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BIOLOGICAL ASPECTS OF ENDEMISM IN HIGHER PLANTS

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INTRODUCTION

Rarity of all sorts piques the curiosity of humans. Rare objects, whether discoveries of natural origin or artifacts of cultures, are avidly sought by collectors and are treasured, housed, and exhibited for the benefit of others. This fascination with that which is rare may partially explain the naturalists' and systematists' time-honored preoccupation with rare and endemic taxa. To be sure, there are sound justifications for acquiring and studying rare organisms. But we suspect that the rarity-seeking syndrome in humans has fostered much of the biologist's preoccupation with rare and endemic plants and animals.

The late twentieth century has witnessed exceptional concern for rare organisms and at the same time has seen many rare plants and animals brought close to extinction (22). The extirpation of rare taxa as well as efforts to preserve rare organisms is the product of the vast human influence on the world's biota. Threatened or endangered taxa have received prime press coverage and, in some instances, legal protection. The Rare and Endangered Species Act of 1973 (US 92nd Congress) and subsequent congressional actions constitute one such response to the threatened loss of the rarer examples of biological diversity. We have no problem, then, in finding a wealth of literature on efforts to conserve rare species. Sources of information on what is rare and on the magnitude of the threat to survival range from the Federal Register's list of

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candidate organisms to the popular press, conservation society journals, symposia (e.g. 68, 92, 100, 105, 114), and books (22, 26, 55, 65).

Biologists welcome the public attention given to the urgent need for action against the threatened extinction of rare biota. But aside from defining their rarity, what can biologists say about the attributes—ecological and evolutionary—of rare taxa? Though we recognize that endemism and rarity have several meanings (20, 21, 37, 72), we direct our reply to this question primarily to that form of rarity called narrow endemism. Narrow endemic taxa are those that occur in one or a few small populations (21) and hence are confined to a single domain or to a few localities. We consider only vascular plants.

If, from some magical Landsat image, we knew the ranges to the nearest square kilometer of all of the world's higher plant species (putting aside the difficulties in delimiting ranges), we could look at their frequency distributions. The variation in ranges would be huge, from plants that are nearly "cosmopolites," such as *Chenopodium album,* to plants that occupy small areas, like *Betula uber,* which resides in less than a hectare. This distribution of ranges would have two tails; although we are concerned mainly with the endemics of the left-hand tail of the curve, comparisons of the two extremes would be of interest too.

Are plants with small ranges a heterogeneous group without other common characteristics or does the term *endemic* reflect an assemblage with special attributes? This review focuses on the biological implications of endemism: (*a*) How and where does endemism occur? (*b*) What properties do endemics have? (*c*) What processes occur uniquely in their populations?

BRIEF REVIEW OF IDEAS ON ENDEMISM

Naturalists and botanists have recognized the existence of rare or endemic plants for centuries. Cain (12) ascribes the origin of the word endemic as it is applied to the distribution of organisms to A. de Candolle (16). The great voyages of discovery from the seventeenth through the nineteenth centuries brought to light countless rare and endemic taxa. Though Linnaeus's *Species Plantarum* of 1753 (53) lists no rarities for North America, his South African listing of Proteaceae contains local endemics in *Protea* and *Leucadendron*. In North America, Torrey & Gray (104) record several rarities; notable among them are *Franklinia altamaha* (their *Gordonia pubescens*) and *Silene polypetala* (their *S. baldwinii*), both from Georgia and one of which is now extinct, the other still rare. However, instances where botanists have addressed the questions of how rare taxa arise, exist, and go extinct are seldom found in the vast number of tabulations of rare and endemic taxa.

Adolph Engler (23) appears to be the originator of the dichotomy of old vs new endemics, which has been used extensively by other plant geographers

ever since (e.g. 94, 97, 101, 112, 115). Willis (112) quantified the idea of the youthful endemic with his J-shaped, or "hollow" curves; they became the backbone of his controversial and largely discredited theory of age and area. The taxon cycle (78, 79, 113) is a modern version of the idea that insular species have an evolutionary progression of stages analogous to the development of an organism (11). The new formulation is as unfalsifiable as earlier concepts.

Stebbins (94) provided a genetical explanation for the epibiotic or relictual endemic. Such taxa, he argued, have depleted their store of genetic variation, a process called biotype depletion, and thus they are unable to expand their ranges. In 1980 Stebbins relied on better genetic evidence to modify the hypothesis of biotype depletion (96).

