scenario (Fig. 2d).

3.2. Earthworm ecological categories

Different trends were found for each ecological category of earthworm. For anecic earthworms (Lumbricus terrestris group), only the interaction of the grazing scenario with the stocking pressure was significant (Table 4). In particular, the presence of anecic earthworms in the sharp grazing gradient was linked to high–stocking pressures (Fig 3a). On the contrary, in the smooth grazing gradient scenario, the presence of anecic communities did not differ along the stocking pressures (Fig 3a). The presence of endogeic communities (Allolobophora, Aporrectodea, Octolasion, Prosellodrilus group) was affected by the stocking pressures and the occurrence of disturbances (Table 4). In particular, higher occurrence of endogeic communities was found within disturbances and also following the gradient of grazing intensity, with the highest occurrence at high–stocking pressures (Fig. 3b). For epigeic communities (Eisenia group) none of the factors or their interactions were significant.

4. Discussion

Our results revealed a significant effect of wild boar rooting disturbances in the structure of earthworm communities depending on pastoral management. Overall, earthworm abundance and diversity were related with the organic matter input from livestock. We found higher abundance and richness of earthworms in areas with high–

stocking pressures. This is in agreement with other studies that reported greater earthworm numbers in fertilized crops (Curry, 1998) and grazed pastures (Schon et al., 2008).

We conducted our study at two grazing scenarios of traditional livestock management, with differences in cattle activity along the respective grazing gradients. Earthworm communities of each scenario responded differently at low–and intermediate stocking pressures. In these areas, earthworm communities were affected by wild boar disturbance almost in opposite directions. In the scenario with smooth grazing gradients, with more homogeneous presence of cattle along the grazing gradient, wild boar disturbance reduced the abundance and richness of earthworms, whereas in the scenario with sharp grazing gradients, wild boar disturbance increased earthworm richness and abundance. This suggests that increased cattle treading may cause habitat degradation for earthworms, overriding any beneficial effects of disturbances, such as increasing niche availability for earthworms. Moreover, areas intensively disturbed by wild boars may be more vulnerable to soil compaction and degradation (Brady and Well, 2002; Bueno et al., 2013), further aggravating habitat degradation.

The alteration of earthworm habitat is known to be directly related to important soil changes (Curry, 1998; Edwards, 1994). For instance, the observed increase in soil moisture and C:N ratio at the sharp gradient could also explain the increased diversity of earthworms, as moisture and main nutrients are important limiting factors for earthworm habitat requirements (Curry, 1998). At the smooth gradient, on the contrary, a more homogeneous distribution of the nutrients, represented by similar C:N ratios along the gradient, would have led to more homogeneous conditions for earthworms. The fertility gradient described at the three levels of stocking pressure (Fillat et al., 2008) is a key factor for earthworm abundance and diversity. We found the highest abundance and richness of earthworms in the most fertile places (high–stocking pressure areas). This suggests that the negative effects of over–trampling, reducing abundance and diversity of earthworms, are not happening at our study sites at high–stocking pressures. However, other factors known to decrease earthworm abundance (Curry, 1998; Lavelle et al., 1998), such as reduced organic matter content and lower pH, were found (Bueno et al., 2013; Fillat et al., 2008). On the other hand, it is known that soil disturbances by wild boars facilitate the establishment of more nitrophilous, ruderal plants transported by cattle, leading to changes in soil nutrient concentrations (Bueno, 2011; Fillat et al., 2008). Thus, one might expect wild boar disturbance to increase earthworm diversity and abundance by habitat amelioration (Curry, 1998), by reducing the environmental constraints of earthworms, but this hypothesis needs to be further evaluated.

