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Special Feature—Ultramafic Ecology 2025: Proceedings of the 11th International Conference on Serpentine Ecology

Disturbance-Driven Shifts in Soil Microarthropod Communities on Serpentine Outcrops in San Luis Obispo, CA, USA

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Received: 21 January 2026 | **Revised:** 24 May 2026 | **Accepted:** 25 May 2026

Keywords: geoecology | microarthropods | mining | serpentine soils | soil biodiversity

ABSTRACT

While the ecological significance of ultramafic environments for plant diversity and endemism is well established, soil microarthropod communities within these systems remain poorly understood. In this study, we examined microarthropod abundance and community composition in adjacent, disturbed, and undisturbed ultramafic sites to assess the long-term impacts of historical chromite mining on soil fauna. Soil samples were collected to a depth of 10 cm under a common shrub *Ceanothus cuneatus* at undisturbed ($n = 12$) and disturbed ($n = 12$) sites. Microarthropods were extracted using the Tullgren/Berlese funnel method and imaged to quantify abundance and taxonomic diversity. Soil physicochemical properties, including texture, pH, electrical conductivity, exchangeable cations, macro and micronutrients, and extractable metals, were also measured on composite samples. We recorded 2592 microarthropods representing 15 arthropod orders. Order-level richness did not differ between disturbed and undisturbed sites; however, community composition differed significantly, with Collembola and Acari showing pronounced loss of abundance following mining disturbance. Our results indicate that historical chromite mining has reduced soil microarthropod abundance and diversity in disturbed serpentine ecosystems.

1 | Introduction

Soil fauna communities represent a significant portion of global biodiversity, as soil is one of the most immense, biodiverse habitats on Earth (Anthony et al. 2023). Belowground, microarthropods play a significant role in soil food webs, such as decomposers, and are vital for understanding ecological functioning (Yahya et al. 2020). Particularly in the rhizosphere, microarthropods (e.g., springtails and mites) play a critical role in regulating microbial processes and influencing plant growth by mediating organic matter decomposition, nutrient cycling and allocation, and plant-pathogen relationships (Jernigan et al. 2023). Analyses of the functional and structural diversity of soil fauna have revealed how microarthropods such as springtails influence root structure and nutrient uptake in plants (Bonkowski et al. 2009). Microarthropods are useful indicators of soil fertility and ecological functioning in disturbed landscapes because they are ubiquitous in soils and vary predictably with soil properties and land-use type (Straalen 1998; Menta et al. 2018; Juan-Overjero et al. 2023). Despite their important role in ecosystem processes, studies of microarthropod communities in extreme environments, such as serpentine soils, remain limited (Guerra et al. 2020).

Serpentine soils, derived from ultramafic rocks, are characterized by elevated heavy metal concentrations and low calcium-to-magnesium ratios, creating stressful conditions for biota (Harrison and Rajakaruna 2011). While the physical and

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chemical constraints imposed by serpentine soils on plants are well documented (O'Dell and Rajakaruna 2011; Garnica-Díaz et al. 2023), their effects on soil fauna communities remain comparatively understudied. Existing evidence from serpentine soils indicates that elevated heavy metal concentrations and low soil organic matter are associated with declines in microarthropod abundance, diversity, and community complexity (Visioli et al. 2019). While previous work suggests that microarthropod diversity is lower in high-metal serpentine soils, more controlled experiments are needed to directly isolate and quantify the effects of metal concentrations and organic matter on these communities (Visioli et al. 2013). Despite the limited attention these communities have received in serpentine systems, monitoring their diversity, abundance, and ecological roles is critical for advancing our understanding of soil health and ecosystem resilience in disturbed landscapes (Parisi et al. 2005; Guerra et al. 2021).

Similar to aboveground flora and fauna, microarthropods are highly susceptible to disturbance; however, substantial knowledge gaps remain regarding how these organisms respond to variation and change in soil conditions. More broadly, it is increasingly recognized that soil biota are vulnerable to biodiversity loss driven by global change, including disturbances such as mining (Tsiafouli et al. 2014; Menta and Remelli 2020; Phillips et al. 2024). In particular, springtail abundance is highly sensitive to disturbances in the litter layer, whether these result from direct removal or from indirect effects such as changes in microclimate or litter quality (Eaton et al. 2004). Additionally, lab-controlled studies of microarthropod species reveal that high levels of heavy metals such as nickel can cause reduced growth, low reproductive output, and high mortality (Scott-Fordsmand et al. 1999). Direct experiments such as these are important to determine which edaphic factors are driving soil microarthropod abundance. Given their sensitivity to land-use and soil variation, serpentine soils provide a unique system for examining microarthropod responses to disturbance and unfavorable soil conditions (Juan-Overjero et al. 2023).

Because of the legacy of mining disturbance in serpentine soils, elucidating the mechanisms governing ecosystem recovery is a critical research priority. Mining activities in serpentine soils contribute to heavy metal contamination and soil toxicity, resulting in vegetation degradation and disrupted nutrient cycling. Centuries of asbestos and nickel mining in serpentine soils have resulted in approximately 11,130 and 19,070 ha of land degradation across 18 countries, respectively (O'Dell and Claassen 2009). The extent of this degradation necessitates comprehensive restoration efforts that address multiple components of ecosystem structure and function. Soil microarthropods have been understudied in post-mining sites despite their utility as bioindicators for assessing site rehabilitation (Sanchez et al. 2021; Fernandes et al. 2024). Several studies have explored the revegetation of mine wastes, but the impact it has on soil fauna community reestablishment has not been thoroughly investigated (Curtis and Claassen 2005; Favero-Longo et al. 2009). Because microarthropods are reliable indicators of soil quality and ecosystem resilience, investigating their abundance and diversity can inform restoration efforts in previously degraded areas.

In this study, we addressed these knowledge gaps by comparing microarthropod abundance and diversity on and off an abandoned mine in a serpentine landscape in California. Our objective was to evaluate the effects of mining disturbance on soil microarthropod abundance and diversity, with particular focus on Collembola (springtails) and Acari (mites). By characterizing soil microarthropods in adjacent disturbed and undisturbed ultramafic sites, we assessed the impacts of mining disturbance on taxonomic richness and community composition. We hypothesized that the abundance and diversity of Collembola and Acari would be reduced in mine soils, resulting in altered microarthropod community composition within surface soils.

