Soil Amelioration In Mediterranean High-Mountains Of Central Spain

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Research Article

Keywords: soil amelioration, Mediterranean high-mountains, soil nutrient content, vegetation patches.

Posted Date: March 7th, 2022

DOI: <https://doi.org/10.21203/rs.3.rs-1302600/v1>

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Abstract

Aim: Link the well-documented information on plant community assembly to the changes in soil properties, a relationship rarely studied in the less studied mountains of Central Spain.

Methods: We assessed the shifts in soil nutrients, soil organic matter (SOM), and soil properties related to texture along an elevation gradient and two transects (Val-CH, Pan-Nav) in Sierra de Guadarrama, central Spain, between bare soil and vegetation-covered patches. Additionally, we calculated the Relative Interaction Index (RII) to evaluate the strength and direction of the dominant life-form effect of each soil variable.

Results: Our results confirmed improved soil properties under vegetation-covered patches compared to bare soils, always irrespective of elevation. Soil properties and RIIs showed no relationship with the dominant life-form. Significant differences in soil chemical properties were found between transects, with more acidic soils, higher nutrients, and SOM in the herb-dominated (Val-CH) than in the cushion-dominated one. The soil amelioration effect was more pronounced at mid-elevations, resembling the humped patterns observed in the Andes, which may be related to the two severity gradients acting in Mediterranean high-mountains.

Conclusions: Maintaining a high C/N ratio among elevations could indicate an excess nutrient input in these systems to benefit vegetation growth. However, we assume slow SOM decomposition rates based on the non-significant differences in the C/N ratio between microhabitats and previously reported decreased microbial activity. These results could directly associate with low mineralization rates and, thus, reduced nutrient availability for plants.

Introduction

The plant-soil relationship is regarded as an essential driver of an ecosystem's dynamics seeing that the growing vegetation drives the environmental variation and, concurrently, shapes the complex spatial and temporal heterogeneity of the soil physicochemical properties (Bagstad et al. 2006; Butterfield and Briggs 2009; Liu et al. 2019; Veen et al. 2018).

In arid and semi-arid ecosystems, it is common to encounter non-uniform vegetation covers exhibiting large spatial and localized structures, i.e., vegetation patterns (Greig-Smith 1979). This spatial distribution may consist of isolated or randomly distributed patches or gaps, with spots of bare soil found within the grass matrix (Bordeu et al. 2016; Tildi et al. 2008). Biomass accumulates in soils beneath vegetation patches, subsequently modifying its biogeochemical processes (Kelly et al. 1996; Schlesinger et al. 1990). This process elicits the so-called "fertility islands" (Jackson and Caldwell 1993; Kelly et al. 1996; Schlesinger et al. 1996). Vegetation patches with sufficient stem and biomass densities can serve as obstructive surfaces that slow and trap runoff water, water- and wind-borne sediments and litter, and nutrients from open inter-patch areas (Schlesinger et al. 2000). These water and nutrient inputs can benefit the vegetation in the patch, enhancing the pulse of plant growth within it (Ludwig et al. 2005).

The positive interactions theory predicts that plants can positively affect other plants through various effects (Lortie et al. 2004; Sotomayor and Lortie 2015). Positive plant-plant interactions may be critical in severe environments, as they influence the structure of plant communities and depend on environmental conditions and functional strategies of the interacting species (Armas and Pugnaire 2005; Brooker et al. 2008; Callaway 1995; Callaway and Walker 1997; Goldberg 1996; Michalet 2007; Soliveres et al. 2011). The identity and characteristics of the species may be of particular importance on the overall balance between the competition and positive effects of sheltering species due to this species-particular ability to transform the environment and interact with others (Baraza et al. 2006; Callaway 1998; Gómez-Aparicio et al. 2004; Tielbörger and Kadmon 2000). The positive effects between species are more likely to occur in stressful environments such as high mountains. Here, the variety of disturbances and severe conditions characteristic of these habitats are the main constrain for plant growth and limit resource acquisition (Körner 2003). Thus, the canopy of certain species may exert ameliorative influences on its neighbors, favoring their growth (i.e., cooling temperatures, lower the evaporative stress, increase soil moisture, high nutrient availability), to the extent it outweighs the negative, competitive impact of growing in close associations (Cavieres et al. 2002). The balance between these effects depends on how the species involved modify their environment, including changes in nutrient dynamics and water availability (Breshears et al. 1998; Hobbie 1992).

According to the stress gradient hypothesis, positive interactions are most beneficial for protégés in harsh environments, where abiotic conditions are typically limiting (Bertness and Callaway 1994). Pioneer nurses in semi-arid habitats could have a higher tolerance to the major environmental stresses (i.e., light intensity and drought), which, in turn, could influence the conditions and

resources provided to their neighbors. In turn, these pioneer nurses could either have slower resource-uptake rates owed to stress-tolerant traits that enable their establishment in inhospitable areas, compared to late-successional nurses. Alternatively, the pioneer nurses could display a higher competitive ability, translating into a faster resource depletion than in late-successional ones, by displaying traits linked to ensuring their fast colonization of open gaps (Grime 1977, 2002; Kazakou et al. 2006).

