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Plant functional type effects on soil function change along a climatic gradient

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Abstract. Global change modifies plant community composition in mountain grasslands through shifts in the balance of plant guilds. Above- and below-ground systems are tightly linked, and changes in plant community composition and structure can be accompanied by changes in soil function and structure. For a thorough understanding of this link, we carried out a study to evaluate the relative importance of regional variables, local soil properties, and local plant diversity on soil activity. We sampled soil and vegetation of six sites along a climatic gradient (334 to 2479 m) in the Eastern Pyrenees. At each site, we sampled patches with the dominant plant functional types (PFTs) in the site, -grasses, legumes and non-legume forbs. We harvested the aboveground biomass and then measured soil chemical variables and the size and activity of soil microbial populations. We performed Variation Partitioning analysis on soil activity variables and tested simple effects between three groups of environmental variables: (a) regional geographical, climatic and management variables, (b) local soil variables, and (c) local plant diversity variables. Our results showed that regional, local soil and local plant biodiversity variables accounted for 64.4%, 64.8 and 15.5% of the total variability of soil activity, respectively. However, the unique effects of the three sets of variables were small compared with the shared variation, with the highest variability being explained by the overlap between regional and local soil variables (45.6% of all variation including unexplained). Thus our findings suggest that plant guild effects on soil activity are modulated by regional environmental variables.

Keywords. Plant guilds – Soil changes – Climatic gradient – Community composition.

Les effets des groupes fonctionnels de plantes sur les fonctions du sol changent à traves d'un gradient climatique

Résumé. *Le changement global modifie la composition végétale dans les prairies de montagne, à travers des changements dans l'équilibre des regroupements végétaux. Les systèmes souterrains et aériens sont étroitement liés, et les changements dans la composition végétale peuvent être accompagnés par des changements de fonction et structure du sol. Pour une compréhension approfondie de cette relation, nous avons réalisé une étude afin d'évaluer l'importance proportionnelle des variables régionales, des propriétés du sol, et de la biodiversité sur l'activité du sol. Nous avons recueilli des échantillons de sol et de végétation de six sites le long d'un gradient climatique (334 à 2479 m) dans les Pyrénées Orientales. Nous avons récolté la biomasse aérienne des colonies dominées par des graminées, légumineuses, et herbacées non légumineuses et mesuré les variables chimiques et l'activité des populations microbiennes du sol. Nous avons effectué une analyse de partition de la variance sur les variables de l'activité du sol, et testé les effets entre trois groupes de variables environnementales : (a) régionales géographiques, climatiques, et de gestion, (b) locales du sol, (c) de la diversité végétale. Nos résultats montrent que les variables régionales et locales du sol, et celles de la diversité végétale représentent 64,4%, 64,% et 15,5% de la variabilité totale de l'activité du sol, respectivement. Pourtant, la plus forte variabilité est expliquée par le chevauchement entre les variables régionales du sol et celles locales. Ainsi, nos résultats suggèrent que les effets des regroupements végétaux sur l'activité de sol sont modulés par les variables environnementales régionales.*

Mots-clés. *Regroupements végétaux – Fonctions du sol – Gradient climatique – Composition végétale.*

I – Introduction

Global change alters plant community composition of grasslands (Aguiar, 2005). Particularly, as a response to climate warming, the balance of forbs and sedges in mountain grassland ecosystems shift (Sebastià, 2007), and an increasing shrub encroachment is observed as a result of both climate change (Sanz-Elorza *et al*., 2003) and grazing abandonment (Casasús *et al*., 2007). Changes in plant community structure and composition imply changes in soil function and structure (Thakur and Eisenhauer, 2015). While several studies suggest that diversity effects on soil processes (e.g. nutrient limitations and/or microbial community composition) are driven by climate (Jing *et al*., 2015), little is known about the relative contribution of the regional climatic conditions, the local soil properties, and the local plant diversity on soil activity. For a thorough understanding of this link, we carried out a study to evaluate the relative importance of regional variables (climate and management), local soil properties (soil water content, pH, total nitrogen, dissolved organic nitrogen, dissolved organic carbon, nitrate, ammonium), and local biodiversity (plant diversity and guild interactions) on soil activity. Mountain ecosystems offer a climatic gradient within a relatively small area, being thus an ideal place to study the diversity-climate effects on ecosystem processes.

II – Materials and methods

1. Study site and experimental design

The six study sites are located in Catalonia, Northeastern Spain along a climatic gradient, ranging from arid up to semi-natural subalpine grasslands with a low-intensity management of extensive seasonal grazing. Altitude, mean annual temperature (MAT) and mean annual precipitation (MAP) ranges are 334-2479 m, 2.4-13.9 ºC and 225-1302 mm, respectively. Sampling was carried out at the peak of vegetation growth in the six study sites during 2014. Sampling points were chosen to represent the dominant plant functional types (PFTs), –grasses, legumes, and non-legume forbs–, with three replicates per PFT. In total, nine points were sampled in each study site by placing nine collars of 25 cm diameter where the vegetation was cut at ground level. In the two sites at lowest altitudes, a total of only six collars (grasses and forbs) were placed because legumes were not dominant at the peak vegetation growth. Vegetation samples were separated into species, then oven-dried at 60°C for 48 hours to obtain dry weight of PFT of each collar. For chemical and microbiological analyses, vertical soil samples were extracted with a spatula from the first soil layer (0-10 cm) of each collar. Soil samples were kept at 4ºC until further analyses.

