The Edaphic Factor in Ecology

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Abstract
The edaphic factor encompasses the physical, chemical, and biological properties of soil that result from biological and geological phenomena or anthropogenic activities. Variations in the edaphic factor contribute to the intriguing patterns of diversity observed in the biotic world. Chemical and physical features of soil greatly influence the ecology and evolution of plants and their associated biota. Extreme soil conditions, such as those found on serpentine outcrops, limestone and gypsum deposits, and even mine tailings, have led to the formation of unique plant communities characterized by both rarity and endemism. Such sites have also provided model organisms for examining the processes of divergence due to adaptation, reproductive isolation, and subsequent genetic differentiation, in some cases resulting in speciation. Ever-expanding agriculture and forestry, mining activity, urbanization, and rapidly changing climate, pose severe threats to the world's unusual edaphic habitats and their biota. While some areas have been preserved for their unique biota associated with unusual edaphic conditions, many more are rapidly being impacted by human activities and climate change. Without strict conservation measures, many edaphic specialist species, including metal hyperaccumulating plants that are useful for innovative, green technologies such as phytoremediation and agromining, may soon be lost.

Introduction

This article describes the crucial roles geology and soil conditions play in the ecology and evolution of plant species and their associated biota. Our objectives are twofold: (1) describe the edaphic factor as a life force responsible for generating and maintaining distinct species assemblages and (2) emphasize the importance of preserving habitats with extreme edaphic conditions due to their rich biological diversity. First, we define the edaphic factor and its role in shaping the biotic world. Then, we review our current knowledge of the ecology of unusual geological formations, focusing on studies conducted within and across biotic kingdoms. Furthermore, we explore plant evolutionary processes on extreme geological substrates, an area that has garnered much interest from evolutionary biologists in recent decades. Finally, we discuss applied ecology and conservation of plants and other biota restricted to distinctive geological environments.

The Edaphic Factor: Its Role in Shaping the Biotic World

Ecologists have long noted the profound influence of geology on the global and regional distribution of organisms. Life exists across a mosaic of geological substrates that vary in space and time, encompassing everything from macro- to microscopic organisms. Geologic phenomena contribute significantly to the maintenance and generation of biotic diversity in two main ways. First, large-scale geological events such as continental drift and the rise of mountain ranges create discontinuous or patchy landscapes. Secondly, within a patchwork of landscapes, different types of parent materials—like igneous, metamorphic, or sedimentary rocks—can become exposed, giving rise to soils with distinct chemical and physical characteristics. This diversity in soil characteristics provides opportunities for species colonization and differentiation.

The concept of the 'edaphic factor' pertains to the physical, chemical, and biological properties of soil resulting from geological processes. Discontinuities in the edaphic factor contribute significantly to the intriguing patterns of diversity we observe in the biotic world. Edaphology is a branch of soil science that specifically examines how soils influence organisms, especially plant growth. It includes agrology, the study of the uses of soils for agriculture, and considers how soil features affect human land use decisions.

According to soil ecologist Hans Jenny, soils derive their distinct characteristics from five interacting factors: climate, organisms, topography, parental rock, and time. If all but one factor (e.g., parental rock) remain constant, then variation in a soil body can be attributed mainly to that one factor. Botanists have long recognized that the distribution, growth habit, and composition of vegetation are greatly influenced by the edaphic factor. The striking effects on vegetation of unusual and often extreme substrates (such as serpentine, limestone, dolomite, gypsum, etc.) are apparent even to amateur naturalists. Whereas climate broadly defines major biomes (e.g., tropical rainforests, temperate deciduous forests, deserts, and tundra), it is geology that enriches diversity within these zones.

The role of the edaphic factor in shaping the distribution of plant species was keenly observed and documented by many 18th- and 19th-century plant ecologists, who considered soils second only to climate as the major ecological determinant of plant distribution. It was not until the 20th century, however, that ecologists fully appreciated the role of the edaphic factor in generating habitats within which plants and their associated organisms live, interact, reproduce, and diverge over time.

Components of the Edaphic Factor

Plants generally rely on soil for obtaining essential nutrients and water, making soil features that influence nutrient availability and water uptake crucial for plant growth. Here is a concise overview of the key soil features that most greatly affect both plant growth and soil microbial life:

Texture

Soil texture refers to the distribution of mineral particles based on their size (diameter). There are three primary particle size classes: clays ($<$ 0.002 mm), silts (0.002–0.05 mm), and sands (0.05–2.0 mm). The percentage of each of these major particle classes determines the texture of a soil. Soil textures range from those predominantly containing one of the three major particle size classes and thus named for them (silt, sand, clay) to various intergradations (sandy clay, etc.). Loam, which is ideal for plant growth, is not named for a predominant particle class because it contains relatively balanced amounts of all three particle classes.

