Received: 2 October 2024 | Revised: 23 April 2025 | Accepted: 13 June 2025

DOI: 10.1002/ecy.70171

REPORT

ECOLOGY
ECOLOGICAL SOCIETY OF AMERICA

The impact of serpentine soils on plant traits and plant–herbivore interactions

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Funding information
Galician Innovation Agency, Grant/Award Numbers: IN607A 2021/03, OTR11097; Oportunius Program; Spanish Ministry of Science and Innovation, Grant/Award Numbers: EUR2023-143463, PID2022-141761OB-I00

Handling Editor: Ayub M. O. Oduor

Abstract

Serpentine soils, known for high heavy metal content and low nutrients, create harsh conditions for plants and herbivores. Although previous research has explored how serpentine soils affect herbivory, most studies have been restricted to a specific region, and the mechanisms involved remain unclear. Here, we conducted a large-scale study across 78 plant species from California, Spain, and Sweden, comparing insect herbivory and leaf traits (chemical, nutritional, and physical) in serpentine and non-serpentine habitats within each region. We also analyzed soil properties—pH, texture, nutrient content, and heavy metal concentrations—to investigate their potential role in mediating soil type effects on herbivory. Our results showed that plants growing in serpentine soils experienced lower herbivory levels and exhibited higher concentrations of phenolic compounds, lower nutrient content, and thicker leaves, compared to their non-serpentine counterparts. Additionally, elevated pH and heavy metal levels in serpentine soils were associated with reduced herbivory, increased concentrations of phenolic compounds, and decreased specific leaf area (SLA) and nitrogen content. However, no indirect link between soil properties and herbivory via leaf traits was found, suggesting that bottom-up effects of soil on plants and herbivores operate independently. Collectively, these findings enhance our understanding of the mechanisms linking plant–soil specialization and aboveground plant–herbivore interactions.

KEYWORDS

California, insect herbivory, phenolic compounds, plant nutrients, soil heavy metals, Spain, Sweden

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INTRODUCTION

Serpentine soils are distributed worldwide, primarily along continental margins and in regions of orogenesis (i.e., mountain building) (Roberts & Proctor, 1992). These soils have unique properties, such as nutrient (e.g., nitrogen, potassium, and phosphorus) deficiency combined with high levels of heavy metals such as nickel, chromium, and cobalt (Proctor & Woodell, 1975), thus creating an inhospitable environment for many plant species (Cacho et al., 2014). As such, for decades, habitats with serpentine soils have served as powerful natural settings for studying plant adaptations to soil-related abiotic stress (Cacho & Strauss, 2014; Harrison et al., 2006), including mechanisms of soil metal sequestration, selective root uptake, and various alterations in metabolic pathways linked to nutrient acquisition and stress tolerance (reviewed by Brady et al., 2005). Research on these plant physiological traits and mechanisms has yielded valuable insights into the ecology and evolution of plant specialization to extreme environments.

Recent studies have found that serpentine soils exert strong bottom-up effects on plant-herbivore interactions, with this in turn having consequences for community structure and ecosystem function (Robinson & Strauss, 2020). Studies in California, for example, have shown that plants growing in serpentine soils often experience lower herbivore abundance compared to those found in nearby non-serpentine environments (Cacho & Strauss, 2013; Lau et al., 2008; Robinson & Strauss, 2018, 2020). This pattern could be partly explained by plant traits that influence herbivore preferences or feeding behavior (i.e., plant-mediated indirect effects). For instance, plants in serpentine soils have been found to produce higher levels of secondary metabolites, such as alkaloids and phenolic compounds (e.g., Cacho et al., 2015), which can in turn result in heightened resistance to herbivory. Despite this, research linking herbivory patterns with changes in plant traits across habitats remains limited, hindering our understanding of soil bottom-up effects on species interactions and plant-associated communities. Moreover, previous studies have focused on single regions (e.g., California), leaving unanswered whether these patterns and their underlying mechanisms behave similarly across serpentine systems with convergent community features. Expanding research to multiple regions while incorporating plant trait and herbivory measurements is essential to achieve a mechanistic understanding of how serpentine soils influence aboveground plant-herbivore interactions and community structure.

