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Plant-topsoil relationships underlying subalpine grassland patchiness

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Abstract

Approximately half of the area in the Spanish Central Pyrenees is dedicated to pastures. A decrease in stocking rate coupled with changes in livestock management in recent decades have favoured the expansion of *Nardus* grasslands, which are considered undesirable for grazing use and for diversity conservation. The objective of this study was to analyse how topsoil properties are related to grassland plant composition occurring in erosion-disturbed (chalk grasslands) and undisturbed (*Nardus* mat-grasslands) soils in a subalpine area of the Spanish Central Pyrenees. We selected six paired sampling points for a side-by-side comparison of both communities. At each point, we 1) estimated the plant cover of each species through inventories and 2) analysed a set of physical-chemical topsoil properties (0-5 and 5-10 cm depth). Data were analysed through multivariate analysis. We found typical species of *Nardus* mat-grasslands in the undisturbed sites growing on non-eroded and well-structured soils that were low in calcium and acidic, with high contents of organic matter. In turn, we found earlier-successional grassland communities growing on slopes recently affected by soil erosion processes. The species composition was mainly species from stony slope grasslands and, to a lesser extent, from the long-term snow-covered environments of the high mountains. These soils were shallower and stonier and had a less-stable structure, higher pH, and lower organic matter and calcium content than undisturbed soils. Our results suggest that the differences between both communities emerge and are maintained by soil-plant feedback mechanisms mediated in *Nardus* mat-grasslands through soil stabilization and acidification and in chalk grasslands through soil erosion and basification. These findings suggest that the subalpine grassland mosaic results from a model of non-equilibrium plant coexistence due to soil disturbance and inexorable succession. Management should be focused on maintaining a disturbance regime, through grazing, sufficient to prevent the spreading of *Nardus* mat-grasslands.

1. Introduction

Mountain grasslands are the basis for the rural economy in much of the world, and livestock farming, e.g., provides a livelihood for millions of people (FAO, 2009). In Europe, extensive grazing has been the traditional use of high mountain areas since Neolithic times, mainly due to the limitations of poor soils, complex topography and harsh climate, which restrict many other land uses (Lasanta, 2010; Egli and Poulénard, 2016). High mountain areas also provide other ecosystem services, including the regulation of hydrological and nutrient cycles, biodiversity conservation, habitat for wild herbivores, soil protection, and soil carbon (C) storage, as well as providing value as cultural landscapes and through tourism and recreation activities (Raudsepp-Hearne et al., 2010; Grêt-Regamey et al., 2012; Bernués et al., 2014).

As in other European alpine mountain ranges (Alps, Carpathians, Apennines, Balkans), the Pyrenees show ancient traces of 7000 years of human activity (Fillat et al., 2008). Most of the original forests have been exploited for centuries to obtain wood and increase the grazing area. Today, pastures are spread over the montane and the subalpine vegetation belts, and grazing takes place there (between 1500 and 2300 m.a.s.l.) between July and October (Gómez, 2008). Most mountain grasslands are therefore secondary plant communities whose conservation requires regular management, especially by mowing, burning and grazing, to avoid shrub and tree re-colonization (Dietl, 1982). However, the socio-economic changes that have occurred since the mid-twentieth century have led to a decline or cessation of traditional practices in large mountain areas in Europe. Livestock densities have become insufficient to prevent plant succession (MacDonald et al., 2000), resulting in a widespread encroachment of woody plants into former grassland areas (Anthelme et al., 2007; Solem et al., 2012; Babai and Molnár, 2014; Gartzia et al., 2014, 2016; Nadal-Romero et al., 2018). The current vegetation is made up of grasslands interspersed with cliffs, ridges, screes and wetland vegetation (Gómez García et al., 1997). In turn, subalpine grasslands are formed by a mosaic of natural and semi-natural herbaceous communities whose structure, distribution, and floristic composition result from the interaction of diverse abiotic parameters (climate, topography, soil) and grazing history. The flat

areas and areas with gentle slopes are occupied by mesophilous pastures, among which the *Nardus* mat-grasslands and the *Festuca-Agrostis* chalk grasslands stand out.

With respect to geomorphology dynamics, erosion processes that occur due to topography and climate are frequent in the Pyrenees at different scales (cryoturbation, solifluction, rill erosion), modifying landforms and the depth and structure of the soil mainly on steep slopes (Del Barrio and Puigdefábregas, 1987; García-Ruíz et al., 2010, 2015). Cryoturbation and solifluction are linked to freeze-thaw cycles and are expected to rise in frequency locally as a consequence of climate change, which is expected to increase the climate variability (Keiler et al., 2010). Erosion is also caused by animal activity (bioturbation), mainly through trampling, excavation or rooting (Gómez-García et al., 1995). Livestock compact the soil and lift and mobilize the topsoil with their hooves, thereby increasing soil losses by erosion (Lasanta, 2010). Rooting by wild boar (*Sus scrofa* L.) and burrowing by moles (*Talpa europaea* L. and *Microtus* spp.), as well as the construction of anthills (*Lasius flavus*, Fabricius, 1782), cause soil disturbance in large areas, thereby affecting plant succession (Gómez García et al., 1995, 1999) and reducing the surface available for livestock grazing (Canals and Sebastià, 2000; Bueno et al., 2013). In the absence of disturbance processes, including decreases in grazing or grazing abandonment, natural succession causes, at first, an increase in the population of potentially dominant species (Bobbink and Willems, 1987), loss of diversity and pastoral value (Bueno et al., 2011; García-González and Gómez García, 2014) and eventually shrub encroachment, currently posing a serious threat to grassland conservation (Nadal-Romero et al., 2018).

Grassland dynamics are inseparably linked to variations in soil quality (Braun-Blanquet, 1948). Moreover, although variations in soil characteristics have been mentioned as promoting succession in different types of grasslands by altering their plant cover, dominant species and diversity (Benito Alonso, 2006; Gómez, 2008), the role of soils and geomorphology in grassland dynamics has received limited attention. Most of the research in the Pyrenees has focused on

the effects of grazing regimes (stocking rate, livestock type, spatial and temporal management) on plant diversity (Gómez et al., 1997; Komac et al., 2014, 2015), spatial patterns (Komac et al., 2011), or vegetation structure (Sebastià et al., 2008). The dominant species of the two types of grasslands mentioned above (particularly *Festuca rubra*, *Agrostis capillaris* and *Nardus stricta*) show an exceptional ecological amplitude (Donald and Perkins, 1968), which allows their expansion in numerous and contrasting habitats. Increasing knowledge of successional processes is essential to understanding grassland dynamics and to improving grassland management and conservation, as has long been noted (Sampson, 1917). The overexpansion of *Nardus* mat-grasslands throughout European mountains to the detriment of chalk grasslands is considered undesirable for grazing use and for diversity conservation and has often been linked to overgrazing, to changes in the grazing regime (Bobbink and Willems, 1987) and, conversely, to the scarcity of herbivore pressure (Montserrat and Villar, 2007). In particular, *Nardus stricta* is a low-nutritive grass largely due to a high silica content in the leaves which makes them unpalatable and rejected by livestock. On the other hand, this plant is very dominant for its type of growth “in phalanx” that, in absence of gaps, limits the establishment of other species and usually gives rise to communities with low diversity. However, long-term monitoring of grazed and ungrazed in the Central Pyrenees has not shown any significant trend of expansion or decrease in *Nardus stricta* (García-González and Gómez-García, 2014; Pardo et al., 2015), which forces us to investigate other factors underlying the grassland dynamics in these communities.