2 | Methods

2.1 | Study Area and Soil Sampling

This study was conducted in the Irish Hills, part of the San Luis Range, a small northwest–southeast–trending mountain range situated between the city of San Luis Obispo and the Pacific Ocean in California (Figure S1). The Irish Hills Natural Reserve (IHNR) occupies the eastern portion of the range and encompasses diverse habitat types, distinctive plant communities, and multiple protected species. San Luis Obispo County has a rich history of chromite exploration and mining that occurred intermittently from 1870 to 1940 (Hamilton 1917; Smith and Griggs 1944). The presence of multiple remnants of pre–World War II mining within the Irish Hills Natural Reserve (IHNR) allows for the study of ecosystem recovery following disturbance and supports targeted restoration efforts (Havlik 2011). Given its potential to host rare species, including two recently described serpentine endemic plant species (Nelson et al. 2019; Keil 2020), IHNR is a valuable site for assessing the ecological impacts of historical mining on serpentine ecosystems (Mulroy et al. 2026). Due to few historical details, little is known about the unnamed mine that was sampled, but it is estimated to be nearly 60 years old (Figure S1). The plant community at this site is noticeably less dense than the surrounding chaparral, as fewer plant species can successfully colonize the mine. Two dominant shrubs at the disturbed site include *Ceanothus cuneatus* (Rhamnaceae) and the serpentine endemic *Arctostaphylos obispoensis* (Ericaceae). These shrubs sparsely cover the mine site, while dense chaparral persists at the undisturbed sampling locations.

Three sampling locations were established: one at an unnamed, abandoned chromite mine (35.25477° N, 120.71255° W) and two adjacent undisturbed reference locations (Figure S1). The first is located approximately 230 m southeast of the chromite mine on the Mariposa Trail, and the second is situated 380 m northwest of the chromite mine. At each disturbed and undisturbed location, eight downslope transects were established to intersect a common nitrogen-fixing chaparral shrub, *Ceanothus cuneatus*. Soil samples were collected under the shrub canopy including the leaf litter to a depth of 10 cm both upslope and downslope (Figure S2). Approximately 250 g of soil was collected per shrub, and geographic coordinates were recorded at each sampling point. Soil samples from each shrub

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were composited to generate 12 disturbed and 12 undisturbed soil samples.

To assess edaphic properties and elemental concentrations, soil samples were further composited by sampling location ($n = 3$ total), thoroughly homogenized, air dried, sieved to 2 mm, and sent to the Analytical Lab and Maine Soil Testing Service at the Maine Agricultural and Forest Experiment Station (MAFES). Analyses for soil texture, pH, organic matter via loss on ignition (LOI [%]), electrical conductivity (EC), total nitrogen (TN [%]), exchangeable P, K, Mg, Ca, B, S, and Na, and metals: Fe, Mn, Zn, Cr, Ni, and Pb were conducted. Soil pH was measured in distilled water. Organic matter was measured by LOI at 375°C. EC was measured in a saturated paste water extraction. TN was determined by combustion analysis at 1350°C. Elements K, Mg, Ca, Al, B, Cu, Fe, Mn, Na, S, Zn, Cd, Cr, Ni, and Pb were extracted in pH 4.8 ammonium acetate (modified Morgan solution). P was determined by Flow Injection Analysis. All other elements were measured by ICP-OES (Ametek/Spectro model Genesis SOP ICP-OES). Particle size analysis was determined after overnight dispersion in Calgon solution. Clay was measured by the hydrometer method. Sand was determined gravimetrically by wet sieving. Silt was calculated as the remainder.

2.2 | Microarthropod Extraction and Identification

Microarthropods were heat-extracted from 200 g of soil per sample using the Tullgren/Berlese funnel method (Potapov et al. 2022) and captured in a solution of 70% ethanol for long term storage. After extracting microarthropods from each sample, they were imaged in a petri dish with 84 mm × 84 mm grid using a high-resolution photo scanner (Epson V600). Images and a dissecting microscope were used to quantify the abundance and diversity of microarthropod taxa. A dissecting microscope, tools, and dichotomous keys were utilized to identify springtails and mites to their respective suborders to determine patterns in their diversity and ecology (Dindal 1990; Moore et al. 2000). Collembola were identified into Entomobryomorpha, Poduromorpha, Symphypleona, and Neelipleona, while Acari were identified into Mesostigmata, Prostigmata, Oribatida, and Astigmata. Taxonomic keys were used to identify microarthropod groups such as Protura, Diplura, Psuedoscorpionida, Araneae, Symphyla, Pauropoda, Chilopoda, Diplopoda, and microarthropods in the larval stage (henceforth "larvae") that could not be further identified (Dindal 1990). When present, the abundance of other taxonomic groups, including Blattodea, Coleoptera, Hymenoptera, and Thysanoptera, was determined. Gravimetric soil moisture was measured on 10 g of soil by oven drying at 105°C for 24 h. We quantified microarthropod abundance per gram of dry soil. Relative abundance was used to describe the average proportion of Collembola and Acari suborders that were present at each site.

2.3 | Statistical Analyses

Data was analyzed using R Version 4.5.2 in R Studio (R Core Team 2025). For soil physical and chemical analysis, undisturbed sampling locations were compared to the disturbed site. Before applying parametric tests to microarthropod abundance and diversity data for some taxa, normality and homogeneity of variances were tested using the Shapiro–Wilk and Levene's test. For normally distributed data, an independent samples *t*-test (t) was used, but if the assumptions were violated and the data were non-normal, the Wilcoxon rank-sum test (W) was used to compare the distribution of the two groups. These tests were conducted to determine if there were significant differences in microarthropod abundance and diversity between sites at the $\alpha = 0.05$ level. Taxonomic diversity of all microarthropods was determined by sample and calculated for order-level richness, evenness, Shannon's, and Simpson's index. Microarthropod community composition differences between samples were visualized using Non-metric Multidimensional Scaling (NMDS), and all analyses were performed using the *vegan* package (Oksanen et al. 2025). To do this, a Bray–Curtis dissimilarity matrix was calculated to determine the dissimilarity between samples, and a pairwise permutational multivariate analysis of variance (PERMANOVA) test was performed to evaluate differences in microarthropod community composition between site types. All visualizations were generated using the *ggplot2* package (Wickham 2016).

3 | Results

3.1 | Soil Analyses

Soil physical and chemical analyses reveal stark edaphic differences between disturbed and undisturbed ultramafic habitats. Soil textures at undisturbed ultramafic sites were clay loams, whereas the chromite mine had significantly altered soil texture with a high percentage of sand (Table 1). Chemical characteristics of the soil, such as pH and EC, were relatively indifferent, while percent organic matter and percent total N were much lower in the disturbed soil (Table 1). Macronutrients, including P, S, Ca, and K, were present at significantly lower concentrations at the mine site compared to the undisturbed ultramafic sampling locations (Table 1). The mine exhibited a notably low calcium: magnesium ratio (0.17), driven primarily by substantially reduced calcium concentrations relative to undisturbed soils (Table 1). At the mine, micronutrients such as Fe, Mn, Zn, Ni, and B were also reduced, with the most pronounced declines observed for Zn, Ni, and B (Table 1). In contrast, heavy metals, including Pb and Al, occurred at higher concentrations than at undisturbed sites, whereas Cr concentrations were lower (Table 1).