To address this gap, we conducted a broad-scale study comparing insect herbivory and plant traits putatively associated with herbivory resistance in serpentine and non-serpentine habitats across California, Spain, and Sweden. To this end, we performed in situ leaf sampling for 78 plant species to quantify leaf damage caused by chewing insects, as well as leaf secondary metabolites, nutrients, and physical traits. We also collected soil samples to measure a suite of abiotic or physical variables, including pH, texture, nutrient content, and heavy metal content potentially affecting leaf traits and herbivory. Based on this, we sought to test for habitat (i.e., soil) type differences in herbivory and plant traits, as well as further tested for plant trait-mediated (indirect) effects on leaf herbivory as a function of habitat type. By examining the relationships between soil properties, plant traits, and herbivory across different regions and plant communities, this study seeks to explore general ecological mechanisms for how plant-soil specialization shapes plant traits and plant-herbivore interactions.

MATERIALS AND METHODS

Field sampling and herbivory measurements

Our sampling resulted in two types of comparisons between serpentine and non-serpentine soil habitats across three distant regions (California, Spain, and Sweden): comparisons of the same species occurring in both soil habitat types ($n = 66$ intraspecific comparisons) and comparisons of species exclusive to each habitat but belonging to the same genus ($n = 6$ congeneric comparisons) (Appendix S1: Table S1, Figure S1). We sampled seven tree species, 27 shrub species, and 44 herbaceous species (Appendix S1: Table S1).

At the end of the summer of 2023, we haphazardly sampled five individuals of each species found at a single population (defined as a group of at least 15 reproductive adults) per soil habitat type, for a total of 617 plants across all species. For each plant, we randomly collected 10 fully expanded leaves of roughly the same age and condition (i.e., position along the branch, color, and consistency). Sampling was conducted at the end of the summer to obtain an estimate of cumulative (total) herbivory over the growing season. Most of the herbivore damage observed on sampled leaves was due to chewing insects (>98% of cases). We photographed all leaves and estimated the percentage of leaf area consumed by chewing insects ("insect herbivory" hereafter) using BioLeaf - Foliar Analysis (Brandoli Machado et al., 2016). We used the average value across leaves per plant for statistical analyses.

Leaf secondary metabolites, nutrients, and physical traits

We selected a subset of five of the above sampled leaves per plant with the requisite that they had little or no herbivore damage, and oven-dried them at 40°C for 48 h to quantify leaf traits. This subsample was aimed at roughly estimating constitutive levels of leaf traits responding to long-term variation in herbivore pressure and abiotic forcing. Namely, we measured specific leaf area (SLA) and the concentration of phenolic compounds (total, as well as separately for condensed tannins and flavonoids) and nutrients (phosphorus and nitrogen) as traits putatively associated with herbivory resistance (see Appendix S2 for more details).

Soil variables

Parallel to leaf sampling, we collected one topsoil sample (0–30 cm depth) at 10–30 cm from the edge of the canopy projection per plant for a subsample of 45 plant species, yielding 39 intraspecific and six interspecific (congeneric) comparisons (Appendix S1: Table S1). For physicochemical analyses, we pooled soil samples from the five individual plants within each population to create a single composite sample per species at each habitat type (i.e., serpentine and non-serpentine). We oven-dried all samples at 40°C for 48 h and homogenized them by sieving to <2 mm to remove large stones and dead plant material. We measured six soil physicochemical properties, namely: pH, electrical conductivity, soil organic matter, and the percentage of clay, silt, and sand content (see Appendix S2 for more details). In addition, we measured the concentration of five soil macroelements (Ca, K, Mg, N, and P) and eight micro-elements (Na, Fe, Cu, Mn, Zn, Ni, Pb, and Cr) (see Appendix S2 for more details). We provide the means (±SE) for these 19 soil properties in both serpentine and non-serpentine soils in Appendix S3: Table S1.