With regard to ecological categories, we found that endogeic earthworms were more associated with soil disturbance by wild boars, while anecic species were more affected by the grazing management (both stocking pressure and the grazing scenarios). Both groups were highly related to high–stocking pressures, especially in the sharp grazing gradient scenario. Specifically, the presence of endogeic earthworms was higher within disturbances, which may be due to the mixing of topsoil with subsoil horizons (Singer et al., 1984). Higher organic matter contents are typically found in the topsoil, although roots can provide organic matter more available in the subsoil (Brady and Well, 2002). This, together with the loosening of the soil followed by its compaction (Bueno et al., 2013), could attract earthworms to areas recently disturbed by wild boar. Similarly, higher abundance of endogeic species has been found in temperate arable lands with tillage treatments (Curry, 1998) and in pastures with higher soil bulk densities (Schon et al., 2011). Regarding wild boar foraging preference, it seems more likely that endogeic species are less predated by wild boar, taking into account the soil depth where the different ecological categories are normally found. Epigeic and anecic categories, being closer to the surface, are probably more exposed and actively searched for by the wild boar.

The abundance of earthworm communities in alpine areas has been quantified by Daniel et al. (1996), Grossi and Brun (1997), and Seeber et al. (2009; 2006; 2005; 2008). However, this is the first time when a study combines the joint effect of traditional livestock activity changes and disturbance by wild boar rooting in mountain areas. The current trend of pastoral abandonment in alpine grasslands of Central Pyrenees is also leading to encroachment of woody species. Extensive areas previously grazed only by sheep are being covered by subalpine shrubs, like Echinospartum horridum (Vahl) Rothm (Komac, 2010). However, this trend may not have a large impact on earthworm communities. For example, in alpine pastures of Switzerland, the population decline of the ubiquitous earthworm Lumbricus rubellus Hoffmeister after pasture abandonment was not related to changes from high quality grasses to poor quality shrub litter (Rief et al., 2012). At the same time, pastures located in valley bottoms are generally overstocked by cattle (Fillat et al., 2008). To which extent this situation can lead to an increase in earthworm abundance that can maintain (or even increase) the attractiveness of the area to wild boars, needs to be investigated. Indeed, wild boar populations and their disturbances are growing in the Central Pyrenees (Bueno et al., 2009; Bueno et al., 2010), with unknown consequences to the encroachment process.

5. Conclusions

Pastoral use and wild boar disturbances have a decisive influence on the composition of earthworm communities in Pyrenean pastures located above the tree-line. Grazing activities, especially in the areas more accessible to cattle, may favour earthworm abundance, except in areas with high-stocking pressures. On the other hand, the effect of disturbances on earthworm communities depends on the stocking pressure and the relative abundance of cattle. When the stocking pressure was not excessively high, the diversity of these communities increased. The presence of the three ecological categories of earthworms was influenced mainly by the stocking pressure and, in some cases, by the presence of disturbances. All these results indicate some complexity in the response of earthworm communities to pastoral management and soil disturbances in alpine and subalpine ecosystems. This should stimulate further research to determine the causes of these responses and accurately predict the trend of earthworm communities and ecosystem characteristics dependent on them.

