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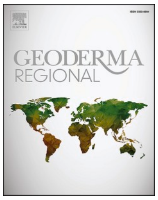

Assessing the occurrence of soil improvement and its relationship to the dominant life form in the high mountains of Central Spain

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ABSTRACT

Soil in mountainous regions is vital to the health and preservation of these unique and diverse ecosystems. In dry and semi-arid regions, vegetation patches play a crucial role in soil nutrient heterogeneity through continuous feedback with soils, acting as barriers to collect runoff water, sediments, and nutrients from bare soil regions. Soil amelioration, an enhancement of soil biogeochemical processes, results in the formation of "fertility islands," the extent of which is contingent on the plant species in question, as well as nutrient dynamics and water availability. Here, we collected soil from across a two-peak altitudinal gradient in the Sierra de Guadarrama high-mountains, each peak featuring a different dominant vegetation type (herbs vs. cushion-like) to compare soil nutrients and properties between bare soil and vegetation-covered patches (microhabitats). Soil improvement was assessed in the microhabitats using the Relative Interaction Index (RII). Fertility islands were shown to be prevalent in high-mountain ecosystems, as soil quality and properties were higher beneath vegetation-covered regions than bare soils. There was a difference in RIIs between the transects, with greater soil improvement in the cushion-dominated transect than the herb-dominated one. Changes in nutrient levels were unrelated to patch successional stage, indicaing that plant generations may not shape the spatial variability of soil attributes. Instead, species variety or the presence of dominant clonal species increased soil nutrients and aggregate stability, highlighting the importance of root shape and high biomass in nutrient retention and soil reinforcement. Finally, our findings imply that the poor, shallow soils in the examined peaks, in comparison to other mountains, may account for the poor facilitative interactions. Competition for the scarce resources at these peaks may intensify as climate warms. Thus, while these plants may grow with minimum assistance under current climate circumstances, their associations may be especially vulnerable to climate change.

1. Introduction

Plants have the ability to modify soil nutrient heterogeneity through continuous feedback with soils (plant-soil feedback), making the plant-soil relationship an important component in the dynamic of plant communities in ecologically stressed systems (Bagstad et al., 2006; Butterfield and Briggs, 2009; Liu et al., 2019; Veen et al., 2018). Biomass accumulation in vegetated patches modifies soil biogeochemical processes (Kelly et al., 1996; Schlesinger et al., 1990), establishing "fertility islands"; patches of vegetation that are richer in nutrients and water availability compared to the spots of bare soil between them (Bordeu et al., 2016; Gavilán et al., 2002; Greig-Smith, 1979; Tildi et al., 2008). In a self-sustaining manner that boosts plant cover, these vegetation clumps act as barriers that slow down and capture runoff water, water- and wind-borne sediments, litter, and nutrients from open inter-patch regions (Schlesinger et al., 1996; Schlesinger et al., 2000). These water and nutrient additions are crucial to the vegetation in the patch because they are expected to promote soil development and plant growth (Ludwig et al., 2005). Natural vegetation patterns that take decades to hundreds of years to emerge provide stabilising features for ecosystems, since they are effective in minimising overland flow and land degradation, and they also aid ecosystems in recovering from disturbance and resisting stressors (Saco et al., 2007, references therein).

Vegetation cover heterogeneity, with both large and small-scale structures (i.e., vegetation patterns), are typical in arid and semi-arid environments (Greig-Smith, 1979; Saco et al., 2007). In these habitats, plant communities typically exhibit a two-phase pattern, with plants

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clustered in patches whose shapes range from stripes to spotted clusters according to the degree of slope anisotropy (Deblauwe et al., 2011; Wiens, 1976). Plant-to-plant interactions control the feedback between biomass and water availability, making these clusters of vegetation a product of self-organizing mechanisms related to the success of the dominant species in the area (Gilad et al., 2004; Lejeune et al., 1999; Meron, 2012). Dominance of a species is associated with its success in the local environment, as demonstrated by its status as the most common or widespread species in the area. Spatial self-organization in plant communities is influenced by species interactions and spatially structured populations (Arnillas et al., 2021). Plant traits, soil composition, and precipitation averages influence this self-organization. Engineering species can facilitate self-organization by creating specialized niches for certain, compatible species (Arnillas et al., 2021; Pescador et al., 2014).

Positive and negative biotic interactions can impact plant species patterns (Armas et al., 2011; le Roux et al., 2012). In stressed environments, plant–plant interactions like facilitation are particularly common (Bruno et al., 2003; Armas et al., 2011). The value of mutually beneficial interactions between plant species varies widely depending on the specific conditions of the environment and the functional strategies of the participating species (Armas and Pugnaire, 2005; Brooker et al., 2008; Callaway, 1995; Callaway and Walker, 1997; Goldberg, 1996; Michalet, 2007; Soliveres et al., 2011). The strength and direction of the balance between positive and negative interactions among plants in a given community can vary with location, time, and the availability of resources, as well as the life histories of individual plants comprising the community (Armas and Pugnaire, 2005). In high-stress environments, such as high-mountains, positive interactions between species tend to become stronger and more frequent than negative ones. High-mountain environments are characterised by extreme climate and a wide range of disturbances, such as cold and fluctuating diurnal temperatures, short growing seasons, intense solar radiation, strong winds, and unstable substrates (Callaway, 1995; Körner, 2003; Körner and Hiltbrunner, 2021), which act as a natural filter for plant establishment by limiting the availability of suitable conditions and to resources for their growth.

Facilitator species, also known as *engineers*, *foundation species*, or *nurses*, can often modulate their environments in ways that encourage the establishment of species that are otherwise poorly adapted to the local conditions (Cavieres et al., 2014). Nurses or facilitators modulate microclimatic and physical conditions in their understories via soil nutrient enrichment, temperature buffering or increasing soil water content, among other mechanisms (Magaña Ugarte et al., 2024). For instance, the shadow of a nurse's canopy minimises thermal amplitudes and soil water evaporation, which may aid seed germination and seedling growth; and their shade also protects understorey plants from photo-inhibition by reducing heat stress and transpiration (Armas and Pugnaire, 2005 and references therein). As a result, the positive effects of some species' canopies may exceed the detrimental effects of growing in close associations in limited environments (Bertness and Callaway, 1994; Cavieres et al., 2002). The life-form of those engineers is either chamaephytic (cushion-like) or hemicryptophytic (perennial herbs), while the neighbours are usually herbs, mostly perennial but annual (Körner, 2003; Körner and Hiltbrunner, 2021). The degree of amelioration appears to be related to the species involved, the successional stage of the vegetation patch, and changes in nutrient dynamics and water availability (Breshears et al., 1998; Hobbie, 1992). For instance, pioneer nurses may be able to establish themselves in open gaps because they are more resistant to stress, display a higher competitive ability or because they could have a reduced resource utilization rate (Grime, 2002; Kazakou et al., 2006).