Statistical analyses

To test for effects of soil habitat type and site variation in leaf traits and herbivore damage, we first ran linear mixed models (LMMs) testing for the effects of soil type (two levels: serpentine and non-serpentine), study site (three levels: Spain, Sweden, California), and their interaction (all treated as fixed factors) on insect herbivory and leaf traits using population-level data (average value across plants per site). Models also included the identity of the conspecific (intraspecific) or congeneric (interspecific) serpentine versus non-serpentine species pairs as a random effect (72 levels, with 66 intraspecific and six congeneric pairs), which controlled for species identity and the congeneric species pairs. We log-transformed herbivory and square root-transformed all the other variables to achieve normality of residuals. Models were implemented using the *lmer* function from the *lmerTest* package (Kuznetsova et al., 2017) in R ver. 4.3.3 (R Core Team, 2024).

To address mechanism behind soil type effects on herbivory, we then ran a piecewise structural equation model (PSEM) (Lefcheck, 2016) using population-level data. Specifically, with this analysis we aimed to elucidate associations between habitat type (serpentine vs. non-serpentine), soil properties, leaf traits, and herbivory, and whether bottom-up forcing (i.e., soil conditions and leaf traits) explained any such soil type differences in herbivory. To this end, we first summarized variation in leaf and soil traits using principal components analysis (PCA). For leaf traits, the first principal component (PC1 traits) explained 50% of the variation and was negatively associated with total phenolics, condensed tannins and flavonoids, and positively associated with SLA and nitrogen concentration (Appendix S4: Figure S1, Table S1). The second principal component (PC2 traits) explained 21% of the variation in leaf traits and was positively associated with condensed tannins (Appendix S4: Figure S1, Table S1). In the case of soil variables, the first principal component (PC1 soil) explained 27% of the variation and was positively associated with electrical conductivity, soil organic matter, and P, K and Zn content (Appendix S4: Figure S2, Table S2), whereas PC2 soil explained 19% of the variation and was positively associated with pH and Mg, Mn, Ni, and Cr content (Appendix S4: Figure S2, Table S2). These analyses were conducted with the *PCA* function from the *FactoMineR* package (Lê et al., 2008) in R (R Core Team, 2024). We then used the standardized z-values from these PCs in the PSEM. In the case of leaf traits, we only used PC1 as this axis accounted for a large portion of the variation and including PC2 did not change results or improve model fit. The PSEM tested for the following: (1) direct associations between soil habitat type (coded as a dummy variable; non-serpentine = 0, serpentine = 1) and soil properties (PC1 and PC2 soil), (2) direct associations between soil properties and leaf traits (PC1 traits), as well as herbivory, and (3) direct associations between leaf traits and herbivory. We also tested for (4) indirect associations between soil properties and herbivory via leaf traits. Direct associations were calculated as path coefficients, and indirect associations were calculated by multiplying intervening direct associations involved in the specified causal pathway. The model also included study site and the identity of the conspecific or congeneric serpentine-non-serpentine species pairs as random factors. We log-transformed herbivory data to achieve normality of residuals and assessed the goodness of fit of the overall model with a "test of direct separation" based on the Fisher's C test (Lefcheck, 2016). We implemented the PSEM and obtained direct association coefficient estimates (i.e., path coefficients) using the *psem* function of the *piecewiseSEM* package (Lefcheck, 2016), and obtained bootstrapped indirect associations (i.e., multiplied path coefficients) and their 95% CIs using the *semEff* function from the *semEff* package (Torchiano, 2020) in R (R Core Team, 2024).

RESULTS

Effects of soil type and site on herbivory and leaf traits

We found a significant effect of soil habitat type on herbivory (Table 1), whereby plants found in serpentine soils exhibited lower leaf damage than those found in non-serpentine soils (mean ± SE of back-transformed log data; serpentine: 0.59% ± 0.10%, non-serpentine: 0.87% ± 0.12%; Figure 1). There was also a significant effect of study site (Table 1), with plants from California having lower herbivory compared to those from Spain and Sweden (California: 0.37% ± 0.14%; Spain: 1.01% ± 0.21%; Sweden: 0.88% ± 0.17%; Figure 1). There was no significant interaction between soil habitat type and site on herbivory (Table 1, Figure 1).

