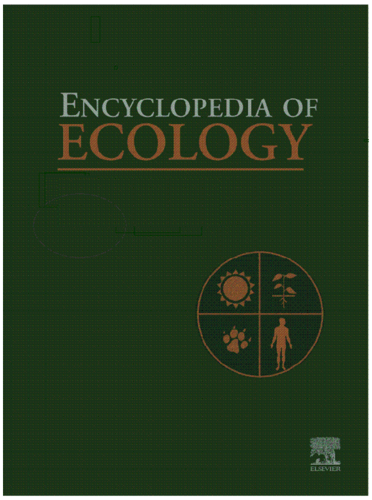

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Edaphic Factor

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Introduction

This article describes the important roles geology and soil conditions play in the ecology and evolution of plant species and their associated biota. We seek to: (1) describe the edaphic factor as a life force responsible for generating and maintaining unique species assemblages and (2) emphasize the importance of conserving habitats with extreme edaphic conditions because of their biological diversity. First, we describe the edaphic factor: its definition and role in shaping the biotic world. Then we review our current knowledge of the ecology of unusual geologies, focusing on studies performed within and across biotic kingdoms. Further, we examine the process of plant evolution on extreme geologies, an area that has generated much interest among evolutionary biologists in the last few decades. Finally, we cover the applied ecology and conservation of plants and other biota restricted to unique geologies.

The Edaphic Factor: Its Role in Shaping the Biotic World

Ecologists have long noted the importance of geology in the global and regional distribution of organisms. Life, ranging from macro- to microscopic, exists on and within a mosaic of geologies that vary across both space and time. The contributions of geologic phenomena to maintaining and generating biotic diversity are twofold. First, large-scale geologic events (e.g., continental drift and rising of mountains) create discontinuous or patchy landscapes. Second, within this patchwork of landscapes, parental geologic materials such as igneous, metamorphic, or sedimentary rocks can become exposed, leading to the development of soils differing in chemical and physical characteristics. This creates opportunities for colonization and differentiation of species. The edaphic factor pertains to physical, chemical, and biological properties of soil resulting from these geologic phenomena. Discontinuities in the edaphic factor have contributed to the intriguing patterns of diversity we see in the biotic world. Edaphology is a branch of soil science that studies the influences of soils on organisms, especially plants. It includes agrology, the study of human uses of soils for agriculture, as well as how the features of soils affect human land use decisions.

According to soil ecologist Hans Jenny, soils owe their distinct characteristics to five interacting factors: climate, organisms, topography, parental rock, and time. If all but one factor (e.g., parental rock) remain unchanged, then variation in a soil body can be attributed to that one factor. Botanists have long recognized that the distribution, habit, and composition of vegetation are greatly influenced by the edaphic factor. The striking effects on vegetation of unusual and often extreme substrates (e.g., serpentine, limestone, dolomite, shale, gypsum) are apparent even to amateur naturalists. Whereas climate broadly defines major biomes (e.g., tropical rainforests, temperate deciduous forests, deserts, tundra), it is geology that enriches diversity within these zones. The role played by the edaphic factor in the distribution of plant species was keenly observed and recorded by many eighteenth- and nineteenth-century plant ecologists, who considered soils second only to climate as the major ecological determinant of plant distribution. It was in the twentieth 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 obtain nutrient elements and water from soil. Thus, soil features that affect the availability and uptake of nutrients and water are of great importance to plants. Below is a brief overview of the soil features that most greatly affect plant growth.

Texture

Mineral particles in soils can be classified on the basis of their size (diameter). Clays are very small (<0.002 mm) particles, silts are larger (0.002–0.05 mm), and sands yet larger (0.05–2.0 mm). The percentage of each of these major particle classes soil determines the texture of a soil. Textures range from those predominantly containing one of the three major particle sizes and thus named for them (silt, sand, clay textures) or various intergradations (sandy clay, etc.). One major textural class (loam), which is ideal for plant growth, is not named for a predominant particle class because loam soils have similar amounts of all three particle classes. Texture is important for plant growth because it influences water availability and soil fertility, that is, the ability of a soil to supply nutrients to plant roots. Open spaces among soil particles represent the pore space of a soil. This pore space may be filled by water, air, or plant roots. Thus, the amount of pore space greatly influences the amount of water that a soil can contain. The tightness with which water is held in pore spaces determines whether or not the 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 large pore spaces that do not hold water tightly enough to prevent gravity from pulling that water into deeper soil layers. Very fine textured soils (e.g., clay soils) have very small pores. Small pores hold water strongly and thus retain much water despite the pull of gravity. However, they also hold water against the pulling power of plant roots and so provide only small 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 essential for plant growth. Soils with higher percentages of clay or silt particles generally have a greater CEC.