Soil in mountainous regions is crucial to the health and preservation of the unique and diverse ecosystems within the mountain ranges (Egli and Poulenard, 2016). Screes, landslides, and avalanches are all examples of morphodynamic processes that contribute to species diversity and landscape features in these areas (Egli and Poulenard, 2016; Körner, 2003; Körner and Hiltbrunner, 2021). Thus, plant community development in mountains is intrinsically linked to the availability of primary substrate and other site-specific variables (Burga et al., 2010; Frei et al., 2010). High mountain ecosystems are thought to be particularly vulnerable to climate change (Nogués-Bravo et al., 2008), so it is important to assess whether the overall warming and associated changes in rainfall patterns, a result of climate change, could impact soil properties and, thus, the local vegetation. (Nogués-Bravo et al., 2008). Vegetation loss or altered vegetation patterns can increase runoff rates and soil erotion (Saco et al., 2007), both of which are detrimental for mountain ecosystems. To better understand how plant community composition and soil properties interact, we undertook a field study in the Sierra de Guadarrama high-mountain areas.

The main objective of this work is to link the available information on plant community assembly from the Sierra de Guadarrama to the changes in soil properties (i.e., physico-chemical properties); a relationship rarely studied in these Mediterranean summits. Vegetation in Mediterranean high-mountains is organized in patches that could be dominated by cushion-like species (e.g., *Jasione centralis, Minuartia recurva, Silene ciliata*) or perennial herbs (e.g., *Festuca curvifolia*) interspersed with bare ground areas (Pescador et al., 2014; Soliveres et al., 2011). The role of vegetation as "vegetation traps" to collect runoff water, water- and wind-borne sediments, litter, and nutrients from open inter-patch regions results in a higher nutrient content and better soil structure in vegetation-covered patches than in bare soils (Bertness and Callaway, 1994; Brooker et al., 2008; Michalet, 2007; Milhoc et al., 2016; Soliveres et al., 2011). It has been hypothesised that the presence of nurse or facilitator species would suggest an amelioration of soil conditions (Cavieres et al., 2002; Cavieres et al., 2006; Cavieres et al., 2008), but summer drought remains an important limiting factor in the plant-soil relationship in these Mediterranean high-mountains (Giménez-Benavides et al., 2007b; Milhoc et al., 2016). Here, we use the term "soil amelioration" to refer to the improvement of edaphic properties, such as an increased nutrient content, soil aggregate stability, improved soil textural properties and increased compaction. Thus, 1) we expect more favourable conditions in vegetation-covered areas (i.e., amelioration effect) than in bare soils, with increased nutrient input and improved soil structure; 2) we also expect that increasing environmental stress gradients in the Sierra de Guadarrama mountains (i.e., low-temperature stress rising with altitude, drought stress strengthening in the opposite direction of elevation; Giménez-Benavides et al., 2007a; Pescador et al., 2015) will be positively correlated to an increasing soil amelioration effect. Since cushion plants are so well-known for their role as nurse species in high mountain environments, we expect that 3) there are strong contrasts between transects, with enhanced soil amelioration in the cushion-dominated transect than in the herb-dominated counterpart (Cavieres et al., 2002; Cavieres et al., 2006; Cavieres et al., 2008).

2. Materials and methods

2.1. Study site and vegetation

The research took place in the Sierra de Guadarrama National Park, in the high-altitude Mediterranean meadows that lie beyond the tree line. The Sierra de Guadarrama (4°44′14" N, 3°43′48" W), is a mountain range in Central Spain running in an *E*-W direction. It has a Mediterranean climate, with very dry summers (June–September, <10% of total yearly rainfall; Gutiérrez-Girón and Gavilán, 2013). Poorly developed and acidic soils (4.7–5.35) of plutonic and metamorphic origin (i.e., granites and gneisses, respectively) predominate in this mountain range owing to the steep slopes. Vegetation tends to colonise soils where precipitation and melted snow are the main sources of moisture, and this moisture begins to decline as summer advances (García-Fernández et al., 2013; Giménez-Benavides et al., 2011; Gutiérrez-Girón and Gavilán, 2013).

In the study site, tree line vegetation (1900–2000 m.a.s.l.) consists primarily of *Pinus sylvestris* L., interspersed with *Cytisus oromediterraneus* and *Juniperus communis* subsp. *alpina*, and perennial herbs, such as *Festuca curvifolia* Lag. *ex* Lange (= *Festuca yvesii* subsp. *lagascae*; Sennen & Pau (Cebolla & Rivas-Ponce) Mart.-Sagarra & Devesa). *F. curvifolia*, a graminoid with stripe-clonal growth that typically forms tightly-packed clumps, or stripes in ground terraces, is a great example of a patchy dry grassland that occurs at higher altitudes (2100–2200 to 2430 m.a.s.l.) and is very prevalent in the study area. In this community, *F. curvifolia* can coexist with >20 high-mountain specialists, being dominant in patches (Gavilán et al., 2002; Pescador et al., 2014). In addition to *F. curvifolia*, there are additional species, chamaephytes with a cushion-like structure, that can live alongside or even outcompete the patches (e.g., *Minuartia recurva*, *Jasione centralis*, *Silene elegans*, *Senecio boissieri*).

The soils in our study region are Rankers soils, which are characterised by their multiform humus and their potential to transform into Humic Cambisols under favourable climatic and topographical conditions. These soil types in the Sierra de Guadarrama are characterised as being low in clay content and high in sand fractions (loamy to sandy loam textures). The predominant gneissic materials of the area can be separated into two groups: metamorphic materials in the strict sense, and the orthogneisses of metagranitic origin. As peculiar inselbergs, the Sierra de la Cabrera and La Pedriza are both major granitic batholiths, with their northern extensions reaching some culminating sections of Cuerda Larga (between Bailanderos and Cabezas de Hierro, our study area). These peripheral areas include plutonic rocks. The La Pedriza batholith is dominated by coarse-grained leucoademellites, whereas the Peñalara and Rascafra outcrops are dominated by porphyritic adamellites (Fernández-González, 1991). Mineral content is high in these mountain soils, which also have a variable humus horizon thickness (from a few centimetres to 0.5 m) and a loose structure that crumbles when wet and is easily blown away by the wind when dry. This means that even though these soils often have little cohesion, they almost always exhibit distinct aggregate formation. Despite their high mineral content, much of this is composed of finely ground, little-weathered minerals that can be easily extracted micromechanically and separated from the organic constituents. Substantial acidification, little clay formation, and low translocation of chemicals are typical of these soils, which also exhibit low chemical weathering (Kubiëna, 1953).

In 2017, we collected samples from 200 individual patches of vegetation in the Sierra de Guadarrama's high-altitude regions (often above 2100 m.a.s.l.). The samples were taken from two distinct elevation transects on slopes with contrasting orientations, due to the changes in the dominant vegetation in these patches (i.e., herbaceous or cushion-like). The first transect covers the region around the hill of Valdemartin and the peak in Cabezas de Hierro from an altitude of 2140 to 2280 m.a.s.l.. Hereafter, it will be abbreviated as Val-CH. The second transect, located in the Loma de Pandasco sector, and henceforth referred to as the Pan-Nav transect, runs from approximately 2100 to 2230 m.a.s.l. and has a general north-westerly orientation (Fig. 1). The selected patches were identified as isolated structures surrounded by bare soil areas. Each patch's total number of species and plant cover, expressed as a percentage, as well as its major and minor diameters, elevation, and exposure, were documented (Table S1). We also took a sample from a barren region adjacent to the patch that was the same size as the patch (Fig. 2). Only ten of the 200 patches of vegetation studied included only a single species, while the rest contained up to nine species (i.e., multi-species patch). Dominant species and life form were identified in each patch. Following the classification provided by Gavilán et al. (2002), the vegetation patches were divided into three distinct stages of patch development based on their floristic composition. These stages are pioneer stage (3–4 species), seral stage (5 species) and climax stage (>6 species).