Texture influences water availability and soil fertility—its ability to supply nutrients to plant roots. Open spaces among soil particles are called pore spaces and may be filled by water, air, organic matter, or plant roots. Thus, the amount of pore space greatly influences a soil's water holding capacity. The tightness with which water is held in pore spaces determines to what extent water and dissolved mineral ions will drain through the soil profile or remain in place and be available for uptake by plant roots.

Coarse textured soils (e.g., sandy soils) have larger pore spaces that do not hold water tightly enough to prevent gravity from pulling that water into deeper soil layers (i.e., the water drains quickly). Fine textured soils (e.g., clayey soils) with small pores hold water tightly and thus retain much water despite the pull of gravity. However, these small pores also hold water against the pulling power of plant roots and so they also provide only small amounts of plant-available water. Soils such as loams, with a relatively even mix of particle sizes, retain water against the pull of gravity but also allow more of the remaining water to be removed by plant roots and thus they provide maximum amounts of plant-available water. Soil texture is also an important determinant of the Cation Exchange Capacity (CEC) of a soil, that is, the ability of a soil to adsorb and exchange mineral ions that are essential for plant growth. Soils with higher percentages of clay and/or silt particles generally have a higher CEC.

Additionally, soil texture also appears to play an important role in microbial soil communities, affecting fungal rather than bacterial alpha diversity, with fungal species diversity increasing in coarse-textured soils. Furthermore, soil texture effects on microbial community structure are taxon-dependent. For instance, the relative abundances of some fungi (Basidiomycota and Eurotiomycetes) and filamentous bacteria (Actinobacteria and Chloroflexi) appear to increase with silt and/or clay content in soil.

Structure

Soil structure refers to the three-dimensional arrangement of soil particles, forming aggregates (lumps of soil material) known as peds. The spaces between peds can be important for water penetration and root development into deeper soil layers.

Depth

Soil depth can greatly influence the types of plants that can grow in them. Deeper soils generally can provide more water and nutrients to plants than more shallow soils. Furthermore, most plants rely on soil for mechanical support and this is particularly true for tall, woody plants (i.e., shrubs, trees). A classic example of the influence of soil depth on plant communities is seen on granite rock outcrops in the southeastern United States. As granite weathers, it can form pools of soil of varying depths that support annual plant communities in shallow soils, whereas deeper soils support herbaceous perennials and still deeper soils are colonized by woody plants. Plant zonation in these soil pools can be striking (**Fig. 1**).