The aim of this work is to analyse the relationships between topsoil properties and grassland plant composition in a subalpine area of the Central Spanish Pyrenees with remarkable erosion dynamics where undisturbed *Nardus* mat-grasslands and disturbed chalk grasslands coexist in a mosaic-like pattern. Our hypothesis is that soil disturbance e.g. by physical erosion or bioturbation is the main cause avoiding *Nardus* grassland expansion in the detriment of chalk grassland.

2. Materials and methods

2.1. Study area and experimental design

The study was performed in La Estiva, at the boundary of the Ordesa y Monte Perdido National Park (Central Pyrenees, Spain). This is a summer grazing area within the subalpine belt at altitudes between 1,700 and 1,900 m.a.s.l. The area is grazed by 200 cows in summer -between July and October- and, later, by flocks of sheep that remain during the autumn until the fall of the first snowfalls. The stocking rate is approximately 1 LAU (large animal units) /ha. The bedrocks is limestone and grey marl from the Middle Ilerdian (Eocene). The climate is subalpine (mean annual rainfall is 1,700 mm and mean annual temperature is 7°C). The snow- and frost-free period extends from May to October (Fillat et al., 2008). Due to the long snow period and history of grazing, the vegetation of the study area is formed exclusively by herbaceous communities, despite being located in the potential domain for black pine (*Pinus uncinata*) forest and *Juniperus communis* shrubland. In the montane and subalpine belts, flat areas and gentle slopes (less than 20 %) sharing the same topographical characteristics are covered by grasslands dominated by *Nardus stricta* and chalk grasslands forming a complex mosaic. The first grassland type (*Nardus* mat-grassland) is classified in the phytosociological alliance *Nardion strictae* and shows a high plant cover (close to 100 %) and low diversity (Shannon index ≤ 2.5). The second grassland type (chalk grassland, alliance *Bromion erecti*) has a lesser plant cover, due mainly to gaps formed by limestone outcrops, livestock dung and animal footprints, and higher diversity (Shannon index ≥ 4). In addition, several species are present which are characteristic of long-term snow-covered grassland (alliance *Primulion intricatae*), which extends into the subalpine and alpine belts replacing *Bromion erecti* above 2000 m.a.s.l. All these grasslands occasionally grow some nitrophilous plants that come from the nearby livestock rest points (alliance *Rumicion alpini*, rest-points grassland). Finally, the adjacent slopes, with rocky and

slippery ground, show sparse grasslands of *Festuca scoparia* (alliance *Festucion scopariae*, stony slope grassland), some of whose plant species are also exported to the dense mosaic grassland aforementioned. The area is affected by gully erosion at many places that generate longitudinal scarps along the slope that are a few metres high on the slipping surface (a young and thin soil or limestone layer) and joined to the old surface by a talus. The result is a mosaic-patterned landscape, with an alternation of patches of tall grasses growing on slightly raised areas (*Nardus* mat-grasslands) and short grasses growing on a lower level of the ground visibly affected by erosion (chalk grasslands) (Figure 1). Soils of the undisturbed sites are classified as Oligoetric Cambisols (Densic, Humic, Endoloamic, Anosiltic) and their depth usually reach more than 100 cm. In the disturbed sites, soil thickness ranged from 15 to 40 cm, and soils are classified as an association of Hypereutric Leptosols and Epileptic Hypereutric Cambisols (Humic, Loamic) depending on the thickness reached in each case (IUSS, WRB, 2015).

The experimental area extends over a surface of 250 ha and is mainly covered by the two target grasslands forming a mosaic. Soil and floristic relevés were sampled on that territory. Six paired sampling sites were selected for a side-by-side comparison of undisturbed and erosion-disturbed sites in the concave relief of La Estiva. Sampling sites were separated by about 100 m and, for each site, sampling points of both grassland types were selected. The sampling was performed in late July 2018. In each case, a plant species inventory was performed using 1 m² grids, visually estimating the plant cover of each plant species on a 1 to 100 scale. At each sampling point three soil sub-samples were collected from the topsoil (0-5 and 5-10 cm depth), and then mixed to obtain a representative and composite soil sample. Thus, the experimental design consisted of 6 replicates x 2 soil depths x 2 grassland types (24 samples in total).

Unaltered soil samples were air-dried and analysed for physical properties: bulk density, mean weight-diameter of aggregates and aggregate stability. The remaining soil material was sieved through a 2 mm mesh sieve for chemical analyses. Coarse fragments (> 2 mm) were separated

from each sample and then quantified. Soil oxidizable carbon was determined using the Walkley and Black (1934) method, and total nitrogen was determined with the Kjeldahl method (Benton Jones, 1991). Soil pH was analysed in a suspension of soil and water (1:2.5, w/v) and soil and KCl (1:2.5, w/v). Electric conductivity was determined using an electrical conductivity metre in a 1:5 (w/v) extract of soil and water. Soluble sulfur was measured in 1:5 aqueous extract by turbidimetry (Bower and Wilcox, 1965). The exchangeable Ca^{2+} , Mg^{2+} , K^{+} , and Na^{+} were analysed after three consecutive extractions with 1 M ammonium acetate buffered at pH 8.2 (ratio 1:20 w/v). The cation exchange capacity was determined after washing the remaining soil samples with ethanol, followed by an extraction and analysis of ammonium by the Kjeldahl method. Available phosphorus was analysed following the method of Olsen and Sommers (1982).

2.2. Data analysis

We analysed the plant species data using a detrended correspondence analysis (DCA) (Lepš and Šmilauer, 2003). DCA is an indirect gradient analysis method used in vegetation analysis to summarize the variation of an abundance data matrix into a few axes that contain most of the covariation and can be assumed to represent the vegetation response to extrinsic environmental gradients. We used another indirect gradient method, a principal component analysis (PCA), to reduce the variation in the soil data to a few axes that summarize the soil response to the environmental gradients. We also used paired Student's t-tests to check for significant differences in soil properties between non-disturbed and disturbed sites for each soil depth and calculated the Spearman correlation coefficients between the soil properties within each type of site. Finally, we used a canonical correspondence analysis (CCA) to relate the soil properties to the plant species composition. Unlike DCA or PCA, CCA is a direct gradient analysis method, i.e., it allows a direct evaluation of the effects of environmental gradients on vegetation by incorporating a second set of environmental variables that are regressed against the vegetation data (Lepš and Šmilauer, 2003). In our case, we used the axes (components) obtained

from the PCA of soil properties as explanatory variables. The axes of the PCA are suitable for this assignment because they are orthogonal (independent) variables, unlike the raw soil data, which are usually highly collinear. The selection of the PCA axes to be included in the regression model was performed by a stepwise procedure, stopping when the inclusion of new axes did not lead to a significant ($P < 0.05$, Monte Carlo tests with 999 permutations) improvement of the model. Once the explanatory variables were selected, the significance of the ordination was tested for the first canonical axis and for all the canonical axes ($P < 0.05$, Monte Carlo tests with 999 permutations). The comparison and correlation tests were performed using IBM SPSS Statistics v.22 (IBM Corporation®, Armonk NY, USA), while the DCA, PCA and RDA were performed using Canoco v. 4.5 (Microcomputer, Ithaca NY, USA).

