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This is the author's manuscript

Original Citation:

Availability:

This version is available http://hdl.handle.net/2318/146912 since 2015-12-09T12:54:36Z

Published version:

DOI:10.1007/s11104-013-1971-y

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14 September 2026

UNIVERSITÀ DEGLI STUDI DI TORINO

This is an author version of the contribution:

Relationships between serpentine soils and vegetation in a xeric inner-Alpine environment

published on:

Plant and Soil(2014), 376:111-128;

DOI: 10.1007/s11104-013-1971-y

The final version is available at:

The final publication is available at Springer via http://dx.doi.org/10.1007/s11104-013-1971-y

Relationships between serpentine soils and vegetation in a xeric inner-Alpine environment

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Abstract

Aims: In serpentinitic areas non-endemic plants suffer from the serpentine syndrome, due to high Ni and Mg concentrations, low nutrients and Ca/Mg ratio. We evaluated the environment-soil-vegetation relationships in a xeric inner-alpine area (NW Italy), where the inhibited pedogenesis should enhance parent material influences on vegetation.

Methods: Site conditions, topsoil properties, plant associations and species on and off serpentinitewere statistically associated (51 sites).

Results: Serpentine soils had higher Mg and Ni concentrations, but did not differ from non-serpentine ones in nutrient contents. The 15 vegetation clusters often showed substrate specificity. Two components of the Canonical Analysis of Principal Coordinates, respectively related to Mg and to Ni and heat load, identified serpentine vegetation. Random Forests showed that several species were positively correlated with Ni and/or Ca/Mg or Mg, some were negatively associated with high Ni, Mg excessaffected only few species. Considering only serpentine sites, nutrients and microclimate were most important.

Conclusions: Ni excess most often precludes the presence of plant species on serpentinite, while an exclusion due to Mg is rarer. Endemic species are mostly adapted to both factors. Nutrient scarcity was not specific of serpentine soils in the considered environment. Considering only serpentine sites, nutrient and microclimatic gradients drove vegetation variability.

Keywords: ultramafic rocks, serpentinite, pedogenesis, serpentine syndrome, soil fertility, Ni

Introduction

Serpentiniteisa metamorphic rock mainly composed of Mg silicates (serpentine minerals, with accessory chlorites, talc, and sometimes olivine and pyroxenes), and often includes magnetites and

chromites. Serpentinite weathering originates soils (normally called “serpentine soils”) typically characterized by chemical and physical properties thatreduce plant productivity and create stress and toxicity to non-adapted species, the so called “serpentine syndrome”(Jenny 1980). Several factors are thought to be responsible of the serpentine syndrome (Alexander et al. 2007),such as a low Ca:Mg ratio caused by the high amounts of Mg released from the parent material and abundant heavy metals (Ni, Cr, Co). In addition, soils often have low macronutrient (N, P, K) concentrationsboth because of their paucity in the rock and of the presence of sparse vegetation. Susceptibility to drought and erosion often characterizes serpentine soils too, because of dark colour, coarse soil texture, rockiness and shallow soil depth (Brooks 1987).

Although vegetation growing on these soils is typically sparse and stunted, plant diversity is often high with abundant endemic taxa (e.g. Kruckeberg 1984). Some of these species hyperaccumulate metals(commonly Nickel) and Ni concentrations in their tissues may be more than 1000 mg kg^{-1} on the dry weight (Van der Ent et al. 2012).Many serpentine endemic species in Europe are known Ni hyperaccumulators(e.g. Brooks and Radford 1978) and often they have a narrow geographical distribution, such as *Alyssum argenteum*(Cecchi et al. 2010),which is a perennial Brassicaceae endemic to serpentine rocky outcrops in the Western Alps. It growsat low altitude on south-facing slopes, from Val Chisone in the south to Aosta Valley in the north (Pignatti 1992).

The role of thefactors involved in the distribution and competitive capacity of serpentinite endemic plants, and of metal hyperaccumulators in particular, has always attracted the curiosity of ecologists, biologists and soil scientists (Roberts and Proctor 1992). The relative importance of each factor of the serpentine syndrome greatly variesdepending on local climate, plant community (Proctor and Nagy 1991) and single species (Lazarus et al. 2011). In particular, the role of heavy metals in influencing serpentine vegetation is unclear. Brady et al. (2005) in their review reported that the serpentine syndrome is mostly associated with low Ca/Mg ratio and with high Mg contents; adaptative traits to high Ni (e.g., hyperaccumulation or, more often, exclusion) are rarer phenomena, evidencing low Ni ecological impacts. Some works pointed out that tolerance to high Ni is readily achieved, reducing its ecological effect on plant communities (e.g.,Proctor 1997). Conversely, other authors have reported that Ni has strong negative effects on plant cover (Lee 1992; Chardot et al. 2007) or on biodiversity (Batianoff and Singh 2001), while it is positively correlated with the number of endemic taxa (Batianoff and Singh 2001).Typically, the workson serpentine ecology explore the edaphic gradients between dry and nutrient-poor barrens and more favourableforestedsites (e.g. Chiarucci 2004, Carter et al. 1987), or the environmental gradients causing vegetation differences within serpentine habitats (Tsiripidis et al. 2010). Common results are that soils in open rocky outcrops or taluses (i.e. serpentine barrens) are nutrient-poor(Chiarucci 2004) and are characterized by a high Mg/Ca molar ratio (e.g. Carter et al.1987). As a

demonstration of low Ni impact on plant life, Ni availability is often higher under the better developed and structured communities (Chiarucci 2004, Tsiripidis et al. 2010) because of enhancedacidification under forest vegetation.

Few works, instead, consider edaphic gradients and their effects on vegetation patterns on serpentinite and on nearby, analogous non-serpentinite habitats (i.e. comparing barren or forested sites on and off serpentinite). In some of these cases,such asin humid, high-altitude subalpine (boreal) forest and alpine habitats, serpentine endemic species or plant communities were well correlated with high levels of available Ni, while the Ca/Mg ratio or the nutrient contentsdid not explain vegetation variability caused by substrate: different nutrient contents and element cycling characterizeddifferently developed soils, both on and off serpentine (D'Amico and Previtali 2012). Element mobility through the profile is high in humid environments, because of both leaching and biocycling; in particular Ca biocycling is enhanced in serpentine-rich soils (Bonifacio et al. 2013), hence effectively decreasing the effect of the Ca/Mg ratio on vegetation. The effect of soil development is thus superimposed on that of the parent material in humid areas, and the final soil characteristics may diverge from those of poorly weathered and poorly leached soils. On the contrary, xeric climates inhibit element leaching from soils, which are typically less developed, thus the ecological effect of the edaphic components of the serpentine syndrome on vegetation should be enhanced, allowing a better evaluation of the soil-vegetation relationships.

Our hypothesis was that soil development and the consequent divergence of chemical properties from those of the parent material may mask the relationships between soil and vegetation, particularly when highly mobile nutrients or metalswith high affinity to organic matter are concerned. The purpose of this study was thus to investigate soil-vegetation relationships on serpentinite in xeric, low altitude habitats in the Western Alps, where element leaching and pedogenesis should be inhibited.To reach this aim, we selected soils from a xeric inner alpine area, both on serpentine and non-serpentine parent materials, evaluated that all soils have a comparable poor development degree and then assessed the relationships between vegetation and those soil properties which are considered the most important in the serpentine syndrome, such as macronutrient availability, Ca:Mg molar ratio, heavy metal availability and rockiness, making use of both well-known statistical tools and recently proposed methods for data treatment. The statistical approach can help to disentangle the respective importance of different factors in soil-vegetation relationships thanks to permutation methods, although direct cause-effect relationships can only be evaluated by lab or field experiments.

Materials and methods

Study area

The central part of the Aosta Valley (RegioneAutonoma Valle d'Aosta), characterized by yearly average precipitation below 750mm, was considered in our study. This region is located in the north-western Italian Alps, close to the French (in the west) and the Swiss border (in the north) (Figure 1). The climate is primarily related to topography: the central part of the region is surrounded by high mountain ranges and it is characterized by rain-shadow effects in every season giving rise to continental, xeric, inner-alpine climate (Mercalli 2003).In the considered xeric area, winter temperatures are between 2° and -5°C, with the lowest values in the valley floors (because of thermal inversions) and at high altitude, while summer temperatures are between 21°C and 10°C (decreasing with altitude). In the lowest parts of south-facing slopes the average temperature is always above 1°C. The average rainfall is below 600-700 mmy^{-1}, and can be as low as 485 mm y^{-1} in the Aosta area. Spring and autumn months have the highest rainfallamounts, while winter and summer minima are typical;the average rainfall of July is below 40 mm (Mercalli 2003).Water scarcity is a strong ecological constraint, particularly on south-facing slopes, where steppe vegetation (dominated by *Bromus erectus*, *Festucavalesiaca*, *Stipapennata* and *Teucriumchamaedrys*) with only scattered trees (*Quercuspubescens, Pinussylvestris* and *Castanea sativa*) is the natural vegetation type at the montane (sub-boreal) phytoclimatic level. Dense *Castanea sativa, Pinussylvestris* and *Quercuspubescens* forests cover the cooler north-facing slopes at the same altitude.Thus, a xericity gradient can be observed within the xeric area. In the driest part of the region, steppe vegetation is found up to 2400 m a.s.l., where steppe species mingle with alpine ones, adapted to low temperatures and short growing seasons.

Several rock complexes are found in the Aosta Valley: serpentinite, mafic rocks and calcschists, included in the PiedmonteseOphiolite Complex, are common in the eastern sector, while the western part is dominated by calcschists and gneiss.Pleistocene glaciers covered large portions of the area until 12,000-15,000 years BP, and mixed glacial till, with a calcareous matrix, is widespread.

Field data collection, soil sampling and analysis

51sites (soil profiles associated with vegetation surveys) were selectedaccording to the average annual rainfall (below 750 mm), among 384 previously observed sites scattered around the whole region, representative of the typical inner-alpine environments. In each site, plant species (identified according to Pignatti 1992) were recordedin homogeneous square areas of 16 m^2, visually estimating the cover (%)of each species.

At each site, the following data werealso collected: altitude, slope steepness, aspect, surface rockiness, bare soil,and tree cover (calculated as % area on a 100 m^2 surface). Surface rockiness, bare soil and tree cover were determined by visual area estimation. Aspect and slope steepness were combined into the heat load factor, a proxy of potential solar radiation and potential evapotranspiration (McCune and Leon 2002). Rainfall data were collected from 12 regional weather stations located close to the sampling sitesand the average annual rainfall was included among environmental parameters.