Structure

The three-dimensional arrangement of soil particles gives rise to soil structure. In many soils, groups of particles are held together to create lumps of soil materials termed peds. The space between peds can be important in allowing penetration of water and roots to 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 especially true for tall woody plants (e.g., shrubs, trees). A classic example of the influence of soil depth on plant communities is seen on granite rock outcrops in the southeastern US. As the granite weathers, it can form pools of soil that vary in depth from a few millimeters at the margin to tens of centimeters in the middle. The shallow marginal soils support certain annual plants, whereas deeper soils support herbaceous perennials and still deeper soils are colonized by woody plants. Plant zonation in these soil pools can be striking (**Figure 1**). Some soils can develop special soil horizons (horizontal soil layers characterized by distinct chemical and physical features) that limit the soil depth available to support plants. These special soil horizons include claypans, zones of soil which contain large amounts of clay, and hardpans, layers of soil particles that have been cemented together by the deposition of mineral materials. Hardpans include calcic horizons (commonly called caliche), in which calcium carbonate cements the soil particles. 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 in which large amounts of water are present.

Organic matter

Organic matter in soils ranges from recognizable plant parts (roots, leaves, stems) to humus, which is partly decomposed plant material that is amorphous and spongy in nature. Organic matter contributes to a soil's ability to retain nutrients and water (i.e., soil's CEC). It aids in holding nutrients because negatively charged compounds in humus attract and hold positively charged plant nutrient ions. It helps provide water because humus can absorb 80–90% of its weight in water and therefore contributes to a soil's ability to hold water under drought conditions.

(a)

(b)

Figure 1 (a) A small soil pool (about 2 m wide) on a granite outcrop in east-central Alabama. Shallow soil at the margins is dominated by lichens. The deepest soil in the center of the pool has been colonized by *Senecio tomentosus*, 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: Jenny 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 *Senecio tomentosus*. Credit: R. S. Boyd.

Organic matter in soils is also an important food source for decomposer and detritivore organisms. Organic matter also contributes to soil color, a factor that affects a soil's thermal properties.

pH

Soil pH is an extremely important ecological parameter. Its most important effect on plant growth is its influence on ion availability in the soil solution. Ions in soils are important for two major reasons. One is that many soil ions contain elements required for plant growth. These elements, called essential nutrients, are primarily obtained from the 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 influence of pH on ion availability stems primarily from the influence of pH on the solubility of the various compounds present in the soil. In general, soil compounds containing some elements are more soluble at some pH values than others. For example, iron is relatively insoluble at pH values of 8 or greater and plants with a high iron requirement may perform poorly in soils with high pH values. Similarly, many heavy metals become increasingly available for plant uptake at pH values of 4–5. Thus, plants growing in low pH soils are more susceptible to heavy metal toxicities.

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) or those that build up in desert soils from evaporative concentration of relatively freshwater (e.g., the Great Salt Lake of Utah). Extensive irrigation of land in regions where there is high evapo-transpiration can also lead to accumulation of salts on the soil surface (i.e., secondary salinization). 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 specific ion effects. Water uptake can be slowed because the high ion concentration in the soil impedes water movement into plant roots. Nutrient uptake can be affected because 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 Ecology

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 features (extreme pH, nutrient imbalances, limited depth, etc.) may be a strong selective force shaping plant evolution. The floras of many unusual soils (serpentine soils, limestone soils, etc.) have at least some taxa that are found only on those soil types, whereas other species may evolve locally adapted populations (ecotypes, races, etc.). In many cases such taxa or populations have evolved in response to particular features of those soils. In other cases, unusual soils may be refugia for taxa that are unable to compete with species that dominate 'normal' soils.

