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Author(s): Arthur R. Kruckeberg
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An Essay: The Stimulus of Unusual Geologies for Plant Speciation

ARTHUR R. KRUCKEBERG
Department of Botany, University of Washington, Seattle, Washington 98195

"Within a given climatic region, the growth of vegetation is mainly determined by the character of the parent material, whether limestone, igneous rock, sand deposit or clayey shale."

Hans Jenny (1941)

ABSTRACT. Though a region’s climate sets the limits for a biota, geology enriches local discontinuity and habitat diversity. When slope, exposure, and physical and chemical properties of rock and soil are arrayed discontinuously, the opportunities for events leading to speciation can occur. Several scenarios can account for evolution in geologically diverse landscapes. They range from ecotypic differentiation and disruptive selection to saltational speciation. I draw upon evidence from microevolutionary response to heavy metals and from serpentine endemism. The western North American genus Streptanthus (Cruciferae), with a number of serpentine endemics, illustrates the possible modes of evolutionary diversification on this demanding substrate.

Imagine a world of life without mountains, valleys, rivers, and all the other topographic intricacies of interesting landscapes. Further, conjure up a world without a mosaic of lithologies—an absence of a mix of sedimentary, metamorphic, and igneous rocks, rich in variant chemical and physical attributes. Without a wealth of geological diversity, the only physical variable on the planet might be the continuous change of climate from poles to equator. Life would then have evolved a dull continuum of response in its tracking of gradual climatic change across a monotonous landscape. But the real biosphere is rich in organic diversity, and much of that diversity, I contend, comes form the wealth of geologic phenomena, expressed through time and space.

The ingredients of the variables fashioned out of geology run the gamut from global events like plate tectonics and the drift of continents to regional and local diversity created out of variant topographies and lithologies. Crucial to the argument that geological diversity begets biological diversity, is the realization that geological events and materials are often arrayed discontinuously. It is this discontinuity that sets the stage for speciation; without isolation, much of the world’s discrete biota—as species—could not have come into being.

The diversification of habitats that can flow from differences in land forms and rock types then becomes the stimulus for evolutionary diversification by speciation. This notion can be conceptualized by paraphrasing Hans Jenny’s (1941) factorial equation for soil formation: $s = f(c_I, o, r, p, t)$. Soil formation is taken as a function of the five independent variables: climate, organisms, topography, parent materials (rocks), and time. Jack Major (1951) adapted the formulation to account for the genesis of vegetation, $v = f(c_I, o, r, p, t)$. I propose taking Jenny’s functional, factorial approach one step farther, to account for plant species diversity in any region. The factorial equation for botanical (or biological) diversity now would read, B.D. = $f(c_I, o, r, p, t)$. Of course, adapting the Jenny equation to biotic diversity has its pitfalls. The most serious omission is the genetic factor. Without the generation of continuity and variety by genes, the biotic diversity, though stimulated by environmental variables, cannot be realized, let alone maintained. For biotic diversity, the equation may call for another independent variable, heredity.

Whether applied to soils, vegetation, or to species diversity, the formulation depends on the action and interaction of the five environmental variables, all of which are under the influence of geological processes and states. Though it is obvious that parent material (p, or rock type) and topography (r) are geological in origin, it can also be argued that the other variables are under the influence of geology. Local climates, though limited by the regional climate, are generated by diverse topographies. And of course, microclimates are the direct
consequence of physiographic differences. The time factor, $t$, puts limits on the start and duration of geological and other processes. But how can one argue that the biotic factor ($o$, organisms) has a geological connection? Other organisms that can influence the course of speciation, had in turn their origins conditioned in part by geology. In a word, I contend that geology begets biotic diversity.

As Jenny pointed out for the process of soil formation, his equation heuristically leads to the analysis of process. By holding all factors but one constant, one can test the effect of variant states of the one variable on the process. In our derived form of the equation for biological diversity, the same prospect for controlled analysis exists.