3.2 | Soil Fauna

We found a significant difference in the mean abundance of microarthropod groups Acari ($W = 139$, $p = 0.000123$) and Collembola ($t(22) = 2.690$, $p = 0.0137$) between the mine and undisturbed reference sites (Figure 1). Other microarthropod groups with the greatest abundance in undisturbed sites were pauropods ($W = 85$, $p = 0.407$) and symphylans ($W = 99$, $p = 0.0683$), though the result is not statistically significant (Figure 2). Significant differences among other taxa were larvae ($W = 23$, $p = 0.00227$) and proturans ($W = 96$, $p = 0.0367$). Significant differences in the relative abundance of groups Entomobryomorpha ($t(22) = 4.56$, $p = 0.000153$) and

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TABLE 1 | Soil chemical and physical characteristics for 1 composite sample each for the chromite mine ($n=1$) and adjacent, undisturbed serpentine outcrops ($n=2$; range shown).

Site	Chromite mine	Undisturbed ultramafic
pH	7.4	6.8–7.2
LOI (%)	4.1	6.6–8.9
EC	0.22	0.24–0.28
TN (%)	0.13	0.25–0.30
P	3.70	0.85–0.90
K	175	225–284
Mg	2698	2408–2502
Ca	457	1518–1629
Al	13	7–11
B	0.2	0.3
Cu	0.07	0.06–0.07
Fe	3.7	4.6–5.4
Mn	11.7	12.7–15.8
Na	37	44–53
S	2.7	3.6–5.3
Zn	0.13	0.36–1.39
Cd	<0.05	<0.05
Cr	0.34	0.61–0.66
Ni	20.7	51.6–65.9
Pb	0.54	0.24–0.26
Sand (%)	51	23–35
Silt (%)	20	31–43
Clay (%)	29	34
Textural class	Sandy clay loam	Clay–clay loam

Note: Organic matter by combustion (LOI) and total nitrogen (TN) are measured as a percentage. Electrical conductivity (EC) was measured as (mmhos/cm). Exchangeable cations (Ca, Mg, K, and Na), other macro and micronutrients, and metals are measured in ppm (μg/g soil).

Poduromorpha ($t(22)=5.07$, $p=0.0000447$) were found between both site types (Figure 3). Entomobryomorpha was relatively more abundant in the undisturbed ultramafic sampling sites, while Poduromorpha dominated chromite mine samples. Acari suborders Mesostigmata, Prostigmata, and Oribatida were relatively more abundant in undisturbed samples, while the relative abundance in Prostigmata ($t(22)=4.092$, $p=0.000482$) and Astigmata ($W=25$, $p=0.00725$) groups was statistically significant between disturbed and undisturbed sites (Figure 4).

There was no significant difference of alpha diversity between each site (Figure S3) for order-level taxonomic richness ($W=74.5$, $p=0.906$), Shannon diversity ($W=91.0$, $p=0.291$), and Simpson's diversity ($W=86.0$, $p=0.443$), except for evenness ($W=107.0$, $p=0.0449$). Microarthropod community composition at the order level was significantly different between the two site types (Stress = 0.038, $F=10.58$, $R^2=0.323$, $p=0.001$; Figure 5).

We recorded 2592 microarthropods representing 15 arthropod orders. Though orders and suborders of microarthropods were recorded for abundance and diversity, several species, genera, and families were observed in samples (Table 2). Notable genera of springtails in both ultramafic sites included *Folsomia* sp., *Isotoma* sp., *Ceratophysella* sp., *Ptenothrix* sp., and the family Onychiuridae. Genus *Proisotoma* sp. was observed in the undisturbed site only, while *Sensillanura* sp. was observed only in the chromite mine (Table 2). Families of Acari that were present in undisturbed samples were predatory mesostigmatid mites like *Macrocheles* sp., members in the Uropodidae family, and *Poecilochirus* sp. There were also various prostigmatid mites at undisturbed sites, including members of Bdellidae, Tetranychidae, and *Procaeculus* sp. Mites in the mine were largely oribatid mites, members of the Acaridae family, and *Procaeculus* sp. (Table 2). Other taxa present at both sites included Pseudoscorpions, Araneae, Symphylans such as *Scutigerella immaculata*, pauropods, chilopods like *Schendyla nemorensis*, and diplopods like *Polyxenus largus*. Additionally, other taxa found at the undisturbed site, but not the disturbed chromite mine, were Proturans and Diplurans (Table 2).

4 | Discussion

4.1 | Site Characteristics

Because soil physicochemical data were composited at the site level, caution is warranted when interpreting relationships between edaphic properties and microarthropod abundance and diversity, as this approach may obscure fine-scale spatial variability. LOI (%) was markedly lower at the disturbed site, likely reflecting the loss of organic matter associated with topsoil removal during mining and its downstream effects on subterranean environments (Geissen et al. 2013). Decreased Cr concentrations in the disturbed site likely reflect localized Cr extraction associated with historical mining activities and enhanced leaching resulting from soil disturbance (Table 1). Though the changes in Cr and Ni concentrations in undisturbed sites are not adequate to disrupt the fecundity of microarthropod groups, it is important to note their decrease in concentration because of mining activities (Scott-Fordsmand et al. 1999). Another notable difference in soil physiochemical data between sites was the textural class, in particular the percentage of sand in the disturbed site (Table 1). The removal of finer-textured topsoil from chromite mining is associated with a stark increase in percent sand and an equivalent decrease in silt and clay.

4.2 | Abundance of Microarthropod Groups

Total microarthropod abundance was found to be lower in the ultramafic site that had been disturbed by chromite mining activities (Figure 1). Because the abundances of Collembola and Acari differed significantly between undisturbed and disturbed sites, our results indicate that even more than 60 years after disturbance, microarthropod communities remain sensitive to

