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AN ESSAY: GEOEDAPHICS AND ISLAND BIOGEOGRAPHY  
FOR VASCULAR PLANTS<sup>1</sup>

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ABSTRACT

"Islands" of discontinuity in the distribution of plants are common in mainland (continental) regions. Such discontinuities should be amenable to testing the tenets of MacArthur and Wilson's island biogeography theory. Mainland gaps are often the result of discontinuities in various geological attributes—the geoedaphic syndrome of topography, lithology and soils. To discover if geoedaphically caused patterns of isolation are congruent with island biogeography theory, the effects of topographic discontinuity on plant distributions are examined first. Then a similar inspection is made of discontinuities in parent materials and soils. Parallels as well as differences are detected, indicating that island biogeography theory may be applied to mainland discontinuities, but with certain reservations.

Key words: acid (sterile) soils, edaphic islands, endemism, geoedaphics, granite outcrops, island biogeography, mainland islands, serpentine, speciation, topographic islands, ultramafic, vascular plants, vernal pools.

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INTRODUCTION

"Insularity is . . . a universal feature of biogeography"—MacArthur and Wilson (1967)

Do topographic and edaphic islands in a "sea" of mainland normal environments fit the model for oceanic islands? There is good reason to think so, both from classic and recent biogeographic studies. Island biogeography theory stretches back beyond MacArthur and Wilson to at least the early 19th century. Wallace, Darwin, von Humboldt, and other early naturalists saw that insularity manifested itself on both oceanic and offshore (continental) as well as on mainland islands. Much more attention has been given to the oceanic island paradigm. Yet MacArthur (1972) in his last major book, *Geographical Ecology*, devotes a section of a chapter on Island Patterns, to "Habitat Islands on the Mainland." Most of the examples of mainland "island" biogeography come from zoology; case-histories for birds and mammals on montane islands in a sea of lowland terrain have been put to the test of island biogeography theory (Brown 1971, 1978; Vuilleumier 1970). But little of a similar vein has been done with vascular plants, though the prospect for testing the theory with plants on mainland islands is promising, given mainland discontinuities of habitat.

I propose here to examine the island-on-mainland problem for plants from two standpoints, both in the context of the geological influence on mainland plant distribution. This context I call the geoedaphic syndrome of factors (Kruckeberg 1986a): it comprises topography, geomorphology (landscape), lithology, and soils; any of these arrayed discontinuously in space. This is the stage upon which biological consequences of drift, adaptive specialization, isolation, and speciation all can be enacted. I first review the few cases where isolated mountains (the "Inselberge" phenomenon) create insularity on continents. Then I examine the

potential of discontinuity in substrate, especially parent material (lithology or rock types) which can engender insularity on mainlands. In both contexts— isolation by montane islands and isolation by edaphic islands—I explore how well island biogeography theory, as developed for oceanic islands, fits the biology of insularity on mainlands.

#### ISLAND BIOGEOGRAPHY THEORY

Island biogeography theory derives from the notion that the numbers of species on islands cannot be accounted for by evolution alone (Pielou 1979). From this premise, it follows that species number on islands could result from an equilibrium between immigration and extinction. We should assume also that subsequent to arrival, a founder may evolve (e.g., speciate); extinction may also be the fate of the founder, before or after evolutionary divergence. A further consideration is that species number at equilibrium is determined by the number of species in the source pool (mainland taxa), by the size of the island, and by its distance from the mainland. Testing of the MacArthur-Wilson theory followed soon after its publication (MacArthur and Wilson 1967); refinements, criticisms, and even rejection have been its fate. Its very survival—and even application to the conservation of rare biota—speaks well for its heuristic value.

It is not my intent to expand on the present status of the theory. Rather, I will turn it to another use. It should be profitable to see how it can be applied to topographic and edaphic insularity on mainlands. Do habitable mainland “islands” within an unfavorable landscape have physical and biologic features not found in the oceanic island context? I perceive the following conditions peculiar to the mainland insularity:

1. Potential source biota surround the “island.” A lowland sagebrush flora laps at the base of a mountain peak, potentially providing recruits. A biota on sandstone is recruitable for occupancy of a serpentine or dolomite outcrop. This proximity of contrasting floras makes for easy dispersal between them; the colonizing of mainland islands by wind or animals will be commoner than for oceanic islands (Ornduff, pers. comm.).

2. As a consequence of (1), mainland “island” biota are likely to be taxonomically related to the surrounding biota. Taxa in such contrasting habitats could be vicariants; similar species of a genus. Unless! The “island” may harbor relictuals. Examples of vicariants: Sandstone vs. dolomite *Erigeron* species in the White Mountains of California (Mooney 1966); serpentine and nonserpentine *Streptanthus* (*S. glandulosus* Hook. subspecies, *S. insignis* Jeps. vs. *S. callistus* Morrison and *S. hispidus* Gray; *S. amplexicaulis* Jeps. and *S. amplexicaulis* var. *barbarae* J. T. Howell in Kruckeberg [1984]). Relictual examples are less common on edaphic islands (e.g., *Cupressus* species on serpentine, according to Raven and Axelrod [1978]), but are frequently encountered in the alpine zone of isolated peaks.