Soil pits were dug at each site, down to the C or R horizon (parent material) and the soil profile was examined to assess soil development and pedogenic processes. The soils found in the inner-alpine, xeric area were usually weakly developedRegosols, Leptosols or, rarely, slightly more evolved Cambisols, Phaeozems and Calcisols (IUSS Working Group 2006). Samples were collected from allgenetic horizons, but only A horizons were considered in this study.

The soil samples were air dried, sieved to 2 mm and analyzed according to the USDA methods (Soil Survey Staff 2004). The pH was determined potentiometrically in water extracts (1:2.5 w/w). Exchangeable Ca, Mg, Kand Ni (Ca_{ex}, Mg_{ex}, K_{ex}, Ni_{ex}) were determined after exchange with NH_4-acetate at pH 7.0. The acid-extractable element concentrations (Ca_T, Mg_T, Ni_T) were determined after HCl-HNO_3 hot acid digestion). In all extracts, the elements were analysed by Atomic Absorption Spectrophotometry (AAS, Perkin Elmer, Analyst 400, Waltham, MA, USA). The total C and N concentrations were evaluated by dry combustion with an elemental analyser (CE Instruments NA2100, Rodano,Italy). The carbonate content was measured by volumetric analysis of the carbon dioxide liberated by a 6 M HCl solution. The Organic Carbon (OC) was then calculated as the difference between total C measured by dry combustion and carbonate-C. Available P (P_{Olsen}) was determined byextraction with $NaHCO_3$with P detection by molybdatecolorimetry.

Rock fragments>5mm were cleaned withsodium hexametaphosphate, sorted according to the lithology and weighted to semi-quantitatively characterize the soil parent material. The frequency distribution of serpentinite clasts in the soils was clearly bimodal: no serpentinite clasts, 21 samples; 10%, 20%, 30% and 50%, 1 sample each; 60%, 3 samples; 70% 1 sample; 80%, 2 samples; 90%, 3 samples and 100%, 17samples.

Data analysis

Statistical analysis were carried out using either SPSS for Windows version 17.0 or R2.15.1 software (R Foundation for Statistical Software, Institute for Statistics and Mathematics, Vienna, Austria).

Based on thebimodal distribution of serpentine content in the parent material, we decided to split soil profiles into two groups depending on whether the parent material was dominated by

serpentinites (>= 60% of serpentinitic clasts by weight) or not.To verify whether clear thresholds existed or if a chemical/ecological gradient was instead present, we also performed additional analyses considering different abundance of serpentine coarse fragments.The differences in soil properties were evaluated by a one-way analysis of variance (ANOVA), using lithology as independent variable. The homogeneity of variance was checked by the Levene test and the variables showing significant differences (i.e. $CaCO_3$, Mg_T, Ca_T/Mg_T,Ni_T, Ca_{ex}/Mg_{ex}, Mg_{ex}, Ca_{ex}/Mg_{ex}, Ni_{ex}, P_{Olsen}) were log-natural transformed for analysis. The correlation between variables was evaluated using the Pearson's coefficient (two-tailed), after a visual inspection of the data to verify that the dependence relationship was linear. In case of non linearity, Spearmann's correlation coefficient was instead used.

The numerical elaborations regarding vegetation and soil-vegetation relationships were performed excluding tree species, which are mostly correlated with climatic and pedoclimatic site properties. Vegetation types were classified using Cluster Analysis (CA), selecting average linkage as agglomeration criteria owing to its highcophenetic correlation value. The best dissimilarity algorithm (Bray-Curtis) was selected according to the function *rankindex* in the *Vegan* package (Oksanen et al. 2011), which correlates the species data with a given gradient (in this case, soil-environmental properties) using many dissimilarity algorithms. To facilitate the ecological interpretation of the clusters, common indicator species (Legendre and Legendre 1998) for each cluster were obtained with the help of the *indval* function, included in the *labdsv*package. Cluster stability was assessed through the "bootstrap" noise-adding and subsetting methods(Hennig 2007): if the resulting ClusterwiseJaccard meanis below 0.5, the cluster is considered "dissolved" and not significant, while it is regarded as "stable" and significant if the value is above 0.75.The number of clusters to be considered during the following analysis was chosen based on the ratio between the total number of clusters and the number of stable ones and according to their ecological significance.The bootstrap method was applied to a variable number of clusters (2-18).

A correlation analysis was performed on the soil-environmental properties, to detectcollinearities (R^2 above 0.75) and select a subset of independent variables to be used in the following elaborations. The selected variables were altitude, surface rockiness, bare soil, N, C/N ratio, available P, molar Ca_{ex}/Mg_{ex}ratio, Mg_{ex},K_{ex},Ni_{ex},$CaCO_3$, tree cover,heat load and average yearly rainfall. Ca_{ex}, pH and C were omitted as strongly collinear with, respectively, $CaCO_3$ and Ca/Mg, and N. Altitude, N, P, K_{ex}, Ca_{ex}, Mg_{ex} and Ni_{ex} were log-transformed prior to analysis.

We used constrained analysis of principal coordinates (CAP, function *capscale*, included in the *vegan* R-package), based on the Bray–Curtis distance, to determine the most influential environmental variables involved in the plant community composition (Anderson & Willis 2003). This multivariate technique offers anappropriate way to apply canonical constraints using a flexible

choice ofdissimilarity measures. The significance tests for each variablewere computed using the marginal testingmethod included. In order to detect the ranking of importance of pedo-environmental factors involved in soil-vegetation relationships, we applied a stepwise analysis on the CAP (function *ordistep*), which shows how much the model is improved wheneach variable is added, with random permutations.

We used the Random Forests (RF) (Breiman 2001), included in the *RandomForest* R library (Liaw and Wiener 2002), to detect the important factors involved in the presence/absence of the species growing in more than 10% of the study sites. RF is an improvement of the Classification Tree method (CART), which shows the optimal distribution ranges of plant species (Vayssiéres et al. 2000). RF is a more robust method than most normally used in ecological niche modelling (Evans and Cushman 2009), and does not need further accuracy estimates (Cutler et al. 2007).The importance of predictive (soil-environmental) variables is estimated by looking at how much the misclassification error (the out of bag error) increases when each variable is permuted while the others are left unchanged. The increase of the error is proportional to the importance of each predictive variable. After checking the optimal number of trees (*ntree*) reducing the out of bag error to a minimum, we modified the *ntree* in the RF from 500 to 3000. The optimal number of randomly selected variables(*mtry*) to be used in each step of the bootstrap process was also checked for each species.

Positive or negative interactions between predictive variables and plant species were checked using generalized linear models (Guisan et al. 1998, *glm*function, family *binomial*), using only the important variables for each considered species.

In order to check if soil-vegetation patterns were substrate-specific or generic for the whole xeric area in Valle d'Aosta, we performed the analyses described above also on the subset of sites with a serpentinite content in the parent material ≥ 60%. This subset was called “serpentine-dominated soils” through the text.

Results

Soils

The A horizons of both serpentine-dominated and non-serpentine soils showed a wide pH range (from 4.4-4.8 to above 8, Table 1) and often had carbonates. Calcium carbonate enrichment in surface soils was common, up to 160 g kg^{-1}, and precipitation of secondary carbonates was often observed in subsurface horizons, mainly in soils derived from non-serpentine parent materials but sometimes also on serpentinic ones.The elemental composition was well related with the parent material: serpentine-dominated soils hadsignificantly higher Mg_T and Ni_T,and a significantly lower

Ca_T/Mg_T ratio (Table 1) than soils formed on other rock types.$Ca_T$and the Ca_T/Mg_T ratio were, however, relatively high and values up to 1.5 were found. The specificity of the parent material was retained also in the available pools of elements: Ni_{ex} and Mg_{ex} were significantly higher on serpentinite, while Ca_{ex} did not differ (Table2). The molar Ca_{ex}/Mg_{ex} ratio was often above 1 also on serpentinite, but it was still significantly lower than on other substrates. While the exchangeable contents of both Mg and Ni were significantly correlated to their total concentration (r_P=0.415 and 0.778, respectively, $p<0.01$),Ca_{ex} and Ca_T were not ($p=0.158$). Tree cover was uncorrelated with all substrate-related edaphic factors and with parent material lithologies.

As expected, all significant differences were also present when a higher threshold was chosen for serpentine-dominated soils and significant differences ($p<0.01$) in carbonate contents and pH appeared (lower on serpentinitic soils)when almost pure serpentinite was selected as a threshold (e.g. ≥ 80% serpentinitic clasts).

Both Ni_{ex}andNi_Twere well correlated with the other typical properties of serpentinitic soil, i.e. Mg_T ($r=0.862$ and 0.656 in the case of total and exchangeable Ni contents, respectively, $p<0.01$), Mg_{ex} ($r=0.678$ and 0.416, $p<0.01$), the total Ca to Mg ratio ($r=-0.477$and $r=-0.398$, $p<0.01$), as well as the Ca_{ex}/Mg_{ex} ratio($r=-0.488$ and -0.398, $p<0.01$). No correlation was instead present between Ni and Ca. When the statistical analysis was performedonly on the serpentine-dominated soils subset (≥60% serpentine clasts),all significantcorrelation were retained in the case of Ni_T, while they became less significant ($p<0.05$) and the one with Mg_{ex} disappeared in the case of Ni_{ex}. The concentrations of organic C, N, P and Kwerenot related to the parent material and better linked to land use. Some grassland soils were in fact particularly rich in nutrients,while forest habitats influenced the C/N ratio. Available P was dependent on the amounts of organic matter (r_P=0.472, $p<0.01$), and negatively associated withbare soil(r_P=-0.296, $p<0.05$)and heat load (r_P=-0.529, $p<0.01$). These two variables were also correlated to each other (r_P=0.307, $p<0.05$).

Considering only serpentine dominated soils, rainfall negatively influenced pH values (r_P=-0.751, $p<0.01$) and $CaCO_3$, while it was positively associated with the C/N ratio (r_P =0.591, $p<0.01$). The C/N ratio was no more related with tree coverand organic carbon was significantly correlated with all nutrients and exchangeable elements (Ca_{ex}, Mg_{ex}, N, K and P). Ni_{ex} was not correlated with any soil or environmental property. All correlations were retained when higher thresholds for serpentine-dominated soils were selected. A large variance of chemical properties characterized therefore also pure serpentinite soils.