The ability of soils to affect ecology or evolution of organisms other than plants is less well known. It is also less likely for many animals, in part because their mobility and aboveground lifestyle render them less influenced by the various properties of soils. One soil feature that in specific cases has been shown to directly influence animal evolution is soil color. In habitats with little vegetation, such as deserts and beaches, the color of some animals has evolved to match the color of the soil. For example, white gypsum dunes, for which the White Sands National Monument in New Mexico is named, host a number of animals that are notably lighter-colored 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 fall victim to predators. The evolution of burrowing and soil-dwelling animals is more likely to be influenced by soil properties due to the greater intimacy of their life histories with those soil features.

These direct effects of soils on biota are supplemented by a variety of indirect ways that soils may influence either 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 endemic to heavy metal-rich serpentine soils harbor unique insect herbivores that are specialized to deal with the high metal concentrations found in the plant tissue (Figure 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, aspen trees suffer significant gopher-caused mortality on deep meadow soils but not on rocky outcrops where pocket gophers do not occur due to the lack of soil deep enough for them to make tunnels.

Figure 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 make up relatively large areas. At this level of ecological scale, the pattern of soil types on a landscape may have important ecological consequences. One of these consequences is diversity (species richness, evenness). In a sense, patches of one soil type in a matrix of another are like islands in the sea (Figure 3), and thus can be subjected to the ideas of Island Biogeography. Island Biogeography holds that the number of species present on an island is primarily determined by the size of the island and by its distance from sources of colonists. Thus, relatively small patches of unusual soils (i.e., edaphic islands) that are far from similar patches would be expected to have fewer species than large patches close to other areas of similar soils. This has been confirmed by recent studies of the flora on patches of serpentine soils in California.

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

Figure 3 Edaphic islands of serpentine outcrops in the Klamath Siskiyou Mountain range in northern California. The relatively barren serpentine outcrops (bare patches with reduced vegetation cover) are embedded in a mosaic of other geologies more favorable for plant growth. Credit: N. Rajakaruna.

soils are an important factor of the environment of 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 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. Recent studies suggest that vehicle emissions along major highways in California may have increased the nitrogen content in serpentine soils. Non-native species, previously excluded from such soils due to nitrogen limitation, could potentially invade these unique habitats.

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 northwestern US, diffuse knapweed (*Centaurea diffusa*; Asteraceae) has a direct soil-mediated impact on competing native plants. This invasive plant 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 but have been introduced in many locations. By consuming soil litter and accelerating its breakdown, these animals increase soil compaction, decrease water penetration, and change 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. Such conditions also foster distinct morphological and physiological modifications leading to characteristic plant communities. One of the most remarkable edaphic habitats in which such unique plant communities are found is 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 found throughout the world, concentrated, however, along continental margins and in regions of orogenesis (i.e., mountain building). Serpentine soils are unique in that they are often high in pH and heavy metals such as magnesium, nickel, and chromium, and generally low in essential nutrients, Ca/Mg ratio, and water-holding capacity. The rocks are often on open, steep slopes exposed to high light and heat conditions, and resulting soils are generally shallow and highly erodable (Figure 4). The serpentine syndrome, the unique biological effects manifested by these extreme geoedaphic conditions, has led to research on plant physiology, ecology, and evolution in many parts of the world. Serpentine soils, although covering a mere few percent of the Earth's surface, host many endemic species. In the Californian Floristic Province, for example, 198 out of 2133 taxa endemic to that province are wholly or largely restricted to serpentine. Tropical islands of New Caledonia and Cuba provide even better examples of plant restriction to serpentine soils. In New Caledonia, 3178 taxa, roughly 50% of the native flora, are endemic to serpentine soils while in Cuba, 920 species, one-third of the taxa endemic to Cuba, have developed solely on serpentine soils. Similar restrictions and remarkable floristic associations are also found in serpentine areas of the Mediterranean, Africa, Australia–New Zealand, and Asia. Studies of metal hyperaccumulators (i.e., plants that accumulate at least 0.1% of their dry leaf weight in a heavy metal) 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 phytoremediation (i.e., the use of hyperaccumulators to extract heavy metals from contaminated soils).