Stanley Cain's now classic work on plant geography (12) set forth the then prevailing notions on the kinds and origins of endemic plant species. His three dicta on endemics merit repeating: (*a*) Endemism includes two types of plants that are confined to single regions–endemics, *sensu stricto,* which are relatively youthful species, and epibiotics, which are relatively old relict species. (*b*) "Youthful endemics may or may not have attained their complete areas by having migrated to their natural barriers. Epibiotics may, but frequently do not, contain the biotype richness that will allow or has allowed them an expansion of area, following their historical contraction of area." (*c*) "A high degree of endemism is usually correlated with age and isolation of an area, and with the diversification of its habitats, as these factors influence both evolution (the formation of new endemics) and survival (the production of relic endemics)" (12, p. 212).

Stebbins & Major (97) recast Cain's two categories as paleoendemism and neoendemism. These authors point to persistent defects in the new vs old endemic dichotomy. First, often little basis exists on which to judge whether an endemic taxon is new or old. On this point, Cain (12, p. 227) has the last word: ". . . the relic nature of an endemic should never be accepted without some form of positive evidence." Second, the mode of origin of either type of endemic taxon remains obscure.

Stebbins & Major based their classification upon the way in which narrow endemics have achieved their restricted distributions, since this varies among species; this system was also proposed by Favarger & Contandriopouplos (24). Stebbins & Major's system incorporates the age of the endemic, its systematic position, and cytological data (chromosome number and ploidal level). In groups of related species, diploids are older than derivative low polyploids, while both high polyploids and diploids are paleoendemics. The several kinds of endemics and their attributes are arrayed in Table 1. Endemics with more than one disjunct population are most likely relictual (paleoendemics), while endemics confined to a single population can be either paleoendemics or neoendemics.

Table 1 A typology of narrow endemics based on three characteristics: systematic position, ploidal level, and age (adapted from 97)

	Isolated			Closely related		
Age	Diploid	Low polyploid	High polyploid	Diploid	Low polyploid	High polyploid
Ancient	Schizoendemic		Paleoendemic	Schizoendemic Patroendemic		
Recent				Schizoendemic	Apoendemic	Apoendemic

Stebbins & Major (97) use the ploidal level and its modes of origin both to categorize endemics and to explain their origins. Paleoendemics are ancient vestiges of taxa that were once more widespread. Their present relictual status is presumably the result of the increasing constriction of their specialized habitats over time. The neoendemics, on the other hand, are recent in origin, have just split off from a parental entity, and may be poised for a further expansion of their ranges and gene pools. *Plantago cordata* (61) and *Stephanomeria malheurensis* (31) demonstrate that both paleoendemics and neoendemics indeed occur, but we currently have no way to evaluate their relative proportion in floras. Between the two extremes in age of endemics, there are, of course, endemics of intermediate age; they remain narrow endemics, confined to a restricted, local habitat.

Recent reviews agree that there are multiple causes of rarity and endemism (20, 21, 73, 96). Neither genetics, ecology, nor history alone will suffice to explain the origin of endemic taxa. Moreover, the interplay among various causal factors will vary in intensity, depending on the particular taxon under scrutiny. Stebbins (96) proposes the gene pool/niche interaction theory to explain origin or rarity and endemism. His notion is grounded on the assumption of multiple causation:

> "According to this theory, the primary cause of localized or endemic distribution patterns is adaptation to a combination of ecological factors that are themselves localized. Factors of soil texture or chemical composition are the most common but by no means the only ones. . . . Next to climatic and edaphic factors, those inherent in the gene pool of the population are of critical importance. They include the total amount of variability, the amount of variability that can be released at any one time, and the amount of variation that can be generated with respect to those particular characteristics that affect most strongly the establishment of new populations" (96, pp. 82–83).

Stebbins (96) uses an abstraction to envision the interaction of these factors: ". . . the niche (is seen) as a depression that is partly filled with a liquid, the gene pool. Variations in the size and steepness of the sides of the niche and the depth to which the liquid gene pool occupies the niche provide the variables that can lead to rarity" (96, p. 83). A deep pool in a niche with a precipitous rim would represent a species that is highly specialized, i.e. endemic.

THE GEOGRAPHY OF ENDEMISM

The narrow or local endemic is the one that best fits the colloquial notion of rarity. However, the term endemism, in its classical biogeographic usage, does not necessarily imply rarity or even small range. Thus, continental or regional endemics need not be, and in fact seldom are, rare. Douglas fir *(Pseudotsuga*

menziesii), canyon live oak *(Quercus chrysolepis),* and Scots pine *(Pinus sylvestris)* are endemic to their respective continents or extensive regions, but they are hardly rare. *Sequoia sempervirens* is a common conifer endemic to the coastal forests of California; *Saponaria ocymoides* is widespread though endemic to the European Alps. But our intuitive perception of rarity is at a much smaller scale of magnitude. A rare species occupies only a small fraction of a regional floristic or geographic province. *Streptanthus niger,* an endemic crucifer, occurs on only one of the many serpentine outcrops in California. It is a recognized rarity, one that Mason (59) would call a narrow endemic.