A two-phase plant community pattern is the expected norm in harsh habitats, with plants grouped in inconspicuous patches with varying patterns going from stripes to spotted clumps as a function of slope anisotropy (Deblauwe et al. 2011; Wiens 1976). These vegetation clumps result from intrinsic self-organized mechanisms related to the performance of the dominant species in the patch, where plant-to-plant interactions control the feedback between biomass and water (Gilad et al. 2004; Lejeune et al. 1999; Meron 2012). As described by Körner (2003), vegetation patches in high-mountain habitats are usually dominated by one or few graminoid or cushion-like species. The great differences in environmental conditions within relatively short distances in high mountain areas offer the appropriate environments to study how the plant-soil relationship changes across relatively small scales (Körner 2003). The soil characteristics in high mountain areas are determined by the environmental conditions and vegetation, coupled with the strong influence of the age and type of the mountains on their ecosystems and soils (Egli & Poulénard, 2016). These variations are owed to the morphodynamic processes in these areas, which create specific habitats (e.g., scree, landslides, avalanches) that influence species richness and landscape elements (Egli and Poulénard 2016; Körner 2003). The development of plant communities in high-mountain areas is closely coupled to the primary substrate and other site factors (Burga et al. 2010; Frey et al. 2010). As different species often co-occur at the same spots, the effect of nurse plants can change between sites due to differences in microclimate and availability of soil resources, especially through an elevation gradient (Cavieres et al. 2008).

Mountain soils play a major role in the functioning and conservation of the unique ecosystems found within the mountain ranges (Egli and Poulénard 2016). Since high mountain ecosystems are considered particularly sensitive to climate change (Nogués-Bravo et al. 2008), it is essential to assess whether the overall warming and associated changes in rainfall patterns could influence soil properties and vegetation. Thus, to further our understanding of the potential effects of plant community composition on soil properties, we performed a field survey in the high-mountain areas of Sierra de Guadarrama (central Spain).

The main objective of this work is to link the well-documented information on plant community assembly to the changes in soil properties, a relationship rarely studied in these summits. Based on the significantly higher water and nutrient input under vegetation patches compared to bare areas reported across biomes (Callaway and Walker 1997; Cavieres et al. 2006; Holmgren et al. 1997; Ludwig et al. 2005; Maestre et al. 2009; Soliveres et al. 2011) we expect 1) a stronger amelioration effect in vegetation-covered patches compared to bare soils, with higher nutrient content and improved soil structure. The stress gradient hypothesis together with the two stress gradients in Mediterranean high-mountains, (low-temperature stress increasing with elevation, drought stress enhancing with decreasing elevation; Giménez-Benavides et al. 2007a) leads us to expect 2) the size of the soil amelioration effect could enhance parallel to the intensification of the environmental stress gradients. Thus, being greater at the highest and lowest limits of the altitudinal gradients. Mediterranean high-mountains occur as biphasic habitats, with plants occurring in clumps, dominated by so-called “engineers,” interspersed in bare ground areas (Milhoc et al. 2016; Pescador et al. 2014). Hence, we expect that 3) the dominant life form in these vegetation patches (i.e., cushion or herbaceous) influences the soil amelioration rate provided by vegetation, having cushions exert a stronger ameliorative effect given their extensively documented facilitative behavior (Cavieres et al. 2014).

Materials And Methods

Study site and selected species

The study area was set in the community of xerophytic Mediterranean high-mountain pastures growing above the tree line, representing the potential vegetation in Sierra de Guadarrama. The Sierra de Guadarrama (Central Spain, 4°44'14" N, 3°43'48" W), is an E-W running mountain range distinguished by a Mediterranean-type climate, with an intense dry season during summer (June–September, less than 10% of total annual rainfall; Gutiérrez-Girón and Gavilán 2013). The predominant lithology in this mountain range is of poorly developed and acidic soils of plutonic and metamorphic origins (i.e., granites and gneiss, respectively), with little depth due to the pronounced slopes.