Figure 4 Serpentine hills of Clear Creek Management Area, San Benito County, California. Serpentine exposures on these steep, open hills are prone to erosion. Credit: N. Rajakaruna.

Gypsum ($CaSO_4 \cdot 2H_2O$), 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, deposits in xeric areas of the American southwest and adjacent Mexico are especially noted for their unique species composition.

Limestone forms by precipitation and lithification of $CaCO_3$, also leads to the formation of unique plant communities. In fact, some of the earliest observations on edaphic-plant relationships were made on landscapes overlying limestone and, by the late twentieth century, studies of limestone plant ecology had yielded a plethora of published work in both 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, Mount Olympus of Greece, the European Alps, and tropical formations of Jamaica, Cuba, Turkey, and parts of Asia.

In addition to habitats formed on geologies with extreme chemical composition, other edaphically influenced habitats, such as savannas, barrens, guano-rich bird nesting rocks, coastal bluffs, alkaline flats, and vernal pools are also important sites that harbor unique communities of plants and animals.

Evolution under Extreme Edaphic Conditions

Plant species or distinct populations belonging to certain species can often be distinguished by their faithfulness to particular edaphic conditions (Figure 5). 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 work on many plant species, demonstrate 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, sets the 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 called edaphic endemics. While most plant species can be found under 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.

Figure 5 An edaphically controlled vegetation boundary at Jasper Ridge Biological Preserve, San Mateo County, California. The yellow-flowered *Lasthenia californica* (Asteraceae) is restricted to serpentine soils. The sharply demarcated boundary between *L. californica* and grasses is defined by a serpentine-sandstone transition. Credit: Bruce A. Bohm.

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 depositing of 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. Current phylogenetic analyses provide strong support for rapid evolution of edaphic specialists as recently illustrated for the species pair *Layia glandulosa*–*L. discoidea* (Asteraceae).

Conservation of the Biota of Extreme Geologies

Habitats on extreme geologies, from natural outcroppings of serpentine rocks to barrens resulting from anthropogenic activity, harbor unique species assemblages. Unfortunately, ever-expanding agriculture and forestry, mining activity, and urbanization have drastically affected the biota of many areas with unusual geologies. Plants associated with heavy-metal-rich geologies (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. The raw material for such endeavors comes from species found on extreme geologies 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 several 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 states of California, Oregon, and Washington, in the Province of Québec in eastern Canada, and in New Zealand and South Africa, have led the way in raising awareness of the immediate need for the conservation of these unique biotas. There has also 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.

See also: Endemism; Island Biogeography.

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Edge Effect

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To consider 'edge effect', one must have a definition of an edge. Edges in ecology are frequently represented by a physical transition from one kind of habitat to another (**Figure 1**). The physical attribute of this edge may be manifested in habitat metrics such as density, size, color, texture, and salinity. Often edges are in the eye of the beholder; that is, an apparent edge between two habitats may be organized at one scale for a human, but at an altogether different scale for, say, a vole – which would arguably detect habitat gradients and edges at finer resolutions and shorter distances than the human. Therefore, as one considers the effect of edge, such consideration is inextricably bound up in scale, and, therefore, requires careful definition of the components of scale (resolution of examination and extent of the edge in question).

The reasons to carefully consider edges and their effects are manifold. These boundaries or transitions from one unit of organization (e.g., habitat, community, ecosystem, depending on your scale of choice) to another often exhibit high levels of species richness or biodiversity and perhaps, most importantly, may be sensitive sentinels of environmental change. These transitional areas, which are also commonly called ecotones, often reveal species composition, structure, and function representative of the unit of organization as compared with the adjacent area as well as having their own unique array of species and characteristics (e.g., species diversity, population dynamics, local extinction rates, sediment geochemistry, and soil processes, to name a few). Moreover, edges are often important controls over a range of ecosystem processes. These boundaries influence the structure and function of landscapes serving as a sort of valve, regulating ecological processes across a wide range of temporal and spatial scales. As in all branches of ecology, choice of