3. Mainland “islands” will have a mix of species—some common to the surrounding “sea” of lowlands (or normal substrates), as well as some endemics on one or more of the “islands.” Western North American examples of ubiquitous taxa (often called “ubiquists” or “indifferent” species) include herbaceous perennials like *Achillea millefolium* L., *Agropyron spicatum* (Pursh.) Scribn. & Sm., and *Antennaria racemosa* Hook.; as well as woody taxa like *Artemisia tridentata*

Nutt., *Amelanchier alnifolia* Nutt., and *Prunus emarginata* (Dougl.) Walp. Their occurrence both on and off "island" habitats usually merits no taxonomic recognition, though they may be differentiated into physiologic races or ecotypes for the respective habitats. Endemics restricted to the topographic or edaphic islands are many, and well known; examples will be given below.

4. The presence of common, edaphically indifferent taxa (in 3) fuels a competition between them and local endemics that may not occur on oceanic islands. Absence of competition on oceanic islands is thought to be a potent ingredient for speciation from the initial founders (Hubbell 1968). Only when the mainland island is an isolated, stressful edaphic habitat like serpentine, may the competition factor be diminished.

5. It follows from (4) that mainland islands may be climatically or edaphically challenging habitats, not simply colonizable habitats like oceanic islands, isolated from a mainland by distance (Carlquist 1974).

6. Should extinction of a rare entity occur on an oceanic island, its replacement by recolonization will be unlikely, given the distance from the nearest source. But on mainland islands, the extinction of a species can be followed by recolonization, especially if the taxon (or its nearest relative) is on surrounding terrain (Ornduff, pers. comm.).

Most of the case histories for biota on mainland islands are for animals (especially birds and small mammals) on isolated mountains. Vuilleumier (1970) confirms the equilibrium theory, in part, for the bird fauna of the northern Andean paramos. But he finds differences too. Bird colonists en route to oceanic islands may drown in the attempt, but they may survive overland migration to new paramo sites with brief stopovers in nonparamo habitats. Further, the dispersal to oceanic islands will be continuous, but only intermittent (e.g., during the Pleistocene) for paramo islands. Brown (1971, 1978) found that boreal mammals on Great Basin mountain "islands" (western U.S.A.) were not in equilibrium. They reached the boreal islands in the Pleistocene, then colonization ceased. Only extinctions have subsequently occurred. These boreal mammals are thus relictual, much like the mountain-top plants of the southern Appalachians, discussed below (White, Miller, and Ramseur 1984). A more striking example of this relictual insularity occurs above timberline in the northern Appalachians in arctic-alpine plant taxa (Bliss 1963; Billings 1988).

#### TOPOGRAPHIC DISCONTINUITIES AS FLORISTIC ISLANDS

Some botanists have begun to look at the island-on-continent syndrome for vascular plants. Thus far the focus has been on the floristics of the "Inselberge" phenomenon—isolated mountains in a "sea" of lowland landscape. Three case histories will illustrate this topographic insularity.

Olov Hedberg's extended study (Hedberg 1970) of the high alpine enclaves of East African mountains is now a classic. Though poor in species, the rigorous, diurnally stressful habitat of the Afroalpine has generated a truly remarkable "Inselberge" flora: Local endemics are on one or more of the isolated peaks. In western North America, alpine islands in a "sea" of prairie or desert abound (Fig. 1). Billings (1978) has discussed these insular floras for the Great Basin of Nevada, particularly in terms of island biogeography. Floras of high Andean paramo habitats have been shown to conform well to the MacArthur-Wilson model; equilib-