Vegetation at the tree line (1900–2000 m.a.s.l.) is dominated by *Pinus sylvestris* L., interspersed in a matrix of shrubs (*Cytisus oromediterraneus*, *Juniperus communis* subsp. *alpina*) and perennial herbs, such as the dominant grass *Festuca yvesii* subsp. *lagascae* (Devesa and Martínez-Sagarra, 2021; = *Festuca curvifolia* Lag. ex Lange). With increasing elevation (from 2100–2200 to 2430 m), *F. curvifolia*, a graminoid with stripe-clonal growth that generally forms tightly-packed clumps, takes over these areas creating an excellent example of a patchy xerophytic pasture, where spots and stripes grow perpendicularly to the slopes due to environmental severity (Pescador et al. 2014). In this community, *F. curvifolia* coexist with more than 20 high-mountain specialists interspersed within the *F. curvifolia* clumps or in the ground terraces between vegetation stripes (Gavilán et al. 2002; Pescador et al. 2014). In the remnants of these communities, there is an evident abundance of cushion-type life forms (e.g., *Armeria caespitosa*, *Jasione centralis*, *Silene elegans*, *Minuartia recurva*) coexisting with hemicryptophytic taxa (e.g., *F. curvifolia*, *Jurinea humilis*, *Senecio boissieri*). The community settles on soils whose primary source of soil moisture comes from rainfall and snow-melting water, seeing a progressive reduction alongside the advancement of the summer season (García-Fernández et al. 2013; Giménez-Benavides et al. 2011; Gutiérrez-Girón and Gavilán 2013).

Field Sampling

We sampled 200 patches from the high-mountain areas in Sierra de Guadarrama, commonly located above 2100 m. The sampling was conducted along two elevation transects in slopes with different orientations which owe to the changes in vegetation. The first transect is generally N-oriented and extends from 2140 to 2280 m, covering the area known as the hill of Valdemartin towards the top of the summit in Cabezas de Hierro. Thus, hereafter it will be referred to as Val-CH. The second transect is generally NW oriented and goes from 2100 to 2230 m, in the sector known as Loma de Pandasco, thus called henceforth Pan-Nav. The selected patches were identified as isolated structures surrounded by bare soil areas. The total number of species, and plant cover, in percentage, was recorded for every patch, together with the major and minor diameters of the patch, elevation, and exposure. Of the 200 patches sampled, 102 contained only one species, while the remaining patches comprised up to nine species (i.e., multi-species patch). Dominant species and life form were identified in each patch. The vegetation-covered patches were classified into three different stages of patch development depending on their floristic composition, following the categorization given by Gavilán et al. (2002).

Soil properties (Physico-chemical)

Soil samples were taken from five soil cores (located in the four corners and the center of the plot) and merged before analysis. As most nutrients are usually confined to the upper 5–10 cm of the profile (Entry and Emmingham 1995), only the first 10 cm were considered for soil sampling. Soil samples were air-dried at room temperature for about one month and then sieved in the laboratory for their analysis.

The following variables were estimated: fine-earth fraction for the total natural soil (< 2 mm), fine gravels (2–20mm), and gravels (> 20 mm), expressed as a percentage. Texture percentages for sand, silt, and clay follow the limits of the Soil Conservation Service (1975), and they were determined by the sedimentation pipette method.

Chemical analyses of pH in H₂O and KCl were made with a glass electrode in a suspension of soil in deionized water (1:2.5 by volume) and 1M KCl, respectively. Soil organic matter content (SOM, %) was determined in the fine-earth fraction using the Walkley and Black dichromate acid oxidation method (Black, 1967). Total nitrogen (N_{TOT}, %) was determined according to the Kjeldahl method and expressed as a percentage. Total phosphorous (P; Burriel and Hernando 1950) and potassium (K) adsorbed to colloid were both determined and expressed in ppm (Soil Salinity Staff 1954).

Relative Interaction Index

The Relative Interaction Index (RII) was estimated to assess the strength and direction of the dominant plant effect of each variable with the following formula (Armas et al. 2004).

$$RII = \frac{P_v - P_0}{P_v + P_0}$$

The terms P_v and P_0 correspond to the parameter for each variable in the vegetation-covered patches and bare soil patches, respectively. The RII varies between - 1 and 1 and, for this study, higher values of each soil variable from vegetation-covered

patches can be interpreted as the evidence of ameliorated, improved soil conditions compared to those from bare patches (i.e., fertility islands; (Jackson and Caldwell 1993; Schlesinger et al. 1996).

Statistical analyses

A one-way PERMANOVA was performed to compare the average values for each soil property under the vegetation-covered patch vs. their bare soil counterparts, establishing the sampling microhabitat (covered vs. bare soil) as the explanatory variable. The PERMANOVAs were performed using the “adonis2” function from the “vegan” package (Oksanen et al. 2019), with the probability of type I error established at 95%, using the Euclidean distance metric and performing 9999 permutations. This robust technique was implemented given the small number of replicates and lack of normal distribution in the data. Pairwise comparisons were conducted to know which patches were significantly different. The Bonferroni posthoc test was used to establish the probability of type I error at 99%.

Before conducting the PERMANOVAs, we checked for multicollinearity among the predictors selected from the PCA (altitude, locality, transect, number of species, cover, dominant life form, and microhabitat) to avoid redundancy among them. The latter was achieved by assessing the variance inflation factor (VIF) with the “vif” function of the “car” package (Fox and Weisberg 2011). Given that maximum VIF values were lower than three, all variables were included in the initial models.