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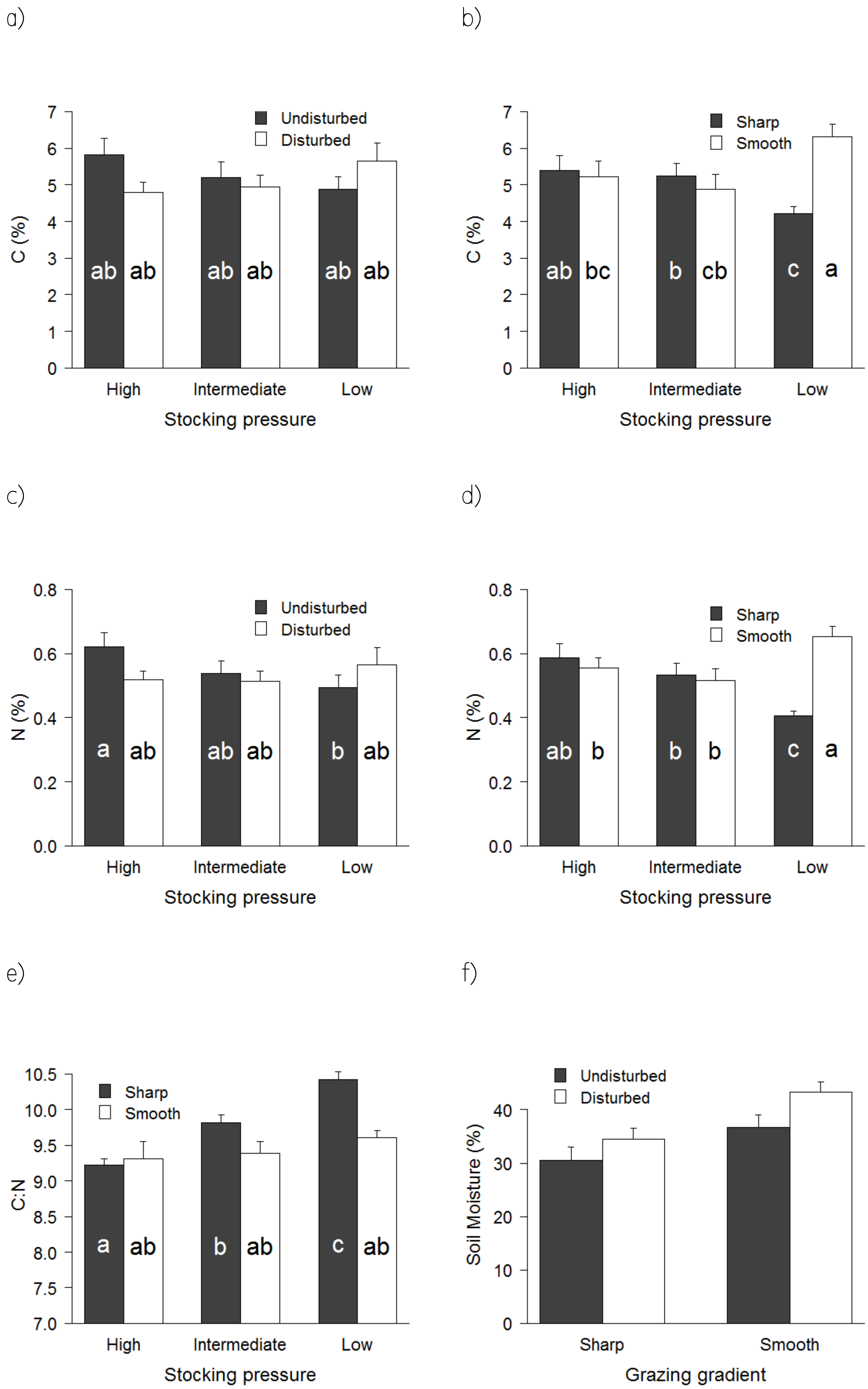
Figure captions

Figure 1. Soil properties (mean ±standard error) in relation with the significant factors and interactions following GLM analyses (Table 2): Carbon (a) and nitrogen (c) concentrations at different stocking pressures in the presence and absence of wild boar disturbances. Carbon (b) and nitrogen (d) concentrations at different stocking pressures, in the two grazing scenarios (sharp and smooth gradients). C:N ratio (e) at different stocking pressures at the two grazing scenarios. Soil moisture (f) in the two grazing scenarios, in the presence and absence of wild boar disturbances. Lowercase letters indicate significant differences among comparative measurements of abundance, based on a Tukey post–hoc multiple test at alpha < 0.05.

Figure 2. Abundance and richness of earthworms (mean ±standard error) in relation with the significant factors and interactions following GLM analyses (Table 3). Effects of stocking pressure and the occurrence of wild boar disturbance for the sharp (a) and smooth (b) gradient scenario. c) Stocking pressure and the occurrence of wild boar disturbances. d) grazing scenario and the occurrence of wild boar disturbances. Lowercase letters indicate significant differences among comparative measurements of abundance, based on based on a Tukey post–hoc multiple test at alpha < 0.05.