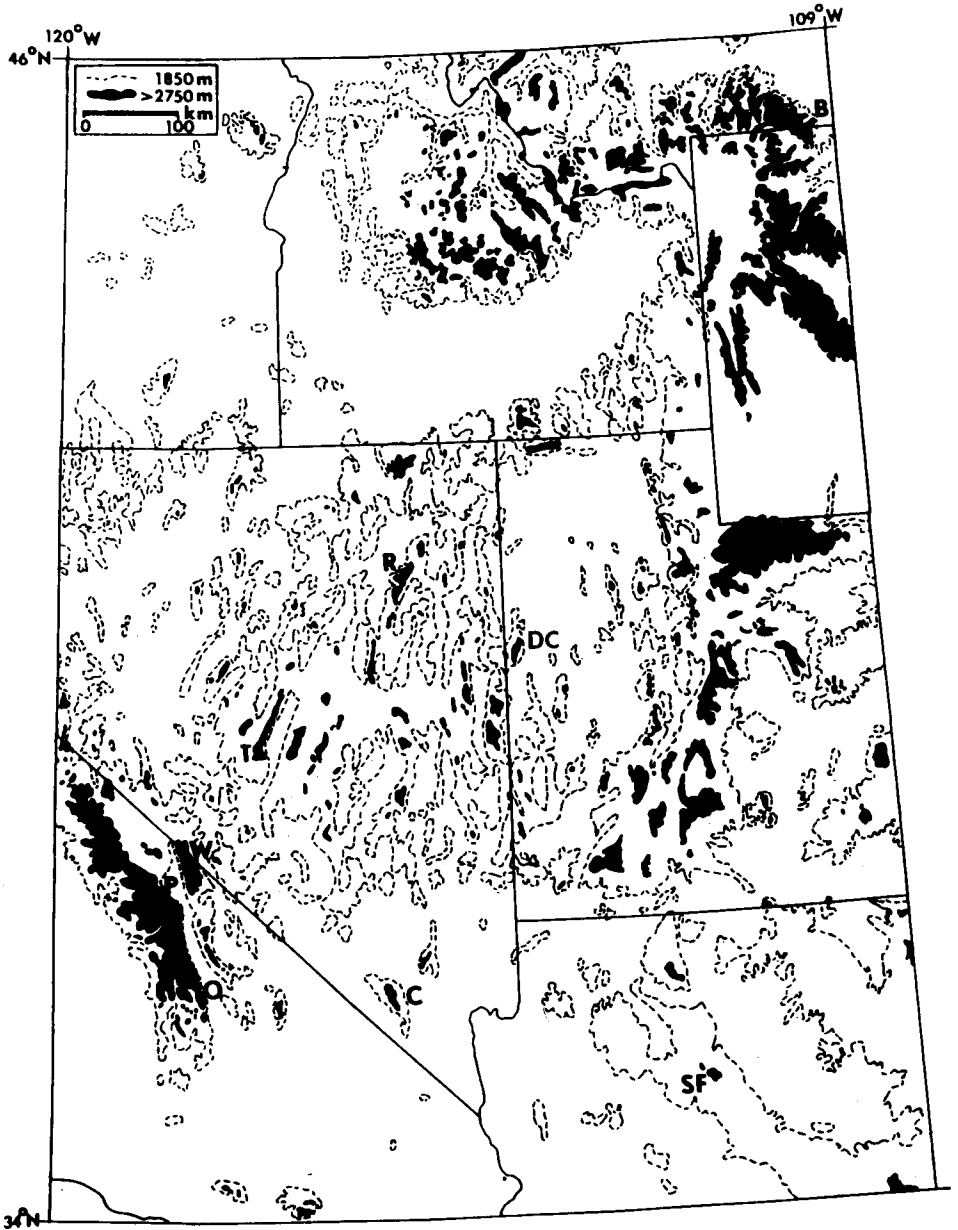


Fig. 1. The summits of mountains in the Great Basin (western North America) display an unmistakable insular distribution (Billings 1978).

rium was reached during glacial periods (Simpson 1974). Awaiting similar scrutiny is the rich array of isolated mountain ranges and single peaks in Montana, east of the continental divide. A hint of what is in store for the biogeographer in this mainland archipelago of "Inselberge" can be found in "Islands on the Prairie" (Meloy 1986).

The last example of topographic islands and their floras comes from the south-

eastern United States—the southern Appalachian high mountain flora (White et al. 1984). They test the hypothesis that on these montane islands “vascular plant richness is related to island size and find that the species/area relationship of these mountain tops has the steep slope (of the MacArthur-Wilson model).” White et al. found species richness to be positively correlated with size of area, number of peaks, maximum elevation, and number of community types present. There is a significant difference between these montane island patterns and that predicted from island biogeography theory. The two smallest montane islands have higher richness than that expected from size alone. Past history of the regional flora can account for this discrepancy. White et al. conclude that “extirpation has been more important than immigration in shaping the recent floristic richness of the high peaks.”

It would seem then that island biogeography theory as applied to plants on mainland topographic islands is just beginning. It can serve as a set of working hypotheses to test biogeographic data derived from mainland island biota. More case histories of this sort are needed to see if the vascular plant floras of mainland islands and oceanic islands share common biogeographic attributes. Parenthetically, it should be pointed out that we need analyses of the floras of oceanic islands. While there are many published floras of oceanic islands, their conformity to island biogeography theory awaits further testing (Carlquist 1974).