3. Results and discussion

3.1. Vegetation analysis

We recorded 65 plant species in the study area. The presence in each area and coverage indexes of the plant species identified are listed in Table 1. The most frequent species were *Festuca nigrescens*, *Galium pumilum* and *G. verum*, which were present in 10 of 12 relevés. According to the site type, the more common plant species in the disturbed sites were *Cirsium acaule*, *Festuca nigrescens*, *Leontodon hispidus*, *Plantago media*, *Trifolium montanum* and *T. pratense*, which occurred in all six relevés. *Nardus stricta*, *Pilosella officinarum* and *Tragopogon lamottei* were present in all the relevés of the undisturbed sites. According to their coverage indexes, the most abundant species in the disturbed sites were *Festuca nigrescens* and *Plantago media*, showing coverages from 10 to 20 %, followed by *Cirsium acaule*, *Alchemilla gr. glaucescens*, *Sanguisorba minor*, *Thymelaea tinctoria* and *Trifolium montanum* with coverages from 5 to 10 %. In the undisturbed sites, the species with the highest coverage was *Nardus stricta* (57 %), followed far

behind by *Eryngium bourgatii*, *Iris latifolia*, *Alchemilla* gr. *glaucescens* (10-20 %), *Festuca nigrescens*, *Cirsium acaule*, *Trifolium alpinum* and *Potentilla erecta* (5-10 %).

The first axis of the DCA summarizes 23.6 % of the variance in the species data and clearly separates the samples from the disturbed and undisturbed sites (Figure 2, Table 2). The species with the highest positive contribution (species score > average + SD) on axis I, and therefore those associated with the undisturbed sites, were *Campanula scheuchzeri*, *Eryngium bourgatii*, *Iris latifolia*, *Nardus stricta*, *Phyteuma orbiculare*, *Polygonum viviparum*, *Potentilla erecta*, *Ranunculus amplexicaulis*, *Tragopogon lamottei*, *Trifolium alpinum*, and *Viola pyrenaica*. Among these species, we found several species (*Campanula scheuchzeri*, *Eryngium bourgatii*, *Nardus stricta*, *Potentilla erecta*, *Ranunculus amplexicaulis*, *Trifolium alpinum*) that are considered characteristics of the *Nardus* mat-grasslands (Braun-Blanquet, 1948).

On the other hand, the species that had the greatest negative contribution on axis I (score < average - SD), and therefore those related to disturbed sites, were *Alchemilla alpigena*, *Anthyllis montana*, *Briza media*, *Erigeron alpinus*, *Gentiana verna*, *Koeleria vallesiana*, *Leotodon hispidus*, *Leucanthemum vulgare*, *Erigeron alpinus*, *Medicago suffruticosa*, *Onobrychis pirenaica*, *Ononis cristata*, *O. striata*, *Oxytropis neglecta*, *Plantago lanceolata*, *Seseli montanum*, *Thymelaea tinctoria* and *Trifolium thalii*. Among this set, we found several species common in stony slopes grasslands, such as *Oxytropis neglecta*, *Seseli montanum*, *Thymelaea tinctoria*, *Koeleria vallesiana*, and *Medicago suffruticosa* (Gómez, 2008; Remón et al., 2009). There are also species (*Alchemilla alpigena*, *Gentiana verna*, *Oxytropis neglecta*, *Trifolium thalii*) of the long-term snow-covered grasslands. *Agrostis capillaris*, *Lotus corniculatus* and *Trifolium pratense*, which are found in a wide range of grasslands, show similar abundances in both undisturbed and disturbed sites (Table 1), as do other species characteristic of chalk grasslands, such as *Carex caryophylla*, *Cirsium acaule*, *Eryngium bourgatii*, *Plantago media*, *Sanguisorba minor* or *Trifolium montanum*.

The other axes of the DCA are of much lower explicative power [explained variances of 9.6 % (axis II), 4.3 % (axis III) and 0.4 % (axis IV)], and we did not identify any trend regarding the distribution of species in either undisturbed or disturbed sites. For instance, in axis II, the species with the lowest score (negative) were *Achillea millefolium*, *Anthyllis montana*, and *Plantago lanceolata*, whereas those with the highest score (positive) were *Alchemilla alpigena*, *Erigeron alpinus*, *Gentiana verna*, *Koeleria vallesiana* and *Leucanthemum vulgare*.

In summary, the samples from both grassland types showed contrasting floristic compositions in the DCA. The vegetation of the undisturbed sites includes plant species that are typical of *Nardus* mat-grasslands. Moreover, the species composition of the disturbed sites was found to be mainly related to the neighbouring stony slope grasslands and, to a lesser extent, to the long-term snow-covered vegetation. These results are consistent with our initial hypothesis that disturbance results in the replacement of *Nardus* mat-grasslands with other communities, including species specialized in growing on shallow calcareous soils (stony slope grassland). This finding agrees with that reported in other studies in the Central Pyrenees (Gómez, 2008; Benito Alonso, 2010), showing that in the absence of disturbances (including grazing), chalk grasslands seem to be replaced by *Nardus* mat-grasslands.

3.2. Soil description and analysis

The paired Student's t-test analysis of the top 10 cm of the soil showed significant differences between both site types for several physical and chemical properties (Table 3). Deep (≥ 100 cm) undisturbed soils under *Nardus* mat-grasslands showed significantly lower contents of coarse fragments, lower bulk density and a trend toward lower values of the mean weight-diameter of aggregates and higher values of aggregate stability (significant at 5-10 cm) compared to disturbed soils. This well-developed soil structure is probably due to the greater slope stability and longer soil evolution under this type of pasture.

The soils of undisturbed sites were significantly ($p \leq 0.01$) more acidic than the disturbed soils, both for real (pH H₂O) and potential (pH KCl) acidity. The presence of *Nardus stricta* in acidic and low-nutrient soils is well documented in other works (Güsewell et al., 2005; Galvánek and Janák, 2008). This acidity is related to the washing of the basic cations to the deeper layers, as this is an area with high rainfall, and soils are older and well-developed on a stable geomorphology (flat areas or gentle slopes) (Badía et al., 2008a). There may also be a greater contribution of protons from the dissociation of carbonic acid caused by the reaction of water with carbon dioxide coming from soil respiration, as well as from soil organic matter decomposition (Ji et al., 2014).

The oxidizable carbon content was higher in the undisturbed soils than in the disturbed soils (significant only in the first 5 cm), while we did not find significant differences in the total nitrogen content. The C/N ratio was significantly higher in the undisturbed soils than in the disturbed soils. For soils in similar climatic zones, the accumulation of organic carbon in grazed soils depends mainly on biotic factors (grazing intensity, type of pasture and livestock), and the soil organic carbon content tends to decrease when grazing intensity is high (Zhou et al., 2017; Abdallaa et al., 2018) because of depletion of plant biomass and decreased incorporation of plant residues into soil (Bilotta et al., 2007).

In La Estiva, the livestock show a clear preference for grasses located in the disturbed sites (chalk grasslands) over those in the undisturbed sites (*Nardus* mat-grasslands) (Figure 1), which livestock (especially sheep) tend to avoid (Grant et al., 1996) due to the low palatability of *Nardus stricta* (Braun-Blanquet, 1948). Thus, we could assume that the grazing intensity is greater in the disturbed areas, which can result in lower organic inputs to soil leading to lower soil organic matter content in these sites than in the *Nardus* mat-grasslands. Moreover, *Nardus stricta* is a slow-growing plant adapted to acidic and nutrient-poor soils that generates residues of low quality and a slow decomposition rate (Güsewell et al., 2005), which is in agreement with

the higher C/N ratio of the undisturbed soils. A lower input of animal excreta related to a lower grazing intensity could also favour a higher C/N ratio in these soils.