Figure 3. Occurrence of the ecological categories of earthworms (endogeic and anecic) in relation with significant factors and interactions following GLM analyses (Table 4): a) effect of stocking pressure and grazing scenarios on anecic earthworms; b) effect of stocking pressure and occurrence of wild boar disturbances on endogeic earthworms.

Lowercase letters indicate significant differences among comparative measurements of abundance, based on a Tukey post–hoc multiple test at alpha < 0.05.



a)
C (%)
0
1
2
3
4
5
6
7
Undisturbed
Disturbed
ab ab ab ab ab ab
High
Intermediate
Low
Stocking pressure
b)
C (%)
Sharp
Smooth
ab bc b cb c a
High
Intermediate
Low
Stocking pressure
c)
N (%)
0.0
0.2
0.4
0.6
0.8
Undisturbed
Disturbed
a ab ab ab b ab
High
Intermediate
Low
Stocking pressure
d)
N (%)
Sharp
Smooth
ab b b b c a
High
Intermediate
Low
Stocking pressure
e)
C:N
7.0
7.5
8.0
8.5
9.0
9.5
10.0
10.5
Sharp
Smooth
a ab b ab c ab
High
Intermediate
Low
Stocking pressure
f)
Soil Moisture (%)
0
10
20
30
40
Undisturbed
Disturbed
Sharp
Smooth
Grazing gradient

Figure 1.