The significance of geological phenomena for organic diversity has not escaped the attention of biologists. The classic generalizations (some say principles or "laws") on the distribution of plants (Cain 1944) place the edaphic factor (broadly taken here as "geo-edaphics", to include soils, geology and topography) second only to climate as the major environmental determiners of plant distribution. Certainly, manuals of regional floras pay tacit homage to edaphic diversity by describing the habitats and ranges of taxa. But acknowledging the profound influence of geoedaphics on diversity is mostly done after the fact. The array of species in all their unique and discrete habitats begs for causal explanation. How does the organic world take advantage of habitat diversity? This evolutionary question can be subjected to analysis in the context of the processes and events of speciation. In anticipation of how speciation is affected (and effected) by geoedaphics, we first look at the nature and effects of those stimuli of speciation generated by geological phenomena.

**The Nature and Kinds of Geological Stimuli for Plant Speciation**

In the functional equation for biotic diversity, $B.D. = f(cl, o, r, p, t)$, three independent variables constitute the major geological influences: topography, parent material, and time. Especially significant for plant speciation, and the elaboration of diversity, is the commonplace reality of the **discontinuous array** of land forms and rock types. Mountain tops, slopes of different aspect, valleys, marshes, alluvial fans, all are separated one from another; and rock types like granites and serpentines can be isolated by intervening sediments or lavas. It is this patchiness or discontinuity of edaphic phenomena that creates a further impetus for biological discontinuity—i.e., speciation.

**Topography and its spatial distribution.** Geological events and processes shape the land, discontinuously. Most evident is the isolating effect seen in mountains; all their various attributes (slope, exposure, elevation, intervening valleys and canyons, etc.) provide an abundance of discrete habitats. Summits of peaks within a mountain system as well as disjunct mountain ranges separated in space are classic spawning grounds for speciation. The isolated volcanic peaks of the Cascades and the separate but parallel desert ranges of the Great Basin illustrate the between-range aspect of isolation.

Other features of land form carve up space discontinuously. Bodies of water, from oceans to lakes and rivers can be potent barriers or sources of isolated habitats. Perhaps the most spectacular discontinuities in land form are islands, especially oceanic. Indeed islands have yielded their own unique evolutionary-ecological theory—*island biogeography.*

**Parent materials, especially rock types.** Rock types exert a selective action on plant life in diverse ways, both direct and indirect. Frequently, especially where outcrops are exposed at the surface, they can act as direct substrates for plants. Color, texture, repose (position via slope, exposure), and chemical composition then can influence the growth of plants. More often, though, a given rock type is translated into a soil by weathering. The derived soil will bear the imprint of its parent material, as features of texture, clay content, water holding capacity, base exchange capacity, and the quality of the mineral ions themselves. It is the difference in these rock and soil factors that can provide unique edaphic habitats for plants, often in discontinuous array.

The effect on plants of sharply contrasting edaphic states is well known. Botanists have long recognized the striking effects of such azonal substrates as limestones, dolomite, shales, gypsum, and serpentinite (fig. 1). They have been found to harbor unique plant associations, endemic species, and to foster morphological and physiological modifications of
plants, as well as unusual distributions of taxa. See Krause (1958), Kruckeberg (1969, 1984), and Proctor and Woodell (1975) for reviews and references.

But not all lithologies have such dramatic, highly visible effects on florals. Zonal soils, derived from parent materials as diverse as granites, sandstones, basalts, schists, etc., usually are normal in the sense of balanced mineral content and optimal (non-extreme) physical characteristics. Yet the effect of these zonal soils on plant-life may simply be more subtle. Less extreme differences in chemical and physical properties may still have a selective action on the biota. Far less is known about the biological effects of contrasts between normal (zonal) substrates where they are proximate in space. Though the agronomic literature abounds with examples, much less is recorded on the effects of such substrates on indigenous florals. The agricultural literature on edaphic differences is biased towards contrasts between alluvial soils, often admixtures of different upland lithologies and soils. Where the botanist can discover the direct biotic consequences of subtle rock and soil differences is on normal upland substrates, formed in residuum. The mountains of western North America offer such contrasts in abundance. Witness the Sierra Nevada of California where lavas and granites commingle, or the North Cascades with their wealth of igneous and metamorphic rock diversity.