Marked differences were found in the exchangeable calcium and magnesium contents. The calcium content was much higher in the disturbed soils than in the undisturbed soils, whereas the opposite was found with magnesium, which was significantly higher in the undisturbed soils. The exchangeable sodium was significantly higher in the first 5 cm of the disturbed soils. The soil bases were positively correlated with the oxidizable carbon, especially in the case of potassium, both in undisturbed ($r = 0.921$, $p < 0.01$) and in disturbed soils ($r = 0.912$, $p < 0.01$), showing that soil bases come mainly from the mineralization of organic matter. In addition, the sum of exchangeable cations was also positively correlated with electrical conductivity (similar values in both soils) ($r = 0.803$; $p < 0.01$ in undisturbed soils; $r = 0.775$; $p < 0.01$ in disturbed soils), indicating the existing relation between soluble and exchangeable ions. Soils under *Nardus* grasslands are generally found on siliceous rocks, but in the Central Spanish Pyrenees, as in some other regions in Europe (e.g., France or Slovakia), they are also found on calcareous parent materials. In such cases, the presence of *Nardus* mat-grasslands is generally associated with a decrease in calcium content in the topsoil that is washed into deeper soil layers due to high rainfall (Stanová and Valachovič, 2002; Bensettiti et al., 2005). The same occurs in the soil pH, which becomes acidic due to the loss of cations. The high calcium content in the disturbed soils is probably due to the mixture of soil horizons after disturbance (erosion and colluviation) and limestone (R-layer) vicinity. Sebastià (2004) also found a lower calcium content and a higher magnesium content in soils (10-20 cm) in the subalpine belt of the south-eastern Pyrenees under *Nardus stricta* grasslands. Soluble sulfur, on the other hand, reached higher values in soils under *Nardus* mat-grasslands than in the other soils, although the difference was only significant at 5-10 cm. Finally, we found no significant differences in the contents of plant-available phosphorus and, moreover, they were low in all cases, which could be explained by the fact that the sites are not a livestock resting area (Badía et al., 2008b) and therefore, the excreta inputs are low.

The principal component analysis (PCA) allows us to obtain a synthetic view of the main gradients of variation in soil properties for both site types. The first two components of the PCA explain 71.2 % of the total variance observed (Figure 3, Table 2).

The first component, with a high explanatory power (44 % of total variance explained), represents a soil gradient related to soil organic matter (oxidizable C and total N), and other parameters related to it, such as cation exchange capacity (CEC), bulk density (BD), aggregate stability (AS), and mean weight-diameter of aggregates (MWD). The highest sample scores along this axis were found in certain samples of the disturbed soil group (C1, C2, C3) associated with a lower content in soil organic matter and a more compact structure with less-stable and higher-size aggregates; the lowest scores were found in some samples of the undisturbed soils group (N4, N5, N6), which show the highest content of soil organic matter, CEC, and magnesium, and a finer, more porous and stable structure. However, this axis does not clearly separate both groups, which intermingle in the centre of the PCA.

Axis II (27.2 % of total variance explained) represents a gradient related to acidity / basicity, exchangeable calcium richness and stoniness. In this case, the highest scores correspond to certain disturbed sites (B4 and B5), whereas the undisturbed samples are located in the negative part of the axis, associated with higher acidity and magnesium content and lower content of coarse fragments. Again, there is no clear separation of both groups in this second component. However, the combination of axes I and II distinguishes the undisturbed group as a group with relatively homogeneous soils compared to the disturbed soils, which are much more dispersed.

Finally, the third axis, which explains only 9.3 % of the variance, is related to the levels of electric conductivity and soluble sulfur and, to a lesser extent, to magnesium. The highest scores on this axis correspond to certain samples of undisturbed soils (N1, N3, N4), but the intermediate and lowest scores correspond equally to samples of both groups.

Despite none of these gradients discriminating the two groups on its own, the undisturbed samples (N) were found to be a distinct, relatively homogeneous group characterized by low scores on the first two axes, contrasting with the disturbed samples (C), which showed greater dispersion in their soil properties.

3.3. Plant species distribution in relation to soil properties

The CCA of the relationship between soil properties and floristic composition considered the first three PCA axes of the soils (axes 1, 2 and 3, in order of decreasing predictive power) as environmental variables and discarded the fourth axis of the PCA, which was statistically non-significant ($P > 0.05$, Monte Carlo test, 999 permutations). The resulting canonical ordination axes were highly significant ($P < 0.01$ for both the first and all the canonical axes), so we can consider the ordering of the species from the first three soil PCA axes to be statistically significant compared to a random model.

The first CCA axis (23 % of variance explained) explains the species composition based on the soil variation represented by the first (related to soil organic matter) and second (related to basicity) axes of the PCA, which contributed almost equally to the canonical axis (Figure 4, Table 2). The first CCA axis produces a clear separation between the undisturbed and disturbed groups, similar to that observed in the first axis of the DCA of vegetation. The species that are negatively related to this axis (score $<$ average - SD) and are therefore associated with the *Nardus* mat-grassland were *Campanula scheuchzeri*, *Iris latifolia*, *Nardus stricta*, *Phyteuma orbiculare*, *Potentilla erecta*, *Polygonum viviparum*, *Ranunculus amplexicaulis*, *Tragopogon lamottei*, *Trifolium alpinum* and *Viola pyrenaica*. As we previously found in the first axis of the DCA, we found species characteristic of the *Nardus* mat-grasslands: *Nardus stricta*, *Campanula scheuchzeri*, *Potentilla erecta*, and *Trifolium alpinum*. On the other hand, the species that are positively related to the first canonical axis (score $>$ average + SD) and, consequently, are

associated with the chalk grasslands were *Anthyllis montana*, *A. vulneraria*, *Briza media*, *Leontodon hispidus*, *Medicago suffruticosa*, *Ononis striata*, *Oxytropis neglecta*, *Pilosella lactucella*, *Plantago lanceolata*, *Seseli montanum* and *Thymelaea tinctoria*. The concordance between the first axes of DCA and CCA indicates that the main gradient in vegetation and the floristic differences among the grassland types can be explained by the variation in soil properties.

The second canonical axis explains 11.9 % of the variance of the species data and is strongly correlated with the third axis of the soil PCA (related to dissolved ion content). The species with the highest scores on this axis (score > average + SD) were *Cirsium eriophorum*, *Galium verum*, *Koeleria pyramidata*, *Merendera montana*, *Poa pratensis*, *Trifolium alpinum* and *Trifolium repens*. These species include some that are typically predominant in chalk grasslands (*Agrostis capillaris*, *Lotus corniculatus*, *Poa pratensis*) and some (*Cirsium eriophorum*, *Trifolium repens*) typical of resting site vegetation. The occurrence of chalk grasslands and, particularly, resting site species was thus related to higher ion contents in the soil solution; these species can be considered indicators of more frequent livestock presence, resulting in larger inputs of excreta leading to higher levels of plant-available soluble nutrients in soils (Badía et al., 2008b).

Finally, the species with the lowest scores (score < average - SD) on the third canonical axis were *Achillea millefolium*, *Campanula scheuchzeri*, *Eryngium bourgatii*, *Euphorbia cyparissias*, *Leontodon pyrenaicus*, *Pilosella officinarum*, *Plantago lanceolata*, *Rhinanthus pumilus*, and *Taraxacum officinale*. Other species, such as *Plantago lanceolata* and *Taraxacum officinale* and several short-lived plants, can be classified as “opportunistic” or “fugitives” that grow in a wide range of environments, temporarily colonizing vegetation gaps (Platt and Weis, 1977; Gómez García et al., 1999).