#### EDAPHIC DISCONTINUITIES AS FLORISTIC ISLANDS

Mineral substrates derived from a variety of parent materials often display a discontinuous distribution in space. One such parent material is the family of ultramafic rocks, especially serpentinite, found world-wide (Brooks 1987). These ferromagnesian rocks typically surface discontinuously over wide areas in the Pacific States (Kruckeberg 1984), and similarly throughout the Atlantic seaboard, from Quebec to Georgia (Reed 1986; Dann 1988). One only has to look at a geologic map (Fig. 2) where ultramafics are present to see the remarkable insularity of the outcrops. Floras of serpentine areas are reasonably well known and often display a number of insular attributes. The distinctive floras and communities are usually markedly set apart from those on adjacent normal substrates; they may have local, narrow endemics and can show racial differentiation of indifferent taxa. Other features include isolation spatially from similar outcrops and ecophysiological from adjacent nonserpentine floras. Species richness may be correlated with size of outcrop, and varying distances separate outcrops (from archipelagos to Inselberge). Such a biogeographic “Eldorado” has scarcely been mined, neither for serpentine floras nor for any other geodaphically discontinuous substrates.

So the best we can do is to propose a protocol for its study and to hypothesize some strategies and outcomes. The serpentine case is a good one to explore. In a given locality, as in the Coast Ranges of California, outcrops of all sizes and proximities to each other can be found (Kruckeberg 1984). Species richness can be gotten for such sites, much like the data for montane islands. My travels on serpentine islands of all sizes leads me to predict that richness will be correlated with size of area and the spatial configuration of outcrops. One attribute of serpentine and similar edaphically stressful habitats is not of prime significance to montane or oceanic insularity. That is, the ecophysiological challenge encountered

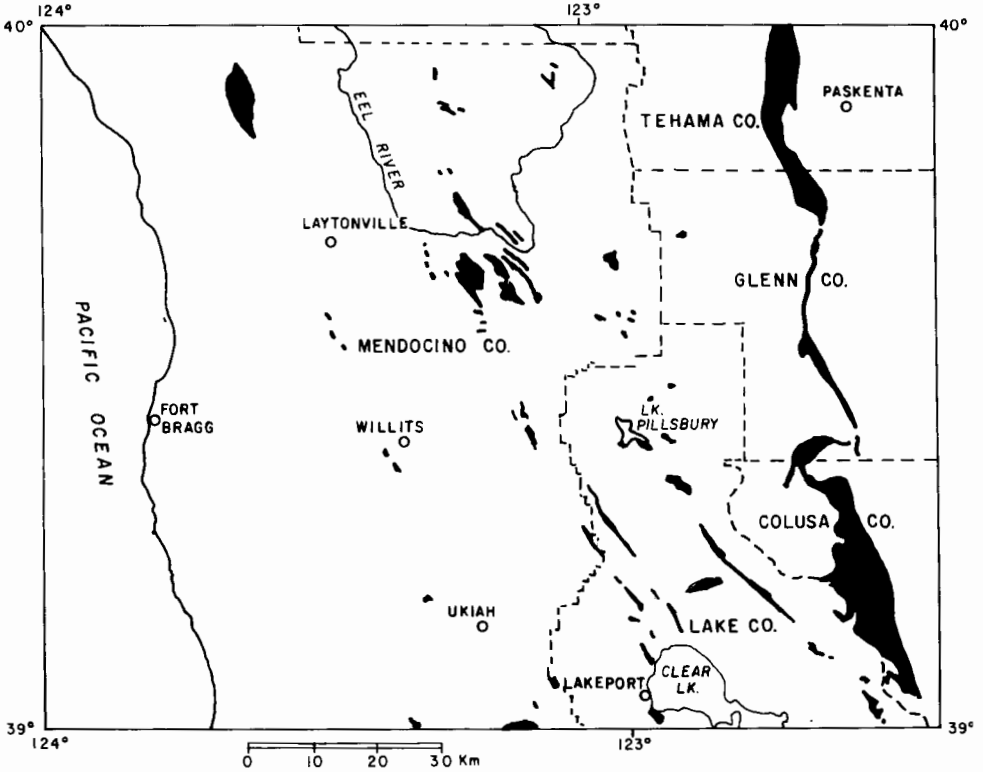


Fig. 2. The distribution of serpentine outcrops is clearly insular as shown from the Ukiah Sheet of the Geologic Map of California (Kruckeberg 1984).

by the presumptive colonists. Plants that may eventually occupy serpentine (or limestone, gypsum, or leadmine tailings) must acquire tolerance to the serpentine (or other stringent edaphic) factor.

All is not left to future research for finding attributes of edaphic islands that illustrate island biogeography. There are data on size of area and distance to neighboring edaphic habitat that can be correlated with species diversity.