Cosmopolitan species constitute a very small proportion of the world's flora. Wulff (115) goes so far as to say that there are no true cosmopolites among flowering plants. A few more than 200 species have ranges that occupy each a quarter or more of the earth's surface (0.001% of the flowering plants) (115). A vast majority of the world's seed-plant flora are endemic on some scale, from regional to local. Good (28) states that endemism, in the sense of restriction to a floristic province, accounts for more than 90% of the world's plant species. Further, endemism manifests itself at various taxonomic levels from variety to higher category. Many of the smaller angiosperm families are endemic [sensu Good (28)] and are found in the tropics and Australasia.

Three primary factors—geographic area, ecological breadth, and isolation (13)—describe the distribution of endemics. Endemics are found on all landmasses of the world, both continents and islands, and in all major biomes. More curious is the well-known fact, first identified by Charles Darwin, that the quantity and quality of endemism differ among the major geographic, topographic, and vegetation types. For instance, while species number is smaller for islands than for areas of comparable size on continents, the islands have higher proportions of endemics (13, 28). Most oceanic (i.e. isolated) islands are far richer in endemics than islands near continents. And by virtue of the small size of most oceanic islands, their endemics would perforce be narrowly distributed—i.e. true rarities.

Endemic plants also are distributed unevenly across the land areas of the world. Some places, like mountains and islands, are rich in endemics, while boreal and arctic regions are relatively poor in them. Many parts of the world are well-known centers of endemism: California, the European Alps, the Mediterranean region, alpine regions of central Africa, New Caledonia, Hawaii, the Cape region of South Africa, and the Sino-Himalayan region. Nonetheless, examples of narrow endemics abound in nearly all floras. A small sampling includes *Shortia galacifolia* and *Pedicularis furbishiae* in the eastern United States; *Fremontodendron decumbens* and *Carpenteria californica* in the western United States; and *Silene diclinis* and *Daphne rodriguezii* in the Mediterranean region of Europe.

TAXONOMIC BIAS AND ENDEMISM

Rare plants hold a special fascination for taxonomists. The quest for local endemics, marginal populations, and kindred rarities is a major concern of taxonomists studying regional floristics, once they have described the common taxa. Indeed, the taxonomist has made the greatest initial contribution to cataloging rare, endangered, or threatened plants, thus providing the basis for their conservation.

A binomial that appears in print is not necessarily an absolute, eternal verity. To paraphrase an old adage, "one person's species is another person's variety," or one may simply demote the binomial to conspecific status. So in the taxonomy of rare plants, the dilemma of evaluating taxonomic judgment is ever present. We like to think that the concept behind any legally named taxon is a hypothesis testable to some degree. The name *Berberis nervosa* implies the existence of a system of populations in nature having particular attributes. Yet most binomials (or trinomials) that appear in the taxonomic literature represent little more than opinions that are subject to counteropinions and to taxonomic inflation or deflation by yet another expert.

The very naming of an exceptional organism or group of organisms confers upon it a sense of uniqueness and discreteness. But a subsequent name change or its relegation to synonomy may submerge a local rarity to obscurity. Rarity surely is not a mere artifact of taxonomic judgment. For well-worked temperate areas of the world, rare taxa at the generic, specific, and infraspecific levels—e.g. *Darlingtonia, Pedicularis furbishiae,* and *Pinus contorta* subsp. *bolanderi*—are often unequivocal concepts.

The potential subjectivity of taxonomic status of rarities may express itself in ambiguities at various levels of the taxonomic hierarchy. The compilation of global endemism at the family or subfamily level is a case in point. What may be a small or even monotypic family to one taxonomist is simply a member of a larger family to another expert. Two monotypic families endemic to North America, the Koberliniaceae and Canotiaceae (as used in 28), are just as justifiably placed in a larger family, Celastraceae, which is more cosmopolitan (48). Examples at the genus level are known to all taxonomists—e.g. *Benthamidia* into *Cornus, Roxira* into *Madia, Vulpia* into *Festuca.* At the species level, differences in taxonomic judgment can alter the apparent status from rare to abundant, or the reverse.