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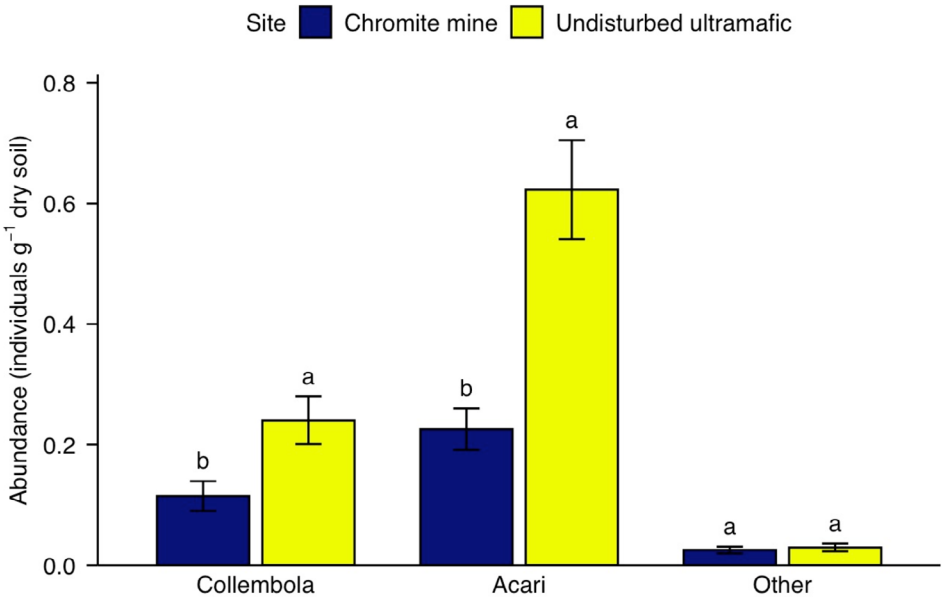


FIGURE 1 | Microarthropod abundance in disturbed ($n = 12$) and undisturbed sites ($n = 12$) measured as individuals per g of dry soil. Bars indicate mean abundance with error bars representing the standard deviation of microarthropod abundance. Different lowercase letters indicate significant differences at $p < 0.05$ level.

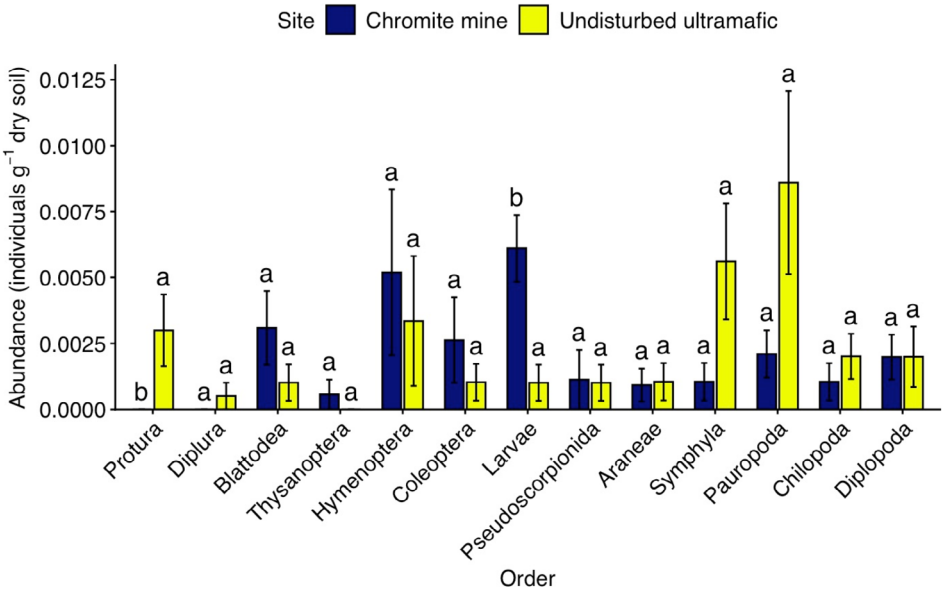


FIGURE 2 | Soil fauna abundance of observed orders in disturbed ($n = 12$) and undisturbed sites ($n = 12$) measured as individuals per g of dry soil. Bars indicate mean abundance with error bars representing the standard deviation across samples. Different lowercase letters indicate significant differences at $p < 0.05$ level.

physically and chemically altered environments. Collembola abundance has been shown to be low immediately following the cessation of mining activities, but populations are able to recover on decadal timescales in some systems (Dunger and Voigtländer 2009; Frouz et al. 2001). In this study, Collembola abundance remained significantly reduced relative to undisturbed reference sites even 60 years post-mining, indicating that edaphic constraints in serpentine soils may limit mesofaunal recovery on decadal timescales. This finding supports our hypothesis and aligns with prior studies that show that Collembola and Acari are susceptible to changes in the soil, such as disturbances to the litter layer (Eaton et al. 2004). Because the chromite mine had less organic matter than the disturbed site (Table 1), we hypothesize that the loss of organic matter likely contributed to changes in Collembola and Acari abundance. However, because physicochemical analyses were completed at a site level, there are limitations to this inference. The abundance of other taxa did not reveal significant differences between sites. This could be due to the low abundance of other taxa in the samples. Protura were significantly more abundant in undisturbed sites, while larvae were more abundant in the chromite mine (Figure 2). Our findings that microarthropod abundances differ between disturbed and undisturbed soils align with other studies (Juan-Overjero et al. 2023), where forests near mine tailings

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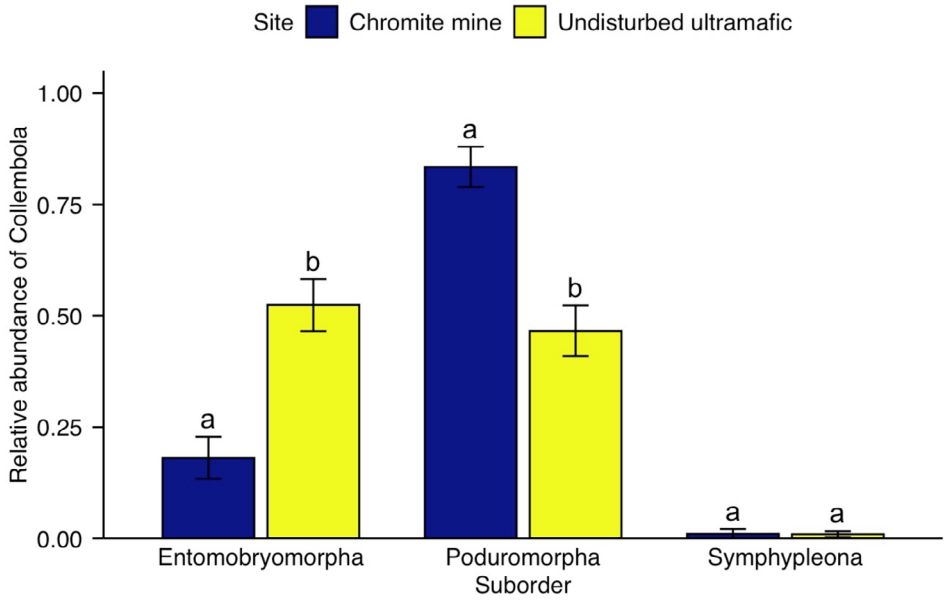


FIGURE 3 | Relative abundance of Collembola suborders in disturbed ($n = 12$) and undisturbed sites ($n = 12$). Bars indicate the mean relative abundance with error bars representing standard deviation across samples. Different lowercase letters indicate significant differences at $p < 0.05$ level.