Vegetation

Plant communities weregrouped into 15 ecologically meaningful clusters (Figure2a). The full list of species associated with the vegetation clusters, and their indicator values are reported in the electronic annex. TheJaccard index was often slightly below 0.75 (electronic annex 1), probably because of the presence of some widespread species such as *Teucrium chamaedrys* and *Bromus erectus*.The first hierarchical cluster subdivisions identified clusters mainly characterised by the dominance of serpentinites (single-site clusters 1, 11, 9 and a group including small serpentine clusters 2, 3, 5 and non-serpentine clusters 12 and 13) and a group of mixed large clusters. Xerophilous prairies or steppe formations, with scarce or absent tree or shrub cover (Figure 3a), mostly on southward slopes (Figure 3b) at different altitudes (Figure 3c), were represented by cluster 14 and cluster 8 (differentiated by a higher shrub cover, mainly *Juniperus communis*, and by past agricultural activities, such as terraces or surface rock removal in cluster 8). These formations occurred both on serpentinite and on non-serpentinite parent material (Figure 3d). Quite similar steppicgrasslands, on stable serpentinite talus slopes at different altitudes (Figure 3d and 3c), were included in cluster 2. Cluster 10 consisted of xerophilous understory communities of montane (sub-boreal) *Pinus sylvestris* forests (Figure 3a). The most important indicator species of this type of community was *Carexhumilis* (electronic annex 1), but many steppe or prairie species grew despite the weak solar radiation. Understory communities of similar forest habitats were also represented by cluster 3, on serpentinite (Figure 3d), often on northward aspects; ferns were characteristic and some were serpentine endemics (i.e., *Asplenium cuneifolium*).Cluster 4included the understory vegetation of low altitude *Quercuspubescens*,*Pinussylvestris*and *Castaneasativa*open forests, with high heat load (Figure 3b) and low tree cover, growing both on calcschists and serpentinite (included in the same cluster even if clearly differentiated by the presence of *Alyssum argenteum*on serpentinite).Rocky outcrops were included in cluster 5 (on serpentinite, characterized by *A.argenteum*), cluster 7 (never on serpentinite), and 13, on different substrates, at higher altitudes (Figure 3).Caryophyllaceae often characterized serpentine vegetation, particularly on rocky outcrops or talus slopes (e.g., *Minuartia laricifolia* and *Cerastium arvense*).Among the endemic ultramafic species, the hyperaccumulator *Alyssum argenteum* was common in low altitude open forests and serpentinite rocky outcrops, but it was also found in montane*Pinussylvestris*forests and open steppe communities (electronic annex 1).

Considering only serpentine sites (Figure 2b), 9 clusters were obtained:4 single-site clusters, a large one (11 sites, including common xerophilous serpentine communities (the main indicator species was *Alyssum argenteum*), another dominated by thick *Pinus sylvestris* forests (4 sites) devoid of endemic species, and other smaller ones separating respectively scree slopes, thick Scots pineforests

with ferns, rocky outcrops. No cluster separated pure serpentine sites from those having between 60% and 90% serpentinite in the soil coarsefragment fraction.

Soil-vegetation relationships: serpentine and non-serpentine sites

The CAP analysis evidenced that plant communities werewell associated with both environmental and soil properties. CAP1 was negativelyassociated withMg_{ex}, CAP2 positively with tree cover and rainfall, CAP3 increased with high available Ni and low heat load (Table 3). If CAP2 identified forest habitats, CAP4was negatively correlated to rainfall and C/N ratio, separating therefore the most steppic grasslands from the most humid forests.The least fertile sites, with low Ca/Mg ratio and available P,were associated to the highest values of CAP5. The space identified by CAP1 and CAP3 well described the clusters previously found and allowed to separate serpentine adapted associationsfrom those that were not present on this parent material (Figure 4). In fact, many sites ofcluster 4 werewell associated with negative CAP1 values (high Mg levels). Similar associations with high Mg levels were observed for most sites belonging to clusters 5, 9 and 15. On the contrary, clusters 1, 8, 10 and 13 appeared mostly negatively associated with soil Mg. The correlation of plant communities with soil Ni was masked by the opposite correlation with heat load: sites apparently well correlated with high or low soil Ni actually were often characterized by, respectively, low or high heat load values. Clusters 1, 5, 10, 13 were mostly associated with high values of CAP3 (high Ni and/or low HL), while clusters 14, 6 and 9 were mostly associated with low values of this axis. The space identified by positive values of CAP1 and negative CAP3 values comprised only non-serpentine sites. The stepwise analysis indicated that the CAPSCALE performance was strongly dependent on Ni, Ca/Mg ratio, elevation, heat load and tree cover, which were thus the most important variables associated with vegetation gradients in the study area (Table 3).

The factors associated with the presence of common species, as well as the separate ecological effect of heat load and Ni,couldbe evidenced by the RF analysis. Taking into account the soil properties that allowed to distinguish between fertility conditions of serpentine and non-serpentine soils, i.e.Ni_{ex}, Mg_{ex} and Ca_{ex}/Mg_{ex}(Table 2), the RF rankings (Table 4)showed that some species were well associated to serpentine conditions, such ashigh Ni_{ex},lowCa_{ex}/Mg_{ex} or highMg_{ex} values, while some others were negatively correlatedto substrate-derived soil properties. In particular, *Alyssumargenteum, Alyssoidesutriculata*and *Cerastiumarvense*were very well correlated with both high Ni and Mg contentsor Ca/Mg ratio.A good association with serpentine soils was shown also by *Biscutella laevigata*, well correlated with high Ni_{ex} and low values of Ca_{ex}, while a good association with high Ni_{ex} levels without any effect of exchangeable basic cations was observed for *Minuartialaricifolia*and *Sedum montanum*(well correlatedalso to elevated Ca_{ex} concentrations).

Some species were correlated to high Mg_{ex} levels and/or low Ca_{ex}/Mg_{ex} ratios without any relationships with Ni contents: *Armeriaarenaria, Anthyllisvulneraria*s.l. and*Stachysrecta*. Negative association with high Ni_{ex} contents was observed on many species: *Achilleamillefolium, Alyssum alyssoides, Berberis vulgaris,Carexhalleriana, Festucavalesiaca, Fumanaericoides, Helianthemumnummularium* and *Koeleriavallesiana*. High Mg_{ex} contentswere negatively correlated only with*Euphorbia cyparissias*and *Teucrium chamaedrys*. The explanatory power of all the considered edaphic and environmental variables was extremely low for some common species, such as*Dianthus carthusianorum,Dianthus sylvaticus, Potentillaneumanniana* (negative correlation with high Ni_{ex}), *Carexhumilis* and *Sempervivumarachnoideum* (negative association with high Mg_{ex}). Available P never helped in explaining species distribution and the effect of K_{ex} was also limited: *Anthyllisvulneraria* was indeed the only species markedly associated to the K-richest sites.

Soil-vegetation relationships: serpentine sites

The CAP analysis evidenced that serpentine plant communities were strongly dependent on climatic factors (rainfall and heat load), which influenced also the few "important" factors retained after the variable selection based on intercorrelation and variance inflating factors (Table 5). In particular, CAP1 identified a Mg gradient associated with an inverse rainfall one, CAP2 represented a $CaCO_3$-heat load gradient, CAP3 was well correlated with negative heat load and with positive $CaCO_3$, P and C/N, making it not easily interpretable; CAP4 was influenced by highP and Mg_{ex}, CAP5 by C/N and Mg, CAP6 by rainfall. Ni_{ex} was excluded as its influence on the overall model fitting was negligible.

RF rankings (Table 6) for presence-absence species data showed a generalized, strong decrease in Ni_{ex} importance compared with the complete data set: only *Alyssoides utriculata* and *Cerastium arvense* kept their positive correlation with high Ni_{ex}, whileno species were negatively associated with it. $Mg_{ex}$was a rather important factor in explaining the presence/absence of many species: the positive correlation obtained when analyzing the whole data set were retained also in this reduced set (*Alyssum argenteum, Cerastiumarvense* and *Stachys recta*), while a positive association with*Helianthemum nummularium* and *Berberis vulgaris* and a negative one with *Minuartia laricifolia* appeared. The negative associations between Ca_{ex} and *Alyssum argenteum* and *Biscutella laevigata* were retained. On serpentine soils, *Festucavalesiaca, Galiumlucidum, Helianthemumnummularium, Teucrium chamaedrys* had negative relationships with Ca_{ex}; the first two species, in particular, had positive correlations with Ca_{ex} on the complete data set. P became an important factor for many species growing on serpentine soils; this nutrient was never important when considering the complete data set.

Discussion

Pedogenesis in xeric soils in mountain habitats

In this work we wanted toevaluate soil-plant relationships in serpentinic areas,taking into consideration the effect that soil development has on element concentration and, more generally, on soil chemical properties.We therefore maximized the possibilities to detect differences by selecting a xeric environment, where no marked element movements should have occurred. Both the lack of carbonate dissolution in A horizons and $CaCO_3$ precipitation in deeper ones confirmed the pedogenic trends of xeric environments. The high acidity observed in the surface horizons of some serpentinitic soils is common also in other dry environments, such as Mediterranean Italy (Bonifacio et al. 1997) and California (e.g. Lee et al. 2004) and in the study area it was related to the presence of organic matter (r_S=-0.591, $p<0.01$, n=20, i.e. excluding the soils where pH was buffered by carbonates), thus more linked to the acidifying capacity of organic matter than to leaching. The differences between parent materials were well visible in the total element concentrations, and also partially retained in the available forms. The Mg_T and Ni_T concentrations were high on serpentinite, although with a very high variance, but $Ca_T$and the Ca_T/Mg_T ratio were much higher than normal in ultramafic soils: in fact, the Ca_T/Mg_Tratio usually variesbetween 0.01 and 0.1 (Brooks 1987). The high ratio we found in the study area may be related to the presence of carbonate inclusions or to aeolian additions. Aeolian inputs in the Alps are common and arise both from Saharan dusts (Goudie and Middleton 2001) and from shorter range intra-alpine sources (Küfmann 2002). However, the lack of correlation between Ca_T and Ca_{ex} suggests a decoupling of Ca availability from direct weathering of the parent material,and indicates that processes affecting only available forms, such as biocycling, likely played an important role. Calcium indeed is one of the elements that undergo important nutrient uplift and biocycling (Blum et al. 2008), which are particularly enhanced on serpentinitic soils due to element deficiency (Bonifacio et al. 2013). Biocycling may thus contribute to increase the Ca available pool in surface horizons, eliminating the differences between parent materials and decreasing therefore the effects that Ca deficiencies have on vegetation. Serpentinitic soils were characterized by much higher availableNiconcentrations than non-serpentinitic ones, even at high pH values and in the presence of carbonates. High Ni_{ex} contents were observed elsewhere in weakly developed soils, and were related to the incipient weathering of Ni-rich primary minerals (Carter et al. 1987). The Ni_{ex} contents and the lack of correlation between Ni_{ex} and pH values were similar to those found in extremely acidic subalpine or weakly developed alpine soils on serpentinite in nearby valleys (D'Amico and Previtali 2012), where it was leached more efficiently from the most acidic soils; in humid subalpine and alpine serpentine soils, Ni_{ex} was well correlated with organic carbon, while in

these xeric soils Ni_{ex} and C were not associated, suggesting that the metal affinity to organic matter is not sufficient to fully explain Ni availability.