Timing of geological processes and events. The vector of time manifests itself on the geologic phenomena that in turn influence plant life in many ways and in varying magnitudes. The effects of duration range from global and regional influences (continental drift, tectonism, vulcanism, glaciation) down to the more short-term local manifestations (advance and retreat of glaciers, local vulcanism, active fault zones, mass-wasting of rock and soil, changes in water courses, etc.). Time becomes critically operative for biota when a geological process runs its course in the biosphere, not deep in the earth’s mantle or crust. As examples, the student of speciational events wants to know how long a montane “rain-shadow” has been in place, how long a serpentine outcrop has been available for colonization, how long the Columbia Basin lavas have been continually receptive to biotas? The greater the time span of any such sur-
ficial geological processes, the longer the time frame for enacting the speciation steps leading to organic diversity.

Jenny’s (1941) original equation for soil formation brings the time factor in focus. By setting time to equal zero, the course of changes in other variables like topography or parent material can be followed. We now have a precisely recorded reference point of time = 0 in the Pacific Northwest, with the eruption of Mt. Saint Helens. Among the changes in plant life that could flow from this disturbance are incipient events leading towards speciation.

**Scenarios on Speciation as Influenced by Geology and Edaphics**

Modern evolutionary theory has elaborated a wealth of modes of speciation. The full range of kinds of speciation can be found in the books by Dobzhansky et al. (1977), Futuyma (1979), Grant (1981), Stebbins (1974), and White (1978). Most kinds of species formation are variants on the neo-Darwinian paradigm: genetic variation arises and is recombined in populations, some of which is preserved by chance or direction (selection); when the preserved variants become arrayed discontinuously, such isolation can lead to the genesis of new species. Selection, combined with isolation can be induced by both physical and biotic factors of the environment. The geodaphic factor, as a potent source of species diversification, is one physical factor singled out of the rest for scrutiny in this essay.

First off, can we find any speciation sequences that are unique to the stimulus of the edaphic factor? So far as I can detect, no new species-forming processes emerge. The body of evolutionary theory appears to be rich enough to account for the variety of origins of distinct lineages arising from the manifold effects of geology. In fact, what follows will be a recounting of the widely accepted stages in the diversification of plants from the origin of variation and its fixation, to speciation and adaptive radiation. At each stage, the effects of geodaphics will be the focus.

*Variation and the edaphic factor.* There is substantial evidence that populations have both the potential—by being preadapted—to tolerate unusual edaphic situations and often do become tolerant to them. The evidence comes from studies on the evolution of tolerance to heavy metals of mine areas (Antonovics et al. 1971) and from work on the ecotypic variation in tolerance to serpentine soils (Kruckeberg 1951, 1967). The research on heavy metal tolerance has demonstrated clearly that some species have the requisite genetic preadaptedness to venture successfully onto soils contaminated with toxic heavy metals (Antonovics et al. 1971). This capacity seems no different than that of any population faced with a new environmental challenge. Either the genetic potential for accommodation exists or it does not. Houseflies do it in the presence of DDT, bacteria do it in the presence of antibiotics, and presumably all other biota that have spread into new habitats started with an initial preadapted genotype.

Tolerance to serpentine (ferromagnesian) soils appears to start in the same way. I found that of all the species tested, only *Achillea millefolium* had in its non-serpentine populations, some preadaptation to serpentine, especially when the non-serpentine race came from areas close to serpentine (Kruckeberg 1951, 1967). The preadaptation of such racial variants may have come about via gene flow from the nearby serpentine-tolerant race.

*Natural selection and the edaphic factor.* Edaphic conditions, particularly when manifested in extreme form, must be potent agents of selection. This statement has to be rendered in a tentative, “must-be” form, for usually there is no evidence that a plant adapted to a substrate, began its odyssey as a favorably selected variant from a largely non-adapted population. For example, limestone, gypsum, and serpentine species are presumably the results of, in part, natural selection. But having long since passed through the formative stages, the evidence for their having arisen via selection is only circumstantial. Populations that achieve tolerance to heavy metals come the closest to revealing natural selection in action, since their origins are so recent. Disruptive selection across a heavy metal-to-normal soil contact can be abrupt, can be strong in selective intensity (s = ca. 1.0) and can produce phenotypically clear-cut genotypes. Moreover, genetic accommodation to a heavy metal environment can be rapid, within a few generations, and can closely track the presence of the toxic heavy metal. The extensive literature on the genetics of heavy metal tolerance is reviewed in Antonovics et al. (1971),