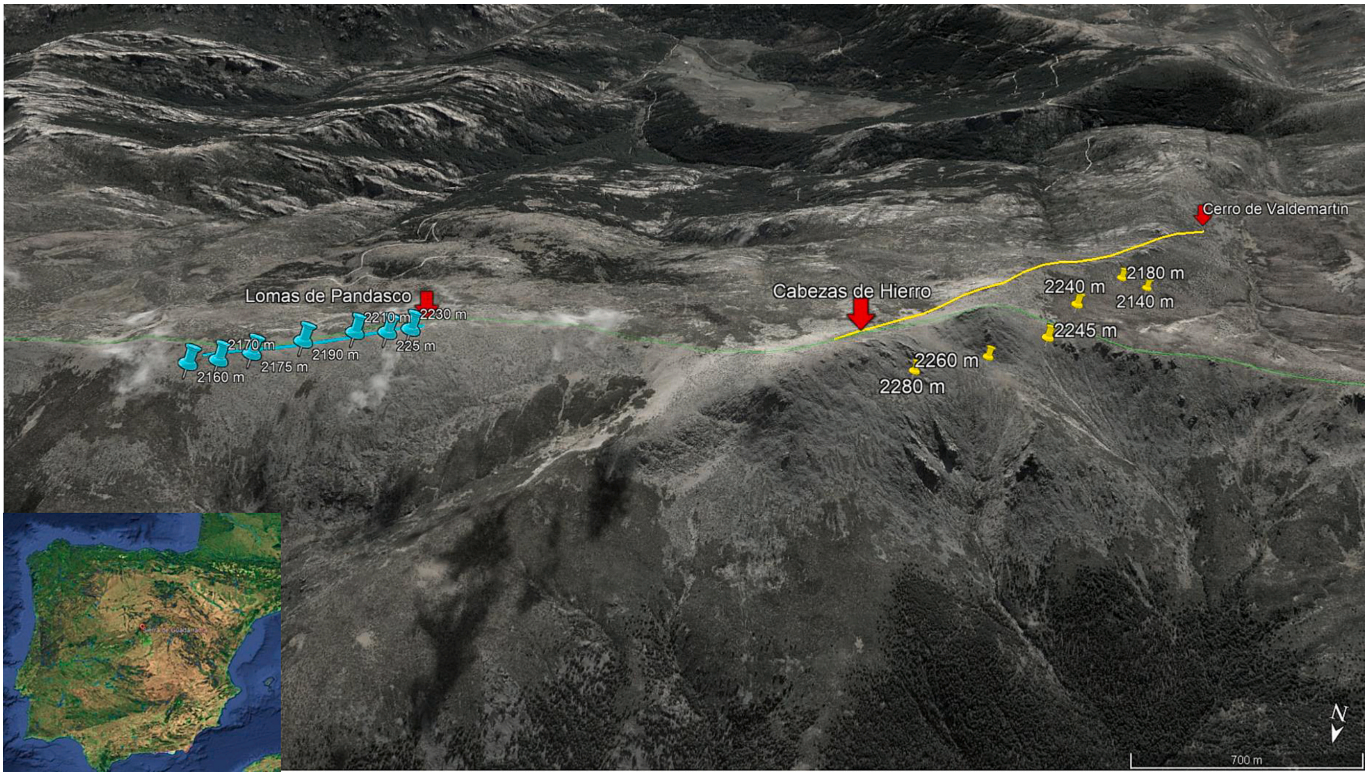

Fig. 1. Distribution of sample plots and elevation gradients along two transects in the Sierra de Guadarrama (Sistema Central, Spain). The Valdemartn-Cabezas de Hierro transect (Val-CH) is marked in yellow, and the Loma de Pandasco-Navahondilla transect (Pan-Nav) is marked in red. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

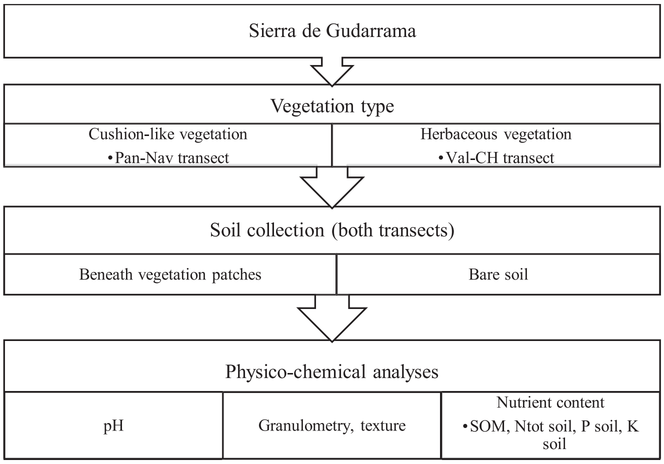

Fig. 2. Schematic illustration of the procedure for collecting soil samples from both transects, which feature contrasting compositions of main plant types and cover types. SOM = Soil Organic Matter; Pan-Nav = Loma de Pandasco-Navahondilla transect; Val-CH = Valdemartn-Cabezas de Hierro transect Total nitrogen in the soil, or Ntot soil. Soil P: Soil Phosphorus; Soil K: Soil Potassium.

2.2. Soil physical-chemical properties

Soil samples were taken during the vegetation sampling under patches and bare ground along the altitudinal gradient. Soil samples were taken from only the top 10 cm, as this is where most nutrients are found (Entry and Emmingham, 1995). We took 65 samples from within vegetation patches and 26 from bare soils, for a total of 103. Before analysis, the samples were air-dried at ambient temperature for about a month and then sieved through a 2 mm sieve in the lab.

The percentages of fine gravels (2–20 mm), gravels (>20 mm), and fine earth (2 mm) in the total natural soil were estimated (FAO-ISRIC, 1990). Soil Conservation Service (Soil Survey Staff, 1995) guidelines for sand, silt, and clay percentages were used in conjunction with the sedimentation pipette method to estimate these values.

Soil suspensions in deionized water (1:2.5 by volume) and 1 M KCl were analysed chemically for pH with a glass electrode. The percentage of organic matter (SOM, %) in the fine-earth fraction of soil was calculated using the dichromate acid oxidation method developed by Walkley and Black (1967). The Kjeldahl method was used to get a percentage value for total nitrogen (N_{TOT}, %). The amount of phosphorus (P; Burriel and Hernando, 1950) and potassium (K; Salinity Laboratory Staff, 1954) adsorbed to the colloid was calculated and reported in parts per million.