Over the last decades, the disturbance regime in the Central Pyrenees has been altered by the decline in grazing pressure and the cessation of traditional management practices (including the

use of fire to keep out bushes and unpalatable grass growth), thus allowing plant succession and the spread of grasses and woody vegetation. However, the vegetation response to grazing changes in high elevation grasslands has been shown to be weak and slow (Pardo et al., 2015). At present, vegetation development is far from uniform, and mosaics of several plant communities are common in the landscape (Gómez, 2008). In this research, we found marked differences in plant composition and soil conditions between disturbed grasslands and stable or undisturbed grasslands growing in close vicinity to each other. Contrasting soil conditions in nearby sites are typical in mosaic vegetation landscapes and are usually indicative of soil-vegetation feedback processes, which tend to stabilize alternative ecosystem states (Ehrenfeldt, 2005; Mora and Lázaro, 2013).

The preference of *Nardus* mat-grasslands for acidic soils is well known (Chadwick, 1960) and, on calcareous parent material, restricts their settlement to only stable, well-leached soils. *Nardus stricta* grows in dense tussocks, producing large amounts of organic matter for the underlying soil. Indeed, we found that the soils under *Nardus* mat-grassland showed a highly permeable crumb structure that resulted in increased infiltration and more leaching and, together with the dense plant cover, prevented the runoff and erosion processes.

In contrast, abundant calcium and moderately high pH excludes the *Nardus* mat-grasslands from sites with young soils with shallow or outcropping calcareous bedrock. In these soils, under chalk grasslands, the organic matter content remains lower than in those soils under *Nardus* mat-grasslands, and the topsoil shows a dense blocky structure that, combined with less-protective vegetation, allows erosion to occur. Livestock also enhance erosion through grazing and trampling resulting from the higher palatability of plants in chalk grasslands compared to those in *Nardus* mat-grasslands. As a result of erosion, the calcareous material will remain shallow or become even more surficial, further excluding the *Nardus* mat-grasslands. The final result is the

stabilization of the patches of both types of vegetation and their persistence in the landscape over long periods of time.

Our results suggest that soil-vegetation feedback mechanisms contribute to generating and maintaining the vegetation mosaic in these high mountain areas with calcareous bedrock. Thus, the plant composition, spatial distribution and dynamics of this mosaic would result from a model of non-equilibrium plant coexistence caused by soil disturbance and relentless succession (Raup, 1957; Pickett, 1980). Our results indicate that an adequate management for the improvement of Pyrenean pastures (to maintain plant diversity, to improve nutritive quality) should be focused on maintaining an appropriate disturbance regime, through grazing, sufficient to prevent the spreading of *Nardus* mat-grasslands.

4. Conclusions

Our findings show that the subalpine grassland mosaic distribution and its dynamics in the Central Pyrenees subalpine belt are closely related to the underlying soil properties, and support the hypothesis that soil disturbance e.g. by physical erosion or bioturbation is the main cause avoiding *Nardus* grassland expansion in the detriment of chalk grassland.

Dense grassland communities, recognized as typical species-poor *Nardus* mat-grasslands, were found to grow on stable or largely undisturbed sites located on slightly raised ground. Due to slope preservation and longer leaching processes, the soils sustaining this grassland were deep, low in calcium and acidic, and showed relatively homogenous topsoil properties: high contents of organic matter and of certain nutrients, such as magnesium, and a fine, porous and stable structure.

In turn, we found species-rich, earlier-successional chalk grasslands growing on young soils on slopes recently affected by water erosion, landslides or other forms of erosion. The soils of these

sites were shallower and stonier and showed higher pH, lower organic matter content, higher calcium content, and a more compact structure, with larger-sized and less stable aggregates, than undisturbed soils under *Nardus* mat-grasslands. The vegetation at some sites also included species typical of rest-point grasslands, indicating a more frequent livestock presence that was related to higher contents of soluble nutrients.

Our findings indicate that the differences between these two grassland types arise and are maintained by soil-plant feedbacks mediated, in one case, through soil stabilization and acidification, and, in the other case, through soil erosion (caused by hillside slides, ravine formation, or animal activities) leading to basification. In this way, the subalpine grassland mosaic (and its plant composition, spatial distribution and dynamic) would result from a model of non-equilibrium plant coexistence caused by soil disturbance and relentless succession.

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Figure captions

Figure 1. Mosaic landscape with an alternation of *Nardus* mat-grasslands (straw coloured, raised areas) and chalk grasslands (in green, lower areas) in the Central Spanish Pyrenees.

Figure 2. Detrended correspondence analysis (DCA) of vegetation. Diagram of the scores of the species and the samples in the first two axes.

Figure 3. Principal component analysis (PCA) of soils. Diagram of the factorial loads of the soil properties and the scores of the soil samples in the first two axes (A) and in the first and third axes (B).

Figure 4. Canonical correspondence analysis (CCA) of soil and vegetation. Diagram of the scores of the species, samples and environmental variables (soil PCA axes) in the first two canonical axes.

Table captions

Table 1. Presence and coverage values (%) of the plant species by site type. Rare species found in less than three inventories are not included.

Table 2. Statistical parameters resulting from the multivariate analysis of soils and vegetation

Table 3. Physical and chemical soil properties under both grassland types at two soil depths and their statistical analysis by paired Student's t-test.

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Highlights

- We explore the factors underlying subalpine grassland dynamics in the Central Pyrenees
- *Nardus* grasslands growing on deep, acidic, Ca-poor soils dominated undisturbed sites
- Species-rich, earlier successional grasslands dominated calcareous eroded sites
- Soil-plant feedbacks can generate and maintain differences between grassland types
- Non-equilibrium plant coexistence contributes to subalpine grassland mosaic



Table 1 Presence and coverage values (%) of the plant species by site type. Rare species found in less than three inventories are not included

	Disturbed sites			Undisturbed sites		
	Presence (% cases)	Coverage (% surface)		Presence (% cases)	Coverage (% surface)	
		Mean	SD		Mean	SD
<i>Agrostis capillaris</i> L.	33	2.5	4.2	50	2.8	4.0
<i>Alchemilla</i> gr. <i>glaucescens</i> Wallr.	83	8.8	11	67	10	11
<i>Anthyllis vulneraria</i> L.	67	2.0	2.4	17	0.2	0.4
<i>Achillea millefolium</i> L.	50	4.0	7.9	33	2.5	4.2