We similarly found significant effects of soil habitat type on all leaf traits except condensed tannins (Table 1). Namely, plants growing in serpentine (relative to non-serpentine) soils exhibited, on average, higher total phenolics (mean ± SE of back-transformed square root data; serpentine: 97.58 ± 6.72 mg g^{-1} DW, non-serpentine: 86.57 ± 6.33 mg g^{-1} DW; Figure 2A) and flavonoids (serpentine: 22.29 ± 2.20 mg g^{-1} DW, non-serpentine: 18.24 ± 1.99 mg g^{-1} DW; Figure 2C), as well as lower phosphorus (serpentine: 1.48 ± 0.09 mg g^{-1} DW, non-serpentine: 1.84 ± 0.11 mg g^{-1} DW; Figure 2D), nitrogen (serpentine: 21.33 ± 1.07 mg g^{-1} DW, non-serpentine: 23.18 ± 1.11 mg g^{-1} DW; Figure 2E), and SLA (serpentine: 54.98 ± 4.06 cm^2 g^{-1} DW, non-serpentine: 66.17 ± 4.46 cm^2 g^{-1} DW; Figure 2F). There was no effect of study site on leaf traits except for SLA (Table 1), whereby plants in California exhibited, on average, lower SLA compared to plants in Spain and Sweden, which themselves did not differ (California: 41.48 ± 5.74 cm^2 g^{-1} DW; Spain: 72.21 ± 8.10 cm^2 g^{-1} DW; Sweden: 70.33 ± 7.05 cm^2 g^{-1} DW) (Figure 2F). Finally, there was no significant interactions between soil habitat type and site for any of the leaf traits studied (Table 1, Figure 2).

Associations among soil properties, leaf traits, and herbivory

The PSEM indicated significant negative and positive associations between soil habitat type and PC1 and PC2 soil, respectively (Figure 3). These results indicated that serpentine soils exhibited lower values of electrical conductivity, soil organic matter, and P, K, and Zn content (PC1 soil), as well as higher values of pH and Mg, Mn, Ni, and Cr content (PC2 soil) (Appendix S4: Table S1, Figure S1).

TABLE 1 Results from the linear mixed models testing for the effects of soil habitat type (two levels: serpentine and non-serpentine soils), study site (three levels: Spain, Sweden, California), and their interaction (all treated as fixed factors) on leaf herbivory (percent leaf area consumed by insects), the concentration of leaf total phenolics, condensed tannins and flavonoids (all used as proxies of chemical defenses), the concentration of leaf nitrogen and phosphorus (a proxy of plant nutritional quality), and specific leaf area (a proxy of physical defense, i.e., leaf thickness or toughness).

	Soil type		Site		Soil type × site	
Response	$F_{1,69}$	p	$F_{2,69}$	p	$F_{2,69}$	p
Herbivory	6.34	**0.014**	4.14	**0.020**	0.01	0.986
Total phenolics	8.16	**0.006**	1.86	0.163	1.06	0.351
Condensed tannins	0.02	0.875	1.32	0.274	0.59	0.557
Flavonoids	15.03	**<0.001**	1.89	0.158	2.42	0.096
Nitrogen	9.42	**0.003**	1.61	0.207	1.76	0.180
Phosphorus	19.40	**<0.001**	2.20	0.119	1.12	0.331
Specific leaf area	15.79	**<0.001**	6.68	**0.002**	0.05	0.949

Note: We also included the identity of the conspecific (intraspecific) or congeneric (interspecific) serpentine–non-serpentine pair as a random effect (see *Statistical analyses*). We log-transformed herbivory and square root-transformed the remaining variables to achieve normality of the residuals. F values with df (numerator, denominator) and associated significance levels (p) are shown. Significant p values ($p < 0.05$) appear in boldface.