It seems reasonable to expect that adaptation to other extreme edaphic situations could follow the heavy metal route: a few preadapted genotypes could become the founders of a tolerant population. For the nutritionally adverse soils weathered from serpentine and other ferromagnesian rocks, I have detected a comparable route to achieving tolerance. Recently introduced weeds that have accommodated to serpentine, suggest genetic preadaptation followed by rapid spread on serpentine. *Prunella vulgaris* and *Rumex acetosella* are two examples where the local serpentine populations have become fully tolerant only since they were introduced following disturbance by man. Nearby genotypes on non-serpentine soils are not tolerant (Kruckeberg 1967). The case of *Achillea* races, mentioned earlier, is less determinate, since some individuals of non-serpentine populations close to serpentine outcrops may show tolerance to serpentine.

Isolation and geodaphics. The most significant causes of local and regional taxonomic diversity are traceable to the isolating effects of discontinuities in geology and edaphics—geodaphics. Discrete populations come into being and in their isolation can diverge further to achieve the state of distinct species. There are undoubtedly several levels of isolation and in turn they can be achieved in several ways. The geodaphic isolates may range from distinct genotypes within species, through detectable local populations or races, upward to uniquely edaphically endemic species or even higher categories.

More than one mode of origin of the edaphic isolates can be envisioned (Stebbins 1942, 1980; Kruckeberg 1984). Two alternative pathways to speciation are open to populations faced with a geodaphic challenge: 1) gradual or abrupt speciation at the diploid level, and 2) abrupt speciation via allopolyplody. Divergence leading to speciation at the diploid level may proceed along different pathways. Figure 2 illustrates the possible pathways; each stage may be an endpoint for a particular population—the scenario need not be played out to its full conclusion. What is more, we can find each stage exemplified in nature (see below).

For edaphic situations where a sharp chemical or physical contact exists between natural substrates, the man-caused analog of genotypic tolerance to toxic heavy metals of mine tailings can be used as a model. I see the heavy metal syndrome applicable equally to the genesis of races tolerant to a variety of natural substrates: limestones, gypsum, saline soils, and serpentsines. Using serpentine soils as an example we can envision four or five stages leading to the establishment of an edaphic-endemic species. Stage 0. Some preadaptation for serpentine tolerance exists in certain non-serpentine populations. Stage 1. Disruptive selection effectively separates a species into serpentine-tolerant and -intolerant gene pools. Stage 2. Further genetic divergence in structural and functional traits occurs within the serpentine-tolerant part of the effectively discontinuous populations. Stage 3. Isolation between serpentine and non-serpentine segments of the species becomes genetically fixed; the two populations are unable to exchange genes. Stage 4. Further reinforcement of genetic-ecologic isolation and consequent further divergence of the serpentine population may occur, put in motion by the initial genetic discontinuity. The sequence encompasses an evolutionary history from the initial compatibility between habitat and certain preadapted variants, to clear-cut species formation.

The "serpentine syndrome" (Jenny 1980) is so striking in its manifestation that it can reveal populations in various stages of diversifi-
speciation. Especially instructive is the evolutionary sequence for species of the mustard genus, *Streptanthus* (Kruckeberg 1984; Kruckeberg and Morrison 1983). Of the 16 species in subgenus *Euclisia*, 14 are facultative or obligate serpentine species, and several are narrowly limited to only a few of the available outcrops. Stage 1 in the sequence given above can be detected in species of *Streptanthus* not obligate to serpentine. For example, the wide-ranging *S. glandulosus*, has numerous populations occurring on and off serpentine. None of its non-serpentine populations are tolerant to serpentine (Kruckeberg 1951, 1954). Thus racial differentiation has already taken place. Other serpentine taxa of the western United States exhibit this early stage of diversification (Kruckeberg 1951, 1954, 1967).