<i>Briza media</i> L.	67	4.2	4.7	17	0.3	0.8
<i>Carex caryophyllea</i> Latourr.	67	1.8	1.9	83	4.0	3.6
<i>Cerastium fontanum</i> Baumg.	0	0.0	0.0	50	0.8	1.2
<i>Cirsium acaule</i> (L.) Scop.	100	8.8	4.3	50	8.3	12
<i>Cirsium eriophorum</i> (L.) Scop.	17	3.3	8.2	33	1.2	2.0
<i>Eryngium bourgatii</i> Gouan	33	1.0	2.0	67	16	19
<i>Euphorbia cyparissias</i> L.	33	1.8	4.0	17	5.0	12
<i>Festuca nigrescens</i> Lam.	100	16	8.6	67	9.2	8.0
<i>Galium pumilum</i> Murray	67	1.2	1.2	100	1.3	0.8
<i>Galium verum</i> L.	83	3.0	2.3	83	4.8	7.6
<i>Iris latifolia</i> (Mill.) Voss	0	0.0	0	50	12	16
<i>Leontodon hispidus</i> L.	83	5.2	4.3	0	0.0	0.0
<i>Linum catharticum</i> L.	67	0.8	0.8	17	0.2	0.4
<i>Lotus corniculatus</i> L.	83	3.2	3.8	33	1.0	2.0
<i>Medicago suffruticosa</i> Ramond ex DC.	67	3.2	3.9	0	0.0	0.0
<i>Merendera montana</i> (L.) Lange	50	2.0	3.9	33	0.3	0.5
<i>Nardus stricta</i> L.	0	0.0	0.0	100	57	14
<i>Oxytropis neglecta</i> Ten.	50	5.2	8.3	0	0.0	0.0
<i>Pilosella lactucella</i> (Wallr.) P.D. Sell & C. West	50	1.0	1.1	0	0.0	0.0
<i>Pilosella officinarum</i> F.W. Schultz & Schultz Bip.	50	1.8	2.5	50	4.3	6.5
<i>Plantago alpina</i> L.	50	3.0	4.0	0	0.0	0.0
<i>Plantago media</i> L.	100	13	6.1	50	2.2	3.9
<i>Polygala vulgaris</i> L.	33	0.7	1.2	33	0.3	0.5
<i>Potentilla neumanniana</i> Rehb.	67	2.8	2.5	0	0.0	0.0
<i>Potentilla erecta</i> (L.) Rauschel	0	0.0	0.0	100	7.8	5.7
<i>Prunella vulgaris</i> L.	67	1.7	1.9	67	3.7	3.8
<i>Ranunculus carinthiacus</i> Hoppe	50	1.0	1.3	67	1.0	1.1
<i>Sanguisorba minor</i> Scop.	83	7.5	5.2	67	2.8	2.5
<i>Seseli montanum</i> L.	50	0.8	1.0	0	0.0	0.0
<i>Taraxacum officinale</i> Weber	67	1.2	1.2	33	1.2	2.0
<i>Thymelaea tinctoria</i> (Pourr.) Endl.	83	7.0	8.5	0	0.0	0.0
<i>Thymus praecox</i> Opiz	83	4.3	3.6	33	0.7	1.2
<i>Tragopogon lamottei</i> Rouy	0	0.0	0.0	50	0.5	0.5
<i>Trifolium alpinum</i> L.	0	0.0	0.0	67	7.8	11
<i>Trifolium montanum</i> L.	100	6.3	4.2	50	4.7	7.8
<i>Trifolium pratense</i> L.	100	5.7	3.6	33	1.0	2.0
<i>Trifolium repens</i> L.	33	1.8	4.0	17	0.3	0.8

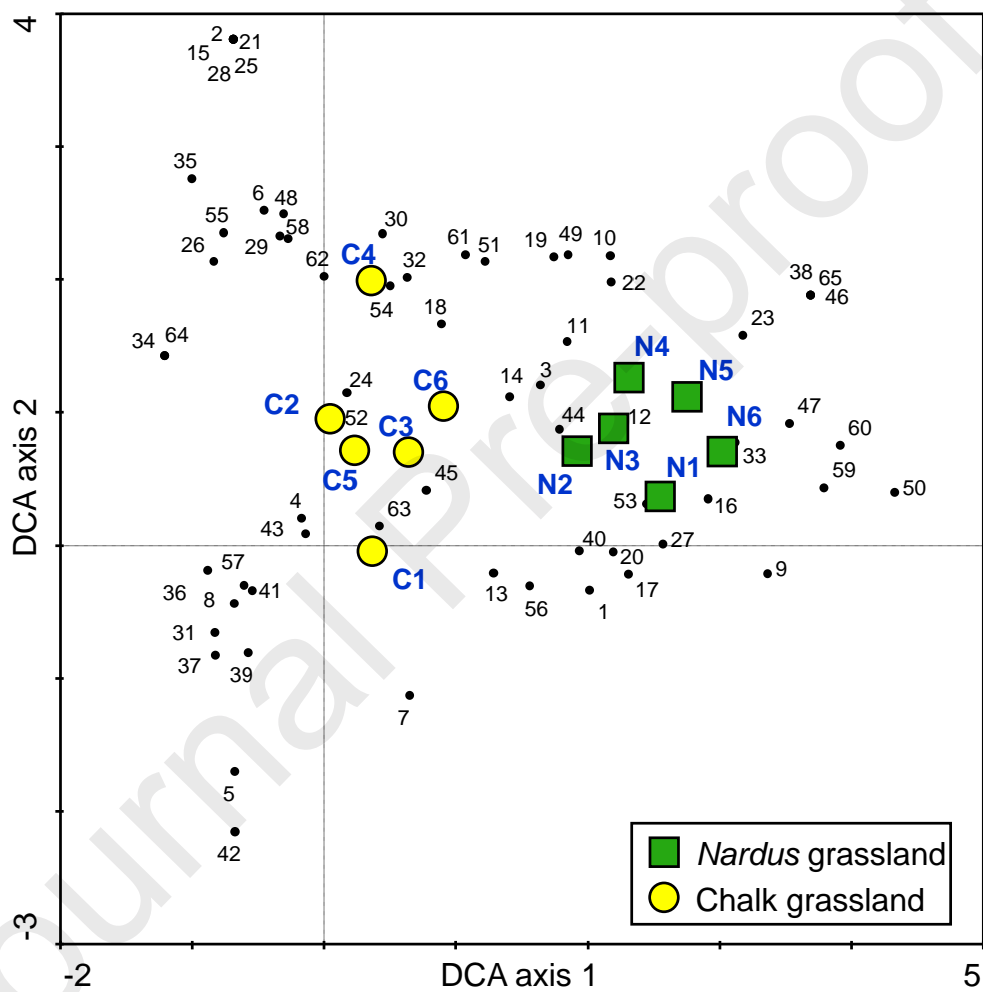
Table 2. Statistical parameters resulting from the multivariate analysis of soils and vegetation

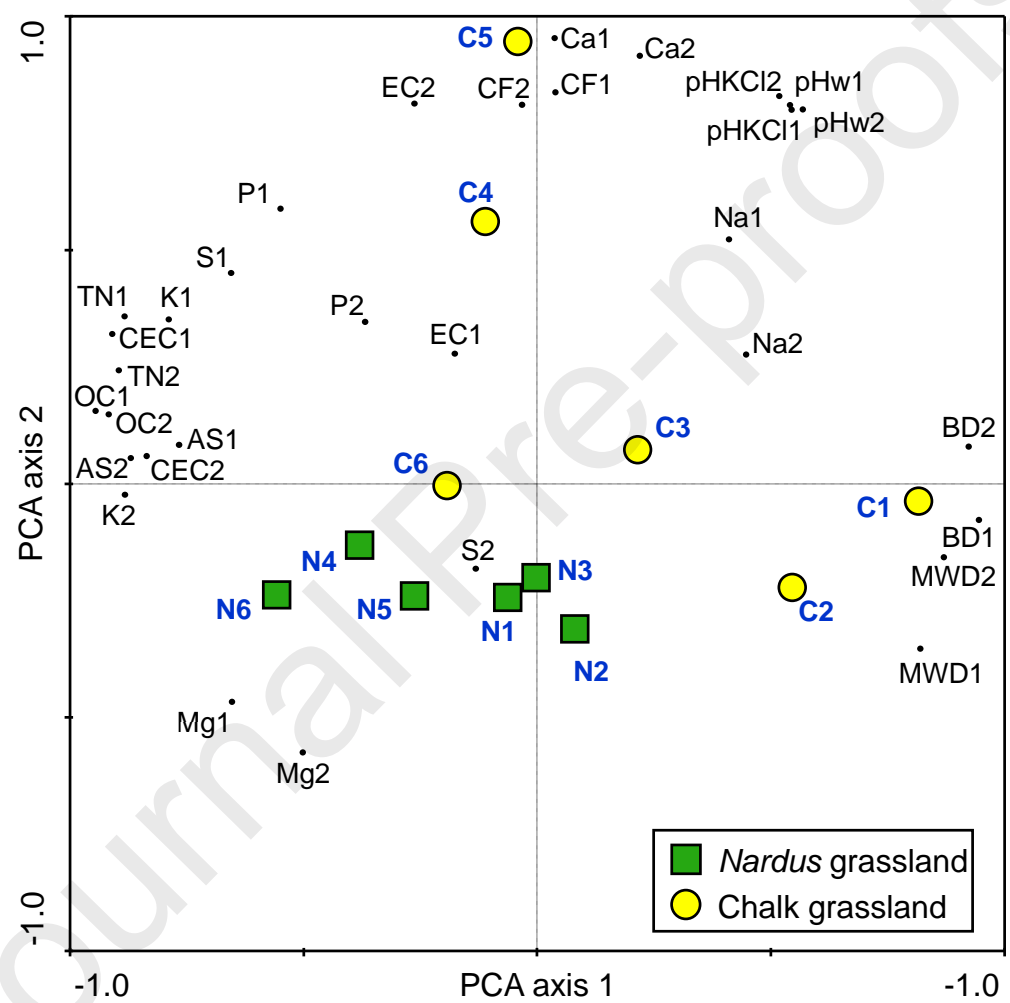
	Axes				Total variance (PCA) or inertia (DCA, PCA)
	1	2	3	4	
PCA of soil properties					
Eigenvalues	0.440	0.273	0.093	0.045	1.000
Cumulative % variance of soil data	44.0	71.2	80.5	85.0	
Sum of all eigenvalues					1.000
DCA of plant species					
Eigenvalues	0.572	0.228	0.103	0.011	2.418