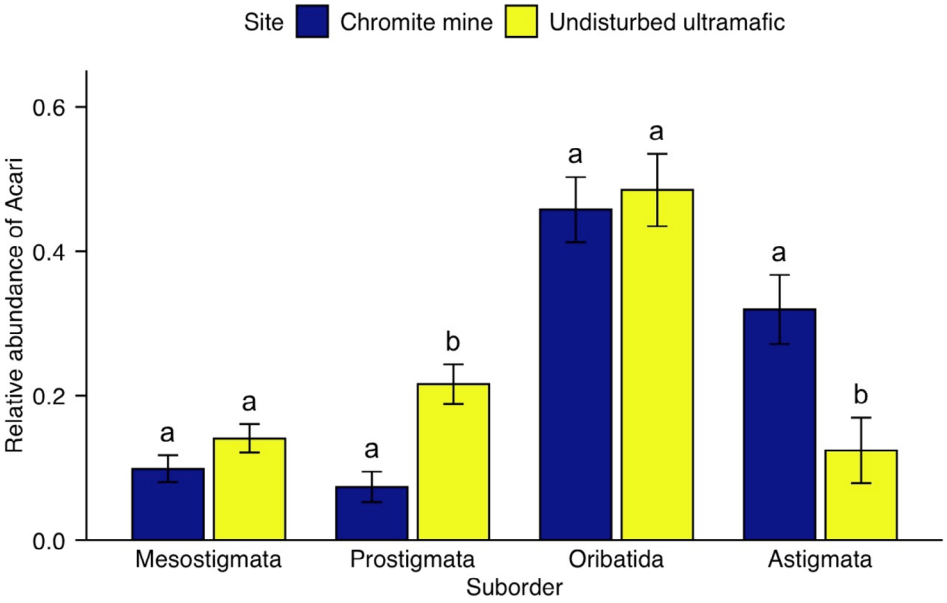


FIGURE 4 | Relative abundance of Acari suborders in disturbed ($n = 12$) and undisturbed sites ($n = 12$). Bars indicate the mean relative abundance with error bars representing the standard deviation across samples. Different lowercase letters indicate significant differences at $p < 0.05$ level.

showed less abundant and complex microarthropod communities than those that were distant. Absence of microarthropods in post-mine soils may be due both to dispersal limitations from adjacent non-disturbed areas (Ponge et al. 2006) or suppressed colonization and establishment in severely altered soils (Dunger and Voigtländer 2009). Microarthropod abundance, however, is not influenced by edaphic factors alone, but also by fecundity and seasonality. It is important to recognize that samples were taken in January during the wet season, and abundance is expected to be higher than if sampling was done during the spring or summer. Considering variable seasonal fecundity across microarthropod taxa, further research is needed to determine how their responses to disturbance in serpentine soils vary across seasons (Begum et al. 2014; Guo et al. 2022).

4.3 | Relative Abundance of Collembola and Acari Suborders

The mean relative abundance of Collembola and Acari suborders revealed shifts in the abundance of each suborder between sites. The abandoned chromite mine had a larger proportion of Poduromorphans than the undisturbed site and had much fewer Entomobryomorphans (Figure 3). Ultimately, the springtail

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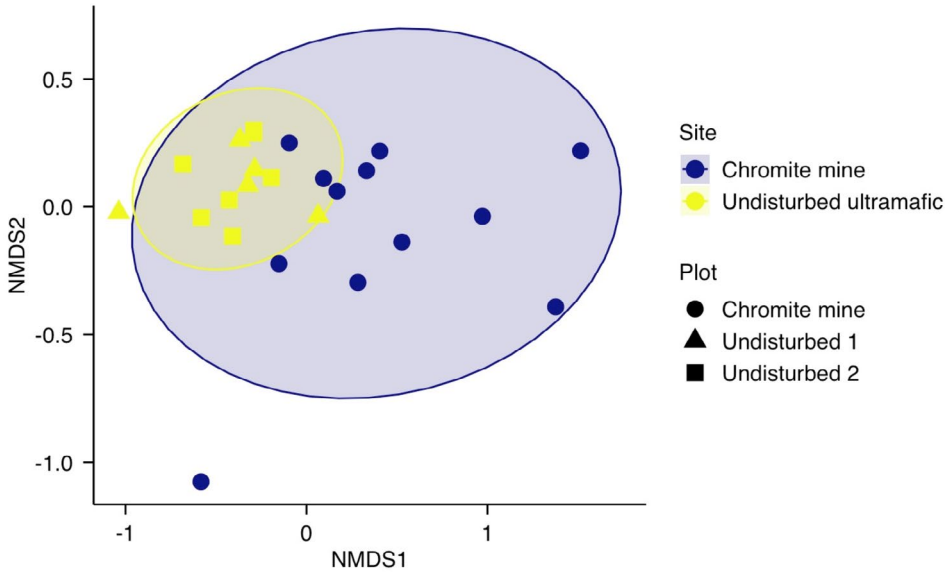


FIGURE 5 | Non-metric multidimensional scaling (NMDS) plot of soil fauna community beta diversity based on Bray–Curtis dissimilarity distances in disturbed chromite mine ($n = 12$) and undisturbed ($n = 12$) sites. Points represent individual soil community samples, colored by site type. Ellipses indicate the 95% confidence interval for each site and PERMANOVA test results indicate significant difference (Stress = 0.038 and p-value = 0.001).

community composition shifted from a higher relative abundance of Poduromorphans to a more evenly distributed abundance between the two suborders. As organic matter can drive changes in springtail abundance, we infer that disturbances disrupt the abundance of different suborders of springtails (Eaton et al. 2004). Relative abundance among Acari suborders further reflects how disturbance alters the balance between springtail and mite communities. Oribatid mites dominated both disturbed and undisturbed sites, whereas Prostigmata were most abundant in undisturbed areas. Mesostigmata showed higher relative abundance in undisturbed sites, though not significantly, indicating that Prostigmata were most affected by mining disturbance. Direct studies of mining impacts on Acari and Collembola are limited; however, research on analogous disturbances such as organic matter loss and soil compaction in forests has documented reduced mesofaunal densities consistent with our findings (Battigelli et al. 2004). Additionally, post-mining restoration techniques in limestone quarries in Spain have been shown to shift microarthropod community composition (Andrés and Mateos 2006). Relative abundance of both Prostigmata and Astigmata was higher in mined sites with minimal post-mining intervention (soil spreading but no planting) relative to an adjacent reference forest (Andrés and Mateos 2006). Astigmata similarly increased in relative abundance in the passively restored chromite mine in our study (Figure 4). However, unlike prior observations that Prostigmata tend to increase in abundance after heavy disturbance in other systems (Clapperton et al. 2002; Battigelli et al. 2004), the relative abundance of Prostigmata was lower in the mined site compared to the undisturbed reference (Figure 4).