Incipient isolation, following racial differentiation is illustrated by the named variants in several species of *Streptanthus*. *Streptanthus insignis* subsp. *insignis* and *S. i. subsp. lyonii*, both on serpentine in the South Coast Ranges of California, are separated by only short discontinuities in the serpentine lithology. They are distinct morphs, but as yet are still highly interfertile (Kruckeberg and Morrison 1983). A distinct species within the section *Hesperides* is *S. drepanoides*; it achieves species distinction for its several singular features and its reduced fertility with its nearest congeners (Kruckeberg and Morrison 1983). Yet a later stage appears fulfilled by *S. barbatus* and *S. howellii*. Both are distinct species endemic to Klamath-Siskiyou serpentine, yet retain features showing their kinship to the wide-ranging arid-land species, *S. cordatus* (subgenus Pleiocarida). A final stage has been reached in subgenus *Euclisia* by *S. polygaloides*, endemic to Sierra Nevada serpentine; it is so distinct a species that it defies alignment with any other Euclisian taxon. Indeed *S. polygaloides* was placed in its own genus, *Microsemia*, by E. L. Greene (1904); and in recent times, that affinity has been supported again on the basis of the species’ exceptional status as a hyperaccumulator of nickel (Reeves et al. 1981).

Thus by direct evidence and by inference, the several stages leading to narrow edaphic endemism are illustrated by different taxa in *Streptanthus*. All have conformed to the diploid speciation model; *Streptanthus* species of subgenus *Euclisia* are uniformly diploid (*n* = 14, Kruckeberg and Morrison 1983, and unpubl.).

Some variations on the above speciational sequence can be expected. A mode of origin that depends on a stressful edaphic habitat coupled with a salient cytogenetic change is catastrophic selection followed by saltational speciation (Lewis 1962; Raven 1964). Speciation by “saltation” is initiated in a marginal population, or one decimated by a severe environmental stress, catastrophic to the bulk of the population. Only particular genotypes survive the catastrophe; should they bear new chromosomal rearrangements, they can be isolated effectively from their nearest relatives. The model has been applied only to *Clarkia* (Lewis 1962), where the edaphic stresses were presumed to be extreme drought and serpentine soils.

Hybridization between populations of different edaphic requirements will, if in the first place successful, blur the distinction between the two gene pools. Of course, effective hybridization may not occur, if the F1, or later hybrids find no edaphic niche to match their intermediate tolerance spans. Species pairs on and off serpentine in California display both possibilities. *Ceanothus ramulosus* or *C. cuneatus* on non-serpentine soils and *C. jepsonii*, a serpentine endemic, often coexist on either side of an edaphic contact. Yet intermediates are rare, and give no sign of local hybrid swarms or introgressant populations (Nobs 1963). The situation is slightly different for *Quercus dumosa* (non-serpentine) which often is sympatric with the serpentine endemic, *Q. durata*. Most such coexistences produce no hybridity; but one exception has been recorded (Forde and Faris 1962). Local introgression has taken place and the introgressant individuals come to occupy a rather sterile non-serpentine ridge in the Vaca Mountains.

Two of the classic case histories that helped put introgressive hybridization on the map appear to have geoedaphic causes. The *Tradescantia* case of Anderson and Hubricht (1938) involved a topo-edaphic sequence of habitats with some human disturbance. The other case history analyzed by Heiser (1949), involved the serpentine endemic sunflower (*Helianthus bolanderi* subsp. *exilis*), *H. annuus*, and its widely introgressed derivative, *H. bolanderi* subsp. *bo-
landeri. In both instances, we would like to know if the success of the introgressant populations depends on their acquiring genes from the parent which was the edaphic specialist.

No doubt there are many other examples where hybridity has extended the range of an edaphic specialist. An illuminating example, worked out by Brayton and Mooney (1966), shows how substrate, topography, and other geoedaphic factors interact to yield a gradient of biotypes. Two species of Cercocarpus are arrayed along a topo-edaphic sequence in the White Mountains of California. The “good” species are at either end of the sequence, while the zone of hybridity lies altitudinally and edaphically intermediate in position.

Speciation by allopolyploidy must take a place on our list of those diversity-making phenomena associated with geoedaphics. Though allopolyploidy does not yield adaptive radiation, its products—the allopolyploid derivatives of lower ploidal species—combine in “crystallized” state, the attributes of both parents. Such reticulate evolution does achieve a kind of newness—the best of two worlds—even though not embarking on wholly new evolutionary paths. Out of the many possible examples of allopolyploid origin stimulated by edaphic variables, I offer three case-histories. 1) Nearly every case of an allopolyploid that borders or occupies a deglaciated area exemplifies the effect of this geoedaphic disturbance phenomenon. Anderson’s (1936) classic case of Iris setosa, Iris virginica, and the derivative allotetraploid, I. versicolor, illustrates the opportunistic effect of deglaciation on the polyploidized hybrid, I. versicolor. 2) Johnson and Packer (1965) found a strong correlation between microedaphic differences and distribution of levels of ploidy in one Alaskan valley. 3) The last case concerns Eriogonum fasciculatum, studied by Stebbins (1950). This species complex includes diploids and polyploids, with the polyploids confined to geologically more recent habitats than their diploid progenitors.