Fluctuations in taxonomic status are recorded in the many catalogs of rare, threatened, or endangered plants that have been compiled in recent years. For examples, *Holodiscus discolor* var. *delnortensis,* a rosaceous shrub, was synonymized as ordinary *H. discolor;* and *Iris tenax* var. *gormanii* was demoted to a *forma* of *I. tenax* (87).

Since taxonomists have been the chief recorders of rarity, their familiarity with taxonomic groups containing endemics should shed light on the origin and diversification of endemic angiosperms. Narrowly construed, the work of the taxonomist is simply to name and classify groups of organisms separated by recognizable discontinuities. But, of course, taxonomists usually do more with their materials. Seeking answers to "Why?" and "How come?" questions, they embark on excursions in ecology, biogeography, and evolution. Systematics is the broad field that attempts to synthesize data from diverse disciplines in order to interpret relationships. Broadly speaking, then, systematic studies of endemics should be able to address questions of their origins and radiations, that is, of their evolutionary history and phylogeny (77). Monographs that have utilized endemics and their attributes in accounting for relationships include those on *Epilobium* (74), *Clarkia* (52), *Lasthenia* (66), *Nigella* (99), and numerous others.

Insufficient field records and changes in taxonomic status owing to monographic revision are other sources of taxonomic error in studies of endemism (77). On the basis of only a single or a few collections, local endemics are identified in lightly explored areas, especially in the tropics; further exploration often discloses that the distribution of the putative local rarity has been underestimated. Of course, as Richardson (77) points out, further field work in a floristically rich but little known region can also increase the number of known narrow endemics. Richardson also gives examples of reductions in the numbers of endemics following monographic revision of a group—for instance, *Canarium* (Burseraceae), earlier thought to consist of 45 species that were all endemic—is now considered to have only 9 species, 4 of which are endemic.

Some kinds of endemism permanently escape taxonomic recognition. Disjunct or outlier/marginal populations, aberrant individuals, physiological races, ecotypes, and even sibling species may be rare in nature and possess unique genetic attributes. Harper (37) stresses this overlooked aspect of rarity and cites the example of *Agrostis tenuis,* with its remarkable heavy metal–tolerant races; these variants do not receive taxonomic recognition, and thus, he claims, may not be included on lists of rare species.

Native plants, rare to a local or regional flora, receive the primary attention of the botanist. Less frequently, the botanists' perception of endemism embraces taxa that are introduced from other floras. Lists of endangered plants, for example, simply do not include localized introduced plants. This sentiment is supportable if the rare adventive is not rare elsewhere, either in its native land or as an adventive in some other place. When stripped of our bias against weeds, however, some introduced plants can be considered genuine rarities, either in their native state or in their adopted environments. Klamath weed, *Hypericum perforatum,* once so common a weed in parts of the western United States, has

become less common locally as a result of biological control, although its range probably has not altered greatly. Should it be on an endangered list too?

THE EVOLUTION AND GENETICS OF ENDEMICS

Rarity enters the evolutionary domain in two distinct ways. The first is the scientists' preoccupation with how narrow endemics come into being. The second concerns the fate, i.e. the evolutionary potential and future, of the local rarity.

Origins of Endemism

Opportunism, an ever-present prospect for living systems, plays a major role in the genesis, perpetuation, and extinction of rare taxa. Given time, space, and environmental heterogeneities, discrete biological capacities will develop opportunistically. Mangroves have arisen independently in 23 families (14), and many have small ranges despite water dispersal, e.g. *Pelliciera rhizophorae*. Genetic potential, tempered by developmental and phenotypic constraints, is the only arbiter on the part of the organism. We see no special, novel mechanism that is needed to generate endemic taxa. Narrow endemics are the product of speciation; in their origins and continued rarity they differ only in degree from commoner species.

Two series of studies provide us with models of the evolution of narrow endemism. A major achievement of field biologists is the observation in nature, several times, of the origins of a geographically restricted taxon. The first series deals with the evolution of heavy-metal tolerance by plants on polluted soils, paralleling the pathway to endemism associated with environmental, especially edaphic, peculiarities (9). The second series focuses on the origin of *Stephanomeria malheurensis* from *S. exigua* ssp. *coronaria* and illustrates the likely developmental path for species that occupy a fraction of a larger potential range (31).

Very localized adaptation to soil toxicity is induced by a variety of substances---e.g. copper, zinc, lead, and nickel. Grasses such as *Anthoxanthum odoratum* and *Agrostis stolonifera* can evolve a tolerance to heavy metals in less than a decade. The work of Bradshaw, McNeilly, Antonovics, and their colleagues, summarized in a recent review (9), has demonstrated that tolerance is a direct selective consequence of the presence of these metals and has high heritability. Populations in nontoxic environments may contain tolerant genotypes preadaptively, so natural variation in the capacity to withstand the metals is present in natural populations. The local differentiation of tolerant genotypes can be maintained despite considerable gene flow from neighboring,

nontolerant populations; limited reproductive isolation by differentiation in flowering times has evolved.