To select the most significant predictors of changes in the soil properties (i.e., nutrients, SOM, and particle size), we performed an overall PCA analysis using the packages “stats,” “Factoextra,” and “FactoMineR” (Kassambara and Mundt 2017; Le et al. 2008; R-Core-Team 2018). An additional PCA analysis was performed only with data from the vegetation patches to decide the predictors of the changes in the soil properties within these patches. The differences in the soil conditions were correlated using Spearman’s rho, allowing assessing whether the strength of the amelioration effect (i.e., RII) varied among elevations. Additionally, the relative plant cover (% cover, no. species) and data related to the successional stage of the patch (i.e., dominant species, patch stage) were correlated with the nutrient and SOM values for each patch via Spearman’s rho correlations to find a possible influence of the vegetation status on the variations in soil conditions.

Results

Effects of vegetation cover on soil properties

As expected, soil properties significantly improved under vegetation-covered patches than bare soils (Fig. 1, Table 1; $p < 0.01$). These differences were always irrespective of elevation ($p > 0.05$; Table 1, S1). The Val-CH soils are more acidic than in the Pan-Nav transect, together with a lower delta pH in the former. As for the soil texture, sand constituted the major soil fraction in both microhabitats, without significant differences between them ($p > 0.05$; Table S2). Differences in the soil’s physical properties did not vary significantly with altitude or microhabitat.

Table 1

Mean values of the soil chemical properties for the studied vegetation patches in both studied transects (Valdemartin-Cabezas de Hierro, Val-CH; Loma de Pandasco-Navalondilla, Pan-Nav). Values for total soil nitrogen (N_{tot}), soil organic matter (SOM), potassium (K), and phosphorus (P) are given in means per site ($n = 5$), with their respective Relative Interaction Index (RII). Different lowercase letters indicate statistically significant differences between microhabitats, and different uppercase letters indicate significant differences among sites (one-way PERMANOVA, $\alpha = 0.05$). Orient, plot orientation; Microhab, microhabitat; C/N, C/N ratio.

Transect	Elevation (m.a.s.l.)	Orient	Microhab	N_{tot}	RII_N	SOM	RII_{SOM}	C/N	K	RII_K	P	RII_P
Val-CH	2140	N	Veg	0.40 ^a	-0.1 ^A	11.33 ^a	0.29 ^A	28.3 ^a	162.61 ^a	0.01 ^A	12.4 ^a	0.04 ^A
			Bs	0.34 ^b		6.17 ^a		18.1 ^a	160.78 ^a		11.33 ^a	
	2180	NE	Veg	0.33 ^a	-0.1 ^A	6.32 ^a	-0.08 ^A	17.7 ^a	80.6 ^a	0.1 ^A	8.89 ^a	0.2 ^A
			Bs	0.43 ^b		7.41 ^b		17.2 ^a	68.8 ^a		5.29 ^a	
	2240	N	Veg	0.55 ^a	0.2 ^A	12.12 ^a	0.27 ^A	22.0 ^a	109.95 ^a	-0.2 ^A	11.6 ^a	0.01 ^A
			Bs	0.34 ^b		6.17 ^b		18.1 ^a	160.78 ^a		11.33 ^a	
	2245	N	Veg	0.54 ^a	0.2 ^A	12.48 ^a	0.2 ^A	23.1 ^a	133.4 ^a	-0.09 ^A	26.17 ^a	0.4 ^A
			Bs	0.34 ^b		6.17 ^b		18.2 ^a	160.78 ^a		11.33 ^a	
	2260	NW	Veg	0.46 ^a	0.03 ^A	9.3 ^a	0.11 ^A	20.2 ^a	86.65 ^a	0.12 ^A	10.86 ^a	0.35 ^A
			Bs	0.43 ^b		7.41 ^b		17.2 ^a	68.7 ^a		5.29 ^a	
	2280	N	Veg	0.42 ^a	0.1 ^A	7.95 ^a	0.13 ^A	18.9 ^a	112.08 ^a	-0.18 ^A	10.01 ^a	-0.06 ^A
			Bs	0.34 ^b		6.17 ^b		18.1 ^a	160.78 ^a		11.33 ^a	
Pan-Nav	2160	NW	Veg	0.23 ^a	0.02 ^A	3.5 ^a	0.11 ^A	15.2 ^a	63.53 ^a	0.19 ^A	11.28 ^a	-0.3 ^A
			Bs	0.22 ^a		3.29 ^b		14.9 ^a	43.04 ^b		20.68 ^b	
	2170	N	Veg	0.18 ^a	-0.1 ^A	4.05 ^a	0.1 ^A	22.5 ^a	80.8 ^a	0.31 ^A	3.69 ^a	-0.70 ^A
			Bs	0.22 ^b		3.29 ^b		14.9 ^a	43.04 ^b		20.68 ^b	
	2175	E	Veg	0.35 ^a	0.23 ^A	6.31 ^a	0.31 ^A	18.0 ^a	160.67 ^a	0.58 ^A	4.11 ^a	-0.67 ^A
			Bs	0.22 ^b		3.29 ^b		14.9 ^a	43.04 ^b		20.68 ^b	
	2190	NW	Veg	0.3 ^a	0.03 ^A	8.51 ^a	0.24 ^A	28.4 ^a	120.30 ^a	0.33 ^A	11.54 ^a	-0.36 ^A