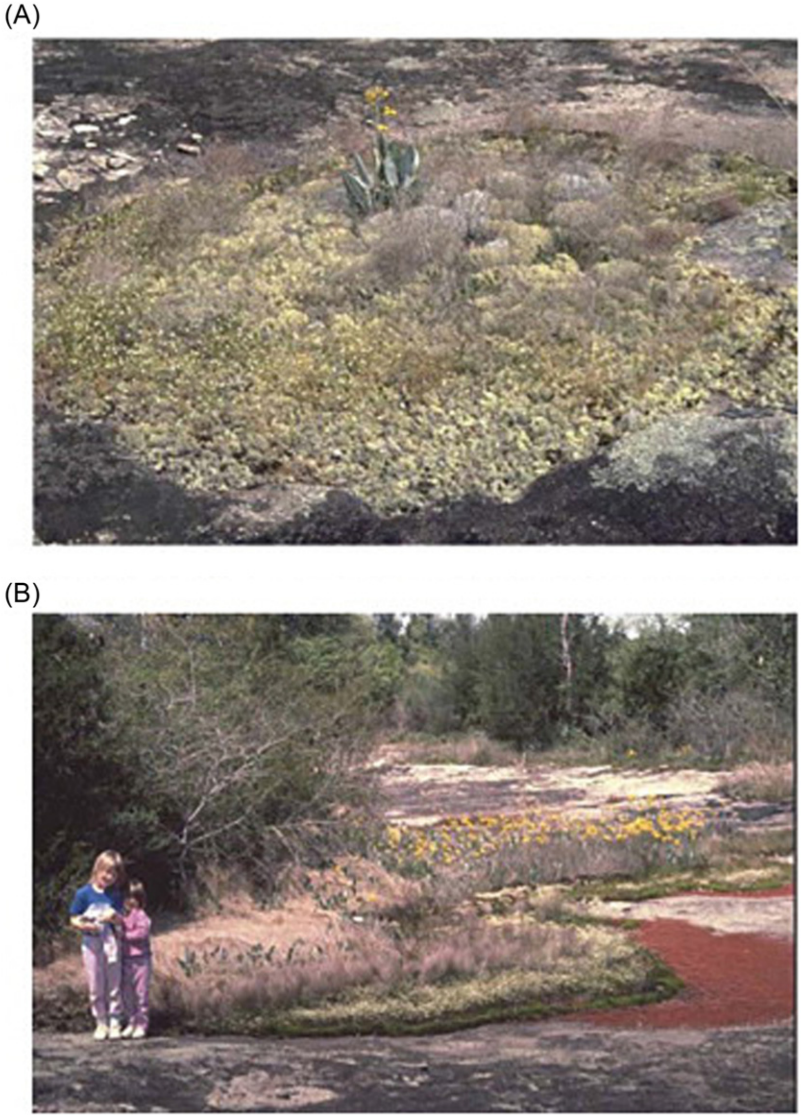

Fig. 1 (A) A small soil pool (about 2 m wide) on a granite outcrop in east-central Alabama, U.S.A. Shallow soil at the margins is dominated by lichens. The deepest soil in the center of the pool has been colonized by *Packera dubia*, a yellow-flowered herbaceous perennial species. (B) A larger soil pool on the same granite outcrop shown in (A). Deep soil on the *left* (behind the children: Jennifer and Kristina Boyd) is occupied by woody plants (shrubs and trees). The soil pool becomes more shallow to the *right*, where striking zonation of smaller plants can be observed. The most shallow soil on the extreme right is occupied by the small red-colored annual *Sedum smallii*. Slightly deeper soil to the left of the *Sedum* zone is dominated by moss (*Polytrichum commune*) and white-flowered annual *Arenaria* species. Still deeper soil between that zone and the woody plants is dominated by perennial grasses along with some *Packera tomentosa*. Credit: R. S. Boyd.

Some soils can develop special soil horizons (horizons are horizontal soil layers characterized by distinct chemical and physical features) that limit the soil depth available for plant growth. Examples include claypans, a compact soil layer that restricts root penetration and water infiltration due to high clay content, and hardpans (calcic horizons or caliche), where layers of soil particles that have been cemented together by the deposition of calcium carbonate impede root (and water) penetration. The net effect of these dense horizons is to impede or prevent root growth and thus limit the effective depth of the soil. They also may affect soil oxygenation by restricting drainage at times when large amounts of water are present in the soil.

Organic Matter

Organic matter in soils ranges from recognizable plant parts (roots, leaves, stems) to humus, which is partially decomposed plant material that is amorphous and spongy in nature. Organic matter enhances soil fertility by improving nutrient retention (via increasing CEC) and increasing water-holding capacity by absorbing water. It aids in nutrient retention because negatively charged surfaces in humus particles attract and hold positively charged nutrient ions. Humus can also absorb 80%–90% of its weight in water and therefore contributes to water-holding capacity. Organic matter is also an important food source for decomposer and detritivore organisms in soil and the soil C:N ratio is a key determinant of soil microbial community structure and function. Further, microbe-derived organic matter accumulation is greatest in soils with higher fungal richness and more efficient microbial biomass production. Organic matter also contributes to soil color, a factor that affects a soil's thermal properties, which can influence plant growth as well as the activity of soil microbes and other soil-dwelling organisms.

pH

Soil pH is a critical ecological parameter that influences ion availability in the soil solution, which is important for two major reasons. First, many soil ions contain elements required for plant growth. These elements, called essential nutrients, are primarily obtained from soil. The second reason is that plants obtain most of their water from soil and the amount of dissolved ions in soil water can influence a plant's ability to take up water (see the following section).

The pH level influences the solubility of various compounds present in the soil. In general, soil compounds containing some elements are more (or less soluble) at certain pH values. For example, Fe is relatively insoluble at pH values above 8, leading to deficiencies in plants with high Fe requirements. Conversely, potentially toxic metals and metalloids become increasingly available for plant uptake at acidic pH values (4–5), increasing the risk of toxicity.

Importantly, soil pH impacts microbial diversity and soil food webs (trophic interactions among soil organisms). Soil bacterial community composition and phylogenetic diversity are directly correlated with soil pH, with diversity peaking in soils with near-neutral pH. Soil nematodes (the most abundant animals on Earth, filling all trophic levels in soil food webs) are also influenced by pH, with global abundance patterns negatively correlated with soil pH. Changes in soil pH can therefore alter the structure and function of soil food webs, influencing processes such as decomposition and nutrient cycling. These effects cascade through ecosystems, impacting and shaping both below-ground and above-ground biodiversity.

Ion Availability

Although we mentioned ion availability under pH (above), we should also mention that some ions are abundant in some soils primarily because they have been deposited in those soils in great amounts. Certain salts (often Na, Mg, or Ca salts) may be abundant in some soils in quantities that greatly affect plant growth. These salts include those from seawater (as in salt marshes, alkali wetlands, or remains of a prehistoric sea, as in Soda Lake, Carrizo Plain National Monument in California, U.S.A.) or those that build up in desert soils by evaporation from relatively fresh water (e.g., the Great Salt Lake of Utah, U.S.A.). Extensive irrigation of land in regions where there is high evapotranspiration can also lead to accumulation of salts on the soil surface (i.e., secondary salinization). Recent data-driven models predict that the dryland areas of South America, southern and western Australia, Mexico, southwestern United States, and South Africa have the highest risk of increased soil salinity in the 21st Century. Salty soils (e.g., saline, sodic, saline-sodic soils) can impact plant growth by affecting water uptake, nutrient uptake, or by causing toxicity due to effects of specific ions. Water uptake can be slowed because high ion concentration (high osmotic potential) in a soil impedes water movement into plant roots. Nutrient uptake can be affected because some ions can competitively inhibit the uptake of essential ions of similar size (e.g., Na^{+} vs. K^{+}, Mg^{2+} vs. Ca^{2+}). Excess ions can also have specific toxic effects on plants by directly inhibiting essential physiological processes.