While the selective regime on toxic mine tailings might seem to be an extreme case, we have no reason to suspect that the evolution of serpentine endemics, for instance, is any different from the pathway to tolerance of toxic soil shown by widespread colonists, such as *Anthoxanthum odoratum*. The studies on heavy-metal tolerance have illuminated evolutionary mechanisms and provided a base of information that workers on edaphic endemism can use for comparison.

Less direct observation is relevant for studying the evolution of endemics that occupy a small portion of a potential range. Some fraction of these endemics must arise rapidly; these derived species would reside within or adjacent to the range of their progenitors. Two annual composites, *Stephanomeria exigua* ssp. *coronaria* and its presumed derivative *S. malheurensis,* are examples of this (31). *S. e.* ssp. *coronaria* has an enormous range and occupies numerous habitats in California and neighboring states. *S. malheurensis* occurs on a single hilltop of 150 acres in Oregon, at the northern edge of *S. exigua* ssp. *coronaria*'s range. In any year, there are probably fewer than 750 individuals of *S. malheurensis* in existence.

A variety of genetic and morphological indicators verify the progenitor-derivative relationship. Although the two species resemble one another very closely, key reproductive traits differ. The achene weight is doubled in the derivative, and its seed number is lower. Self-pollination is the rule in the derivative, but the progenitor is an obligate outcrosser. Several chromosomal differences, including a reciprocal translocation, occur in the derivative. *S. malheurensis* probably experienced a genetic bottleneck and evolved "after a rapid and abrupt series of events initiated by the occurrence of a mutation at the self-incompatibility locus" (31). Presumably, a self-pollinating individual of *S. exigua* ssp. *coronaria* arose, and this led to the development of an inbreeding lineage and to chromosomal rearrangements that produced reproductive isolation. Although the information on other documented cases is not as complete, this evolutionary route to neoendemism is undoubtedly representative of other cases.

Genetic Variation in Endemics

Are endemics genetically depauperate? Stebbins (94) and others have previously argued that the answer is yes. We need to distinguish a variety of possible causes of lowered genetic variation in endemics. Reduction in genetic variability, or in polymorphism, may be the result of reduced heterozygosity, decrease in mean number of alleles per locus, or reduction in the proportion of polymorphic loci. One explanation for a reduction in polymorphism is that lowered heterozygosity is a response to selection, for both neoendemic and

paleoendemic species. Precise adaptation to narrow ecological conditions—the niche–variation hypothesis (106)—is the most commonly cited route, but there are several possibilities.

Factors other than selection, however, affect heterozygosity. Under selectively neutral circumstances, heterozygosity is influenced by effective population size. Endemics may have small effective population sizes for three reasons. The simplest is that endemics may have smaller total populations than widespread species. In this case, the lowered heterozygosity may be equilibrial and is likely to be permanent. Another explanation is our previous scenario (the *Stephanomeria* case) that implies a genetic bottleneck as the origin of neoendemism. Such a bottleneck associated with rapid speciation might produce a current low level of genetic variation, but this condition could be transitory. With expansion after a bottleneck, heterozygosity would rise and equilibrate as a result of mutation. A third possible avenue to neoendemism is inbreeding. Selfing reduces effective population size and hence heterozygosity.

Endemics might be selfers because their progenitors as founders benefited from self-compatibility (43). At a later stage in divergence, selfers more readily become reproductively isolated from their parent population. The degree of selfing also may vary within a restricted population. Wyatt (116) found that peripheral populations were more self-compatible than central populations in granite outcrop species of *Arenaria*. Some endemics may be selfers because of their mode of origin, not because of their range restriction per se.

We can turn this last point around and ask a related but separate question: Can lowered genetic variation be the cause of restricted range? A lack of ecological flexibility may preclude range expansion in a neoendemic or it may cause range contraction in a paleoendemic. Thus, the answer is a conditional "yes" for some cases, but we have no reliable information by which to judge.

Several examples will illustrate levels of genic variation in endemics. *Stephanomeria malheurensis* shows reduced electrophoretic variation in comparison with its progenitor, *S. exigua* ssp. *coronaria* (31). The alleles in *S. malheurensis* are a subset of those in *S. exigua* ssp. *coronaria*. In the widespread progenitor, 60% of the 25 loci were polymorphic with 45 alleles, but only 12% of the loci with 7 alleles were polymorphic in the endemic derivative. Here, the endemic's lower variability may be a product of a genetic bottleneck associated with the speciation event and/or a result of selfing in the derivative in contrast to the progenitor's outcrossing (30).