2.3. Relative interaction index

To quantify the differences between soils with and without vegetation, the Relative Interaction Index (RII) was computed (Armas et al., 2004). Any kind of net interaction (including but not limited to competitive exclusion and symbiosis) can be measured using RII. Because of its well-defined range (from −1 to 1), its symmetry around zero (having the same absolute value for competition and facilitation), and its suitability for use in statistical operations (being linear without discontinuities), the RII has been designated as an appropriate index for analysing plant interactions (Armas et al., 2004). The RII is calculated with the following formula:

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

Where the parameters for each soil variable in the vegetation-covered and bare soil patches correspond to P_v and P_0, respectively. Higher RII values from patches of vegetation are evidence that these regions have improved soil versus their bare equivalents (RII values range from −1 to 1; Jackson and Caldwell, 1993; Schlesinger et al., 1996).

2.4. Statistical analyses

We used the packages “stats,” “Factoextra,” and “FactoMineR” to perform an overall PCA analysis to identify the most significant predictors of soil property changes (nutrients, SOM, and particle size) to calculate the strength of soil amelioration (Kassambra and Mundt, 2017; Le et al., 2008). An additional PCA analysis was done just with vegetation patch data to determine soil property change estimations. The differences in the soil conditions were correlated using Spearman’s rho, to assess whether the strength of the amelioration effect (i.e., RII) varied among elevations. To determine if vegetation status affects soil conditions, Spearman’s rho correlations were used to correlate the relative plant cover (% cover, no. species) and patch successional stage (dominant species, patch stage) with nutrient and SOM values for each patch.

Average values for each soil property were compared between the vegetation-covered patch and the bare soil using a one-way PERMANOVA with the sampling microhabitat (vegetation-covered vs. naked soil) as the explanatory variable. Two PERMANOVA analyses were performed: (1) an overall analysis comparing soil properties under vegetation patches and bare soils between both transects, and (2) a separate analysis for each transect comparing soil properties under vegetation-covered and bare soils among sites within transect. The “adonis2” function of the “vegan” package (Oksanen et al., 2019) was used to perform PERMANOVAs with 9999 permutations, 95% type I error, and the Euclidean distance metric. This robust method was used due to the short number of replicates and non-normal data (checked for normality with a Shapiro-Wilks test, “shapiro.test” function from the “nortest” package; Gross and Ligges, 2015). Pairwise comparisons were conducted to know which patches were significantly different. The Bonferroni post-hoc test was used to establish the probability of type I error at 99%.

To prevent redundancy, we evaluated for multicollinearity among the PCA predictors (altitude, locale, transect, number of species, cover, dominant life form, and microhabitat) before running PERMANOVAs. The variance inflation factor (VIF) was compared to the “vif” function of the “car” package (Fox and Weisberg, 2011). Since maximum VIF values were below three, all variables were included in initial models. All statistical analyses were conducted in R-Core Team (2022).

3. Results

3.1. Effects of vegetation cover on soil properties

Soil properties showed higher levels under vegetation-covered patches than bare soils, specially N_{tot}, SOM and K (Fig. 3; Table 1; $p < 0.01$). The differences existed regardless of altitude ($p > 0.05$). When compared to soils from the Pan-Nav transect, Val-CH soils have a lower pH and are more acidic. Sand was the predominant soil fraction in both microhabitats, with no statistically significant differences between the two ($p > 0.05$; Table S1). Soil physical parameters did not significantly differ by either height or microhabitat.

Compared to the Pan-Nav transect, the Val-CH transect had considerably higher soil nutrient and SOM values ($p < 0.001$; Figs. 4, 5; Table 1). Soil organic matter (SOM) and nutrient levels varied significantly among microhabitats along both transects. ($p < 0.01$). Increases in N_{tot} were correlated to elevation, while changes in SOM were correlated with the successional stage of the patch. Nonetheless, none of these variations were statistically significant ($p > 0.05$; Table 2). Similarly, analysis showed a strong correlation between N_{tot} and SOM at study locations (Table S2).

Although there were some outliers, for the Val-CH transect, Ntot and SOM were both significantly different between microhabitats ($p < 0.01$; Figs. 4a, b), with the former being higher in the vegetation-covered

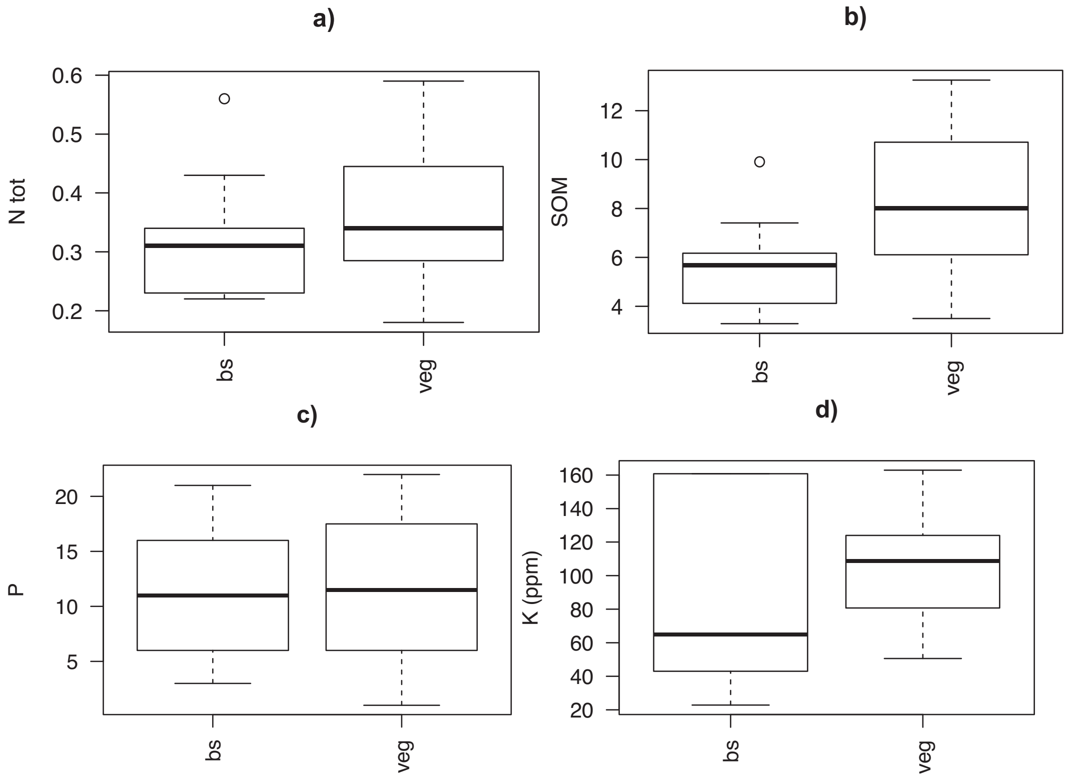

Fig. 3. Boxplot comparing soil samples taken from bare (bs) and vegetation-covered (veg) areas for total soil nitrogen (N_{tot}, %), soil organic matter (SOM, %), phosphorus (P, ppm), and potassium (K, ppm). In a box plot, the centre line serves as the median, the outside box's range is the interquartile range, and the whiskers show the range of values outside the upper and lower quartiles. Open circles indicate outliers. Fig. 3 presents the results of differences in soil properties beneath vegetation patches and bare soils.