The concentration of organic carbon and of N, P and K, whose availability in forest soils is mainly linked to the turnover of organic matter (Lal et al. 2007), was not related to the parent material. Therefore, nutrient scarcity is not a specific feature of serpentine soils in Alpine environments. The negative correlations between available P and bare soil or heat load suggested that nutrient scarcity was more linked to the limitation to vegetation productivity of the hottest and driest areas, where drought stress associated with topographic position is frequent. The correlations between P, bare soiland heat load were retained also amidst serpentine habitats, confirming the poor primary productivity and the slow nutrient biocycling in the most xeric habitats. Vegetation development on serpentinitic outcrops in Tuscany (Chiarucci 2004) was also inhibited by topographic positions, causing heat and drought stress. In xeric environments of the western Alps, however, this drought stress was not dependent on the substrate lithology and thus could not be considered part of the serpentine syndrome.

The effect of serpentinite soils on vegetation: different approaches, different results

The effect that parent material has on vegetation development was well depicted by cluster analysis, although mainly the smallest clusters showed substrate specificity, while most of the largest ones embraced sites on different substrates. In most cases, single site and small clusters identified serpentine plant communities, pointing to a marked heterogeneity among serpentine vegetation. Such high local diversification of serpentine plant communities is common to other serpentine habitats, such as dry areas in the American Pacific Northwest (del Moral 1972) or dry subtropical South African mountains (Reddy et al. 2009).Some of these small clusters included serpentine-endemic species, such as *Aethionemathomasianum*, *Notholaenamarantae* and *Asplenium cuneifolium*, or serpentine-adapted species (*Silene vulgaris* with peculiar morphological characteristics including small stature, thickened and purple leaves, which may represent a unique serpentine ecotype, as described in D'Amico and Previtali 2012).

The Canonical Analysis of Principal Coordinates allowed to better evidence the relationships between site and soil characteristics and vegetation clusters, although the proportion of inertia explained by the model was rather low (28.02%). This was probably due to the typical disorder of ecological systems hypothesized by other authors (e.g. Chiarucci et al. 2001 and Tsiripidis et al. 2010), associated with a weak differentiation in species composition and to the spatial distribution of some species in a complex mountain area; many xerophilous species were actually confined to small parts of the study area, probably because of Pleistocene glaciations history rather than of present environmental conditions. We cannot exclude however that the omission of other

environmental properties, such as winter snow depth, human disturbances, localized grazing, fire history, etc., which may deeply influence vegetation composition (Guisan et al. 1998, Tsiripidis et al. 2010), might have contributed to the low inertia explained. Although the analysis was useful in showing how both substrate (Mg_{ex} and Ni_{ex} in particular), and land use-related (C/N and P) chemical properties were important for plant community distribution, the effects that Ni has on species and community distribution was partially masked by the opposite effect of heat load, and therefore a definitive result was obtained only using RF.

A good association with serpentine soils was shown by several species, some of which are well known on serpentinite in various areas. *Biscutella laevigata*was well associated with high Ni and low values of exchangeable Ca also in nearby humid alpine valleys (D'Amico and Previtali 2012).Many species belonging to the *Cerastium* genus seem well adapted to serpentine soils in Mediterranean (Marsili et al. 2009) and in boreal habitats, where they showed adaptation to high concentrations of both Ni and Mg (Nyberg Berglund et al. 2004).Adaptation to serpentine conditions is reported also for *Minuartia*and*Stachys* genera: endemic subspecies of *Minuartialaricifolia* and *Stachys recta* grow in Mediterranean Italian ophiolitic outcrops, but they have not been recorded in serpentine soils on the Alps (Pignatti 1992). Both species (*M. laricifolia* and *S. recta*) in the study area are well associated with serpentine edaphic properties, respectively to high Ni_{ex} and high Mg_{ex} values. The presence of these species was correlated with, respectively, Ni_{ex} and Mg_{ex} also considering only serpentine soils.The adaptation of hyperaccumulator species was also well depicted.Considering all substrate lithologies, the presence of high concentrations of exchangeable Ni and Mg seems a favourable factor involved in the distribution of *Alyssum argenteum* in the xeric inner-alpine environment in the north-western Italian Alps. In fact, this species confirmed its selectivity for serpentinitic areas, but even if it typically grows in steppe or rocky outcrops (Pignatti 1992), it was able to thrive also under forest vegetation, although with smaller cover values. The localized inclusions of carbonates or allochtonous materials causing enrichment in exchangeable Ca did not inhibit the growth of this serpentine endemic Ni-hyperaccumulator species. Adaptation has been shown in other European serpentine areas for different Alyssum species: in particular, Gabbrielli et al. (1989) demonstrated a positive effect of high soil Ni on the metabolic efficiency of *Alyssum bertolonii* in Mediterranean Italy. *Alyssoides utriculata*, most common on serpentinite but growing also on non-serpentinic soil in the study area, has been sometimes observed hyperaccumulating Ni on particularly Ni-rich serpentinic substrates in North-western Italy (Roccotiello et al. 2010).High Mg was negatively associated only with*Euphorbia cyparissias* and*Teucrium chamaedrys*. Thus, high available Mg does not appear to be an important limiting factor for vegetation in the study area, when comparable poorly developed soils both on serpentine and on other parent materials are considered.The effect of Ni on species

distribution was more marked than that of Mg based on the number of species that were negatively correlated with high Ni. The RF was extremely powerful in disentangling the respective importance of different factors, while taking into account the full set of soil and environmental properties, but the results were confirmed when only the typical factors of the serpentine syndrome were taken into account. The results are also visible observing the differences in the most important soil properties in the sites where the same species grow (Figure 5 and electronic annex 2). The ratios between the average values of Ni_{ex}, Mg_{ex} and Ca_{ex}/Mg_{ex} in the sites where the species were present or absent are reported in Figure 5 (distribution data in electronic annex 2) and clearly show a great discriminating ability of Ni_{ex} with respect to both Mg_{ex} and the Ca to Mg ratio. Ni_{ex} therefore seems the most important factor of the serpentine syndrome characteristics in shaping vegetation distribution on and off serpentinite in xeric inner-Alpine environment.

However, when only serpentine-dominated sites were considered, the main ecological gradients were mostly related with microclimatic features, nutrients (whose cycling and bioaccumulation are related with xericity gradients) and Mg_{ex}. Ni_{ex}, able to characterize serpentine soils as a whole despite its large concentration variability, disappeared from the important edaphic factors explaining both vegetation community distribution and species presence/absence. These results are similar to the ones obtained by many studies performed in many serpentine environments in the world, and appeared with a threshold of serpentinite abundance in the parent material of 60%. Above 60% serpentinite, significant differences were found between Ni, Mg and Ca/Mg compared to soils with less than 60% serpentinite, serpentine endemics appeared and their frequency remained more or less stable above the threshold, indicating that relatively low amounts of serpentine may deeply influence soil and vegetation properties, without any measurable gradient at higher contents. The differences between the two approaches to the study of the relationships between soil properties and vegetation in serpentinitic soils are therefore striking. Nutrient deficiencies were not specific of serpentinitic areas in the Alpine environment we have studied, and neither were the harsh site conditions depicted by e.g. heat load or rockiness. Ni therefore was probably the most important single edaphic factor in differentiating serpentine vegetation from non-serpentine. Its primary importance is verified by the strong decrease in model performances when this element was excluded from the analysis. Within the serpentinitic sites, many species which were negatively correlated with high Ni disappeared or became extremely rare, and the presence of the remaining ones was mainly associated to particularsite conditions, such as bare soil or low tree cover (*Helianthemumnummularium, Festucavalesiaca, Koeleriavallesiana, Potentillaneumanniana*) or thick tree cover with large amounts of exchangeable Mg in the soil (*Berberis vulgaris*). Other fertility factors became more important for species presence, such as macronutrient and Ca

abundance, which were not correlated to Ni availability when the serpentine-dominated subset was considered.

Conclusions

Soils developed in xeric, inner-alpine climates in the Alps underwentno important base and metal leaching,thus serpentine soils werestill particularly rich in total and exchangeable Ni and Mg. Even though the Ca/Mg ratio was lower than on non-serpentine soils, the values werenever excessively low, thanks to Ca bioaccumulation and carbonate inclusions.N, P, K scarcity characterizedbarren soils on every substrates, and didnot characterize serpentine soils in particular, being associated with south-facing aspects, steep slopes and high heat load.Plant communities on serpentinite had a higher heterogeneity than non-serpentinite ones, thanks to the presence of severalendemics, and differences in vegetation between serpentine and non-serpentine sites were correlated with Mg and Ni.Ni excess most often precluded the presence of plant species, while an exclusion due to Mg is rarer. Endemic species were instead mostly adapted to both factors.
When only serpentine-dominated areas were considered, vegetation variability was mostly linked with nutrient concentration gradients and microclimatic features.
Different approaches to the study of the "serpentine syndrome" thus lead to differently comparable results, in particular on the role of Ni as a driver for vegetation pattern. Nickel availability discriminated between serpentinitic and non serpentinitic areas, while climate and small variations in nutrient cycling and availability predominated at the high Ni background of serpentine soils.

Acknowledgement

This study was performed thanks to the research agreement between the University of Turin, NATRISK centre, and RegioneAutonoma Valle d'Aosta, Department of Soil protection and WaterResources. We also thank two anonymous reviewers and the Editor of Plant and Soil journal for the useful comments on previous versions of this paper.