The Edaphic Factor in the Ecology of Plants and Other Biota

Given the importance of soil features to plants, the edaphic factor's influence on plant ecology and evolution is unsurprising. In particular, soils with unusual characteristics (extreme pH levels, nutrient imbalances, toxic elements, limited depth, poor texture, etc.) may act as strong selective forces shaping plant evolution. Unusual soils (serpentine, limestone, gypsum, etc.) often harbor species that are found exclusively on such soil types (edaphic endemics), whereas others may evolve locally adapted populations (ecotypes). These adaptations create functional diversity of species as they respond to specific soil features. In other cases, unusual soils may also serve as refugia for taxa that are unable to thrive in more competitive, herbivory intensive, or pathogen-prone environments typical of "normal" soils.

Plants inhabiting 'harsh' soil environments (serpentine, gypsum and other carbonates, and sodic/saline flats) are often exposed to a common suite of stressors in bare habitats, including high evapotranspiration rates, UV radiation stress, herbivore exposure, and osmotic challenges resulting from high ionic strength soil solutions. Consequently, it is likely that plants across different 'harsh' soil environments employ similar mechanisms to deal with these common stressors, suggesting a stress resistance syndrome. Exploring whether there is a common genetic basis among distinct plant lineages for similar edaphic stressors — across different 'harsh' soil environments — has significant agricultural and ecosystem restoration applications.

In contrast, the ability of soils to affect the ecology or evolution of organisms other than plants is less well known, primarily due to the mobility and aboveground lifestyle of animals that render them less influenced by the various properties of soils. However, soil color has been documented to directly impact the evolution of certain animals, particularly in habitats lacking vegetation such as deserts and beaches, where animals may evolve to match the color of their surroundings for camouflage. For example, the white gypsum dunes, for which the White Sands National Monument in New Mexico, U.S.A., is named, host a number of animals that exhibit lighter coloration than those living on darker surrounding soils. These animals include insects, spiders, scorpions, lizards, amphibians, and mammals. The main selective advantage of this color matching is to provide camouflage that makes color-matched animals less likely to be detected and thus fall victim to predators.

The evolution of burrowing and soil-dwelling animals is more likely to be influenced by soil properties as their life histories are intertwined with soil features. For example, the sandfish skink (*Scincus scincus*) of the Sahara Desert and Arabian Peninsula inhabits sand dunes and can dive into sand and move through it with swim-like movements (giving it its common name). This ability helps it escape predators (a survival strategy) and also avoid temperature extremes (providing thermal regulation), but its ability to move in this way through soil is obviously dependent on the texture of the sand dunes that it inhabits.

These direct effects of soils on biota are supplemented by a variety of indirect effects which can influence animals or plants by affecting organism interactions. This is easily imagined when one considers the importance of plant communities in providing habitat for animals and other organisms. There are several intriguing cases of special plant–insect interactions under extreme edaphic conditions. Some plants that are endemic to serpentine soils have high metal concentrations in their tissues, and in turn harbor unique insect herbivores adapted to deal with those high plant tissue metal concentrations (**Fig. 2**). It is rare to find cases in which the effects of soil on other organisms indirectly affect plants, but this does occur. For example, pocket gophers tunnel through soil and consume aboveground, and especially belowground, plant parts. In mountain meadows of Arizona, U.S.A., aspen trees suffer significant gopher-caused mortality on deep meadow soils but not on rocky outcrops where pocket gophers cannot occur due to the lack of soil deep enough for them to tunnel.

Soils directly influence microbe diversity and community composition (see soil texture, pH, and organic matter). A comparison of bacterial and fungal diversity in biological soil crusts from serpentine and non-serpentine soils, along a precipitation gradient of the Barberton Greenstone Belt in South Africa, recorded no differences in bacterial richness and community structure. Nevertheless, taxon-specific patterns were observed for selected bacterial taxa (such as *Candidatus* or *Solibacter*) which were more abundant in biocrusts of serpentine or lower precipitation sites. Conversely, fungal community structure was distinct between biocrusts of serpentine and non-serpentine soils and between high and low precipitation sites. Furthermore, fungal diversity was lowest in dryer serpentine biocrusts. As with bacteria, fungal patterns were also taxon-specific, with *Ramimonilia* and *Vishniacozyma*, which are known to be resistant or tolerant to potentially toxic metals and metalloids as well as other environmental extremes, were more abundant in serpentine biocrusts, with the latter genus being an indicator of serpentine habitats.