Table 1
Mean soil chemical parameters for the examined vegetation patches in both transects (Valdemartin-Cabezas de Hierro, Val-CH; Loma de Pandasco-Navahondilla, Pan-Nav). The averages for each site ($n = 5$) are provided for total soil nitrogen (N_{tot}), soil organic matter (SOM), potassium (K), and phosphorus (P), as well as their corresponding Relative Interaction Indices (RIIs). High, positive RII indicates improved soil conditions in covered patches than those under the corresponding bare soil patches. Different lowercase letters indicate statistically significant differences between microhabitats within transect (one-way PERMANOVA, $\alpha = 0.05$). Microhab, microhabitat; C/N, C/N ratio.

Transect	Elevation (m.a.s.l.)	Microhab	N_{tot}	RII_N	SOM	RII_{SOM}	C/N	K	RII_K	P	RII_P	Patch stage
Val-CH	2140	Veg	0.27^{a}	−0.1	13.25^{a}	0.29	28.3^{a}	162.61^{a}	0.01	12.4^{a}	0.04	3
		Bs	0.34^{b}		6.17^{b}		18.1^{b}	160.78^{b}		11.3^{a}		–
	2180	Veg	0.33	ND	6.32	ND	19.5	80.6	ND	8.89	ND	1
		Bs	ND		ND		ND	ND		ND		–
	2240	Veg	0.6^{a}	0.28	12.12^{a}	0.33	20.2^{a}	130.5^{a}	−0.1	9.79^{a}	−0.07	3
		Bs	0.34^{b}		6.17^{b}		18.1^{b}	160.8^{b}		11.3^{a}		–
	2245	Veg	0.57^{a}	0.25	12.48^{a}	0.34	21.9^{a}	176^{a}	0.05	9.8	0.04	3
		Bs	0.34^{b}		6.17^{b}		18.1^{b}	160.8^{b}		11.3^{a}		–
	2260	Veg	0.46^{a}	0.03	9.3^{a}	0.11	20.2^{a}	86.7^{a}	0.12	10.9^{a}	0.35	3
		Bs	0.43^{b}		7.41^{b}		17.2^{b}	68.7^{b}		5.3^{a}		–
	2280	Veg	0.42^{a}	0.11	7.95^{a}	0.13	18.9^{a}	112.1^{a}	−0.18	10.0^{a}	−0.06	3
		Bs	0.34^{b}		6.17^{b}		19.7^{b}	160.8^{b}		11.3^{a}		–
Pan-Nav	2160	Veg	0.2^{a}	−0.02	3.5^{a}	0.03	17.5^{a}	37.9^{a}	−0.06	9.28^{a}	−0.7	1
		Bs	0.22^{b}		3.29^{b}		14.9^{b}	43.0^{b}		20.7^{b}		–
	2170	Veg	0.18^{a}	−0.1	4.05^{a}	0.1	22.5^{a}	80.9^{a}	0.31	3.69^{a}	−0.38	3
		Bs	0.22^{b}		3.29^{b}		14.9^{b}	43.0^{b}		20.7^{b}		–
	2175	Veg	0.35^{a}	0.23	6.31^{a}	0.31	18.0^{a}	160.7^{a}	0.58	4.1^{a}	−0.67	3
		Bs	0.22^{b}		3.29^{b}		14.9^{b}	43.0^{b}		20.7^{b}		–
	2190	Veg	0.30^{a}	0.03	8.51^{a}	0.24	28.4^{a}	120.3^{a}	0.33	11.5^{a}	−0.36	3
		Bs	0.28^{b}		5.18^{b}		18.5^{b}	61.02^{b}		24.7^{b}		–
	2210	Veg	0.59^{a}	0.44	12.87^{a}	0.52	21.8^{a}	162.9^{a}	0.75	ND	ND	1
		Bs	0.23^{b}		4.12^{b}		17.9^{b}	22.8^{b}		9.5		–
	2225	Veg	0.19^{a}	−0.1	3.7^{a}	−0.05	19.5^{a}	50.6^{a}	0.38	7.2^{a}	−0.14	1
		Bs	0.23^{b}		4.12^{b}		17.9^{b}	22.8^{b}		9.5^{b}		–
	2230	Veg	0.32^{a}	0.16	8.09^{a}	0.33	25.3^{a}	127.7^{a}	0.70	8.34^{a}	−0.07	1
		Bs	0.23^{b}		4.12^{b}		17.9^{a}	22.8^{b}		9.54^{b}		–