2. Soil analyses

Ammonium and nitrate pools were determined in 2M KCl extractions by a segmented flow analyser AA3 and microbial biomass C and N (MBC and MBN) by chloroform fumigation-direct extraction (Davidson *et al.*, 1989). Nitrification potential (NP) was determined following the soil-slurry method. Soil enzyme activities were determined in homogenised and sieved (2 mm) soils. β- glucosidase and acid phosphatase activities were measured using a 96-well microplate approach (Tian *et al.*, 2010) based on p-nitrophenol release after breaking up a synthetic substrate (p-nitrophenyl glucoside and p-nitrophenyl phosphate, respectively). Urease activity was determined following Kandeler and Gerber (1988).

3. Data analysis

We performed a Variation Partitioning Analysis (PA) on soil activity variables (urease, phosphatase, glucosidase, microbial biomass nitrogen, microbial biomass carbon, potential nitrification) using CANOCO 5. We tested simple effects among three explanatory environmental sets of variables: (a) regional-geographical, climatic and management variables: mean annual temperature

(MAT), mean annual precipitation (MAP), mean annual minimum temperature (TMIN), mean annual maximum temperature (TMAX), mean summer temperature (MST), mean summer precipitation (MSP), sheep grazing, and cattle grazing; (b) local soil variables: soil water content (SWC), pH, total nitrogen, nitrate, ammonium, dissolved organic nitrogen (DON), dissolved organic carbon (DOC); and (c) local plant diversity variables: species richness (S), grass, legume and non-legume forb biomass proportion, and the binary interactions between the three plant functional types. The three datasets of potential explanatory variables had a similar number of variables (8 regional, 7 soil and 7 biodiversity variables).

III – Results and discussion

Variation Partitioning Analysis showed that regional variables accounted for 64.4% of the total variability of soil activity, of which TMIN was the best predictor for soil activity (it adds 57.1 % to explanatory power of this set), followed by management (22% for sheep grazing and 12.8% for cattle grazing). None of the precipitation variables were needed to improve the fit and therefore were not included in the final model. Local soil variables accounted for 64.8% of the variability of soil activity, of which soil ammonium content added 69.3% to the explanatory power of this set. Local plant diversity variables accounted for 15.5% of the variability of soil activity, of which species richness was the single first variable selected by the forward procedure and adds 26.4% to the explanatory power of this set. Nonetheless, PFT and their interactions were the most explanatory variables, as they accounted for the rest of the variability in the biodiversity set. PFT binary interactions were more explanatory than the main effects, overall adding 55.4% to explanatory power of the biodiversity set, as compared to 19.46% of main effects. Among them, the effects of forbs were the most relevant (16.8%). The interaction between legumes and non-legume forbs added 24.3%, being the second single most explanatory variable. The unique effects of the three sets of variables were small compared with the shared variation (Fig. 1), with the highest variability being explained by the overlap between regional and soil variables (55.6% of all variation including unexplained), and followed by the overlap among the three sets (12.7%; Fig. 1).

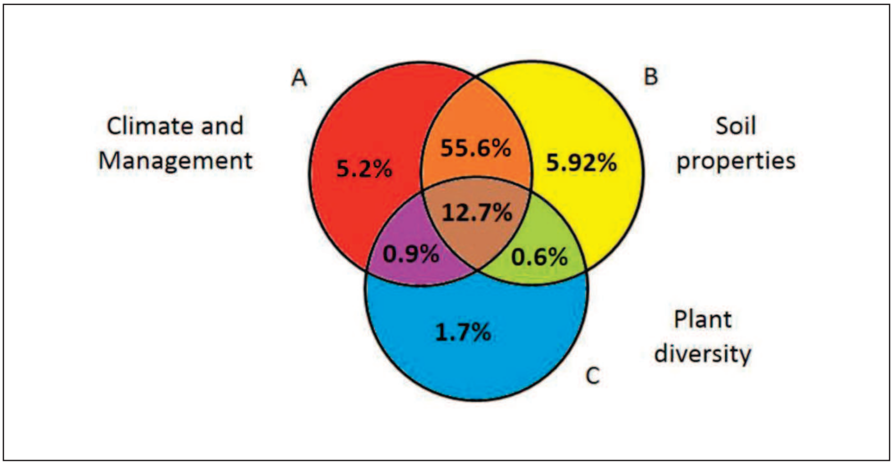

Fig. 1. Distribution of explained variation of soil activity by the three sets of variables. A: regional variables related to climate and management (MTMIN, Sheep, Cattle, MST, MAT); B, local soil variables (Ammonium, pH, Moisture, Total N, Nitrate, DOC, DON); C, local plant diversity variables (S, FL, GL, GF, Forb, Grass, Legume).

Classen *et al.* (2015) distinguished between direct and indirect effects of climate change on ecosystem processes, indirect effects being defined as those mediated by shifts in diversity, community composition and functional traits. These authors hypothesize that indirect effects of climate change on microbes mediated through plants may be stronger than direct effects of climate on shaping microbial community composition and function. Our results show that soil activity is better explained by the combined effects of climate, management, soil properties and plant diversity and that no unique factor can explain the variability of soil activity. On the contrary, Thakur *et al.* (2015) found that soil microbial biomass carbon is driven by plant diversity and that no interactions with global environmental change factors occur. The relative importance of management as a driver of soil activity should be pointed out, suggesting a relevant role of management to attenuate global change effects on soil activity.

IV – Conclusions

The effects of plant guilds on soil activity are modulated by regional environmental variables. The combination of climate, management, soil properties and plant diversity explains the variability of soil activity better than any of the single factors.

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