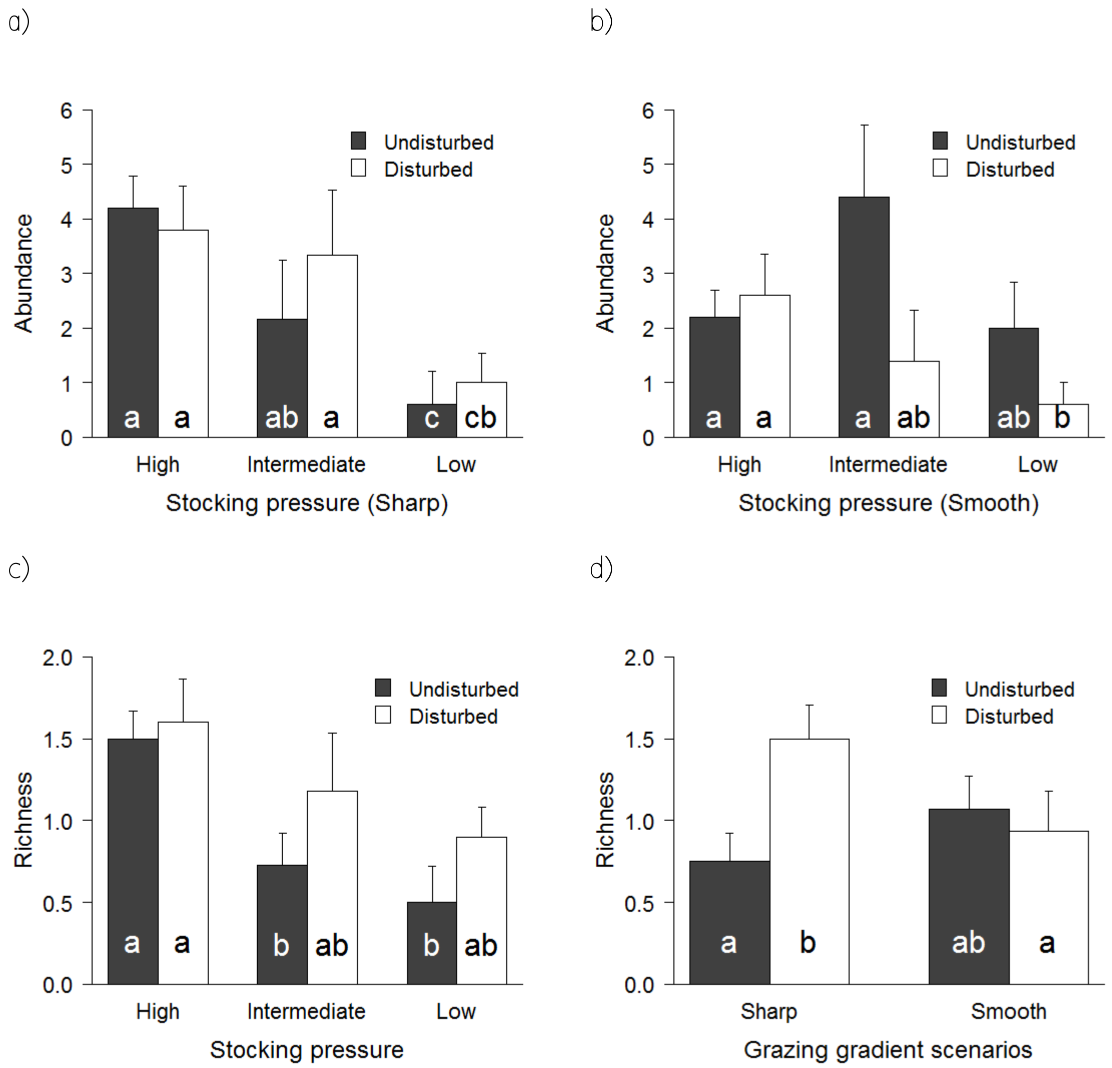

a)
b)
c)
d)
Abundance
Richness
Undisturbed
Disturbed
High
Intermediate
Low
Sharp
Smooth
Stocking pressure (Sharp)
Stocking pressure (Smooth)
Stocking pressure
Grazing gradient scenarios

Figure 2.

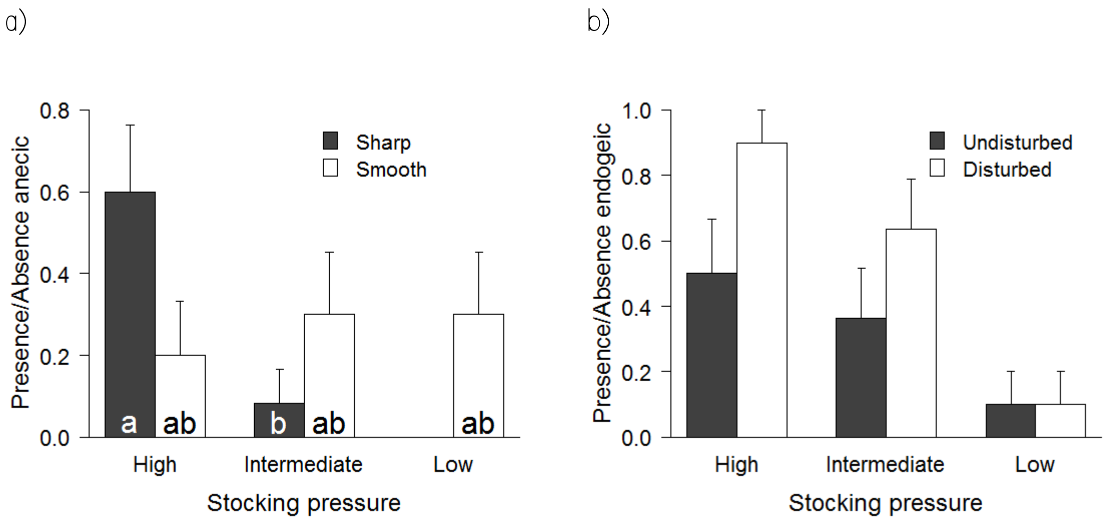

a)
Presence/Absence anecic
0.8
0.6
0.4
0.2
0.0
Sharp
Smooth
a
ab
b
ab
ab
High
Intermediate
Low
Stocking pressure
b)
Presence/Absence endogeic
1.0
0.8
0.6
0.4
0.2
0.0
Undisturbed
Disturbed
High
Intermediate
Low
Stocking pressure

Figure 3.