Lupinus subcarnosus and *L. texensis* provide similar, but not as extreme, results. The former is an edaphic endemic on sandy soils in east-central Texas; the latter occurs on a variety of soils over a larger range (2). For 6 loci, the average number of alleles per locus was 1.84 for the endemic and 3.12 for the more widespread species. Again, the endemic lupine is probably more inbred than the widespread lupine. We cannot associate lowered genetic variation with

endemism per se, however, because we cannot discern whether these endemics are any more genetically depauperate than selfing, widespread nonendemics.

Conifers of restricted range may also have reduced genetic diversity. Ledig & Conkle (49) found no heterozygosity or polymorphisms in the two populations of the highly local Torrey pine *(Pinus torreyana)*. The same workers report (personal communication) that another narrow endemic conifer, Monterey cypress *(Cupressus macrocarpa)* is quite variable, as are the less restricted California conifers, *P. sabiniana* and *P. coulteri.*

Oenothera organensis also is allozymically depauperate, being polymorphic at only 1 of the 15 loci examined; that single locus displayed only 2 alleles (50). In contrast to the two previous cases, this narrow endemic of the Organ Mountains in New Mexico has an extensive self-incompatibility system and functions as a panmictic unit over the estimated 5000 individuals in existence.

Still other endemics—e.g. *Oenothera argillicola* (51) and *Clarkia lingulata* (29)—exhibit moderate genic variation (see 50 for a recent review). All seven species of the California endemic grass genus, *Orcuttia,* had as much genetic variability as more widely distributed members of the Gramineae (33). Because such electrophoretic evidence is equivocal, Stebbins (96, p. 80) concluded that "there appears to be no recognizable correlation, either positive or negative, between the amount of genetic variation within populations of plant species and the rarity or commonness of the species as a whole." See recent reviews on the genetic structure of plant populations (35, 54).

Genetic systems that promote inbreeding or outbreeding often are associated with particular reproductive strategies and life histories (95). Do rare taxa show a particular bias towards one kind of reproductive biology and life history? Though a number of the case histories discussed in this review examine this question for the particular taxon, we know of only one attempt at synthesis of relevant data (38). It appears from this compilation that "a syndrome of life-form and reproductive characteristics separates a rare and common species." Using lists of rare and endemic taxa of Utah, California, and Colorado, K. T. Harper found woody plants to be underrepresented and herbs to be in excess of expectation (38). Flowers of rare species are more often bilateral than radially symmetrical. From this, he infers that most rare taxa that are bilateral also are outcrossing and depend on healthy insect populations for pollination. Any factors that diminish effective pollination would adversely affect the rarity.

THE DYNAMICS OF ENDEMICS

Shifts from Common to Rare and the Reverse

We endorse the notion that rarity need not be permanent, as Harper (37) reminds us. Taxa once common become rare, and local endemics can become widespread in time. The fossil record abounds with instances of formerly wide

distributions that have become markedly constricted over time. The three sequoias are good examples. *Sequoia sempervirens,* now restricted to coastal California, was once found throughout western North America, from Alaska to southern California and the Rocky Mountains. The highly restricted big tree, *Sequoiadendron giganteum,* now in isolated groves in California's Sierra Nevada, was once more extensive in the California Floristic Province and eastward to Nevada (73, 115). *Metasequoia glyptostroboides,* now found only in a very local relictual area in central China, once grew in both the Old and the New Worlds (25).

The packrat midden record also illustrates this shift from a common to a restricted distribution. Spaulding et al (93) found that the bristlecone pine *(Pinus longaeva)* and the Texas pinyon pine *(P. remota)* were widespread in the Great Basin and northern Chihauhuan deserts during the late Wisconsin glacial period; their present ranges have been drastically reduced. The authors further suggest that the reverse trend, from rare to common, has been the fate of the creosote bush *(Larrea divaricata)* and the ponderosa pine *(P. ponderosa).*

A. S. Watt (109) provides the best documented example on a very local scale of the increase and decrease in the abundance of several species. When he began to observe a single 6 × 6 m plot of East Anglian breckland in 1936, *Hieracium pilosella* was absent and then quite rare after an initial invasion. In 1947, it began to spread; from 1950 to 1958, it was the dominant species in the plot. The incidence of *H. pilosella* then declined very rapidly after 1963, and it remained rare for the next decade, after which observations ceased.