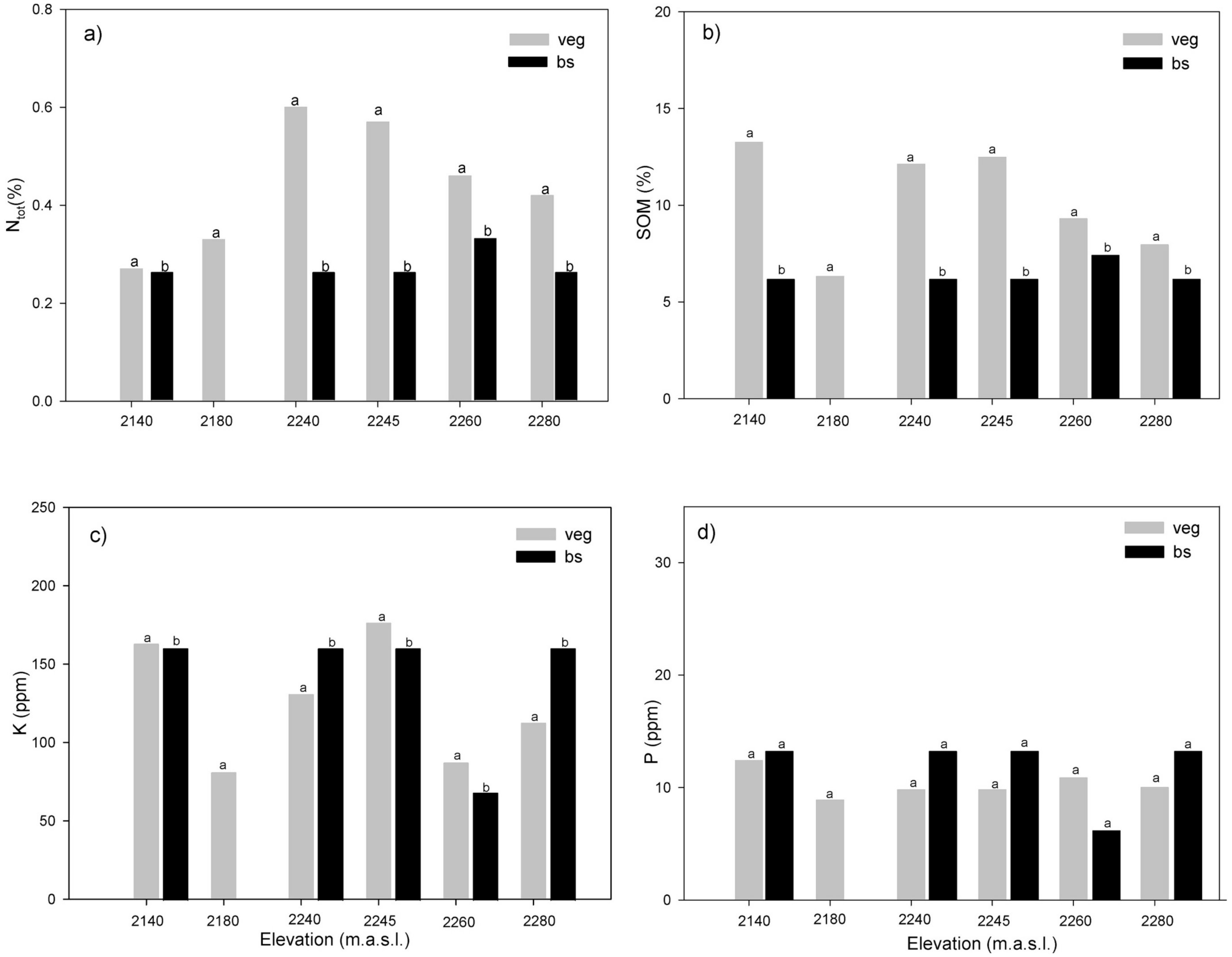

Fig. 4. Comparison of bare soil (black bars) and vegetation-covered patches (grey bars) throughout the elevation gradient in the Valdemartn-Cabezas de Hierro transect (Val-CH) in terms of total soil nitrogen (N_{tot}), soil organic matter (SOM), potassium (K, ppm), and phosphorus (P, ppm). Different lowercase letters represent significant differences between microhabitats (veg, vegetation patches; bs, bare soil, $p < 0.01$). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

regions. In this transect, the soil K also differed significantly between microhabitats, generally with higher K values in bare soils than vegetation patches ($p < 0.01$). There were no real significant differences found between microhabitats for soil P, nor among elevations.

Changes in SOM were favourably impacted by vegetation along the whole elevation gradient of the Pan-Nav transect (Fig. 5b). Higher amounts of Ntot and SOM were found in vegetation-covered than in bare soil sections in Pan-Nav ($p < 0.01$; Figs. 5a, b), but these differences did not occur with increasing altitude ($p = 0.22$). In addition, the Pan-Nav transect observed statistically significant changes in K and P among microhabitats ($p < 0.01$; Table 1), however these showed no discernible trend with elevation. *P* values were generally lower under vegetation-covered patches than in bare soils, and the differences grew in the opposite direction as elevation increased (Fig. 5d), while the differences weren't statistically significant ($p > 0.05$).

With significant differences between microhabitats, the C/N ratio remained relatively high overall in both transects (Table 1; $p < 0.05$), ranging between 18.9 and 28.3 for vegetation patches and 17.2–18.2 for bare soils in the Val-CH transect and between 14.9 and 28.4 in patches and 8.7–18.5 in bare soils from the Pan-Nav transect. This metric did not vary significantly ($p > 0.05$) between transects or elevations ($p > 0.05$).

Soil organic matter (SOM), total nitrogen (N_{tot}), total potassium (K), and the transect all contribute to the first principal component as indicated by the PCA (Fig. 6a, b), thus it may be interpreted as a proxy for soil quality. The second principal component (PC2), distinguishes between the dominant life form, microhabitat (vegetation patch, bare soil), and the fine gravel content. This means that PC2 can be understood as a measure of the community processes within patches, namely the stabilisation of loose substrates and their enrichment via the establishment of specialists.

3.2. *Amelioration effect, RII*

The magnitude of the soil improvement (RII values) varied throughout the transects, with the Pan-Navs transect yielding greater RIIs than the Val-CH transect. Compared to their values at the extremes of the elevation gradients, RII_N, RII_{SOM}, and RII_P were all significantly higher at the middle of the elevation range (Table 1). Changes in nutrient and SOM levels were not related to the successional stage of the patch (Table S2). There was little variation between patches in terms of soil properties and RIIs (Table S1). Strong amelioration effects were observed at intermediate elevations, which could relate to the positive correlation found between elevation and soil nutrients (i.e., N_{tot}, K, and P; Table S2).