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Table 1:Differences in pH, carbonates and total element contents in soils developed on different parent material

	Parent material	N	Mean	Standard deviation	Min	Max	P*
$CaCO_3$ (g kg^{-1})	Serpentinites	26	15.5	36.3	0.0	160.0	0.206
	Others	25	38.1	52.3	0.0	146.6	
pH	Serpentinites	26	6.68	1.06	4.40	8.10	0.242
	Others	25	7.02	0.99	4.79	8.50	
Ca_T (g kg^{-1})	Serpentinites	23	16.75	19.85	1.00	85.52	0.243
	Others	21	23.29	16.44	4.41	58.60	
Mg_T(g kg^{-1})	Serpentinites	23	57.51	25.60	19.29	128.00	0.000
	Others	21	20.44	13.46	7.47	59.00	
Ca_T/Mg_T	Serpentinites	23	0.37	0.40	0.01	1.52	0.000
	Others	21	1.43	1.28	0.31	4.90	
Ni_T (g kg^{-1})	Serpentinites	24	0.76	0.47	0.10	1.66	0.000
	Others	21	0.17	0.15	0.03	0.62	

*P probability of equality of mean (one-wayAnova)

Table 2:Differences in C, C to N ratio and contents of exchangeable elements in soils developed on different parent material

	Parent material	N	Mean	Standard deviation	Min	max	P*
C(g kg^{-1})	Serpentinites	26	46.2	48.7	9.4	218.0	0.426
	Others	25	37.5	25.1	8.3	101.3	
C/N	Serpentinites	26	16.1	7.6	9.0	49.0	0.346
	Others	25	14.5	4.2	9.1	24.1	
Ca_{ex}($cmol_c$ kg^{-1})	Serpentinites	26	12.36	16.40	1.86	87.33	0.755
	Others	25	13.58	10.66	0.62	39.49	
Mg_{ex}($cmol_c$ kg^{-1})	Serpentinites	26	2.86	2.36	0.76	8.80	0.010
	Others	25	1.36	1.53	0.22	7.64	
Ca_{ex}/Mg_{ex}	Serpentinites	26	5.86	5.50	0.53	19.32	0.007
	Others	25	15.98	15.18	0.83	50.63	
K_{ex}($cmol_c$ kg^{-1})	Serpentinites	26	0.19	0.13	0.06	0.48	0.855
	Others	25	0.20	0.15	0.04	0.69	
Ni_{ex}($cmol_c$ kg^{-1})	Serpentinites	26	0.031	0.028	0.002	0.109	0.000
	Others	25	0.002	0.002	0.000	0.006	
P_{Olsen} (mg kg^{-1})	Serpentinites	26	5.69	5.25	0.87	27.83	0.299
	Others	25	4.50	2.35	1.93	12.07	

*P probability of equality of mean (one-wayAnova)

Table 3: Biplotscores for the most significant canonical axes of the Canonical Analysis of Principal Coordinates (CAP). *: ranking of importance derived from the stepwise analysis; Ca_{ex}/Mg_{ex} ratio, Ni_{ex}, elevation, tree cover and heat load were equally the most important (ranking 1), followed by rainfall (6) etc.

	Ranking*	CAP1	CAP2	CAP3	CAP4	CAP5
		Biplot scores for constraining variables				
$CaCO_3$	9	0.07	0.13	0.17	0.14	-0.07
N	13	-0.09	0.01	0.16	-0.08	-0.18
C/N	8	0.09	0.09	0.11	-0.66	-0.34
Mg_{ex}	11	-0.55	0.10	0.18	0.33	0.28
Ca_{ex}/Mg_{ex}	1	-0.07	-0.01	-0.06	0.33	-0.45
K_{ex}	12	0.08	0.13	0.09	-0.05	-0.06
Ni_{ex}	1	-0.21	0.02	0.62	-0.31	0.18
P_{Olsen}	7	-0.16	0.24	0.32	-0.06	-0.42
Elevation	1	0.25	-0.02	0.11	-0.20	0.31
Rainfall	6	0.15	0.44	0.16	-0.66	0.07
Tree cover	1	0.10	0.85	-0.03	0.04	-0.22
Bare soil	14	-0.14	-0.04	-0.07	0.14	0.08
Surface rockiness	10	-0.28	-0.15	0.07	-0.19	0.36
Heat load	1	-0.29	-0.06	-0.54	-0.20	0.13

Table 4: Random Forest rankings of the main environmental and edaphic factors- The numbers represent positive/negative correlation on an arbitrary scale (1-7) of decreasing importance of the factor in the presence/absence of the species. Only species growing in 10% or more of the sampling plots were considered

	pH	$CaCO_3$	C	N	C/N	Ca_{ex}	Mg_{ex}	Ca_{ex}/Mg_{ex}	K_{ex}	Ni_{ex}	P_{Olsen}	Elevation	Rainfall	Tree cover	Bare soil	Surface rockiness	Heat load
Achilleamillefolium						2+				4-				1-		3-	5+
Allium sphaerocephalon			4+	1+		3+								2-			5+
Alyssoidesutriculata	5+		4+	3-				2-	6+	1+							
Alyssum alyssoides						3+		4+		2-				5-		1+	
Alyssum argenteum						3-	2+			1+		4-					5+
Anthyllisvulneraria		6+					5+	3-	1+			2+					4+
Armeriaarenaria				5+			3+	2-						4-			1-
Artemisia campestris			3-	4-								5-		1-			2-
Aspleniumtrichomanes			1+	2-		3+			4-	5+						6+	7-
Berberis vulgaris										2-			3-				1-
Biscutellalaevigata						2-			4+	1+		3+					
Bromus erectus				2+	4-								5-	1-			3+
Carexhalleriana					2-			4-		1-			5+	3-			
Carexhumilis	4+	2-				6+	5-					3-		1+			
Cerastiumarvense						4-	1+	2-		3+		7+	5-				6+
Dianthus carthusianorum		3-	5+							2-				4+		1+	
Dianthus sylvaticus										1-						2+	
Euphorbia cyparissias		7+		4+	5-		2-	3+		6+		1+					
Festucavalesiaca		3+			6+	4+				2-				1-			5-
Festucavaria	3-	5-							2+				4+				1-
Fumanaericoides	2+	5+		6-				4+		1-							3+
Galiumlucidum				2+	5+	3+		4-									1+
Helianthemumnummularium		2+								4-					1+		3+
*Hieraciummurorum*aggr.	2-												3+	1+			4-
Koeleriavallesiana										2-		3-	5-	1-	4+		
Lactucaperennis	5+		1-									2-		3-	4+		
Minuartialaricifolia					3+					2+			1+				
Potentillaneumanniana	3-	2-						7-		6-		5-		1-	4+		

Sedum album		2+			4-				3-							1+	
Sedum montanum			5-	1-		4+			3-	2+							
Sempervivumarachnoideum						2-	7-					4+		1-	6+	3+	5-
Sempervivumtectorum		3-	6-		4-			5+					2+	1-			
Stachys recta				3-	4-		2+							1-			
Stipapennata		5+	3-	4-	2-									1-			
Teucrium chamaedrys	5+		6-				3+	1+					2-				4+
Verbascumlychnitis									4+					2-	1+		3-

Table 5: Biplotscores for the most significant canonical axes of the Canonical Analysis of Principal Coordinates (CAP) for serpentine dominated sites (serpentine >= 60% in the parent material). *: ranking of importance derived from the stepwise analysis.

	Ranking*	CAP1	CAP2	CAP3	CAP4	CAP5	CAP6
			Biplot scores for constraining variables				
Mg	1	0.70	-0.12	0.19	0.47	-0.45	0.19
C/N	6	-0.36	-0.09	0.53	0.20	0.68	0.28
CaCO3	2	-0.07	0.67	0.55	-0.31	-0.06	-0.38
P	5	-0.22	-0.45	0.43	0.56	-0.35	-0.37
Heat Load	3	-0.05	0.74	-0.65	-0.09	-0.04	0.11
Rainfall	4	-0.74	-0.03	0.16	0.26	0.03	0.60

Table 6: Random Forest rankings of the main environmental and edaphic factors on serpentine sites.The numbers represent positive/negative correlation on an arbitrary scale (1-7) of decreasing importance of the factor in the presence/absence of the species. Given the smaller number of samples, only species growing in 25% or more of the sampling plots were considered

	pH	$CaCO_3$	C	N	C/N	Ca_{ex}	Mg_{ex}	Ca_{ex}/Mg_{ex}	K_{ex}	Ni_{ex}	P_{Olsen}	Elevation	Rainfall	Tree cover	Bare soil	Surface rockiness	Heat load
Alyssoidesutriculata			4-	3-		5+		1-		2+							
Alyssum argenteum		4-				1-	3+					2-	5-				
Artemisia campestris			3+	4-			2+							1-			
Aspleniumtrichomanes			4-	3+					1-		2+						
Berberis vulgaris							1+							2+			
Biscutellalaevigata	4-		3-			2+		5-				1+					
Bromus erectus		6+									3+		2-	5-	4-	1-	
Carexhumilis	5+	2-				3-			4-					1+			
Cerastiumarvense							1+			2+			3-				
Festucavalesiaca						1-								2-			
Festucavaria											1+						2-
Galiumlucidum			5+			3-					2-			4-			1+
Helianthemumnummularium		3+				1-	2+								4+		
Koeleriavallesiana														1-			
Minuartialaricifolia				2+			1-						3+				
Potentillaneumanniana						4+					1-	3-		5-	2+		
Sedum album		2-														1+	
Sedum montanum																1+	
Sempervivumarachnoideum											4+			2-	1+		3+
Sempervivumtectorum					2-						1-			3-			
Stachys recta							1+					2-					
Teucriumchamaedris	5+					3-		4+			1-						2+

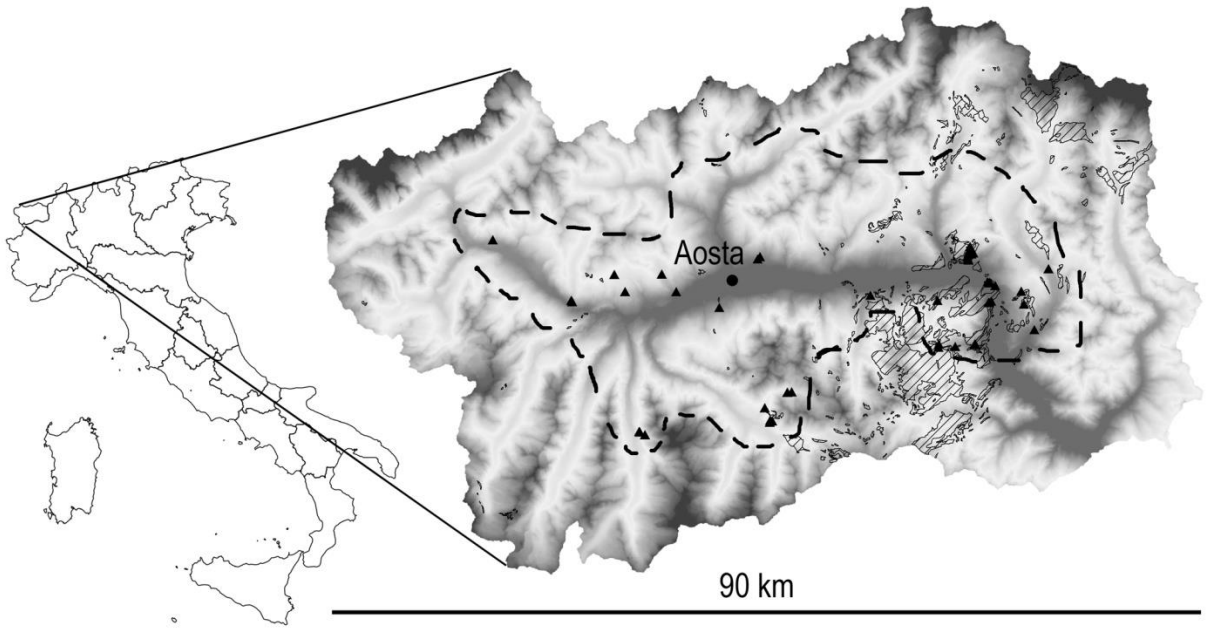

Fig. 1: the study area in the central part of the Valle d'Aosta region. The area characterized by inner-alpine xeric climate is roughly markedby a dotted line; soil and vegetation sampling sites are represented by triangles (several overlaps due to scale); serpentine outcrops are evidenced by shaded areas