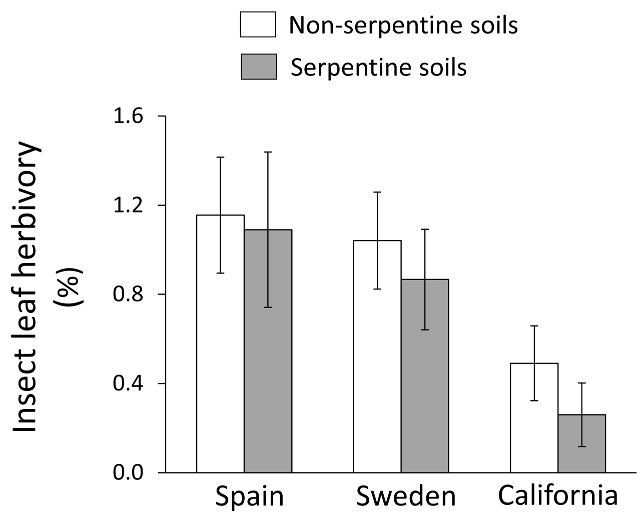

FIGURE 1 Effects of soil habitat type (two levels: non-serpentine and serpentine soils) on the percentage of leaf area consumed by chewing insects across plant species, separately for Spain, Sweden, and California. Bars are back-transformations of log-transformed least square means ± SE (n = 72). Statistics are shown in Table 1.

In turn, we found a negative association between PC2 soil and PC1 traits (Figure 3), indicating that plants growing in soils with higher pH and Mg, Mn, Ni, and Cr content (i.e., serpentine soils) exhibited higher total phenolics, condensed tannins, and flavonoids, and lower SLA and nitrogen (Appendix S4: Tables S1 and S2, Figures S1 and S2). There was no association between PC1 soil and PC1 traits (Figure 3).

We also found a significantly negative direct association between PC2 soil and herbivory (Figure 3), whereby plants growing in soils with higher pH and Mg, Mn, Ni, and Cr content (i.e., serpentines) exhibited lower levels of herbivory (Appendix S4: Table S2, Figure S2). In contrast, there was no association between PC1 soil and herbivory (Figure 3), and there was no association between PC1 traits and herbivory (Figure 3). Lastly, and despite the observed associations between PC2 soil and both leaf traits and herbivory, we found no indirect association between these soil-related properties and herbivory via leaf traits (Figure 3).