Transect	Elevation (m.a.s.l.)	Orient	Microhab	N _{tot}	RII _N	SOM	RII _{SOM}	C/N	K	RII _K	P	RII _P
			Bs	0.28 ^b		5.18 ^b		18.5 _a	61.02 _b		24.74 _b	
2210	NW	Veg		0.59 ^a	0.44 _A	12.87 ^a	0.52 _A	21.8 _a	162.93 _a	0.75 ^A	ND	ND
		Bs		0.23 ^b		4.12 ^b		17.9 _a	22.82 _b		9.54	
2225	SW	Veg		0.19 ^a	-0.1 _A	3.7 ^a	-0.05 _A	19.5 _a	50.62 _a	0.38 ^A	7.24 _a	-0.14 ^A
		Bs		0.23 ^b		4.12 ^b		8.7 _a	22.82 _b		9.54 _b	
2230	NE	Veg		0.32 ^a	0.16 _A	8.09 ^a	0.33 ^A	25.3 _a	127.74 _a	0.70 ^A	8.34 _a	-0.07 ^A
		Bs		0.23 ^b		4.12 ^b		17.9 _a	22.82 _b		9.54 _b	

The analyses showed significant differences in soil nutrients and SOM between transects, with significantly higher values in the Val-CH than in the Pan-Nav transect ($p < 0.001$; Figs. 2, 3; Table 1). Differences in soil nutrients and SOM between microhabitats were significant between both transects ($p < 0.01$). In addition, changes in N_{tot} and SOM were positively correlated with elevation (Supplementary Table S3); however, these differences were always non-significant ($p > 0.05$; Supplementary Table S1). Likewise, the analyses revealed a strong correlation between the N_{tot} and SOM in the study sites (Supplementary Table S3).

The presence of vegetation positively influenced changes in SOM throughout the entire elevation gradient in the Pan-Nav transect (Table 1). The N_{tot} and SOM were significantly different between microhabitats in Pan-Nav sites, with significantly higher values in vegetation-covered than in bare soil patches ($p < 0.01$; Figs. 3a, b), but irrespective of elevation ($p = 0.22$; Table 1). For the Val-CH transect, the N_{tot} and SOM were usually higher in the vegetation-covered patches, with few exceptions (see Table 1), and significantly different between microhabitats ($p = 0.01$; Table 1). Overall, the C/N ratio maintained relatively high values in both microhabitats without significant differences (Table 1; $p > 0.05$), ranging between 17.1–22.5 in the Val-CH transect (with one exception at 2140 m) and between 14.9–28.4 in the Pan-Nav transect. Differences were non-significant between transects or elevations for this parameter ($p > 0.05$).

Similar to the results for SOM and N_{tot}, the soil K and P showed to differ significantly between transects ($p = 0.001$, Table 1). Overall, K was significantly higher in the Pan-Nav than in the Val-CH transect ($p = 0.001$) with the highest K values measured at mid-elevations of the Pan-Nav transect, and always with higher content under vegetation-covered patches than bare soils (Fig. 3c).

Moreover, significant differences in the K and P were found between microhabitats in the Pan-Nav transect ($p < 0.001$; Table 1), while in the Val-CH transect, the substantial differences were non-significant regarding microhabitat or elevation ($p > 0.05$) and had no clear pattern with elevation. Overall, P values were lower beneath vegetation-covered patches than in bare soils, with the discrepancies augmenting opposite to elevation, particularly in sites from the Val-CH transect (Fig. 2d). Significant differences between microhabitats were found in P in soils from the Pan-Nav transect (Table 1). Moreover, P showed to be positively correlated with elevation (Supplementary Table S3), though changes were non-significant (Supplementary Table S2).

Both PCA analyses revealed that the first principal component increases with increasing SOM, N_{tot}, and K, which could be viewed as a general measure of soil nutrients (Fig. 4a, b). Soil nutrients and SOM values increased with elevation in both vegetation-covered and bare soil patches, but these were non-significant. These results show that soils from patches located at higher elevations tend to have considerably greater SOM and N_{tot}. In contrast, those in lower sites have reduced contents of these chemical features. The PCA within vegetation patches showed that the second principal component is related to physical features, increasing proportionally to the content of coarse gravels and decreasing fine gravels. Thus, the PC2 can be interpreted as a measure of the

soil particle size in terms of changes in the type of vegetation cover. Lastly, the increases in the PC3 with the successional stage of the patch and soil P show that the patches with a more advanced successional stage have higher P content beneath them than younger patches.