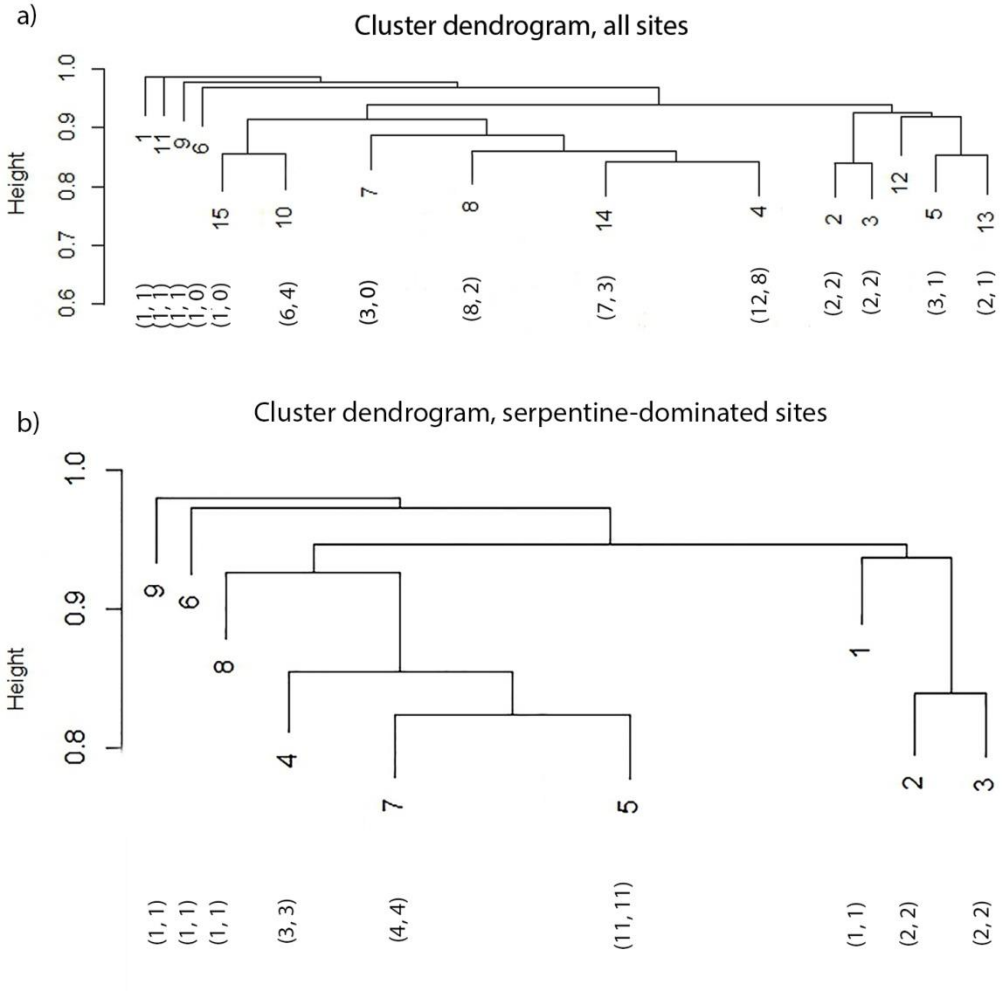

Fig. 2: cluster dendrograms of the total vegetation relevèes (a) and of serpentine-dominated sites (b), (hierarchical clustering, based on Bray-Curtis distance algorithm and on average linkage method).The first number in the parenthesis indicates the number of sites in each cluster, the second one the number of serpentine-dominated clusters.

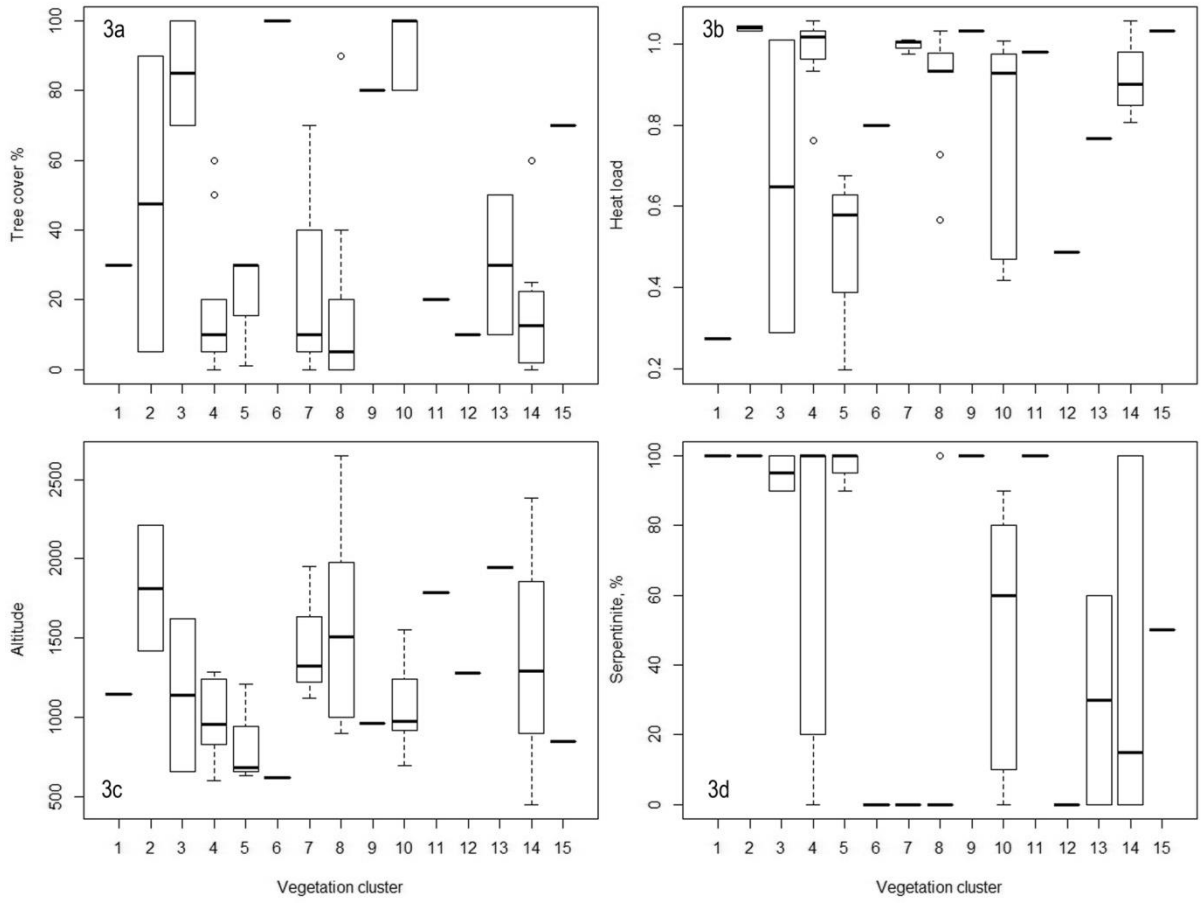

Fig. 3: tree cover (%), heat load, altitude (m) and serpentinite content (%) in the soil parent material characterizing the 15 vegetation clusters.

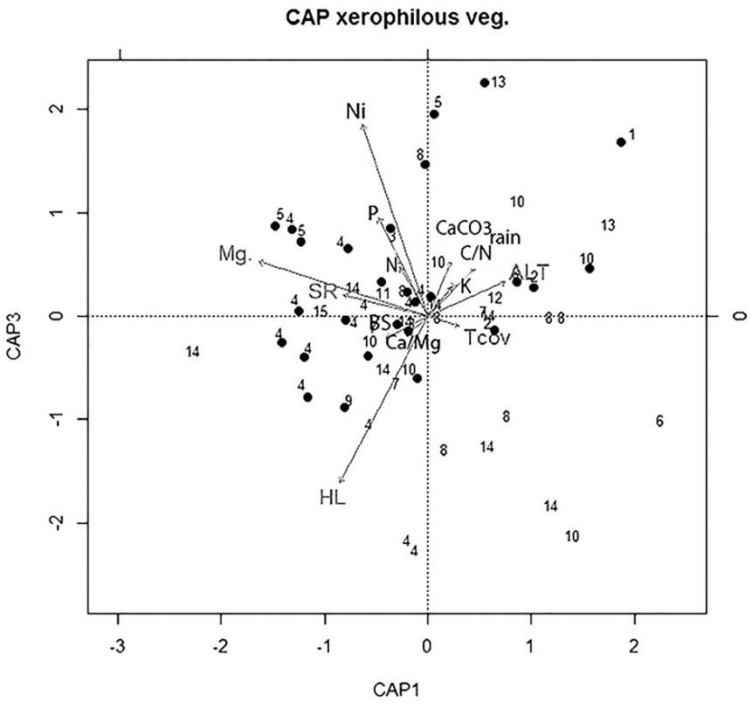

Fig. 4: CAP scatterplots of xerophilous vegetation; the combination of axis 1 (CAP1) and 3 (CAP3) is shown, as most representative of serpentine habitats. Sites are represented by cluster numbers andserpentinite-dominated sites are indicated by a black dot. The following abbreviations have been used: SR = surface rockiness; ALT = altitude; HL = heat load; BS = bare soil.