4.4 | Microarthropod Community Composition

Alpha diversity metrics were not significantly different between mined and undisturbed ultramafic sites (Figure S3). While existing studies of microarthropod diversity are limited, these findings align with responses of other soil fauna (nematodes) to changes in serpentine soils (Kitagami et al. 2021). Significant differences in soil fauna community composition among sampling locations indicate that disturbance has strongly influenced overall community structure. Undisturbed ultramafic samples clustered consistently in NMDS ordination space, whereas chromite mine samples showed substantially greater dispersion, reflecting increased community heterogeneity (Figure 5). Because microarthropod abundance, diversity, and community composition differed significantly among habitat types, these results indicate that mining disturbances occurring nearly 60 years ago continue to shape the structure of soil fauna communities. However, as soil samples were composited and sieved by site for physical and chemical analyses, additional testing at the individual sample level is required to identify the specific edaphic drivers of these patterns. Nonetheless, these observations suggest that shifts in soil texture, loss of organic matter, and elevated heavy metal concentrations likely contribute to reduced microarthropod community complexity in mined serpentine soils, consistent with findings from other studies (Hasegawa 2001; Ashford et al. 2013). Future analyses that directly link per-sample soil physicochemical properties with microarthropod abundance and diversity are needed to better resolve the mechanisms underlying the observed differences in community structure.

5 | Conclusions

Our study demonstrates that historical chromite mining has had significant and lasting effects on multiple facets of soil microarthropod communities within the IHNR. By examining the abundance and diversity of microarthropods, we show that soil fauna and, by extension, soil health, can be effectively assessed many decades after disturbance. These

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TABLE 2 | List of microarthropod taxa found in chromite mine and undisturbed serpentine outcrops.

Class/Order	Family/Genus/Species	Chromite mine	Undisturbed ultramafic
Protura			X
Diplura	*Campodea montis*		X
Collembola	Isotomidae	X	X
	Hypogasturidae	X	X
	Onychiurinae	X	X
	Neanuridae	X	
	Katiannidae	X	
Pseudoscorpionida	Cheliferidae	X	X
Araneae		X	X
Acari	Labidostommatidae	X	X
	Parasitidae	X	X
	Macrochelidae	X	
	Uropodidae	X	X
	Tetranychidae	X	X
	Caeculidae	X	
	Bdellidae	X	X
	Acaridae	X	X
Symphyla	*Scutigerella immaculata*	X	X
Chilopoda	*Schendyla nemorensis*	X	X
Diplopoda	*Polyxenus largus*	X	X
Larvae		X	X
Hymenoptera	Formicidae	X	X
Blattodea		X	X
Coleoptera		X	X
Thysanoptera		X	

Note: Individuals were identified to the order and then further identified to the family, genus, and species if possible. Larvae represent microarthropods in the larval stage that could not be further identified.

findings reinforce the value of soil microarthropods as sensitive indicators of long-term ecosystem alteration. However, more integrative approaches are needed to identify the specific soil physical and chemical parameters driving observed changes in microarthropod communities and their associated ecosystem functions. In particular, applying comprehensive taxonomic frameworks is critical, as soil fauna can be difficult to distinguish using morphology alone (Lienhard and Krisper 2021). Emerging molecular tools, such as DNA metabarcoding, hold strong potential to enhance species-level resolution and build robust reference libraries for ecological investigations (Cuartero et al. 2025).

Future research combining per-sample soil physicochemical analyses with multivariate statistical approaches would further clarify relationships between microarthropod abundance, community composition, and edaphic factors. Incorporating molecular tools would further enhance understanding of soil biodiversity and inform restoration strategies for disturbed ultramafic sites and mine tailings. Ultimately, the monitoring of soil microarthropod communities is essential for making advancements in improving soil health, understanding biogeochemical cycles, and preserving ecosystem services (Parisi et al. 2005; Guerra et al. 2021). Such knowledge will support effective conservation, restoration, and bioremediation efforts in ultramafic landscapes and beyond, with implications for ecosystem management and human well-being across both natural and managed systems.

Acknowledgments

We acknowledge that the field work in the Irish Hills was conducted on land of the Northern Chumash, who have historically been stewards of these lands. We thank the Biological Sciences Department, the Bill and Linda Frost Fund, and the Office of Research's Teacher-Scholar Mini Grant at California Polytechnic State University, San

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Luis Obispo, for financial support of this project. We extend a huge thanks to the Natural Resources Management and Environmental Sciences Department and Dr. Chip Appel and Craig Stubler, who offered lab equipment and space to carry out this project. We thank the many individuals who directly contributed to the successful completion of this research, especially Bruce Hoskins, Assistant Scientist at MAFES, for carrying out soil testing; Robert Hill, Sustainability and Natural Resources Official for the City of San Luis Obispo, for permission to sample at Irish Hills Natural Reserve; John Merriam, for assistance with lab materials; Russell White, for help with obtaining historical documents; and Kyle Nessen for drone aerial footage of the mine site. We thank Dr. Alexandra Yep and Nevia Stickney for input and support in this project, and Emily Fischer for assistance with soil sampling. We thank two anonymous reviewers for their constructive feedback on an earlier version of this manuscript.

Funding

This work was supported by the College of Science and Mathematics, Cal Poly San Luis Obispo, Bill and Linda Frost Fund, and the Teacher Scholar Mini Grant Program of the Office of Research, Cal Poly San Luis Obispo.

Conflicts of Interest

Nishanta Rajakaruna is an Associate Editor-in-Chief for the Special Issue on Serpentine Ecology and will take no part in the peer review and decision-making processes for this paper.

References

Andrés, P., and E. Mateos. 2006. "Soil Mesofaunal Responses to Post-Mining Restoration Treatments." *Applied Soil Ecology* 33, no. 1: 67–78. https://doi.org/10.1016/j.apsoil.2005.08.007.

Anthony, M. A., S. F. Bender, and M. G. A. van der Heijden. 2023. "Enumerating Soil Biodiversity." *PNAS* 120: e2304663120. https://doi.org/10.1073/pnas.2304663120.

Ashford, O. S., W. A. Foster, B. L. Turner, E. J. Sayer, L. Sutcliffe, and E. V. J. Tanner. 2013. "Litter Manipulation and the Soil Arthropod Community in a Lowland Tropical Rainforest." *Soil Biology & Biochemistry* 62: 5–12. https://doi.org/10.1016/j.soilbio.2013.03.001.