Rarity followed by commonness is a pattern that is implicit in our notions of speciation, yet difficult to detect in the fossil record. If we subscribe to the orthodoxy of monophyletic origins, every new taxon must start out as a local endemic. Yet because of their very scarcity, the beginnings of new species are seldom recovered, let alone recognized, from fossil beds.

This sequence—from rare to common—is not documented often, either because it happens infrequently or is difficult to observe. Harper (37) cites a few examples, some of which must be considered in the special category of introductions to other floras, i.e. of initially rare adventives whose numbers and ranges subsequently increased dramatically. No doubt many weedy taxa throughout the world began as tenuous local introductions, which then spread in varying degrees. Newly arisen alloploid taxa—e.g. *Spartina townsendii* and *Tragopogon mirus*—similarly start as rarities and become more widespread over time. But what about rare native taxa? Are there records of their numbers increasing to the point that they are no longer considered rare? Drury (21) gives the example of *Epigaea repens,* trailing arbutus, once considered rare in New England; it became "an abundant weed after a fire in the oak-pine woods of southern New England" (21, p. 21).

There is good reason to predict that some rarities will remain rare indefinitely. Insular endemics like the Haleakala silversword *(Argyroxyphium*

macrocephala) of Hawaii or *Lobelia elgonensis* of the Afro-alpine are unlikely to increase or decrease their ranges so long as their local habitats are maintained. But one must acknowledge that even status quo rarities may fortuitously break out of their limited ranges. Accidental dispersal to another compatible habitat, increase in the area of a specialized habitat, or a genetic revolution accompanying change in selection within the endemic may trigger the expansion of a local range. Another possible fate for an endemic is a variant of the stasis condition. We can envision a rare taxon moving gradually, all the while closely tracking an environment that itself is moving spatially. At no time then, would the endemic appreciably change in population size or range, only in location.

Extinction: Are Endemics Precarious?

Are small populations in greater hazard of going locally extinct than large ones? Several ideas and some evidence suggest that the answer is "yes." A limited range means that a single disturbance can carry away an endemic. A team of woodcutters could easily remove the entire habitat of *Shortia galacifolia,* and dammed lakes can be larger than the range of the organisms they might drown---e.g. *Pedicularis furbishiae*. Further, we think that taxa on their way to extinction for whatever reason must pass through a period of contraction. Therefore, somewhere between high levels of abundance and extinction, small populations must appear. The notion of demographic stochasticity is relevant here (60, 62). Small populations, if they are as responsive to environmental variation as large ones, are more likely to hit the zero point and go locally extinct. This small population process is analogous to genetic drift.

Observing contemporary natural extinctions is indeed difficult (26), and it is unclear whether extinctions caused by humans—for instance, Hawaiian Malvaceae—function like natural ones. Simberloff (89) provides the only relevant experimental data. According to his study, when tiny mangrove islands were cut in half, the smaller insect populations that resulted were more likely to go locally extinct. Extrapolating from these studies to endemic plants is clearly risky.

Other Forms of Rarity Useful for Understanding Endemism

Having concluded that there is no one kind of rarity, we think it is useful to organize the attributes that generate different kinds of rarity into the form of a matrix (72; Table 2). The cells yield an array of rarity in seven forms, as the outcome of local population size (large vs small), geographic range (large vs small), and habitat specificity (wide vs narrow). Of the kinds of rarity that emerge from the matrix, the categories of sparse species are particularly interesting. A taxon that is subordinate in the community, common nowhere, and yet widespread and with rather wide habitat tolerances, could be viewed as

Table 2 A typology of rare species based on three characteristics: geographic range, habitat selection, and local population size (from 72)

	Geographic range and habitat specificity			
	Large and wide	Large and narrow	Small and wide	Small and narrow
Large, dominant in some places	Locally abundant over a large range in several habitats	Locally abundant over a large range in specific habitat	Locally abundant in several habitats but restricted geographically	Locally abundant in a specific habitat but restricted geographically
Small, nondominant	Constantly sparse over a large range and in several habitats	Constantly sparse in a specific habitat but over a large range	Constantly sparse and geographically restricted in several habitats	Constantly sparse and geographically restricted in a specific habitat

rare by local naturalists. Yet, in fact, sparsity
mism!

Because the narrow endemic species is only one manifestation of rarity, we would like to know whether information on other small populations is instructive about plants with small ranges. Harper (37) contends that rarity depends on the scale of observations: What is rare in a hectare of a county may not be rare over a larger region. Furthermore, this scale factor may have a political or chauvinistic flavor. Pointing to the rare occurrence of *Fritillaria camschatcensis* in Washington State, for instance, ignores its increasing commonness to the north, as well as in eastern Asia. Harper, writing as a population biologist, also notes that in examining rarity a taxonomic bias leads the scientist to overlook manifest or hidden genic diversity within species, some forms of which can be exceedingly rare.