### *Serpentine Examples*

Three ferns are commonly found on Pacific Coast ultramafics (*Aspidotis densa* (Brackenr.) Lellinger, *Polystichum lemmonii* Underw., and *Adiantum pedatum* L. subsp. *calderi* W. J. Cody). Of the three, *Aspidotis densa* tells a good biogeographic story (Kruckeberg 1964). It is found on all major serpentine areas from southern California to British Columbia. It has found its way to the more isolated outcrops in central Oregon and is a tell-tale indicator on serpentine outcrops of moderate to large size, especially where the outcrops form island clusters (archipelagos). Only on very small, isolated outcrops is it absent, e.g., at the northern perimeter of the Klamath-Siskiyou massif in southwestern Oregon, in Whatcom and mainland Skagit counties in Washington, and very local outcrops in southern British Columbia. Since *A. densa* is not strictly confined to serpentine, there are

intervening nonserpentine sources for even these more remote, small outcrops. Presumably *Aspidotis* spores are widely dispersed and fall out on a variety of substrates. The sporelings become established mainly on serpentine, despite the availability of open habitats on granite, basalt, and other lithologies. Further, a single sporeling can be the start of a colony, for *Aspidotis* like most homosporous ferns, is partially autogamous, producing some maternal progeny (Smith 1975). So, given its ease of dissemination and partial uniparental reproduction, it is not surprising that it is found widely on serpentines. What is open to conjecture is why it is missing on smaller, isolated outcrops. My guess is that purely by chance, spores have not yet found a given lone outcrop.

The other two ferns are widespread on more mesic, midmontane serpentines throughout much the same range. Again, they fail to appear on the smaller, more isolated outcrops.

These fern case histories suggest other facets of emigration to serpentine. The near universal presence of fern spores in the "rain" of airborne disseminules onto substrates will include spores of nonserpentine ferns landing on serpentine. Common Pacific Coast ferns like *Athyrium filix-femina* (L.) Roth, *Polystichum munitum* (Kauf.) Presl., *Polypodium glycyrhiza* D. C. Eat., and *Cryptogramma crispera* R. Br. must reach serpentine outcrops repeatedly—but to no avail. In this instance immigration is aborted by substrate inhibition. Serpentine islands are prevented from being colonized by nonserpentine airborne taxa because of the stringent selective nature of the habitat. Failures of colonization of this sort must be the fate of other airborne migrants (e.g., terrestrial orchids, certain ericads, etc.). Successful colonization of an edaphic island thus requires more than fortuitous arrival of a migrule. Some degree of preadaptedness to the substrate will be required. This requirement may be nonexistent or at least less stringent for migrules reaching oceanic islands.

The fate of migrules reaching serpentine has been tested. For years, I have attempted to establish seed-plant populations on serpentine, mostly to determine the physiological tolerance of both serpentine and nonserpentine "inocula." Most of the tested taxa have failed to gain even a modest toehold on serpentine. The one exception has been *Silene paradoxa*, a serpentine indicator from southern Europe. Initial transplants of this species onto serpentine in Washington State not only became established but have locally expanded their population by sexual reproduction (Kruckeberg 1986b). Similar emigration onto serpentine can be inferred for introduced species in California (Kruckeberg 1984). Mediterranean annuals (e.g., grasses like *Avena* spp., *Bromus* spp. and *Festuca* spp.) have become established on serpentine, especially where disturbed (roadcuts, borrow pits, mine areas, etc.). While the *Silene paradoxa* L. example involves established, built-in genetic tolerance to serpentine (the species is common on serpentine in Europe), the invasion of Mediterranean annuals onto serpentine suggests a recent acquisition of serpentine tolerance. These grasses have made it onto serpentine islands, possibly because of genetically fixed tolerance in the preadapted colonists.

Once established on an edaphic island, like a serpentine outcrop, what is the fate of the venturesome genotype? One way to answer this question is to determine if the founder gene pool differs from its source gene pool. Some kind of genetic change should be detectable. Genes affecting physiological tolerance, reproductive isolation, or other adaptive traits may have accumulated, as will have gene dif-



ferences simply resulting from drift. One can further postulate that the edaphic founder may be more or less variable than its source gene pool. Despite the rapid and facile approach via electrophoresis of isozymes, I would prefer to get genetic data based on breeding tests. Analysis of  $F_1$  and  $F_2$  progeny of crosses between serpentine and nonserpentine genotypes would tell us much about the genetic change following initial colonization onto edaphic islands. Examples of such genetic tests are limited, and come mostly from the heavy-metal-tolerance literature (reviewed by Antonovics 1975). Metal tolerance is polygenic (or oligogenic in *Mimulus*, MacNair and Cumbes 1989) and its expression often is dominant; the tolerance mechanism is unique to a given metal element. Yet to be done is testing the effects of selection for increased genetic tolerance as well as finding evidence for reproductive isolation (incipient speciation).

Isozyme fingerprinting may also detect genetic differences between island isolates and source populations. Such has been done for Jeffrey pine (*Pinus jeffreyi* Grev. & Balf. in A. Murr.) in California. Its populations are restricted to serpentine in northwestern California and southwestern Oregon; populations in the Sierra Nevada are on normal substrates (especially granodiorites) and are widely distributed more or less continuously from south to north. Isozyme variation for the two contrasting edaphic populations differs significantly (Furnier and Adams 1986). The more isolated and discontinuous serpentine populations are less heterozygous than the Sierran populations on normal soils. The only serpentine population from the Sierras was more like the Klamath serpentine populations in allele frequency than its nearby Sierran populations widespread on granodiorite.