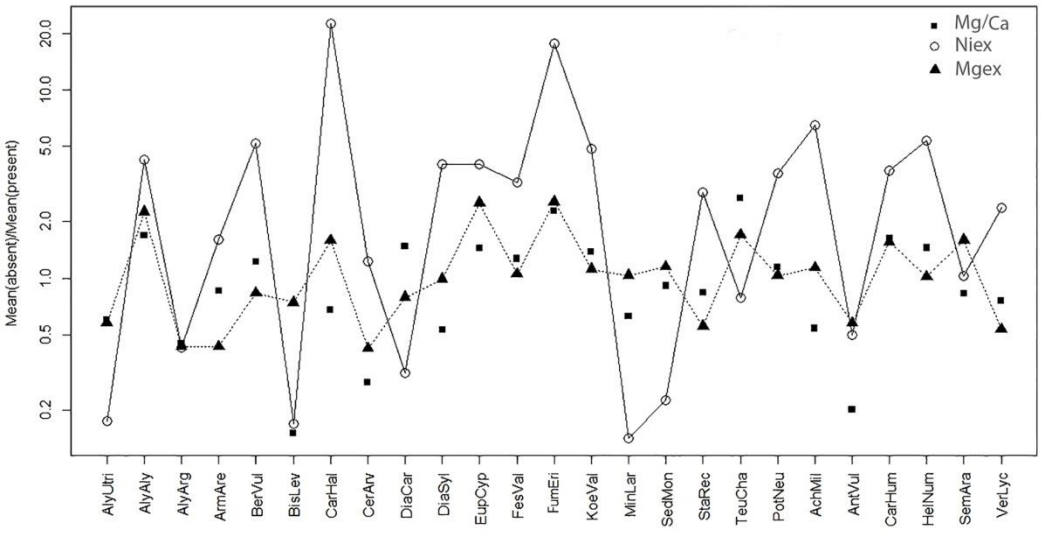

Fig. 5: Ratios between mean values of serpentine syndrome factors (Ni_{ex}, Mg_{ex} and Mg_{ex}/Ca_{ex}) in the areas where the same species was absent or present; given the negative correlation values between Ca/Mg and Ni, the Mgex/Caex ratio is shown, in order to make the rankings of importance easier to be compared. The species shown are those having a rank of positive or negative correlations with the same serpentine factors in Table 3.

The serpentine syndrome in a xeric inner-Alpine environment: relative effect of nutrients and Ni on vegetation

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Plant communities (from cluster analysis) and their specific composition. The column "const" indicates the fraction of samples in each cluster all species occurs in. The indicator species (Legendre and Legendre 1997) of the cluster are also shown (IndVal). The number of sites included in each cluster is shown, as well as the Jaccard cluster stability index (Hennig 2007). The Jaccard stability and species Indicator values are not shown for single-site clusters.

	Cluster																													
	1		2		3		4		5		6		7		8		9		10		11		12		13		14		15	
	ind val	const	ind val	const	ind val	const	ind val	const	ind val	const	ind val	const	ind val	const	ind val	const	ind val	const	ind val	const	ind val	const	ind val	const	ind val	const	ind val	const	ind val	const
Number of sites		1		2		2		13		3		1		3		9		1		6		1		1		2		8		1
Jaccard				0.82		0.74		0.59		0.85				0.96		0.63				0.68						0.84		0.66		
Achillea millefolium								0.23								0.22											0.23	0.5		
Achillea tomentosa																0.11														
Acinos alpinus																0.11									0.34	0.5		0.12		
Aethionema thomasianum																					1									
Agropyron intermedium																0.22														
Agrostis capillaris																												0.12		
Ajuga reptans																			0.17											
Allium sphaerocephalon					0.23	0.5		0.15		0.33						0.11														
Alyssoides utriculata				0.5						0.33				0.33							1							0.25		
Alyssum alyssoides								0.0					0.2	0.3		0.2						1								

								8					2	3		2														
Alyssum argenteum							0.2	0.62	0.23	1						0.11		1		0.33								0.38		
Amelanchier ovalis								0.08											0.29	0.33										
Antennaria dioica			0.5	0.5																										
Anthoxanthum odoratum					0.47	0.5										0.11														
Anthyllis vulneraria			0.5	1												0.11												0.38		
Arabidopsis halleri																									0.5	0.5				
Arabis ciliata								0.08																						
Arabis hirsuta								0.08																				0.12		
Arctostaphylos uva-ursi																0.22														
Arenaria ciliata																0.11														
Armeria arenaria										0.33						0.11											0.37	0.63		
Artemisia absinthium								0.08								0.22												0.12		
Artemisia borealis																0.11												0.12		
Artemisia campestris								0.23		0.33						0.44										0.5		0.25		
Asperula aristata								0.15														1								
Asperula purpurea								0.08																						
Asplenium adiantum-nigrum								0.08																						
Asplenium cuneifolium					0.35	0.5			0.21	0.67																				
Asplenium ruta-muraria								0.08		0.33															0.27	0.5				
Asplenium septentrionale								0.23					0.2	0.33																
Asplenium trichomanes					0.2	0.5		0.23	0.36	0.67																				
Astragalus leontinus																				0.17										
Astragalus monspessulanum																			0.33	0.33										

Astragalus sempervirens														0.33														0.13		
Athamantha cretensis				0.5																		1			0.27	0.5		0.13		
Avenella flexuosa						0.5						1																		
Berberis vulgaris						0.5		0.23				1		0.33		0.11				0.67						0.5	0.22	0.75		
Biscutella laevigata				0.5	0.26	0.5		0.08								0.11						1						0.13		
Brachypodium pinnatum			0.46	0.5				0.08																				0.13		
Brachypodium sylvaticum								0.08																						
Bromus erectus				0.5				0.46		0.33				0.67		0.44				0.17						0.5	0.63	1		1
Bunias orientalis								0.15								0.11														
Bupleurum ranunculoides			0.27	0.5																0.17								0.25		
Calamagrostis arundinacea					0.47	0.5														0.17										
Campanula cenisia																0.11														
Campanula cochleariifolia			0.2	0.5												0.11									0.2	0.5		0.13		
Campanula glomerata																0.11														
Campanula rotundifolia								0.08												0.17										
Campanula scheuchzeri																0.11									0.34	0.5		0.13		
Carduus defloratus																0.11														
Carex flacca																		1												
Carex halleriana								0.08						0.33		0.11												0.25		1
Carex humilis								0.54		0.33				0.33				1	0.69	1								0.13		1
Carex liparocarpus								0.08																						
Carex ornitopodioides																											0.25	0.25		
Carex sempervirens																0.11														
Carlina acaulis																0.1														

															1															
Centaurea cyanus								0.08		0.33			0.21	0.33																
Centaurea nervosa																0.11														
Centaurea scabiosa								0.08		0.33															0.27	0.5				
Cephalanthera longifolia																				0.17								0.12		1
Cerastium arvense									0.25	0.67						0.11									0.28	1		0.5		
Ceterach officinarum								0.08	0.27	0.33																				
Cleistogenes serotina								0.08								0.11														
Clematis vitalba								0.38		0.33						0.11														
Colchicum autumnalis																				0.17										
Colutea arborescens								0.08												0.33										1
Daphne mezereum																0.11														
Dianthus carthusianorum								0.23												0.17				1				0.25		
Dianthus sylvaticus								0.15				1		0.33		0.11												0.13		
Dictamnus album										0.33																		0.13		
Digitalis lutea																												0.12		
Diplotaxis tenuifolia																									0.5	0.5				
Doronicum grandiflorum			0.5	0.5																										
Draba siliquastrum																									0.5	0.5				
Echium vulgare									0.25	0.33						0.11														
Eryngium campestre								0.08								0.22														
Euphorbia cyparissias														0.67		0.22				0.33					0.39	1		0.13		
Euphorborbia seguieriana								0												0.17										
Festuca ovina								0.15										1												

Festuca valesiaca								0.31		0.33				0.33	0.71	1										0.5		0.5		
Festuca varia			0.23	1	0.57	1		0.15		0.67						0.11				0.17				1				0.13		
Fragaria vesca												1							0.22	0.33										
Fumana ericoides								0.31								0.11														1
Fumana procumbens								0.08								0.11														
Gagea fragifera								0.08																						
Galium album						0.5		0.08								0.11														
Galium anysophyllon																0.22														
Galium lucidum								0.77						0.33		0.33				0.33						0.5	0.26	0.63		
Galium mollugo												1																0.12		
Gentiana ciliata																												0.12		
Gentiana ramosa			0.49	0.5												0.22														
Gentiana verna																0.22														
Geranium robertianum									0.33	0.33																				
Geranium sanguineum								0.08										1												
Geranium sylvaticum																												0.12		
Globularia punctata													0.2	0.33		0.11												0.13		
Gypsophyla reptans														0.33		0.44										0.5		0.13		
Hedera helix					0.28	0.5						1																		
Helianthemum nummularium								0.46				1		0.33		0.44				0.33						1	0.28	0.75		1
Hieracium angustifolium			0.2	0.5												0.11												0.13		
Hieracium murorum			0.35	0.5		0.5				0.33						0.11				0.5										
Hieracium pilosella																0.44												0.13		

Hieracium sabaudum												1																		
Hieracium villosum																												0.12		
Hypericum perfoliatum																											0.25	0.25		
Jasione montana													0.33	0.33																
Juniperus communis													0.94	1		0.22												0.13		1
Juniperus sabina						0.5		0.38						0.67		0.78				0.33								0.13		
Knautia arvensis														0.33														0.25		
Koeleria vallesiana								0.62		0.33				0.67	0.21	0.56								1		0.5		0.5		
Lactuca perennis								0.23						0.33		0.11												0.13		
Laserpitium halleri			0.5	0.5																										
Laserpitium latifolium																						1								
Laserpitium siler													0.27	0.67											0.6	1				
Leontopodium alpinum																0.11									0.73	1		0.25		
Ligustrum vulgare												1																		1
Linaria alpina																						1								
Lonicera nigra																0.11				0.17										
Lotus corniculatus													0.21	0.33														0.38		
Lotus corniculatus subso. Alpestris																0.11														
Medicago sativa								0.08																						
Melica ciliata								0.15																						
Melica nutans								0.08	0.27	0.33																				
Melilotus albus												1																		
Minuartia laricifolia		1	0.23	1				0.15		0.33						0.11														
Minuartia recurva																0.11														
Minuartia verna													0.2	0.3														0.1		

													4	3														3		
Molinia coerulea														0.33				1												
Muscari comosum								0.15																						
Notholaena marantae								0.15		0.33																				
Ononis natrix								0.15																						
Ononis reptans																												0.12		
Orobanche mayeri								0.08																						
Oxytropis halleri																0.22														
Petrorhagia saxifraga								0.08		0.33						0.11														
Peucedanum oreoselinum								0.08																						
Phyteuma betonicifolium																0.11														
Pimpinella nigra																			0.24	0.33								0.13		
Pimpinella saxifraga												1																		
Plantago alpina																0.11														
Plantago serpentina														0.33		0.22										0.5		0.13		
Poa nemoralis												1														0.5				
Polygala chamaebuxus					0.5	0.5																								
Polygonatum odoratum								0																				0.12		
Polypodium vulgare					0.47	0.5				0.33						0.11				0.17										
Potentilla argentea								0.08																						
Potentilla neumanniana								0.69						0.33		0.33											0.2	0.63		
Prenanthes purpurea					0.5	0.5																								
Primula hirsuta									0.33	0.33																				
Prunella grandiflora														0.33														0.13		