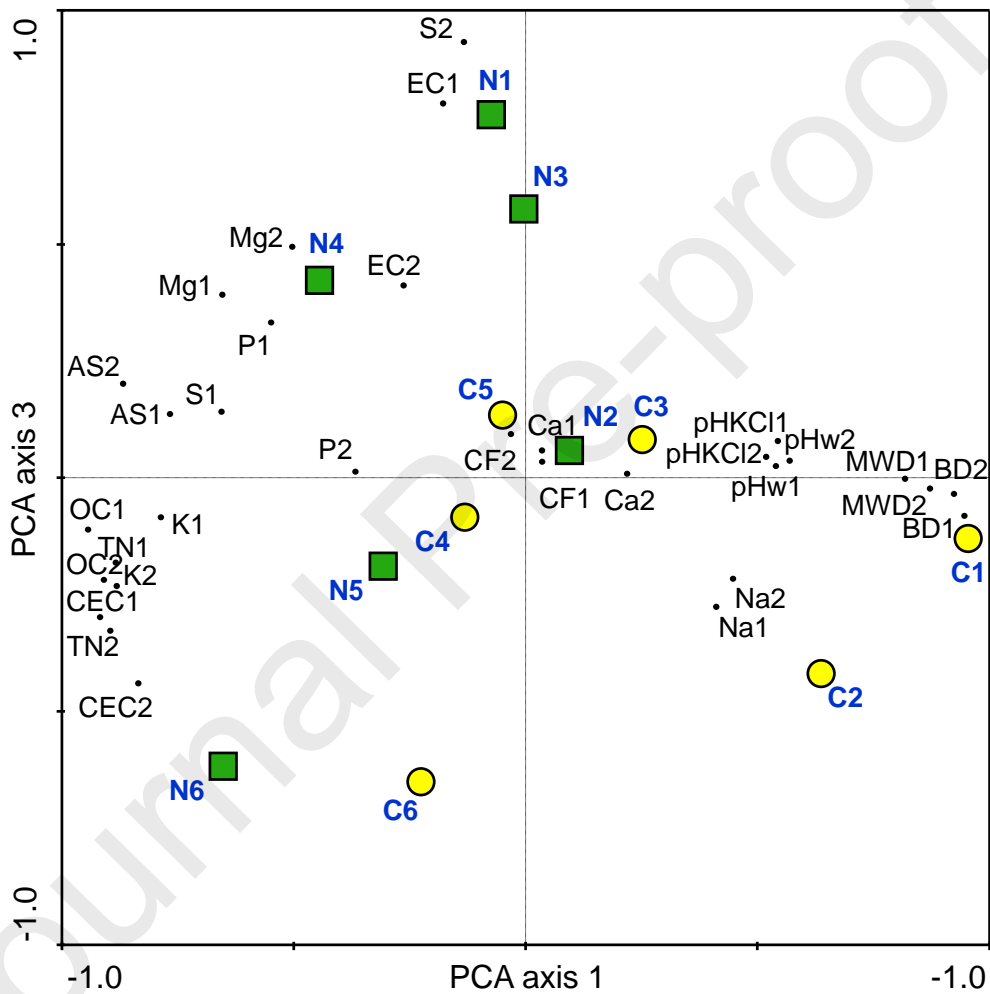
Lengths of gradient	2.999	2.037	1.980	1.449	
Cumulative % variance of species data	23.6	33.1	37.4	37.8	
Sum of all eigenvalues					2.418
CCA of plant species and soil properties					
Eigenvalues	0.517	0.268	0.179	0.311	2.252
Species-environment correlations	0.974	0.929	0.979	0.000	2.252
Cumulative % variance of species data	23.0	34.9	42.8	56.6	
Cumulative % variance of species-soil relation	53.7	81.5	100.0	0.0	
Sum of all eigenvalues					2.252
Sum of all canonical eigenvalues					0.963
Test of significance of first canonical axis	Eigenvalue =	0.517			
	F-ratio =	2.088			
	P-value =	0.0030			
Test of significance of all canonical axes	Trace =	1.112			
	F-ratio =	1.708			
	P-value =	0.0020			