### *Other Edaphic Islands*

Most variations in land forms and lithologies are discontinuously arrayed in space. Islands of habitability result. This is particularly true of the display of rock types and other discrete substrates, as we have just seen for serpentines. Other rock types, those that produce nutritionally normal soils, as well as those with unique chemical properties, often yield insular patterns. We now examine a few other case histories where unique substrates are isolated in space, as islands.

1. Limestone and dolomite outcrops. Pick a continent and you can be sure of finding examples of calcicole floras restricted to carbonate rocks. Two North American examples illustrate the syndrome. Erickson's (1943, 1945) study of populations of *Clematis fremontii* Wats. var. *reihlii* Erickson, in the Ozarks of Missouri, is a classic; it gives a graphic display of field observations to show the close tracking of a plant to substrate. The plant is confined to rocky, barren openings (glades) on outcrops of thin-bedded dolomite. The character of the edaphically defined distribution is strikingly portrayed by Erickson's sequence of range maps, from region to local aggregate (Fig. 3). The ultimate local habitat is the single aggregate, a colony of *Clematis* at a given glade. The insular character of the distribution includes a hint of island size and species diversity. Erickson compiled records of the plant's absence as well as its presence. At least the number of *Clematis* plants is lower for small glades, or the taxon is absent altogether from some smaller glades.

Limestone and dolomite substrates elsewhere are a rich source of phytogeographic patterning. In western North America, local marble outcrops in the Sierra Nevada have significant Rocky Mountain disjunctions (Major and Bamberg 1963).

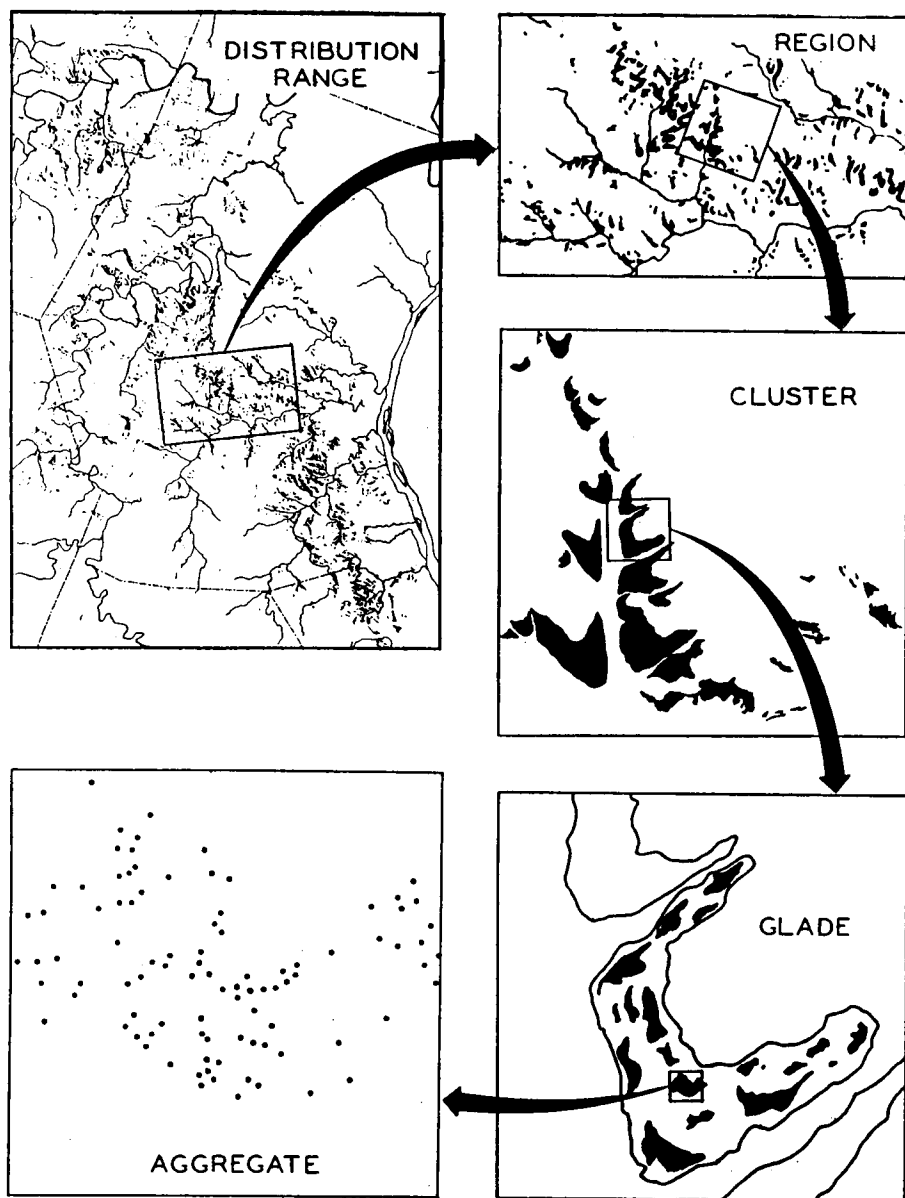


Fig. 3. Sequence of maps with increasing resolution dramatizes the insular pattern of distribution for *Clematis fremontii* var. *reihlii* on isolated limestone outcrops in the Ozarks (Erickson 1945).