Battigelli, J. P., J. R. Spence, D. W. Langor, et al. 2004. "Short-Term Impact of Forest Soil Compaction and Organic Matter Removal on Soil Microarthropod Density and Oribatid Mite Diversity." *Canadian Journal of Forest Research* 34, no. 5: 1136–1149. https://doi.org/10.1139/x03-267.

Begum, F., R. M. Bajracharya, B. K. Sitaula, et al. 2014. "Seasonal Dynamics and Land Use Effect on Soil Microarthropod Communities in the Mid-Hills of Nepal." *International Journal of Agronomy and Agricultural Research* 5, no. 2: 114–123.

Bonkowski, M., C. Villenave, and B. Griffiths. 2009. "Rhizosphere Fauna: The Functional and Structural Diversity of Intimate Interactions of Soil Fauna With Plant Roots." *Plant and Soil* 321: 213–233. https://doi.org/10.1007/s11104-009-0013-2.

Clapperton, M. J., D. A. Kanashiro, and V. M. Behan-Pelletier. 2002. "Changes in Abundance and Diversity of Microarthropods Associated With Fescue Prairie Grazing Regimes." *Pedobiologia* 46, no. 5: 496–511. https://doi.org/10.1078/0031-4056-00155.

Cuartero, J., I. Brunner, M. Schaub, et al. 2025. "Comparing Soil Microarthropod Communities Derived Directly From Soil DNA Metabarcoding With Those From Morphological Assessment in Drought-Prone and Irrigated Pine Forests." *Applied Soil Ecology* 209: e106042. https://doi.org/10.1016/j.apsoil.2025.106042.

Curtis, M. J., and V. P. Claassen. 2005. "Compost Incorporation Increases Plant Available Water in a Drastically Disturbed Serpentine Soil." *Soil Science* 170, no. 12: 939–953. https://doi.org/10.1097/01.ss.0000187352.16740.8e.

Dindal, D. L., ed. 1990. *Soil Biology Guide*. Wiley-Interscience.

Dunger, W., and K. Voigtländer. 2009. "Soil Fauna (Lumbricidae, Collembola, Diplopoda and Chilopoda) as Indicators of Soil Eco-Subsystem Development in Post-Mining Sites of Eastern Germany—A Review." *Soil Organisms* 81, no. 1: 1–51.

Eaton, R. J., M. Barbercheck, M. Buford, and W. Smith. 2004. "Effects of Organic Matter Removal, Soil Compaction, and Vegetation Control on Collembolan Populations." *Pedobiologia* 48, no. 2: 121–128. https://doi.org/10.1016/j.pedobi.2003.10.001.

Favero-Longo, S. E., E. Matteucci, and C. Siniscalco. 2009. "Plant Colonization Limits Dispersion in the Air of Asbestos Fibers in an Abandoned Asbestos Mine." *Northeastern Naturalist* 16, no. 5: 163–177. https://doi.org/10.1656/045.016.0514.

Fernandes, K., S. Clark-Ioannou, B. J. Majer, et al. 2024. "Mining Exploration Infrastructure Affects Biophysical Habitat Characteristics for Ground-Dwelling Arthropod Communities." *Biodiversity and Conservation* 33: 2465–2486. https://doi.org/10.1007/s10531-024-02865-2.

Frouz, J., B. Keplin, V. Pižl, et al. 2001. "Soil Biota and Upper Soil Layer Development in Contrasting Post-Mining Chronosequences." *Ecological Engineering* 17, no. 2–3: 275–284. https://doi.org/10.1016/S0925-8574(00)00144-0.

Garnica-Díaz, C., R. Berazaín Iturralde, B. Cabrera, et al. 2023. "Global Plant Ecology of Tropical Ultramafic Ecosystems." *Botanical Review* 89: 115–157. https://doi.org/10.1007/s12229-022-09278-2.

Geissen, V., S. Wang, K. Oostindie, et al. 2013. "Effects of Topsoil Removal as a Nature Management Technique on Soil Functions." *Catena* 101: 50–55. https://doi.org/10.1016/j.catena.2012.10.002.

Guerra, C. A., R. D. Bardgett, L. Caon, et al. 2021. "Tracking, Targeting, and Conserving Soil Biodiversity." *Science* 371: 239–241. https://doi.org/10.1126/science.abd7926.

Guerra, C. A., A. Heintz-Buschart, J. Sikorski, et al. 2020. "Blind Spots in Global Soil Biodiversity Research." *Nature Communications* 11: 239–241. https://doi.org/10.1126/science.abd7926.

Guo, Z., H. Chang, and R. Liu. 2022. "Response of Soil Microarthropod Community to Seasonal Changes in Urat Desert Steepe, Inner Mongolia." *Frontiers in Environmental Science* 10: 893913. https://doi.org/10.3389/fenvs.2022.893913.

Hamilton, F. 1917. *Mines and Mineral Resources of Portions of California*. California State Printing Office.

Harrison, S. P., and N. Rajakaruna. 2011. *Serpentine: Evolution and Ecology in a Model System*. University of California Press.

Hasegawa, M. 2001. "The Relationship Between the Organic Matter Composition of a Forest Floor and the Structure of a Soil Arthropod Community." *European Journal of Soil Biology* 37: 281–284. https://doi.org/10.1016/S1164-5563(01)01099-8.

Havlik, N. 2011. *Adoption of the Conservation Plan Update for Irish Hills Natural Reserve, and Environmental Determination*. Council Agenda Report City of San Luis Obispo.

Jernigan, A., J. Kao-Kniffin, S. Pethybridge, and K. Wickings. 2023. "Soil Microarthropod Effects on Plant Growth and Development." *Plant and Soil* 483: 27–45. https://doi.org/10.1007/s11104-022-05766-x.

Juan-Overjero, R., J. Álvarez-Rogel, A. Peñalver-Alcalá, R. A. Verweij, C. A. M. van Gestel, and M. N. González-Alcaraz. 2023. "Microarthropod Communities Act as Functional Mediators of Ecosystem Recovery in Abandoned Metal(Loid) Mine Tailings in Semiarid Areas." *Science of the Total Environment* 881: 163394. https://doi.org/10.1016/j.scitotenv.2023.163394.

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Keil, D. J. 2020. "*Erythranthe serpentinicola* (Phyrmaceae), a New-Serpentine Endemic Species From San Luis Obispo County, California." *Phyton* 33: 1–13.

Kitagami, Y., K. Kawai, and T. Ekino. 2021. "Soil Physiochemical Properties Shape Distinct Nematode Communities in Serpentine Ecosystems." *Pedobiologia—Journal of Soil Ecology* 85–86: 150725. https://doi.org/10.1016/j.pedobi.2021.150725.