Fig. 2 The Ni tolerant insect *Melanotrichus boydi* (Heteroptera: Miridae) on a flower of its host plant, the California Ni hyperaccumulator *Streptanthus polygaloides* (Brassicaceae). The plant is found only on serpentine soils in California, and the insect is found only on *S. polygaloides*. The insect is tolerant of the high levels of Ni found in the plant tissues (usually $>$ 3000 μg Ni/g dry mass). The insects, about 5 mm long, contain about 800 μg Ni/g dry mass, enough to make them toxic to crab spiders that hunt for prey on flowers of *S. polygaloides*. Credit: R. S. Boyd.

Soils and Biogeography

Landscape ecology is a subfield of ecology that examines the patterns and interactions between communities that constitute relatively large areas. At this ecological scale, the distribution pattern of soil types across a landscape may have important ecological consequences, such as generation of biological diversity (species richness, evenness). In a sense, patches of one soil type in a matrix of another are akin to islands in the sea (**Fig. 3**), and thus can be considered through the lens of Island Biogeography.

Island Biogeography holds that the number of species on an island is primarily determined by its size and its distance from potential sources of colonists. Thus, relatively small patches of unusual soils (i.e., edaphic islands) that are distant from similar patches would be expected to harbor fewer species compared to larger patches closer to other areas of similar soils. This has been confirmed by studies on the flora of serpentine soil patches in California, U.S.A. Recent studies of calcareous spring fens in Slovakia and the easternmost area of the Czech Republic, acidic alpine grasslands in northwestern Spain, and shallow-soil acidophilous grasslands in the southern Czech Republic, also confirm that isolation affects species richness of edaphic islands, with species richness generally decreasing with increasing isolation.

Soils and Invasive Species

Invasive species are non-native species that become abundant enough to cause significant negative effects on some native species or the function of native ecosystems. Because soils are an important environmental factor for organisms, it is no surprise that soil features can affect the ability of non-native species to become invasive. In many cases, disturbance of native communities (including changes in soils caused by disturbance) provides inroads for invasive species. Some studies have contrasted the susceptibility to invasion of unusual soils (such as serpentine soils) and more normal soils. The general conclusion is that the features of the unusual soils that make them challenging for plant growth often inhibit the invasiveness of non-native species. Anthropogenic activities, however, can directly influence soil chemistry of some unusual edaphic habitats, making such habitats conducive for colonization by invasive species.

This appears to be the case for atmospheric nitrogen deposition on serpentine sites in California, U.S.A., where wet and dry nitrogen deposition can occur in the range of 10–15 kg N ha^{-1} $year^{-1}$, greatly exceeding the critical load (6 kg N ha^{-1} $year^{-1}$) at which invasive species can become problematic and altering community structure as a result. Vehicle emissions along major highways, along with widespread use of NH_3-based fertilizer and the combustion of fossil fuels, all contribute to increased nitrogen loads in many locations, with severe consequences for plant-plant, plant-insect, and plant-microbe interactions, especially in low nutrient soils such as serpentine. Another source of nitrogen input, which is of increasing concern, is the frequent use of Long-Term Fire Retardants (LTFRs), such as *Phos-Chek®*, which are chemically similar to nitrogen fertilizers. Due to increased nitrogen input, non-native species, previously excluded from such soils due to nitrogen limitation, are invading these unique habitats, as shown for serpentine grasslands in California, U.S.A., and native heathland vegetation in eastern Australia. The effects of nitrogen deposition and resulting soil acidification can also influence soil nutrient and metal bioavailability, further impacting plants, soil microbes, and their mutualistic partnerships. It is common for invasive species, particularly plants, to impact soils and, through changes in soil characteristics, affect other organisms in those communities. For example, in the northwestern U.S.A., diffuse knapweed (*Centaurea diffusa*; Asteraceae) has a direct soil-mediated impact on competing native plants. This invasive plant