Pteridium aquilinum																		1												
Pulsatilla alpina																												0.12		
Pulsatilla montana								0.08								0.11														
Rhinanthus alectorolophus								0.08																						
Rumex acetosella		1																												
Rumex scutatus								0.08														1						0.25		
Salvia glutinosa					0.25	0.5						1																		
Sanguisorba minor								0.08											0.21	0.33								0.13		
Sanguisorba officinale									0.33	0.33																				
Sanguisorba officinalis										0.33																				
Saponaria ocymoides								0.15																						1
Saxifraga paniculata									0.36	0.67										0.17		1				0.5				
Scabiosa columbaria																												0.12		
Sedum album								0.38	0.36	1						0.11				0.17					0.36	1				
Sedum atratum																												0.12		
Sedum dasymphyllum										0.33															0.3	0.5				
Sedum montanum								0.46		0.67				0.67		0.11				0.17								0.25		
Sempervivum arachnoideum				0.5				0.54						0.33		0.22								1		0.5		0.13		
Sempervivum tectorum								0.54		0.33				0.67		0.44								1				0.63		
Senecio inaequidens								0.15																						
Senecio ovatus								0.08																						
Seseli annuum								0.08								0.11												0.12		
Sesleria caerulea																										0.5		0.13		
Silene armeria								0																				0.1		

																			2	
Silene nutans						0.08	0.33	1			0.22								0.13	
Silene rupestris	1					0.08														
Silene vulgaris														1						
Solidago virgaurea						0.08							0.17							
Stachys recta						0.31	0.67		0.67								0.5		0.5	
Stachys sylvatica											0.22									
Stipa pennata						0.38			0.33		0.44						0.5		0.5	
Taraxacum officinalis					0.5	0.15					0.11								0.13	
Teucrium chamaedris			0.5			0.21	0.92		1		0.44		0.83		1				0.38	
Teucrium montanum											0.22								0.25	1
Thalictrum foetidus																			0.12	
Thalictrum minus				0.4	0.5														0.13	
Thesium linifolium						0.08													0.12	
Thymus froelichianus						0.23					0.33									
Thymus serpyllum		0.26	0.5				0.33				0.22						0.21	1	0.13	
Thymus vulgaris						0.48	0.62	0.67					0.17							
Tragopogon pratensis															1				0.12	
Trifolium alpinum													0.17							
Trifolium pratense											0.22									
Trinia glauca						0.15														
Trisetum distichopyllum			0.5											1						
Turritis glabra						0.08														
Vaccinium myrtillus				0.5	0.5															

Velar ochroleocum				0.08											0.25	
Velar virgatum				0.15				0.11								
Verbascum lychnitis								0.33				0.23	0.5	0.25		
Veronica arvensis								0.11								
Veronica prostrata								0.11								
Veronica urticifolia										0.17						
Vicia hirsuta				0.15				0.11								
Vicia onobrychoides				0.08				0.11		0.33						
Viola kitaibelliana				0.08				0.11								
Viola biflora												0.5	0.5			

The serpentine syndrome in a xeric inner-Alpine environment: relative effect of nutrients and Ni on vegetation

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Median, mean values of Ni_{ex}, Mg_{ex} and Ca_{ex}/Mg_{ex} ratio, and their 25% and 75% quartiles, in the soils where some common species grow (Present) or not (Absent). Only the species associated with these serpentine-typical soil properties are shown (obtained from the Random Forest elaborations on the complete data set). The 25% and 75% quartiles of variables showing strong discriminating power between presence or absence of the species are underlined.

		Ni_{ex}		Mg_{ex}		Ca_{ex}/Mg_{ex}	
		Median-mean	25%-75% quartile	Median-mean	25%-75% quartile	Median-mean	25%-75% quartile
Achillea millefolium	Present	0.63-2.50	0.01-4.5	1.85-1.91	1.29-2.67	4.27-10.29	3.39-8.23
	Absent	1.56-16.23	0.66-11.38	1.34-2.17	0.78-2.57	4.77-10.31	2.15-15.22
Alyssoides utriculata	Present	23.38-52.52	5.26-94.28	2.60-3.46	1.32-5.46	1.22-6.46	0.65-2.97
	Absent	1.34-9.12	0.60-5.72	1.36-2.00	0.78-2.63	5.27-10.79	2.76-15.13
Alyssum alyssoides	Present	0.06-3.54	0.00-1.38	0.95-1.00	0.62-1.05	16.22-16.30	9.53-21.44
	Absent	1.63-15.001	0.65-8.71	1.44-2.24	0.78-2.67	4.27-9.69	2.15-13.38
Alyssum argenteum	Present	6.31-22.57	4.41-18.13	2.62-3.43	1.88-4.36	3.38-5.71	1.71-5.41
	Absent	0.84-9.63	0.23-1.58	0.95-1.48	0.72-1.52	6.68-12.60	2.76-17.53
Anthyllis vulneraria s.l.	Present	8.56-25.18	2.71-14.37	1.30-3.46	0.94-6.14	2.21-2.28	1.44-2.96
	Absent	1.34-12.53	0.47-5.72	1.40-2.00	0.76-2.57	5.60-11.31	2.75-15.35
Armeria arenaria	Present	7.50-9.11	0.42-14.48	2.67-4.21	1.65-7.20	2.04-9.00	1.38-3.51
	Absent	1.38-14.66	0.64-6.76	1.29-1.82	0.77-2.32	5.57-10.50	2.64-15.16
Berberis vulgaris	Present	1.00-3.67	0.04-4.22	1.38-2.40	0.80-2.47	3.95-11.71	5.47-18.85
	Absent	2.50-19.07	0.73-11.59	1.41-2.00	0.78-2.57	5.17-9.60	2.32-13.00
Biscutella laevigata	Present	18.25-53.55	13.81-92.72	1.99-2.76	1.09-2.62	1.46-1.68	0.65-2.11
	Absent	1.18-9.00	0.15-4.98	1.36-2.05	0.76-2.57	5.60-11.38	3.08-15.35
Carex halleriana	Present	0.57-0.69	0.01-1.31	1.41-1.40	0.90-1.59	6.49-7.25	2.62-11.59
	Absent	2.69-15.60	0.64-9.29	1.38-2.22	0.78-2.60	4.52-10.69	2.24-15.35
Carex humilis	Present	1.42-4.94	0.80-4.22	1.36-1.55	1.03-1.77	11.73-13.84	3.56-18.30
	Absent	2.38-18.44	0.37-9.92	1.53-2.42	0.76-2.81	3.54-8.54	2.15-8.72
Cerasium arvense	Present	11.38-11.68	0.99-19.75	2.16-4.10	0.95-7.64	3.32-3.25	0.51-3.63
	Absent	1.3-14.39	0.35-4.94	1.34-1.73	0.78-2.47	5.63-11.72	2.34-15.73
Dianthus carthusianorum	Present	0.50-34.58	0.03-4.82	1.65-2.60	1.09-2.49	11.18-14.35	3.50-23.29
	Absent	1.63-10.87	0.66-8.20	1.39-2.06	0.77-2.57	4.48-9.70	2.21-13.62
Dianthus sylvaticus	Present	1.47-3.77	1.10-1.61	1.20-2.15	0.87-1.52	3.54-5.81	2.54-8.13
	Absent	1.65-15.21	0.37-8.90	1.40-2.12	0.78-2.60	4.66-10.87	2.24-15.35
Euphorbia cyparissias	Present	1.27-3.97	0.65-3.75	0.76-0.94	0.58-0.95	8.45-13.81	3.94-16.40
	Absent	1.63-15.93	0.50-6.71	1.54-2.36	0.94-2.67	4.26-9.61	2.13-15.09
Festuca valesiaca	Present	0.64-5.82	0.31-7.80	1.12-2.06	0.72-2.60	5.88-11.88	3.57-15.76
	Absent	1.18-18.71	0.95-18.85	1.42-2.16	0.92-2.55	3.45-9.38	2.14-14.66
Fumana ericoides	Present	0.38-0.88	0.00-1.03	1.04-1.03	0.72-1.30	20.38-20.58	14.04-28.12
	Absent	1.81-15.57	0.64-9.29	1.48-2.62	0.78-2.67	3.78-9.02	2.15-11.73
Helianthemum nummularium	Present	0.99-3.98	0.17-2.66	1.03-2.11	0.66-2.11	8.45-12.53	1.30-17.20
	Absent	4.38-21.33	0.80-12.63	1.54-2.14	0.95-2.62	3.63-8.66	2.14-9.70
Koeleria vallesiana	Present	0.74-4.24	0.02-4.22	1.54-1.99	0.69-2.57	5.91-12.32	3.40-20.13
	Absent	3.73-20.61	0.91-11.89	1.31-2.22	0.83-2.52	4.10-8.92	2.10-11.45
Minuartia laricifolia	Present	12.25-55.31	6.45-65.06	0.94-2.07	0.85-2.83	2.38-6.80	1.88-9.55
	Absent	1.27-7.78	0.44-5.03	1.41-2.14	0.77-2.52	4.77-10.83	2.61-14.48
Potentilla neumanniana	Present	0.28-5.07	0.00-6.91	1.59-2.08	0.98-2.65	4.52-11.21	2.29-7.96
	Absent	1.47-18.37	0.80-9.92	1.24-2.15	0.78-2.24	4.52-9.85	2.33-15.12
Sedum montanum	Present	2.69-24.05	0.66-18.13	1.59-1.92	1.09-2.47	5.20-9.59	3.33-13.80
	Absent	1.29-5.40	0.46-7.73	1.26-2.20	0.78-2.67	4.21-10.56	2.24-14.17
Sempervivum arachnoideum	Present	1.50-13.69	0.21-1.22	1.25-1.48	0.67-1.84	4.36-8.91	2.29-8.94
	Absent	1.43-14.03	0.59-8.48	1.40-2.35	0.78-2.68	4.52-10.80	2.33-15.12
Stachys recta	Present	1.38-5.83	0.26-5.13	1.64-3.21	0.58-5.55	3.45-8.96	2.04-9.53
	Absent	1.56-16.65	0.65-9.44	1.34-1.78	0.78-2.16	4.77-10.73	2.89-15.09
Teucrium chamaedrys	Present	1.27-15.47	0.38-4.38	1.29-1.61	0.78-1.65	9.53-16.76	4.26-21.44
	Absent	4.50-12.16	0.81-11.38	1.90-2.73	0.78-3.76	3.15-6.29	1.62-5.57
Verbascum lychnitis	Pres	4.24-6.30	0.51-8.41	1.81-3.63	0.79-6.68	3.42-8.04	1.78-5.50
	Abs	1.47-14.89	0.59-6.66	1.40-1.94	0.78-2.50	4.66-10.59	2.32-15.12