Amelioration effect, RII

The size of the amelioration effect (RII values) exerted by the dominant life form differed between transects. The successional stage of the patch showed no relationship with the changes in the nutrients or SOM. The values for soil properties and RIIs did not vary significantly with the dominant life form in each patch (Supplementary Table S1). In general, high RII_N and RII_{SOM} values between 2140–2245 m.a.s.l. showed a strong amelioration effect at mid-elevations of both transects that contrasted the observed deterioration in soil conditions towards the extremes of the elevation gradient based on the low RIIs. The dominant life form and plant cover were also positively correlated with the changes in SOM ($p < 0.05$; Supplementary Table S3), related to the strong amelioration effect found at mid-elevations.

There was a significant effect of vegetation on ameliorating the soil nutrients and SOM content ($p = 0.002$) only in the Pan-Nav transect. However, these differences did not change significantly through the elevation gradient or among sites ($p = 0.38$ and 0.2 , respectively). As for the Val-CH transect, the effect of soil amelioration by the vegetation patches decreased towards the extremes of the elevation gradient. A stronger amelioration effect was observed at mid-elevations, as shown in the higher values for RII_N , RII_{SOM} , RII_P compared to their values at the extremes of the elevation gradient in this transect. Generally, higher RIIs were obtained for the Pan-Navs transect compared to the Val-CH one. Nevertheless, and similar to the Val-CH counterpart, the soil amelioration effect was stronger at mid-elevations (2175–2210 m.a.s.l.; Table 1) and decreased towards the ends of the elevation gradient. None of the changes in the RIIs were significant with elevation (Val-CH, $p = 0.26$; Pan-Nav, $p = 0.33$).

Discussion

Plants create buffered microsites

Plant communities growing in adverse areas are expected to be structured by the stress tolerance of the individual species that comprise them (Lortie et al. 2004). Consistent with the widespread presence of fertility islands in high-mountain environments (Cavieres et al. 2006; Escudero et al. 2004), our findings confirm that the expected improved soil properties remained constant beneath vegetation-covered patches. However, the amelioration effect was not associated with the type of dominant species in the patch (cushion or herbaceous), nor did it differ significantly through the elevation gradients.

Contrasting the observations in bare soils, the spatial heterogeneity of soil properties was gradually shaped by the generations of pioneer vegetation, generally causing an improvement in the soil environment beneath vegetation patches in advanced stages of development (Fig. 5, Supplementary Table S1). A case in point is the relationship found between the increases in P content with the maturity of the patch successional stage, which may be related to a faster resource depletion by pioneer nurses within young vegetation patches compared to their late-successional counterparts, to prompt the colonization of open gaps (Grime 1977, 2002; Kazakou et al. 2006). These results provide further information on how the plant-soil interaction contributes to plant establishment in adverse environments (Li et al. 2021).

Despite differences in soil amelioration across the elevation gradient being generally non-significant, differences were greater in intermediate elevations (Fig. 5). Our results resemble the humped patterns observed by Milhoc et al. (2016) in a larger elevation gradient in the Mediterranean Andes and may be attributed to the two severity gradients in Mediterranean high-mountains: freezing stress increasing with altitude; drought stress increasing as elevation declines (Cavieres et al. 2006; Giménez-Benavides et al. 2007b). Additionally, and similar to the findings by Cavieres et al. (2002), we observed an increase in the abundance and number of species within vegetation patches proportional to elevation. These findings suggest an enhanced ameliorating role of certain species in the vegetation patches at higher elevations, possibly in response to the aggravation of the severity gradients. This increased amelioration would thus favor recruitment within these patches and plausibly improve the associated species' performance. In general, our results suggest the high-mountain communities from Sierra de Guadarrama show endurance to current

environmental-induced shifts, resembling the positive interaction reported by Lloret and Zedler (2009) and Lloret et al. (2012) in other Mediterranean habitats and plant communities.