In the nearby White Mountains, the contrasts between dolomite with bristlecone pine (*Pinus longaeva* D. K. Bailey) and siliceous sandstone with sagebrush has been well documented (Wright and Mooney 1965; Mooney 1966; Lloyd and Mitchell 1973). Old World case histories abound; thus, the chalklands of Great Britain (Lousley 1950; Sankey 1966) are well known for their distinctive floras; and in Japan, Shimizu (1962, 1963) has found similar floristic diversity on limestones.

2. Granite outcrops. The granite "flat rocks" of southeastern United States are exposed, floristic islands surrounded by mesic forest. Even a single granite outcrop can take the form of an archipelago of microisland communities. Burbank and Platt (1964) focus on these intra-outcrop islands of vegetation, calling them "island communities." They are in depressions with soil, scattered across the face of the bare rock. Depending on the depth of soils, they support four distinct community types. The prospect for testing island biogeography theory on these island chains is promising. Burbank and Platt did look at size of island community, but chose to relate it to soil depth rather than to species diversity. Murdy (1968) sees the disjunction of granite outcrops as a propitious condition for both speciation and extinction. Endemic taxa may be on one outcrop, but missing on a nearby outcrop. If extinction is really involved, then this suggests the Lewis (1960) model of catastrophic selection leading to saltational speciation for the survivors.

Wyatt and Fowler (1977) subjected their floristic data on North Carolina granite outcrops to the MacArthur-Wilson model for islands. They found a positive, linear relationship between area and species number. To the west, granitic outcrops in the central mineral region of Texas were found to have fewer endemics than on the southeastern U.S.A. outcrops (Walters and Wyatt 1982). They ascribed this difference to the greater geographic isolation and the sharper discontinuity with surrounding vegetation for the southeastern granite outcrop floras. Though the outcrops of the two areas harbor different floras, they were nearly identical in life-form spectra (a predominance of annuals).

Granite outcrops occur on other continents. Some examples are the "kopjes" of South Africa and the granitic domes of Australia. Ornduff (1987) gives an extensive and fascinating account of the latter edaphic islands in southern Western Australia. The flora of these granite domes is not simply "a random subset of the Western Australian flora." Some families are underrepresented, while others are overrepresented on granitic outcrops. Further, there is a bias in life-form: nearly two thirds of the native vascular flora on granite outcrops are annuals, while annuals are only one twelfth of the Western Australian floras as a whole. Geophytes and "resurrection" plants are conspicuous elements of the outcrop floras. Ornduff, using island/area analysis, found that the species number/area prediction did not hold for these granitic outcrops. Even the smallest outcrop (Nettleton Rock) supported the largest number of species.

It is well to point out here, as does Ornduff (1987:19), that MacArthur and Wilson (1967) exempted mainland islands from some of their conclusions for oceanic islands. They argued, as I have in this paper, that mainland "habitat islands" are surrounded by land areas with potential immigrants and competitors, unlike oceanic islands.

3. Locally acid soils as islands. At numerous sites in western North America, there occur local habitats with soils markedly more acid than their surrounding substrates. The causes of the local acidity are various: unusual parent materials or exceptional topographies. Whatever the cause, the vegetation of the acid sites can differ markedly from the surrounding vegetation. These islands of acid soils can support both endemics as well as species widely disjunct from their usual ranges. Hydrothermally altered volcanics in the Great Basin foster unique vegetations, primarily disjunct conifer stands with subalpine herbaceous taxa in sagebrush country (Billings 1950; Salisbury 1964). The lateritic Ione formation of the

Sierra Nevada foothills in central California adds a different twist to the acid soil-vegetation story. Here the typical blue oak-Digger pine, or chaparral types on normal soils are replaced by an acid heath scrub on soils of pH 2.9–3.9 (Gankin and Major 1964). These floristically depauperate outcrops can be dominated by one species of ericad, the endemic Ione manzanita (*Arctostaphylos myrtifolia* Parry). The only other endemic is *Eriogonum apricum* J. T. Howell; a scattering of annual herbs and cryptogams (mosses and lichens) makes only a modest showing on barrens, especially in open places not occupied by the heath.