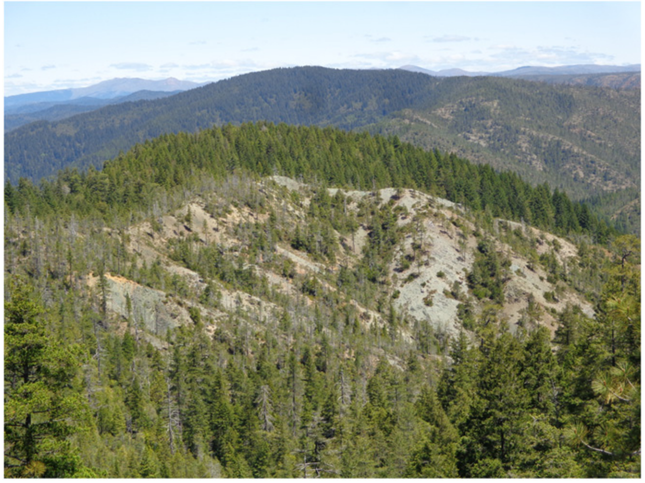

Fig. 3 Edaphic islands of ultramafic rock outcrops at the Western geologic boundary of the Josephine peridotite, Rowdy Creek Road, Del Norte County, California, USA. The sparsely vegetated ultramafic rock outcrop (center, middle ground) contrasts sharply with the densely vegetated non-ultramafic soils (background) more favorable for plant growth. Credit: R. E. O'Dell.

produces 8-hydroxyquinoline, a chemical that builds up in soils occupied by *C. diffusa* and poisons native plants growing in those soils. Invasive animal species have also been shown to alter soil features that then impact many other organisms in a habitat. For example, earthworms are not native to the forests of Minnesota, U.S.A., but have been introduced in many locations. By consuming soil litter and accelerating its breakdown, these animals increase soil compaction, decrease water penetration, and alter the nature of the litter layer habitat in ways that reduce its suitability for some native animals, herbaceous plants, and tree seedlings.

Plant Life on Selected Edaphic Conditions

Unusual edaphic conditions harbor unique plant associations often characterized by rarity and endemism. These conditions also foster distinct morphological and physiological adaptations, resulting in characteristic plant communities. One of the most remarkable edaphic habitats where such unique plant communities thrive is found on serpentine soils derived from ultramafic and related rocks (i.e., rocks high in iron and magnesium silicates). Ultramafic rocks such as serpentinite and their associated serpentine soils are globally distributed but are concentrated, however, along continental margins and in regions of orogenesis (mountain building). Serpentine soils are unique due to high pH and high levels of potentially toxic metals and metalloids such as magnesium, nickel, and chromium, and are generally low in essential nutrients, Ca/Mg ratio, and water-holding capacity. The associated rocks are often found on open, steep slopes exposed to high light and heat conditions, resulting in generally shallow and highly erodible soils (**Fig. 4**). The biological effects manifested by these extreme edaphic conditions, known as the serpentine syndrome, have spurred research in plant physiology, ecology, and evolution worldwide.

Serpentine soils, although covering a mere few percent of the Earth's surface, host many endemic species. For instance, in the California Floristic Province (U.S.A.), 255 taxa (193 full species of plants, as opposed to subspecies or varieties) endemic to that province are largely restricted to serpentine (i.e., 14.7% of California endemic species). Of these, 148 (c. 60%) come from only ten plant families, concentrated mostly in one or two genera per family. Tropical islands such as New Caledonia and Cuba exemplify even higher levels of plant endemism on serpentine soils. In New Caledonia, serpentine soils host over 2100 plant species, with more than 60% of these species that are serpentine endemic, while in Cuba, 920 species, one-third of the island's endemic taxa, are exclusively found on serpentine soils. Similar restricted distributions and remarkable floristic associations are also found in serpentine areas of the Mediterranean region, Africa, Australia–New Zealand, and parts of Southeast Asia. Over 500 serpentine-associated species accumulate metals from the soil. Studies of metal hyperaccumulators (i.e., plants that accumulate at least more than 100 times the concentration found in a normal plant) of serpentine soils have not only led to the discovery of novel physiological pathways and their underlying genetic bases, but have also laid the foundation for the development of innovative technologies such as agromining, which uses hyperaccumulators to extract heavy metals from contaminated soils.

Gypsum ($CaSO_4 \cdots 2\,H_2O$), a substrate formed by the evaporation of saline waters, is also widely known for its distinctive indicator flora. The plant response to gypsum (gypsophily) manifests itself as unique communities consisting of gypsophilic endemics. While gypsum-associated plant communities are found in parts of Europe and coastal Southwest Africa (e.g., Namibia, South Africa), deposits in xeric areas of southwestern North American and adjacent Mexico are especially noted for their unique species composition. Gypsophiles (gypsum endemics) accumulate elements found in excess on gypsum soils (S, Ca, and Mg) in their leaves, while gypsovags (widespread species also found on gypsum) seem to block the uptake of these elements at the root