Table captions

Table 1. Characteristics of the level of stocking pressure along the grazing gradient in the two grazing scenarios studied in the Spanish Pyrenees. Plant richness was 'low' (<20 plant species), 'medium' (15–25 species) or 'high' (>30 species). Mean values (elevation and slope) are given ±1SD except those for which other measure is indicated. Data based on previous studies (Bueno, 2011; Fillat et al., 2008). Botanical nomenclature according to Gómez–García et al. (2005).

Table 2.- Significant factors and interactions affecting the soil properties (C, N, C:N ratio and soil moisture) of subalpine grasslands of the Spanish Central Pyrenees, resulting from GLM analyses. All values are F–values from the analysis of deviance tables for the GLM with Gaussian distributions. Stocking pressures (SP), wild boar disturbance (D), grazing scenarios (GS).

Table 3.- Significant factors and interactions affecting the abundance and richness of earthworms in subalpine grasslands of the Spanish Central Pyrenees, resulting from GLM analyses. Abundance values are Chisq–values, where richness vales are F–values, from the analysis of deviance tables for the GLM with Poisson and Gaussian distributions, respectively . Stocking pressures (SP), wild boar disturbance (D), grazing scenarios (GS).

Table 4.–Significant factors and interactions affecting the ecological categories of earthworms (anecic, epigeic and endogeic) in subalpine grasslands of the Spanish Central Pyrenees, resulting from GLM analyses. All values are Chisq–values from the analysis of deviance table for the GLM with binomial distribution. Stocking pressures (SP), wild boar disturbance (D), Grazing scenarios (GS).

Table 1

Characteristics	Sharp grazing gradient (Aisa)			Smooth grazing gradient (Goriz)		
Stocking pressure	High	Intermediate	Low	High	Intermediate	Low
Elevation	1760.7±136.2	1696.2±102.8	1968.7±169.6	1896±19.8	1956.8±83.3	1921.9±35.3
Slope	18.9±12.1	23.1±8.8	24.4±9.9	6.3±6.0	11.6±6.6	13.0±6.9
Dominant aspect	Southwest	Southwest	Southeast	Southeast	Northeast	Northeast
Total extent (ha)	15.7	129.2	158.5	3.3	434.8	70.2
% disturbed by wild boar	18.9 %	13.1 %	3.8 %	33.3 %	5.1 %	0.5 %
Plant richness	Medium	High	Low	Medium	High	Low
Plant community	Rumicion	Bromion	Nardion	Rumicion	Bromion	Nardion
Dominant plant species	Chenopodium bonus–henricus, Trifolium repens, Poa supina	Festuca rubra, Agrostis capillaris, Trifolium pratense, Lotus corniculatus	Nardus stricta	Chenopodium bonus–henricus, Trifolium repens, Poa supina	Festuca rubra, Agrostis capillaris, Trifolium pratense, Lotus corniculatus	Nardus stricta

Table 2.

Soil	SP	Dist	GS	SP x Dist	SP x GS
C	0.646	0.404	3.043+	3.231 *	7.519 **
N	1.126	0.914	5.734 *	3.381 *	11.344 ***
C:N	12.915 ***	n.s.	10.480 **	n.s.	4.561 *
Moisture	n.s.	5.394 *	11.022 ***	n.s.	n.s.

p values: + < 0.1; * < 0.05 ; ** < 0.01 ; *** < 0.001 . ´n.s.´ non-significant factors.

Table 3.

Earthworms	SP	Dist	GS	SP x Dist	SP x GS	Dist x GS	SP x Dist x GS
Abundance	25.598 ***	1.151	0.599	1.086	3.977	5.712 *	7.155 *
Richness	7.124 **	2.240	0.748	n.s.	n.s.	5.934 *	n.s.

p values: + < 0.1; * < 0.05 ; ** < 0.01 ; *** < 0.001 . ´n.s.´ non-significant factors.

Table 4.

Categories	SP	Dist	GS	SP x GS
Anecic	3.9	n.s.	0.194	9.729 ***
Endogeic	16.979 ***	4.364 *	n.s.	n.s.

p values: + < 0.1; * < 0.05 ; ** < 0.01 ; *** < 0.001 . ´n.s.´ non-significant factors.