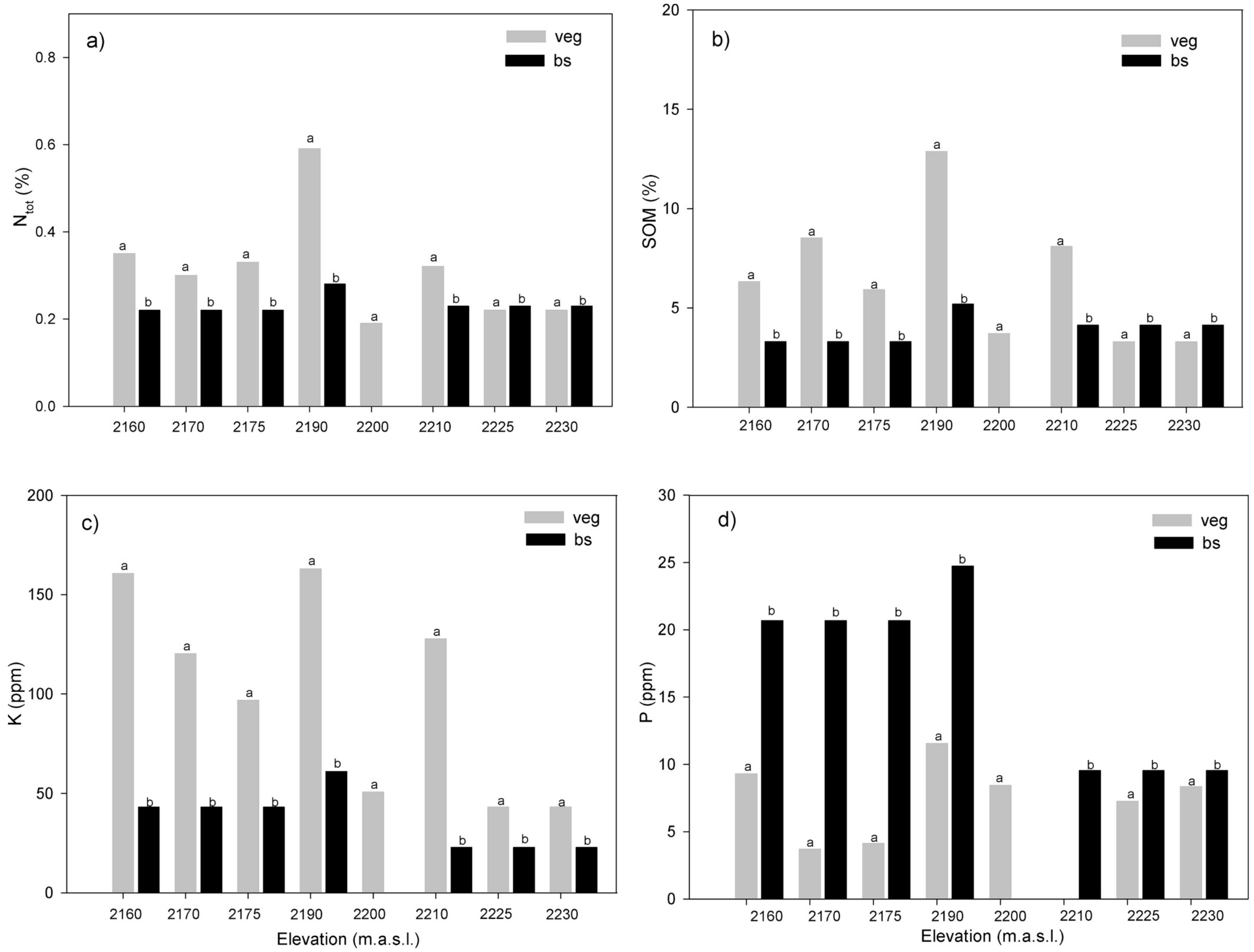

Fig. 5. Elevational trends in the Loma de Pandasco-Navahondilla transect (Pan-Nav) soil chemical properties. Graphs comparing total soil Nitrogen (Ntot, %), soil organic matter (SOM, %), potassium (K, ppm), and phosphorus (P, ppm) between bare soil (dotted line, open symbols) and vegetation-covered patches (continuous line, closed symbols). Different lowercase letters represent significant differences between microhabitats (veg, vegetation patches; bs, bare soil, $p < 0.01$).

Table 2

Data from vegetation-covered patches with the respective values for soil nutrients and SOM per patch. Information on the successional stage of the patch (i.e., patch stage) was retrieved from Gavilán et al. (2002). Elev, elevation in m.a.s.l.; O., orientation; No sp., number of species in the patch; D, major diameter; d, minor diameter; Cover, percentage cover; Dom. Sp, Dominant species in the patch; Ntot, total soil nitrogen content given in percentage; SOM, soil organic matter given in percentage; P, phosphorus; K, potassium. Different lowercase letters indicate statistically significant differences with elevation (one-way PERMANOVAs, α = 0.05).

Transect	Elev.	O	D	d	No sp	Cover (%)	Dom. Sp	N_{tot}	SOM	P (ppm)	K (ppm)	Patch stage
Val-CH	2140	E	30	25	4	95	*Festuca curvifolia*	0.3	13.25	12.8	118.26	3
	2180	NE	46	35	4	75	*F. curvifolia*	0.3	6.32	8.89	80.57	1
	2240	N	37	22	8	95	*F. curvifolia*	0.6	12.12	9.8	130.5	3
	2245	N	33	24	5	85	*F. curvifolia*	0.81	16.11	22	203	3
	2245	N	33	24	5	85	*F. curvifolia, Hieracium myriadenum*	0.57	12.48	12.37	176	3
	2245	N	23	22	5	80	*Agrostis truncatula*	0.36	8.26	11.97	135.13	2
	2260	NW	70	34	7	80	*F. curvifolia*	0.46	9.3	10.86	86.65	3
	2280	N	37	25	8	95	*F. curvifolia*	0.42	7.95	10.01	112.08	3
Pan-Nav	2160	NW	34	25	4	90	*Silene ciliata*	0.2 ^{a}	3.5 ^{a}	9.28^{a}	37.9^{a}	1
	2170	N	58	35	6	85	*T. penyalarensis*	0.18 ^{a}	4.05 ^{a}	3.69 ^{a}	80.86^{a}	3
	2175	E	33	24	6	80	*S. ciliata*	0.35 ^{a}	6.31^{a}	4.11 ^{a}	160.67^{a}	3
	2190	NW	25	25	6	90	*S. ciliata*	0.3 ^{a}	8.51^{a}	11.54 ^{a}	120.3^{a}	3
	2200	N	29	20	9	75	*F. curvifolia*	0.33 ^{a}	5.91^{a}	8.42^{a}	96.79 ^{a}	3
	2210	NW	ND	ND	3	50	*T. penyalarensis*	0.59	12.87	ND	162.93	1
	2225	SW	30	19	5	60	*Senecio boissieri*	0.19	3.7 ^{a}	7.24 ^{a}	50.62 ^{a}	1
	2230	NE	48	20	5	85	*S.boissieri*	0.32	8.09	8.34 ^{a}	127.74 ^{a}	1

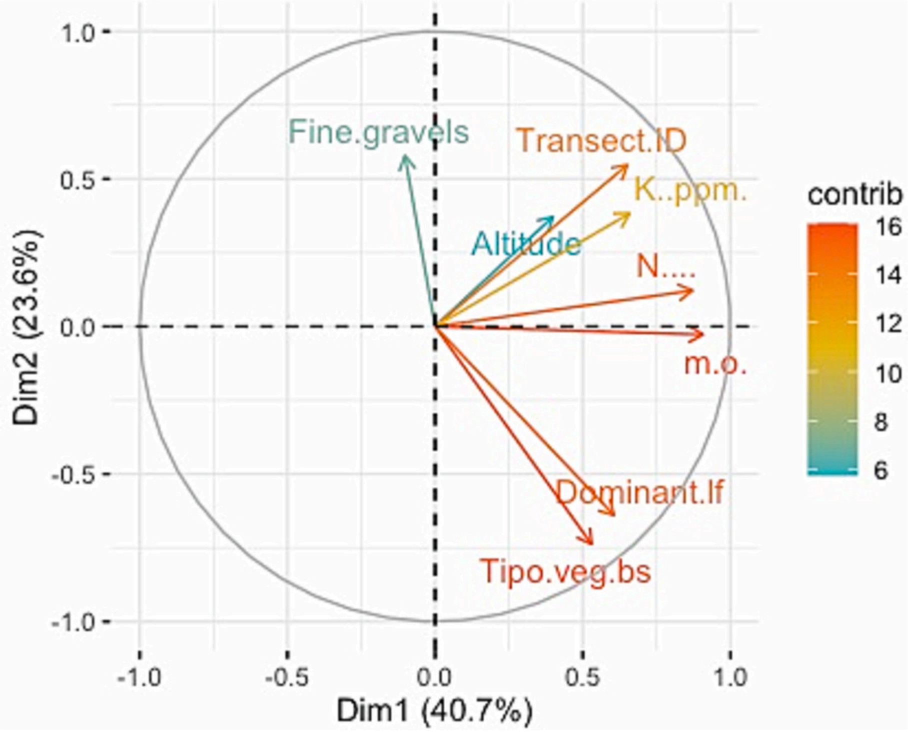

Fig. 6. Biplot showing the principal component analysis (PCA) used to determine the factors influencing soil property and nutrient changes along the Val-CH and Pan-Nav transects in the Sierra de Guadarrama. Each variable's "contrib" in the biplot represents its relative importance in explaining the data.

4. Discussion

Our findings confirm that the expected improvement of soil quality remained consistent beneath vegetation-covered patches, confirming the prevalence of fertility islands in high-mountain ecosystems (Cavieres et al., 2006; Escudero et al., 2004). This ameliorating effect, however, was not linked to the dominating species in the patch (cushion or herbaceous) or significantly different across elevation gradients. As a result, Körner and Hiltbrunner (2021) hypothesis that low-stature plants will be conserved despite an overall microhabitat response to atmospheric changes, resulting in a shift in thermal habitat mosaics, is related to this lack of association to the growth form.