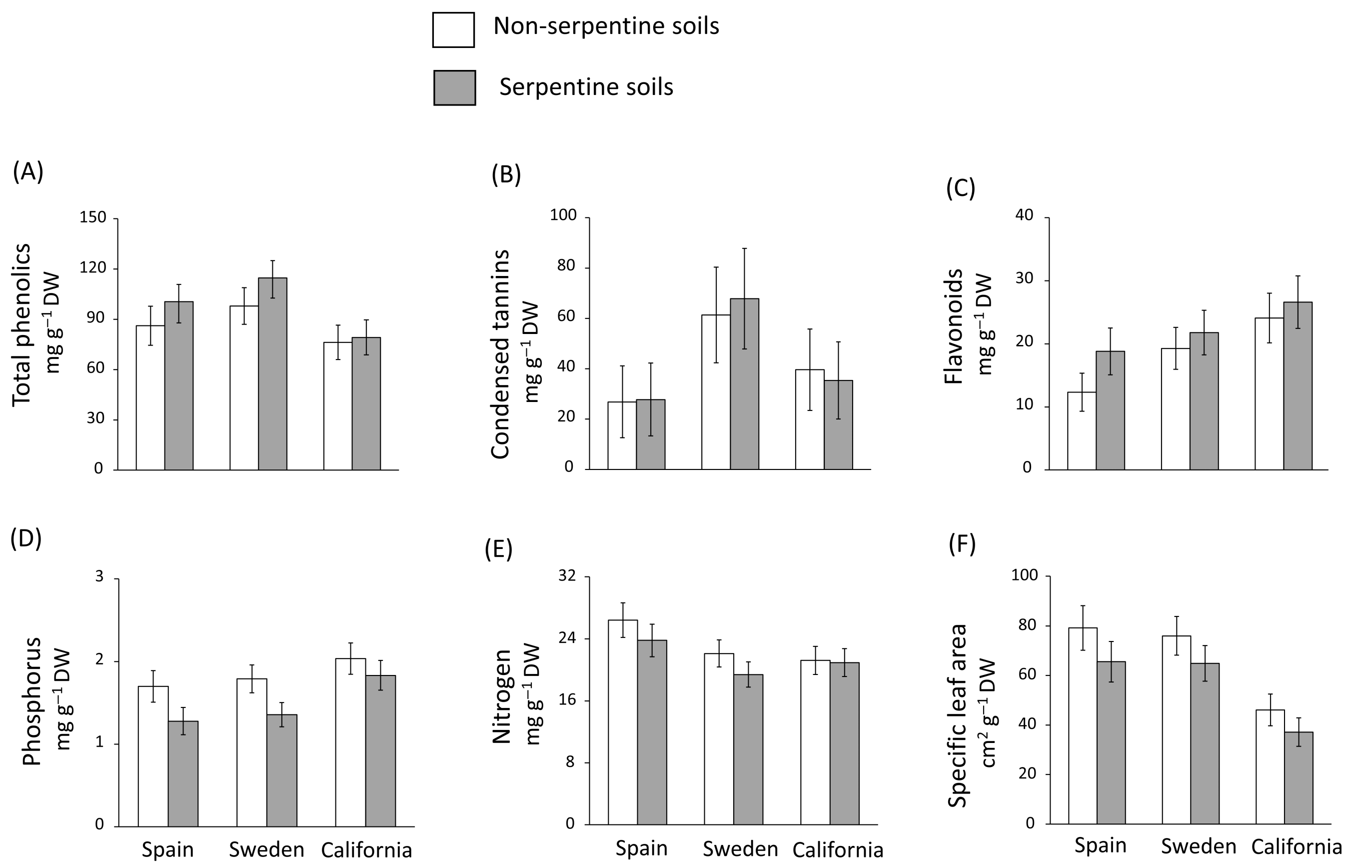

FIGURE 2 Effects of soil habitat type (two levels: non-serpentine and serpentine soils) on the concentration of leaf (A) total phenolics, (B) condensed tannins, (C) flavonoids, (D) nitrogen and (E) phosphorus, and (F) specific leaf area across plant species, separately for Spain, Sweden, and California. Bars are back-transformations of square root-transformed least square means ± SE (n = 72). Statistics are shown in Table 1. DW, dry weight.