Compared to bare soils and patches with other dominant species, the substantially richer soils found underneath *F. curvifolia* (Table 1; Supplementary Table S1) further support previous studies stating that *F. curvifolia* patches behave as “islands of fertility,” ameliorating soil conditions beneath them (Escudero et al. 2004; Pescador et al. 2014). Nevertheless, and despite the presence of these “fertility islands,” our findings further support the report by Pescador et al. (2014) indicating *F. curvifolia* does not act as a nurse or facilitator species in these summits. The latter occurs since it blocks the growth of other species within its clumps, exerting an allelopathic effect or “repulsion halo” (Gutiérrez Girón and Gavilán 2010; Pescador et al. 2014). Instead, this species should be considered a primary colonizer, forming monospecific bands of vegetation, thanks to its clonal growth, and improving the soil underneath to promote its expansion in austere circumstances (i.e., poor soils; (Gavilán et al. 2002). As per its allelopathic effect, the thick litter and leaf mats created by *F. curvifolia* may add to its dominant nature by reducing or impeding seedling emergence of alternative species (Suding and Goldberg 1999). These thick leaf mats could be counterbalancing the positive effect of the ameliorated soil conditions found beneath its canopy with considerable light limitations (Suding and Goldberg 1999).

Enhanced biological activity and soil processes can improve soil aggregation and macroporosity, which increase soil infiltrability and, consequently, the ability of vegetation patches to obstruct, capture, and store runoff water and nutrients (Ludwig et al. 2005). Altitude and vegetation must also be accounted for in high-mountain environments since they lead to differences in organic matter decomposition rates (Gutiérrez-Girón et al. 2015). In this line, other factors such as litter and root extension may also play a significant role in controlling runoff-run-on processes. The buildup of litter and substantial SOM values found in patches with *Thymus penyalarensis* as the dominant species (Supplementary Table S1) could be the effect of the antimicrobial properties attributed to this genus, limiting fungi or bacterial development or activity (Dorman and Deans 2000). These antimicrobial properties might be slowing down the SOM decomposition and lowering the mineralization rates, which could explain the high C/N ratio found in these patches (Dorman and Deans 2000; Kalbitz et al. 2003). Our findings relate to those by Gutiérrez-Girón et al. (2015) reporting a high soil organic carbon accretion under *Juniperus* shrubs that correlates with a reduced respiration rate of soil microorganisms. The high SOM content found in the understory of *T. penyalarensis*, coupled with an absence of significant differences in the soil C/N ratio between microhabitats, could also be related to high chemical recalcitrance of C substrate (Duboc et al. 2014; Gutiérrez-Girón et al. 2015; McCulley et al. 2004). Taken as a whole, the present findings suggest a pattern of generally high recalcitrancy of the litter in these mountains, though further studies focusing on each species are required.

Chemical weathering comprises the processes of mineral dissolution, alteration, and transformation of initial mineral phases to those that are more stable at the surface of the earth (Egli et al. 2014). Wind could significantly influence critical soil-related effects at high elevations, such as soil erosion and surface drying. The common incidence of strong winds in the Sierra de Guadarrama summits and limited chemical weathering typical of old and flat topographies like the one of this mountain range could trigger the lifting of lighter substrates leading to a stripped soil surface (i.e., dry soils, deficient in nutrients (Egli et al. 2014; West et al. 2005). The incidence of these conditions could explain the lack of significant differences found between microhabitats in the present study. K is a monovalent cation abundant in the lithological material from the area that in soils with a high sand percentage wash away easily with water. Thus, chemical weathering could explain the generally lower K values found in bare soils than in those covered by vegetation. Furthermore, the high amounts of accumulated biomass found in vegetation patches (high SOM, see Supplementary Table S1) could suggest a seemingly soil cover, retaining a certain amount of soil aggregates against the runoff be caused by the effect of wind, rain, and snow melting and enhanced nutrient enrichment. However, the high C/N ratios calculated in all vegetation patches and the slackened microbial activity described by Gutiérrez-Girón et al. (2015) put forward this alleged excess nutrient input may not necessarily translate into higher mineralization rates, adding to the scarce significant differences between microhabitats.

Cushion plants are well-known ecosystem engineers (Cavieres et al. 2006; Jones et al. 1994) as they strongly modify their surrounding environment and affect community assembly processes (Badano and Cavieres 2006; Schöb et al. 2012). Cushions are the dominant life-form in the Pan-Nav transect (Supplementary Table S1) inferring the observed soil amelioration results from the “nursing” effect of cushions in these patches. The lack of significant differences with elevation verifies a pattern of soil amelioration by cushions in these high-mountains which appears to be robust to the broad-scale environmental gradients and more related to site-specific conditions (i.e., neighboring species, soil microbial activity). The latter is based on the observed lack of significant