Another Californian acid-heath vegetation is the remarkable pygmy conifer-heath flora in Mendocino County. Here the decisive edaphic control of acid, sterile, and poorly drained soils is induced by a unique topography (Westman 1979). Five terraces underlain by sandstone were elevated during the Pleistocene and then stayed in place. The slopes bordering the terraces are clothed with mesic, mixed coast redwood forest: the windward edges of the terraces, aeolian in origin, are of Bishop pine (*P. muricata* D. Don.) and *Rhododendron* heath. The terraces proper, though, are the startling feature: pygmy conifers and ericaceous heath on acid (highly podzolized) soils underlain with an impervious hardpan. The pygmy conifers, *Pinus contorta* Dougl. var. *bolanderi* (Parl.) Vasey and *Cupressus goveniana* Gord. var. *pygmaea* Lemmon, both endemics, coexist with a heath vegetation, including the endemic *Arctostaphylos nummularia* Gray.

A remarkable case of edaphic endemism on discontinuous “islands” of substrate has recently been described for the unique Lake Wales sand ridges of Florida (Huck, Judd, Whitten, Skean, Wunderlin, and Delaney 1989). Xeric, residual sand hills, beach ridges, and dune fields occur discontinuously along the low ridge system, interrupted with numerous sinkhole lakes and basins. The vegetation of sand pine and sclerophyllous oak scrub is rich in endemics. Besides the newly described endemic *Dicerandra christmanii* Huck & Judd, there are 27 other endemics, herbaceous as well as woody taxa. The authors propose that the isolated xeric sand “islands” came about in one of two ways: either fragmentation of once widespread taxa, or short-distance dispersal may have occurred, possibly by water. The initial dispersal event to one or more of the “ecological islands” could have been followed by further genetic divergence of the isolates.

These disparate variants of islands (with acid or sterile substrates) have a common theme—isolated and unique habitats. In common with other stringent, chemically demanding habitats, their relevance to oceanic island biota must be tempered with reservation. Most telling is the difference in the founding biota. Far more on the edaphic island than on the oceanic island, the founder must run the physiological gauntlet of acquiring tolerance, instantly and preadaptively available in order for establishment to occur.

4. The vernal pools of California are mainland edaphic islands, harboring distinctive floras (Holland and Jain 1981). The pools are usually arrayed in archipelagolike groupings, separated by large areas unsuitable edaphically for pool formation. Analysis of species composition within and between pools (and archipelagos) reveals some intriguing biogeographic notions. Despite the high endemism of vernal pools, species diversity in individual pools is low. Size of pool had only a small but significant effect on species richness.

The catalog of other kinds of mainland edaphic sites as islands could be much amplified. Other special topographic features include dunes, lakes, wetlands, cliff-

faces, alluvial fans, catenas, etc. And to the list of chemically or physically distinct substrates can be added gypsum, alkaline-saline sites, metalliferous soils with zinc, copper, lead, cobalt, etc., hot springs (solfataras, fumaroles, etc.), volcanic substrates (pumice, tephra), silicate-rich materials, alumina soils, phosphate-deficient soils, and so forth. Still other discontinuities in the geodaphic fabric of the mainlands come from sites locally altered by man. So the inventory that piques phytogeographic speculation is enriched. It remains to be seen if common biogeographic threads can be detected among the diverse kinds of isolation on mainlands.

#### CONCLUSIONS

It seems reasonable to expect that island biogeography theory fashioned by MacArthur and Wilson (1967) should apply to mainland islands. The parallels between oceanic islands and islands of altitude, topography or substrate on continents are indeed provocative. Features of spacing between islands, size of islands, and distance from source biota apply to both oceanic and mainland islands. In fact, the major part of this essay addresses the prospectus of these parallels. And yet the outcome of the comparisons seems less than wholly satisfying. The comparison leans heavily on the analogy between real islands and islandlike spaces on continents. The analogy serves mostly to urge upon us a testing of island biogeography theory. But there are dangers in stretching analogy too far. I see two attributes of mainland islands that distinguish them from oceanic islands.

First, mainland islands are not at sea in a void of vascular plant recruits. Rather, they are surrounded by potential founders, a point developed earlier in this essay. Often, then, a mainland island will have a mix of species, some unique to the "island" and some taxonomically identical to the surrounding biota. A second caveat has also been stressed earlier: Mainland island habitats, whether topographic or edaphic, demand a genetic accommodation to their environments by the founder colonists. This may—or may not—be true for their reception on oceanic islands.

Island biogeography theory also concerns itself with the speciation and adaptive radiation phases of island stocking (Ch. 7 in MacArthur and Wilson 1967). For oceanic islands—and indeed for mainland islands—the intriguing questions dealing with events beyond colonization have to do with genetic accommodation to insular, often unique, habitats. Evolutionary theory offers strategies for this accommodation, at every stage from ecotypic adjustment of a wide-ranging species to the genesis of species and beyond. To paraphrase MacArthur and Wilson (1967, preface), I am unable to see any real distinction between biogeography and evolution.

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## FOOTNOTE

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