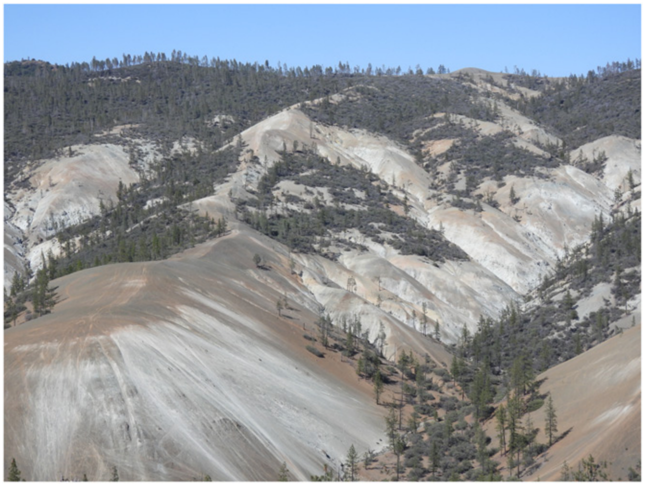

Fig. 4 Barrens of New Idria Serpentinite Mass, Clear Creek Management Area, San Benito County, California, U.S.A. The highly pulverized natural (undisturbed) serpentinite exposures on these steep, open, rolling hills are prone to erosion yet are home to several serpentine-endemic and rare species. Credit: N. Rajakaruna

Fig. 5 Sodic, vertic clay-adapted annual plant community of Cantua Creek, western Fresno County, California, U.S.A. Strong contrasting differences in soil depth and chemistry at fine spatial scales across this desert landscape create a high diversity of edaphic niches. Each native annual plant species has a narrow fundamental edaphic niche and dominates in that specific niche, creating a dazzling rainbow display of color. Non-native annual grass invasion results in a smaller realized niche for each native annual plant species and the color intensity (native annual abundance) is reduced. Purple = *Phacelia tanacetifolia*, Dull Orange = *Amsinckia furcata*, Bright orange = *Eschscholzia hypecoides*, Dull Yellow-Green (left) = *Deinandra halliana*, Blue = *Phacelia ciliata*, Bright Yellow = *Madia radiata*. Credit: R. E. O'Dell.

level, resulting in lower foliar concentrations. Gypsophiles have specific adaptations related to water and nutrient use that enhance plant fitness on these harsh soils.

Limestone, formed by precipitation and lithification of $CaCO_3$, also leads to the formation of unique plant communities globally. In fact, some of the earliest observations on edaphic-plant relationships were made on limestone landscapes and, by the late twentieth century, studies of limestone plant ecology had yielded a plethora of published work in North America and Europe. Limestone and associated materials such as dolomite ($CaMgCO_3$) have exerted a profound influence on regional floras across the world resulting in unique vegetation compositions. Of interest are those temperate formations found on the White Mountains of eastern California (U.S.A.), Mount Olympus (Greece), the European Alps, and tropical formations of Jamaica, Cuba, Turkey, and parts of Africa and Asia, including the limestone karsts of China and southeast Asia.

In addition to habitats formed on geological substrates with extreme chemical compositions, other edaphically influenced habitats, such as barrens, mine tailings, guano-rich bird nesting rocks, coastal bluffs, alkaline flats, solfatara fields, sodic vertic clays (**Fig. 5**), sand dunes, granite inselbergs, and vernal pools are also important sites that harbor unique communities of plants, microbes, and animals.

Evolution Under Extreme Edaphic Conditions

Plant species or distinct populations belonging to certain species can often be distinguished by their fidelity to particular edaphic conditions (**Fig. 6**). Plants that grow on chemically or physically extreme substrates are often derived from populations found off such substrates, suggesting the role extreme soil conditions can play in generating plant diversity. Influential work conducted during the mid-twentieth century on the grasses of heavy metal-contaminated mine tailings provides a classic demonstration of the role natural selection plays in maintaining diversity. This work, and subsequent studies on many plant species, demonstrated that populations can evolve tolerance to extreme edaphic conditions and that this may lead to reduced gene flow between the ancestral population and the divergent, edaphically specialized population. Such reproductive isolation, followed by further divergence, lays a foundation for the origin of new plant species. Plants that have either evolved *in situ* (i.e., neoendemics) or those that have had broader distribution but are currently restricted to extreme substrates (i.e., paleoendemics) are examples of edaphic endemics. While most plant species can be found growing in a range of edaphic habitats, it is these edaphically specialized taxa and their ancestral species that have attracted the attention of plant physiologists and evolutionary ecologists alike.

Edaphic endemics provide a model system to examine the process of plant evolution, from adaptation and reproductive isolation to genetic divergence. Closely related species pairs are often distinguished by their distinct edaphic preferences. Such pairs can be found on adjacent yet contrasting soils formed naturally due to variation in parental rocks or by anthropogenic acts such as quarrying, mining, and even by depositing chemical waste in landfills. The process of divergence might proceed as follows: some individuals of a species have genetically determined traits that allow them to successfully survive in adjacent, chemically harsh soils. These individuals could become founders of a distinct population characterized by their tolerance to the extreme edaphic condition. Such a transition to a new habitat, if accompanied by a reduction in gene flow, can bring about full-fledged speciation. Evolution of tolerance to extreme conditions can occur quite rapidly, even within a few generations. Therefore, edaphic specialists