As a result of pioneer vegetation generations affecting the spatial diversity of soil physical attributes, the soil environment beneath vegetation patches often improves with the patch successional stage. The crucial role of root shape and tensile strength in the soil reinforcement (Huck et al., 2013, references therein) may explain the inverse link found between fine gravel content and the dominant life form and microhabitat (Huck et al., 2013, references therein). Increased species diversity or the formation of dominant clonal species through patch development both enhance root density, which in turn increases soil aggregate stability (Huck et al., 2013; Körner, 2003). These findings provide further evidence on how a dense plant cover aids in slope stability, soil conservation and plant establishment in adverse environments (Körner, 2003; Li et al., 2021).

Although there were typically insignificant changes in soil amelioration along the elevation gradient, the discrepancies were more pronounced at intermediate elevations. The two severity gradients in Mediterranean high-mountains—freezing stress increasing with altitude and drought stress increasing as elevation declines (Cavieres et al., 2006; Giménez-Benavides et al., 2007b)—may explain why our findings resemble the humped patterns observed by Milhoc et al. (2016) over a larger elevation gradient in the Mediterranean Andes. Furthermore, we found that the diversity of species within vegetation patches increased in a way that was both height- and form-independent, replicating the results of Cavieres et al. (2002).

Cushion plants, known for their ability to alter their surroundings and influence community assembly processes (Badano and Cavieres, 2006; Schöb et al., 2012), have gained recognition as ecosystem engineers (Cavieres et al., 2006; Jones et al., 1994). In the Pan-Nav transect, cushions were the most common life form, but their moderate amelioration at intermediate altitudes (2170, 2175 m.a.s.l.) was similar to that of herbs in the Val-CH gradient at moderate altitudes (Table 1, S1). This suggests that cushions in the studied Sierra de Guadarrama gradients have limited impact on improving soil quality. Thus, the high-mountain plant communities from Sierra de Guadarrama continue to thrive as they are optimised for their local environment, as these plants have adapted their phenology to track snowmelt timing and photoperiod adequacy, allowing them to withstand adverse environmental conditions (Körner and Hiltbrunner, 2021; Körner, 2003). However, as temperatures rise, their resilience to climate change may be a key selective factor. Species in the Sierra de Guadarrama are able to maintain their niche and avoid extinction due to climate change because they are more adaptable to the shifting climate. However, the short altitudinal range and *E*-W orientation of Sierra de Guadarrama, restricts their migration making them vulnerable to the introduction of species from lower altitudes (Jiménez-Alfaro et al., 2014; Gottfried et al., 2012).

Soil infiltration and vegetation's capacity to slow, collect, and store runoff water and nutrients both benefit from increased biological activity and soil processes (Ludwig et al., 2005). Litter and root expansion may also influence run-off-run-on processes. In high-mountain environments, clonal organisms like *F. curvifolia* stabilise ecosystems, reduce steep slope erosion, and are more resilient to perturbations (Cornelissen et al., 2003; Körner, 2003). Tussocks (thick litter and leaf mats; Huck et al., 2013; Körner, 2003; Suding and Goldberg, 1999) rich in necromass are created by dominant (and often clonal) high-mountain plants like *F. curvifolia* to shield themselves and their less robust neighbours. In Sierra de Guadarrama, *F. curvifolia*-dominated patches are located in small terraces and had particularly high fine gravel, fine earth, and nutrient accumulation (see Table S1), resembling previous observations in the Alps and Caucasus that *Festuca* grasses stabilise erosion edges due to their dense root system and enrich the soil via humus, nutrient, and water runoff (Huck et al., 2013). Our findings showing *F. curvifolia* leaf mats improved soil conditions and "nurse" other species, further support its role as a facilitator species in these poor soil environments (Pescador et al., 2014). However, when evaluating associations with neighbouring vegetation, *F. curvifolia*'s clonal dominance drives competition and pushes other species into an interphase habitat around its clumps (Gutiérrez-Girón and Gavilán, 2013; Pescador et al., 2014). Our data verifies this species as a primary coloniser, forming monospecific bands of vegetation by clonal growth, promoting stable substrate and specific topographic niches to improve soil properties (Gavilán et al., 2002). However, strong root competition (enlarged root system of *F. curvifolia*) due to low nutrient conditions in the study area (poor soils) and further reducing the possibility of positive effects on neighbouring species. The shallow soils in our system may also lead to more severe competition, limiting soil resource intake from the same depth (Dornbush and Wilsey, 2010; Martorell et al., 2015) and further explaining the limited soil amelioration (low RIIs) found beneath *F. curvifolia* vegetation-covered patches.

Chemical weathering involves mineral dissolution, alteration, and transformation to more stable surface mineral phases (Egli et al., 2014). At high elevations, wind can considerably affect soil erosion and surface drying (Larcher, 2003). Strong winds in the Sierra de Guadarrama summits and limited chemical weathering typical of old and flat topographies like this mountain range could lift lighter substrates and leave a stripped soil surface with low nutrient levels (Egli et al., 2014; West et al., 2005). Thus, chemical weathering may explain the lower K values in Pan-Nav transect bare soils compared to Val-CH ones. The high biomass in *F. curvifolia* patches, compared to Pan-Nav cushions, may indicate a more adequate soil cover that retains more soil aggregates and nutrients. However, Gutiérrez-Girón et al. (2015) suggest that this alleged extra nutrient input may not increase mineralization rates due to high C/N ratios in all vegetative patches and slackened microbial activity.

The current results imply soil amelioration occurs regardless of the dominant life form and elevation, which is consistent with findings by Milhoc et al. (2016) and Escudero et al. (2004). These results provide evidence that the shallowness of the soils and their comparatively weak nutrient content, compared to other habitats, may be attributed to a minimal effect of facilitative interactions in the examined gradient. As a result, we may infer that a more intense competitive effect takes place at these peaks because of the limited supply of resources (such water and nutrients). The plants that thrive there are therefore able to withstand the stress without any help from the species around them (Maestre et al., 2009). However, more research is needed to fully define these dynamic processes in Sierra de Guadarrama by examining the balance between the ameliorative effects and competitive implications in these plant associations under shifting climatic conditions (Callaway and Walker, 1997).

5. Conclusions

Our findings that vegetation-covered soils were consistently better than bare soils from the same elevation, further evidence the existence of "fertility islands" in these mountains. By changing the spatial heterogeneity of soil parameters in plant patches, specialist species enhanced soil ecology in comparison to bare soils. Cushions had a minor, but detectable, effect on soil quality, suggesting that soil improvement is independent of dominant life form and elevation. This suggests that the shallow soils and poor nutrient content along the gradient may be the result of weak facilitative interactions in Sierra de Guadarrama. The shallowness of soils and limited availability of water and nutrients at these mountains may produce a more intense competitive effect as consequence of climate change, shifting plant community composition.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Rosina Magana Ugarte reports financial support was provided by Government of Spain Ministry of Universities. Rosario Gavilan reports financial support was provided by Madrid Regional Government. Agustin Rubio reports financial support was provided by Spain Ministry of Science and Innovation. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.geodrs.2023.e00744.

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