differences in the C/N ratio between microhabitats indicating a slow SOM decomposition rate. The fair amount of residue (pers. obs.) and maintenance of a high C/N ratio found throughout the elevation gradients (Table 1) further indicates an overall declined SOM decomposition due to a reduced microbial activity (priorly described in these summits Gutiérrez-Girón et al. 2015) which directly associates with low mineralization rates. Thus, these findings could translate into a reduced nutrient availability for plants in these habitats that plausibly favors the enhancement of competition rather than facilitation, implying cushions exert a meager impact on ameliorating soil conditions in the Pan-Nav transect (Escudero et al. 2004; Gutiérrez-Girón et al. 2015). Species of *Festuca* growing in the Andean highlands (i.e., *Festuca orthophylla*) are characterized by a shallow rooting system covering up to 6-fold the area of the above-ground canopy, which allows the plant to access resources in a total area equivalent to 6-fold that of their canopy (Monteiro et al. 2011). Generally, tussock grasses (e.g., *Festuca* species) are thought of as strong competitors due to their vast above- and below-ground biomass (Grime 2002). Their root network is the most important mechanism for capturing resources in scarce environments and allowing for their distinctive high competitiveness (Bordeu et al. 2016). Modeling studies have shown how the spatial organization of tussock vegetation in semi-arid ecosystems is mediated by the competitive interactions and a reduction in aridity (Bordeu et al. 2016). Similar to the observed in *F. orthophylla* (Monteiro et al. 2011), we assume that *F. curvifolia* has an enlarged root system covering larger areas than the canopy to enable soil exploration. The latter could result from a strong root competition driven by the low nutrient conditions in the study area (i.e., poor soils), further reducing the possibility of positive effects on neighboring species. That could be why we observe scarce significant differences between soil nutrients between vegetation-covered dominated by this tussock and bare soil patches (i.e., Val-CH transect; Table 1). An additional explanation could be the possibility of a more intense competition occurring within the shallow soils in our system. This enhanced competition could be reflecting limited root segregation due to a lack of space and high species richness in these vegetation patches. Thus, this could be restricting the uptake of soil resources from the same depth as observed in other grasslands (i.e., niche overlap over the soil depth gradient; Dornbush and Wilsey 2010; Martorell et al. 2015).

Similar to Mihoc et al. (2016) and Escudero et al. (2004), the present results suggest soil amelioration occurs irrespective of the status of the vegetation patch and elevation. These findings allow suggesting a minor effect of facilitative interactions in the studied gradient that could be related to the shallowness of the soils and their relatively poor nutrient content, compared to other habitats. In turn, we could assume a stronger competition effect occurs in these summits due to stress caused by the lack of a resource (e.g., water, low nutrient availability). Consequently, the plants growing in these sites tolerate the stress and do not require its amelioration by neighboring species (Maestre et al. 2009). Nonetheless, more studies exploring in-depth the balance between the ameliorative effects and competitive impacts in these plant associations are required to accurately describe these dynamic processes in Sierra de Guadarrama (Callaway and Walker 1997). These studies should be carried out mainly focusing on cushion species dominating in alternative patches in Sierra de Guadarrama due to their well-known facilitative nature and seeing as these interactions may vary in function of changing environmental factors in space-time, life stages of the dominant species, or shifts instigated by a dynamic and spatial organization (Holmgren et al. 1997; Meron 2012; Pescador et al. 2014; Soliveres et al. 2010).

Declarations

Acknowledgments

This project has been partially funded by the Madrid Regional Government through the REMEDINAL TE-CM (S2018/EMT-4338) project and by the Spanish Government with the FORADMIT Project (AGL2016-77863-R). Additional funding has been granted by the ECOSINK project (2019-T1/AMB-12782) to cover the staff salary expenses.

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Figures

Figure 1

Boxplot showing the overall differences under bare (bs) vs. vegetation-covered (veg) patches for a) total soil nitrogen (N_{tot} , %), b) soil organic matter (SOM, %), c) phosphorus (P, ppm), and d) potassium (K, ppm) in the soil samples. The solid line in each box diagram indicates the median, the box enclosure is the interquartile range, and the whiskers represent the variability outside the upper and lower quartiles. Outliers are represented as open circles.

Figure 2

Changes in the a) total soil Nitrogen (N_{tot}), b) soil organic matter (SOM), c) potassium (K, ppm), and d) phosphorus (P, ppm) between bare soil (dotted line, open symbols) and vegetation-covered patches (continuous line, closed symbols) along the elevation gradient in the Valdemartín-Cabezas de Hierro transect.

Figure 3

Changes in the soil chemical properties along the elevation gradient in the Loma de Pandasco-Navalondilla transect. Graphs show the differences between bare soil (dotted line, open symbols) and vegetation-covered patches (continuous line, closed symbols) for a) total soil Nitrogen (N_{tot} %), b) soil organic matter (SOM, %), c) potassium (K, ppm), and d) phosphorus (P, ppm) contents in the soil samples.

Figure 4

Biplots for the PCA analysis applied to the Sierra de Guadarrama data sets identifying a) the predictors of the changes in soil properties and nutrients between both studied transects (Val-CH, Pan-Nav); and b) the predictors for changes in soil properties and nutrients within vegetation patches, grouped by the dominant life form. Symbols represent the sites, and the size of the symbol accounts for the quality of each sample on the factor map. In biplot a), “contrib” refers to the contribution of each variable to the explanation of data

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Figure 5

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Supplementary Files

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