Fig. 6 An edaphically controlled vegetation boundary at Jasper Ridge Biological Preserve, San Mateo County, California, U.S.A. The yellow-flowered *Lasthenia californica* and *L. gracilis* (Asteraceae) are restricted to serpentine soils. The sharply demarcated boundary between *L. californica-L. gracilis* and grasses is defined by a serpentine-sandstone transition. A more 'invisible' yet sharp boundary also exists between *L. californica* and *L. gracilis*, with *L. gracilis* only in the upper reaches of the outcrop (dry serpentine soils) and *L. californica* restricted to the bottom swale (wet, ionically-rich serpentine soils). Credit: Bruce A. Bohm.

are model organisms to explore the genetics of adaptation as well as speciation. Current phylogenetic analyses suggest that edaphic specialists may be suitable candidates for the study of parallel (or repeated) evolution of functional traits, as well as traits contributing to reproductive isolation. When changes in traits conferring edaphic tolerance are associated with changes in traits associated with reproductive compatibility, a case for parallel ecological speciation can be made.

Climate Change and Edaphic Specialists

How a changing climate may influence edaphic specialists is an area of active research. Will changes in temperature and precipitation further restrict the distribution of edaphic specialists due to increased competition from other taxa, or will they expand their ranges, if preadaptations to drought, high temperature, or other abiotic stressors render them more competitive under a novel climate? Climatic and edaphic factors interact to control local adaptation and substrate endemism. For example, serpentine endemism is highest in wet regions in California, U.S.A., likely resulting from increased competition on 'normal' substrates under climates that are more favorable for plant growth. At the community level, there is also more species, functional, and phylogenetic turnover across edaphic boundaries in mesic relative to arid regions of California.

Climate change will clearly have differential effects on the ranges of edaphic specialists, and predicting how each species may respond to the multitude of climatic variables (and other biotic interactions) they experience is challenging without species-specific experimentation. Moreover, numerous climatic factors need consideration—precipitation, temperature, wind, and CO_2 levels; as well as atmospheric deposition of toxic pollutants and nutrients. Designing experiments to explore the synergistic effects of the multitude of climatic stressors is challenging and findings may not universally apply across different plants, geographic regions, or soil-plant associations.

Given the high diversity of edaphically-specialized species across all climatic regimes, particularly in Mediterranean and tropical climes, it is critical that species distribution models used in the prediction of climate change responses of plants incorporate edaphic factors. However, as soil physical and chemical features are often not mapped at a high enough spatial resolution, models can lead to inaccurate predictions. Additional work is necessary to investigate best approaches to climate change response, including the feasibility of assisted migration (or conservation translocation) for highly restricted species with limited dispersal abilities or those with suitable soil habitats that are far beyond their usual dispersal distances.

Conservation of the Biota of Extreme Geologies

Habitats on extreme geological substrates, from natural outcrops of serpentinite rocks to habitats resulting from anthropogenic activity, harbor unique species assemblages. Unfortunately, ever-expanding agriculture, forestry, mining activity, and urbanization have drastically affected the biota of many disturbed areas with unusual geology. Plants associated with heavy-metal-rich rock types (i.e., metallophytes) are not merely biological novelties—they are the optimal choice for the restoration of metal-contaminated sites across the world. Phytoremediation is a growing field that uses metal-hyperaccumulating plants in the remediation of metal contaminated sites. More recently, agromining, the use of metal-hyperaccumulating plants to extract metals, metalloids, and rare earth elements from soils at an agricultural scale, has also received much attention, with experimental 'metal farms' now in operation in Albania, Greece, and Malaysia. The raw material for such green technologies is species found naturally on extreme rock types such as serpentine outcrops, pointing to an immediate need for the conservation and detailed study of these habitats. Fortunately, recent years have seen the declaration of some preserves, set aside primarily due to their unique edaphic habitats and associated biota. Although they are spotty in their distribution and inadequate in number on a global scale, several preserves in the U.S. states of California, Oregon, Maine, Maryland, and Washington, in the Province of Québec in eastern Canada, and in New Zealand, Italy, Sri Lanka, and South Africa, have led the way in raising awareness of the immediate need for the conservation of these unique biotas. For example, Mount Kinabalu on the Island of Borneo, Malaysia is a UNESCO Geopark, set aside for the conservation of many serpentine endemic species, including pitcher plants and orchids, as well as nickel hyper-accumulating species. Other examples are the Sesia Val Grande UNESCO Global Geopark in Italy and Barberton Makhonjwa Mountains UNESCO World Heritage Site in South Africa. There has been an urgent plea from those associated with research on metallophytes, advocating the prioritization of future research needs for the conservation of metallophyte diversity as well as the sustainable uses of metallophyte species in restoration and remediation of contaminated sites worldwide, as well as for agro-mining to extract much-needed metals such as nickel and scandium via the use of metal-hyperaccumulating plants.

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