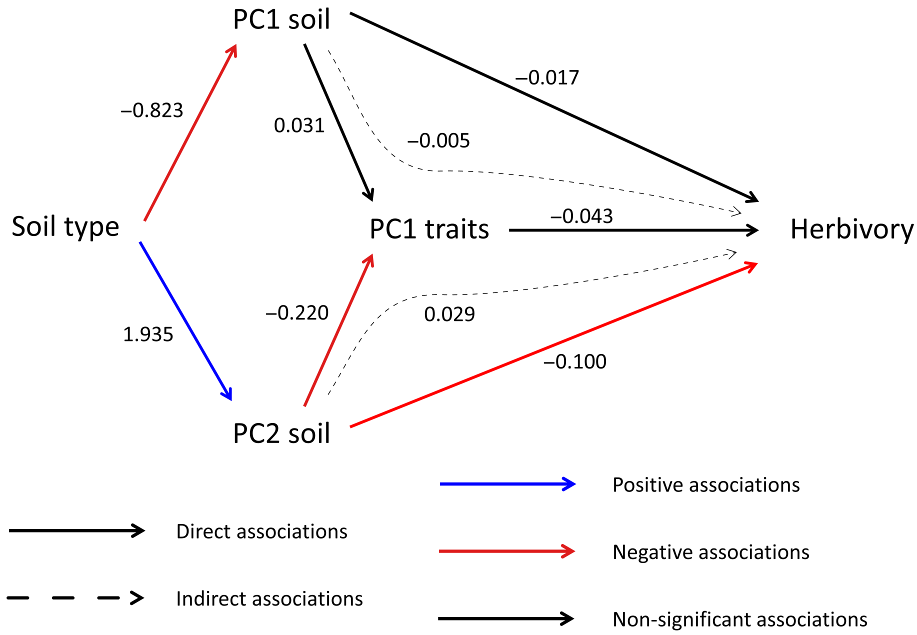

FIGURE 3 Diagram showing the path coefficients from a piecewise structural equation model testing for direct and indirect associations between soil habitat types (serpentine and non-serpentine), soil properties (PC1 soil and PC2 soil), leaf traits (PC1 traits), and herbivory across three sites (Spain, Sweden and California). PC1 soil was positively associated with electrical conductivity, soil organic matter, and P, K and Zn content, whereas PC2 soil was positively associated with pH and Mg, Mn, Ni, and Cr content. PC1 traits was negatively associated with total phenolics, condensed tannins, and flavonoids, and positively associated with specific leaf area (SLA) and nitrogen concentration. Continuous arrows indicate direct associations, while broken arrows indicate indirect associations (between soil properties and herbivory via leaf traits). Significant associations ($p < 0.05$) are shown in blue (positive) or red (negative), while nonsignificant associations are shown in black. Explained variance based on marginal R^2: PC1 soil = 0.03; PC2 soil = 0.20; PC1 traits = 0.05; Herbivory = 0.11. Fisher's $C = 6.49$, df = 6, $p = 0.37$, corrected Akaike information criterion (AIC_c) = 1102.05. PC1, first principal component; PC2, second principal component.

DISCUSSION

Our results showed that plants growing in serpentine soils—characterized by high concentrations of heavy metals (e.g., Mn, Ni, and Cr) and elevated pH—exhibited higher levels of total phenolics, condensed tannins, and flavonoids compared to their non-serpentine counterparts. This pattern aligns with the known physiological and biochemical strategies plants use to cope with the stress imposed by serpentine soils (reviewed by Peralta-Videa et al., 2009), including the production of secondary metabolites (Anjitha et al., 2021; Bali et al., 2020). Phenolic compounds, in particular, are known to chelate heavy metals, thereby reducing their toxicity and preventing them from interfering with key physiological functions (Jung et al., 2003). These metabolites also help mitigate oxidative stress caused by reactive oxygen species generated during heavy metal uptake (Chen et al., 2020). In addition to detoxification roles, certain phenolic compounds such as phenolic acids and flavonoids can influence nutrient dynamics, including nutrient uptake and mobilization. For example, they may modify root exudates to enhance nutrient acquisition, helping plants counteract nutrient imbalances or deficiencies (e.g., in Ca or K) associated with high-pH serpentine soils (Kidd et al., 2011). Lastly, some classes of secondary metabolites like condensed tannins may influence nutrient cycling and retention in soils, highlighting implications for ecosystem-level nutrient dynamics (Madritch & Lindroth, 2015). Collectively, this evidence suggests that the higher concentrations of phenolics observed in our study may contribute not only to stress tolerance but also to partially mitigating nutrient limitation in plants growing in serpentine soils (see discussion next).

Plants growing in serpentine soils also had lower nitrogen, phosphorus, and SLA compared to plants in non-serpentine soils. High pH and the presence of heavy metals present in serpentine soils have been shown to reduce the availability and hinder the uptake of macro- and micronutrients (e.g., Zhang et al., 2014). Nutrient-limited soils select for conservative resource use strategies (Abrahão et al., 2019; Aerts & Chapin, 1999), characterized by slow growth and low nutrient concentrations, the latter consistent with findings in serpentine plants. This strategy is also reflected in functional traits such as observed lower SLA (thicker leaves) in serpentine plants, favoring water conservation and nutrient efficiency (McBurney, 1992). Alternatively, it is possible that higher investment in secondary metabolites (see above) limits plant growth if the latter trades off with chemical defenses (Hu et al., 2021), an indirect mechanism that could also contribute to conservative strategies in serpentine soils (Blanchard et al., 2024). Further investigations on plant physiological responses and functional traits (including growth-related variables) are required to address linkages between the production of secondary metabolites, tolerance to metal toxicity, and nutrient limitation. Ultimately, this will shed mechanistic insight into the effects of serpentine soils on plant life history evolution associated with growth and defense.