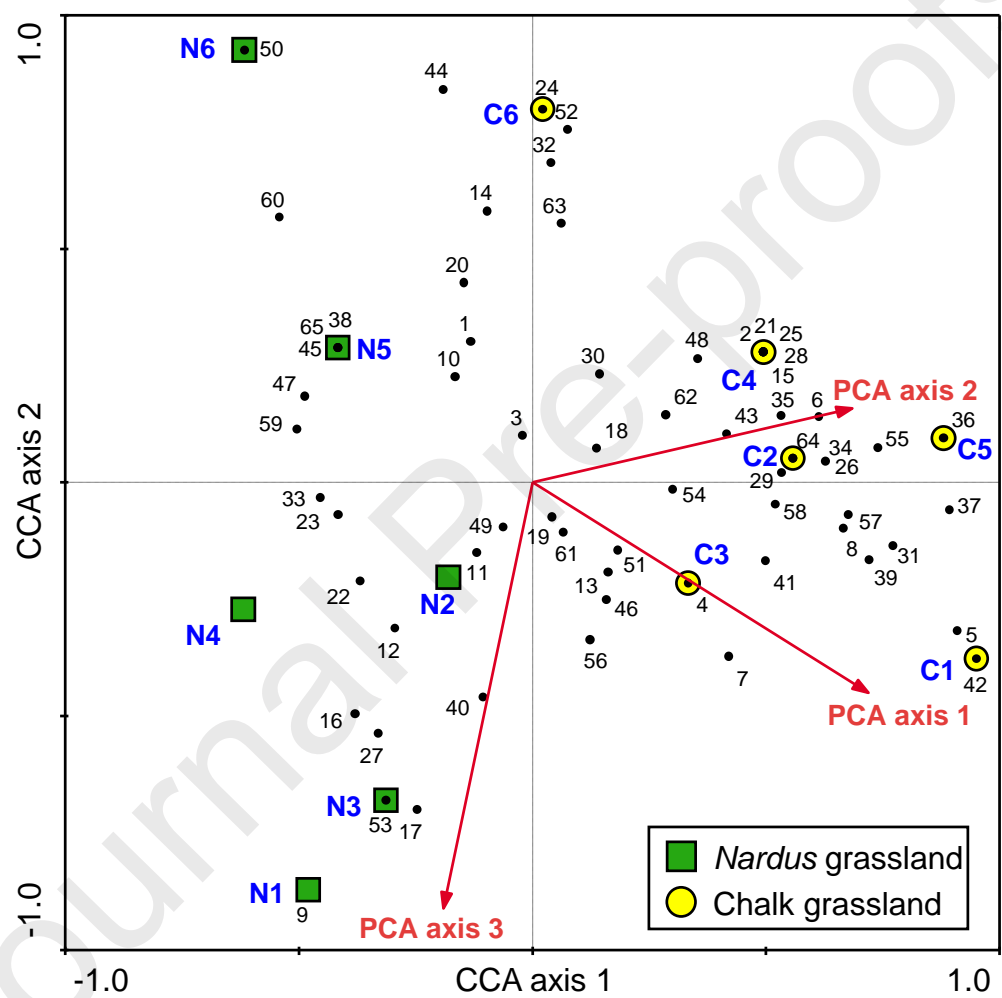
Soil property	Soil depth (cm)	Disturbed sites	Undisturbed sites	<i>P</i> (paired t-Student)
Coarse fragments (% w/w)	0-5	3.55 (1.85)	0.77 (0.15)	0.010
	5-10	8.10 (6.95)	0.29 (0.08)	0.049
Bulk density (g/cm ³)	0-5	0.84 (0.09)	0.64 (0.04)	0.043
	5-10	1.08 (0.07)	0.89 (0.05)	0.010
Mean diameter of aggregates (mm)	0-5	2.80 (0.52)	2.19 (0.27)	0.168
	5-10	3.74 (0.53)	2.81 (0.31)	0.138
Aggregate stability (% w/w)	0-5	90.2 (5.7)	97.1 (0.3)	0.394
	5-10	83.2 (7.8)	96.7 (0.4)	0.009
pH (H ₂ O) 1:2.5	0-5	6.17 (0.24)	5.15 (0.09)	0.002
	5-10	6.40 (0.22)	5.21 (0.12)	0.003
pH (KCl) 1:2.5	0-5	5.65 (0.29)	4.43 (0.13)	0.003
	5-10	5.84 (0.33)	4.26 (0.15)	0.030
EC (μS/cm) 1:5	0-5	159 (21)	190 (20)	0.221
	5-10	104 (16)	96 (4)	0.655
C _{ox} (g/kg)	0-5	68.7 (14.3)	91.1 (9.6)	0.041
	5-10	39.3 (6.8)	48.8 (5.0)	0.071
Total nitrogen (g/kg)	0-5	6.23 (1.15)	7.00 (0.79)	0.236
	5-10	4.15 (0.64)	4.69 (0.51)	0.240
C/N ratio	0-5	10.8 (0.41)	13.0 (0.33)	0.015
	5-10	9.3 (0.25)	10.4 (0.24)	0.034
P Olsen (mg/kg)	0-5	4.18 (0.90)	4.14 (0.52)	0.861
	5-10	2.02 (0.27)	1.83 (0.40)	0.735
S (mg/kg)	0-5	79 (22)	102 (13)	0.102
	5-10	36 (4)	60 (11)	0.040
CEC (cmol _c /kg)	0-5	24.2 (2.8)	26.3 (1.8)	0.173
	5-10	17.6 (1.8)	19.5 (1.6)	0.082
Ca ²⁺ exchang. (cmol _c /kg)	0-5	10.7 (1.7)	5.9 (0.6)	0.021
	5-10	9.3 (1.2)	4.0 (0.5)	0.015
Mg ²⁺ exchang.	0-5	0.50 (0.10)	1.34 (0.18)	0.016

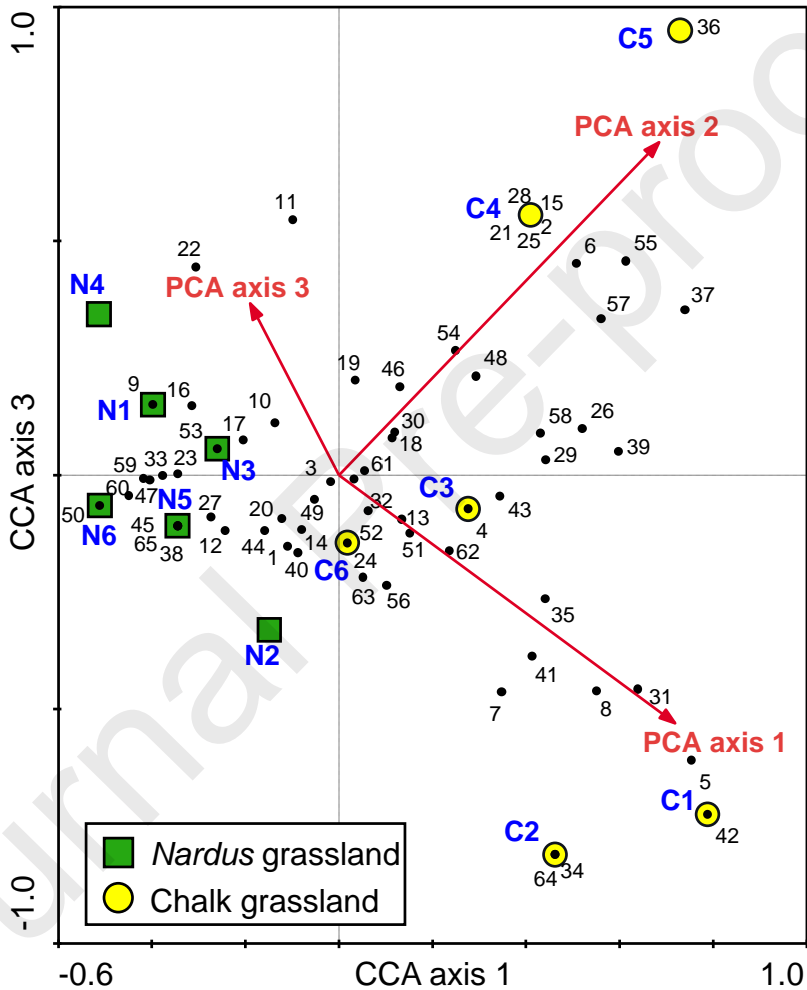
(cmol _c /kg)	5-10	0.32 (0.07)	0.85 (0.10)	0.024
K ⁺ exchang. (cmol _c /kg)	0-5	0.340 (0.045)	0.370 (0.050)	0.425
	5-10	0.155 (0.018)	0.188 (0.020)	0.134
Na ⁺ exchang. (cmol _c /kg)	0-5	0.0400 (0.0045)	0.0267 (0.0021)	0.010
	5-10	0.0333 (0.0021)	0.0267 (0.0033)	0.175
Sum of bases (cmol _c /kg)	0-5	11.6 (1.7)	7.7 (0.7)	0.052
	5-10	9.8 (1.2)	5.0 (0.6)	0.025
Saturation of bases (%)	0-5	48.2 (3.9)	29.9 (3.2)	0.005
	5-10	55.9 (5.2)	27.8 (4.6)	0.005











Mat-grassland

Chalk grassland