The “take-home” message coming from these several modes of evolutionary diversification seems clear. The edaphic factor as one significant set of environmental stimuli fosters evolution and speciation along several pathways. Although no new mechanism for generating diversity can be linked to geoedaphic influences, they, as major environmental stimuli, shape newness in a full range of modes and mechanisms. One only has to examine a book like Grant’s (1981) which deals with the many variant modes of diversification and speciation to see that geoedaphics can serve as the environmental trigger for most every model.

Conclusions and Summary

The elaboration of plant species diversity should be viewed as a two-way street: environmental challenges are met, then responded to, by biological invention—read, evolution! A salient point of this essay has been to remind the evolutionary biologist of the profound influence of the diversity of the physical world on the outcomes of evolutionary opportunism. Self-evident, perhaps, but there is a tendency for the evolutionary biologist to become preoccupied with the living component of the duality—to look for biological mechanisms and outcomes, rather than those non-living agents of selection and isolation fashioned out of geological processes.

I have attempted to fit the diverse elements of geological process and product as evolutionary stimuli to those components of the neo-Darwinian paradigm that create diversity in the world of higher plants. Discontinuities in the displays of geological phenomena fashion discontinuities in living systems, from discrete gene pools to highly unique and endemic species or higher categories. The term geoedaphics has been used here to encompass the array of geological processes and end-products sensed by plants: diverse topographies, lithologies, mineral types, and their weathered derivatives, soils. Time must be reckoned in with geological process, for the duration and age of the landform, the soil, rock outcrop, etc. influence the nature of biological response. I have adapted Jenny’s (1941) soil-formation equation to the diversity-making processes in the plant world: Biological Diversity = f(cl, o, r, p, t). This conceptual formulation underscores the five independent but interactive variables (climate, organisms, topography, rock type, and time) in the evolutionary process.

The rich variety of pathways to distinct species as formulated by contemporary neo-Darwinian theory can all be fitted to the geoedaphic challenge. No new speciational scenarios appear, though some may be particularly
exploited due to the discontinuities of geology and soils. Thus, disruptive selection, catastrophic selection, and saltational speciation may be frequent outcomes for plants challenged by stresses and discontinuities created by geodaphics.

Two geodaphic systems have been used here to illustrate the effects of physically unique habitats on gene pools. The first, toxic heavy metals in soils of mine tips/tailings, affords the best model for testing the genetic potentialities for survival in certain plant gene pools. Acquisition of genetically fixed tolerance to heavy metals can be taken as illustrating the first stage in isolation of lineage. The other set of examples comes from the highly endemic flora on serpentine soils. Genera of the California flora that have diversified on serpentine (e.g., Streptanthus, Linum, Fritillaria, etc.) illustrate possible stages in isolation and speciation of edaphic specialists.

Finally, I contend that botanists will unearth many more linkages between plant species diversity and regional geodaphics, some more subtle than the heavy metal or serpentine responses. Such further understanding can come from an initial recognition that the myriad of habitats induced directly or indirectly by geology is a rich array of evolutionary stimuli.

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LITERATURE CITED


FORDE, M. B. and D. G. FARIS. 1962. Effect of introgression on the serpentine endemism of Quer-


GREENE, E. L. 1904. Certain west American Crucif-

erae. Leaflets of Botanical Observation and Critic-

icism 1:81–90.

HEISER, C. H. 1949. Study in the evolution of the sunflower species Helianthus annuus and H. bolan-


———. 1954. The ecology of serpentine soils: A symposium. III. Plant species in relation to serpen-


LIU, E. H. and M. W. GODT. 1983. The differentiation of populations over short distances. Pp. 78–95 in Genetics and conservation, eds. C. M. Schone-