Our results also indicated that plants found in serpentine soils experienced less herbivory, consistent with previous work, particularly that conducted in California (e.g., Cacho & Strauss, 2013; Robinson & Strauss, 2018, 2020). However, contrary to expectations, we found no indirect associations between soil properties and herbivory via leaf traits, rejecting the idea of plant-mediated effects on herbivory and suggesting soil effects on leaf traits do not cascade to affect herbivory but rather operate independently in each case. This contrasts with findings from Robinson and Strauss (2018), who found that leaf defensive and nutrient-related traits contributed to the differences in herbivore performance between plant species growing in serpentine versus non-serpentine soils. Consistent with our findings, work in other types of systems has reported no relation between soil effects on leaf traits and herbivory, as in our own work with *Quercus robur* sampled along elevational gradients in temperate forests in northwestern Spain (Abdala-Roberts et al., 2016). It is plausible that some types of leaf secondary metabolites play a role in abiotic tolerance (see above), rather than anti-herbivore resistance, thus explaining these patterns. That said, further research is needed before discarding the idea of plant-mediated effects on herbivory, including measurements of other leaf defensive traits (e.g., different classes of secondary compounds such as alkaloids and terpenoids), heavy metals (to address toxicity effects on herbivores), as well as biomass-related traits and plant architecture or vegetation complexity possibly influencing microhabitat conditions for herbivores. It is important to also note that the percentage of leaf area consumed by chewing insects was quite low across all systems (mean ± SE: 1.10% ± 0.14%; range: 0%–9.35%), which could have imposed a limitation to detect correlations with leaf traits. Future work might benefit from considering other herbivore guilds, such as sucking insects or browsing mammals, which may exert greater pressure in some cases and respond differently to soil features and measured traits, potentially revealing other plant trait–herbivory relationships. Finally, other nonexclusive explanations for soil effects on herbivory include patch-scale features, including differences in plant composition or density, and source-sink spatial dynamics. For instance, the scarcity of palatable and nutritionally adequate plants in serpentine soils may force herbivores to adopt different foraging strategies, such as moving longer distances, feeding on less preferred species, or increasing overwintering by shifting their feeding times. Likewise, serpentine habitats are usually fragmented or isolated within the landscape (Harrison et al., 2006; Roberts & Proctor, 1992), with this potentially influencing herbivore immigration to and population size within serpentine fragments. Joint tests of plant traits and these patch- or landscape-level drivers would allow testing the relative contributions of these mechanisms and, in so doing, build a more robust understanding of soil-based bottom-up effects on plant-associated consumer interactions.

ACKNOWLEDGMENTS

We are grateful to Cathy Koehler and Zoe Wood for assisting with the fieldwork. We also thank the UC McLaughlin Natural Reserve for allowing us to use their field sites. This research was supported by grants from the Spanish Ministry of Science and Innovation (PID2022-141761OB-I00 and EUR2023-143463 projects) and the Galician Innovation Agency (IN607A 2021/03 and OTR11097) to Xoaquín Moreira.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Moreira et al., 2024) are available in Figshare at https://doi.org/10.6084/m9.figshare.26545675.v1.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Moreira, Xoaquín, Luis Abdala-Roberts, Carla Vázquez-González, María Rúnarsdóttir, Kaori Shiojiri, Beatriz Lago-Núñez, Asier R. Larrinaga, et al. 2025. "The Impact of Serpentine Soils on Plant Traits and Plant–Herbivore Interactions." *Ecology* 106(7): e70171. https://doi.org/10.1002/ecy.70171