Lienhard, A., and G. Krisper. 2021. "Hidden Biodiversity in Microarthropods (Acari, Oribatida, Eremaeoidea, *Caleremaeus*)." *Scientific Reports* 11: 23123. https://doi.org/10.1038/s41598-021-02602-7.

Menta, C., F. D. Conti, S. Pinto, and A. Bodini. 2018. "Soil Biological Quality Index (QBS-Ar): 15Years of Application at Global Scale." *Ecological Indicators* 85: 773–780. https://doi.org/10.1016/j.ecolind.2017.11.030.

Menta, C., and S. Remelli. 2020. "Soil Health and Arthropods: From Complex System to Worthwhile Investigation." *Insects* 11, no. 1: 54. https://doi.org/10.3390/insects11010054.

Moore, J. C., B. B. Tripp, R. T. Simpson, and D. C. Coleman. 2000. "Springtails in the Classroom: Collembola as Model Organisms for Inquiry-Based Laboratories." *American Biology Teacher* 62, no. 7: 512–519. https://doi.org/10.2307/4450960.

Mulroy, M., I. Suhr, J. Dart, E. Balderas, Z. Raposo, and N. Rajakaruna. 2026. "Slow Succession: A Comparison of the Saxicolous Lichens of a 50-Year-Old Abandoned Chromite Mine and a Nearby Undisturbed Ultramafic Outcrop." *Ecological Research* 41, no. 4: e70095. https://doi.org/10.1111/1440-1703.70095.

Nelson, K. M., D. J. Keil, and R. A. Hill. 2019. "*Chorizanthe aphanantha* (Polygonaceae: Eriogonoideae), a New Serpentine-Endemic Species From the San Luis Range of Western San Luis Obispo County, California." *Madrono* 65: 184–191.

O'Dell, R. E., and V. P. Claassen. 2009. "Serpentine Revegetation: A Review." *Northwestern Naturalist* 16, no. 5: 253–271. https://doi.org/10.1656/045.016.0519.

O'Dell, R. E., and N. Rajakaruna. 2011. "Intraspecific Variation, Adaptation, and Evolution." In *Serpentine: Evolution and Ecology in a Model System*, edited by S. P. Harrison and N. Rajakaruna, 97–137. University of California Press.

Oksanen, J., G. Simpson, F. Blanchet, et al. 2025. "vegan: Community Ecology Package." R package version 2.6-10.

Parisi, V., C. Menta, C. Gardi, C. Jacomini, and E. Mozzanica. 2005. "Microarthropod Communities as a Tool to Assess Soil Quality and Biodiversity: A New Approach in Italy." *Agriculture, Ecosystems and Environment* 105, no. 1–2: 323–333. https://doi.org/10.1016/j.agee.2004.02.002.

Phillips, H. R. P., E. K. Cameron, N. Eisenhauer, et al. 2024. "Global Changes and Their Environmental Stressors Have a Significant Impact on Soil Biodiversity–A Meta-Analysis." *iScience* 27, no. 9: 110540. https://doi.org/10.1016/j.isci.2024.110540.

Ponge, J. F., F. Dubs, S. Gillet, J. Ponge, J. Sousa, and P. Lavelle. 2006. "Decreased Biodiversity in Soil Springtail Communities: The Importance of Dispersal and Landuse History in Heterogeneous Landscapes." *Soil Biology & Biochemistry* 38, no. 5: 1158–1161. https://doi.org/10.1016/j.soilbio.2005.09.004.

Potapov, A. M., X. Sun, A. D. Barnes, et al. 2022. "Global Monitoring of Soil Animal Communities Using a Common Methodology." *Soil Organisms* 94, no. 1: 55–68. https://doi.org/10.25674/so94iss1id178.

R Core Team. 2025. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing.

Sanchez, S. P., R. Courtney, and O. Schmidt. 2021. "Soil Meso- and Macrofauna Indicators of Restoration Success in Rehabilitated Mine Sites." In *Handbook of Ecological and Ecosystem Engineering*, edited by M. N. V. Prasad. John Wiley & Sons Ltd.

Scott-Fordsmand, J. J., P. H. Krogh, and S. P. Hopkin. 1999. "Toxicity of Nickel to a Soil-Dwelling Springtail, *Folsomia fimetaria* (Collembola: Isotomidae)." *Ecotoxicology and Environmental Safety* 43: 57–61. https://doi.org/10.1006/eesa.1998.1758.

Smith, C. T., and A. B. Griggs. 1944. "Chromite Deposits of the Southern Coast Ranges of California." In *Strategic Minerals*, vol. 945, 23–44. U.S. Government Printing Office.

Straalen, N. M. 1998. "Evaluation of Bioindicator Systems Derived From Soil Arthropod Communities." *Applied Soil Ecology* 9, no. 1–3: 429–437. https://doi.org/10.1016/S0929-1393(98)00101-2.

Tsiafouli, M. A., E. Thébault, S. P. Sgardelis, et al. 2014. "Intensive Agriculture Reduces Soil Biodiversity Across Europe." *Global Change Biology* 21, no. 2: 973–985. https://doi.org/10.1111/gcb.12752.

Visioli, G., C. Menta, C. Gardi, and F. D. Conti. 2013. "Metal Toxicity and Biodiversity in Serpentine Soils: Application of Bioassay Tests and Microarthropod Index." *Chemosphere* 90, no. 3: 1267–1273. https://doi.org/10.1016/j.chemosphere.2012.09.081.

Visioli, G., A. M. Sanangelantoni, F. D. Conti, B. Bonati, C. Gardi, and C. Menta. 2019. "Above and Belowground Biodiversity in Adjacent and Distinct Serpentine Soils." *Applied Soil Ecology* 133: 98–103. https://doi.org/10.1016/j.apsoil.2018.09.013.

Wickham, H. 2016. *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag.

Yahya, M., M. Afzal, M. Z. Majeed, et al. 2020. "Differential Impact of Land-Use, Season and Soil Characteristics on the Abundance of Edaphic Springtails (Insecta: Collembola) and Mites (Arachnida: Acari)." *Pakistan Journal of Zoology* 52, no. 4: 1483–1491. https://doi.org/10.17582/journal.pjz/20190817120809.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Map of sampling locations at Irish Hills Natural Reserve (a), map of study area with respect to California (b), and aerial imagery of the chromite mine from the northeast (c). **Figure S2:** Soil sampling schematic for each *C. cuneatus* sampled (a) and leaf litter at the soil surface (b). Each target shrub had soil collected upslope and downslope from a depth of 10cm and then composited to obtain a representative sample. **Figure S3:** Diversity measured as richness, Shannon index, Simpson's index, and evenness across disturbed ($n = 12$) and undisturbed ($n = 12$) sites. Bars represent mean values with error bars representing standard deviation. Different lowercase letters indicate significant differences at $p < 0.05$ level.

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