Two other sorts of small populations are especially relevant for an understanding of endemism: populations on the margin of a large range (91) and isolated disjuncts distant from a larger central range (34). The genetic structure of marginal populations has revealed how divergence and isolation arise. Ecological processes in small disjunct populations should be similar to those for narrow endemics, but little is known about either group. A notable exception is Donald Pigott's work on *Tilia platyphyllos* (67). Pigott pieces together climatic, ethnographic, edaphic, biogeographic, systematic, and physiological information on widespread European populations to infer the native status and historic pathway to extreme isolation of "perhaps the rarest native species in northern Europe" (67, p. 305). Thus, isolated disjuncts provide a model, not yet used, for understanding endemics, because in some cases they provide replicate populations for experimentation; the consequences of manipulating them are not as hazardous as those stemming from tampering with a single remaining population.

THE ENVIRONMENTAL DETERMINANTS OF NARROW ENDEMISM

While numerous factors—e.g. history, area, and isolation—limit distribution, the ultimate arbiter of the success in occupying space of any organism, whether endemic or not, is its inherited tolerance to environmental factors. Organisms do not occur where they cannot, but often they do not occur where they might. Thus a major question about endemics is: Are they restricted to the places in which they reside because they cannot exist beyond these bounds, or could they occur over large areas if they were brought there? Are endemics ecologically or physiologically narrow or fastidious? Are the restricted ranges of endemics a reflection of their small niches?
through climate, geology (both topography and soils), or the presence of other

organisms; when environments are narrow in breadth, compatible organisms may be similarly restricted.

Climate

When microclimatic diversity is superimposed on a regional climate, the diversity of organisms can escalate. Differences in microclimates arrayed from forest floors to upper canopies in the tropics promote microhabitat variation that is exploited by distinct biotas. Rock outcrops in deserts create local climates, as do waterfalls, streamsides, and lakes in forest habitats. When local climates are highly discontinuous or uniquely set apart from prevailing climates, some plants will be endemic to the site. In the tropics, epiphytic orchids, aroids, gesneriads, and bromeliads can be microclimate specialists; vernal pool species (in *Downingia, Navarretia,* and *Pogogyne*) and terrestrial orchids found in bogs are good microclimate specialists in temperate floras.

Geological Determinants of Rarity

Geological phenomena relevant to rarity include events associated with the plate tectonics that create mountains and raft continents, with the genesis of discrete lithologies, with processes of land formation, and with the chemical and physical constitution of rocks. Soil formation, especially the genesis of unique soil types, is but one geological setting for the evolution of discrete forms of plant life.

When the products of geological processes are displayed discontinuously, as discrete land forms or as chemically and physically distinct substrates, they may provide the necessary isolation for the genesis of unique biotas. Island endemics are spectacular outcomes of geological events that are arrayed discontinuously over time and space. On continents, topographic, lithological, and pedological discontinuities achieve the ecological isolation essential to species diversity. Isolated mountain ranges on continents often harbor local endemics, owing to the geological events of discrete orogenies—e.g. isolated batholiths, emergence of volcanoes, and separated cordilleras. The Cascade Range of western North America provides some good examples, especially on its isolated volcanic peaks. Some taxa are endemic to a single volcano (e.g. *Pedicularis rainierensis* on Mount Rainier), while other endemics have less narrow ranges and occur on two or more of the isolated volcanoes (e.g. *Arnica viscosa* on Mount Shasta, the Three Sisters, Mount Thielson, and Mount Mazama). Discontinuous distributions similar to those on isolated volcanic peaks are known for the remarkable tree lobeliads of the alpine zone of central African peaks—e.g. *Lobelia elgonensis* on Mount Elgon vs *Lobelia gibberoa* on several Afro-alpine peaks (28).

Edaphic factors—i.e. chemical, physical, and biological properties of soils—are the phenomena most commonly used to draw the link between

environments and endemic taxa. Endemics that are associated with unusual substrates like gypsum, serpentine, limestone, alkaline, and heavy metal soils are well known to field botanists in many parts of the world. Mason (58, 59) was one of the first to articulate the close tie between unusual soils and narrow endemics. He described instances of narrow edaphic endemism in order to illustrate the interplay between genetically determined tolerances and edaphic influences.

Plants endemic to soils derived from serpentinite and other ferromagnesian rocks are found in many parts of the world. Two areas in the tropics are noted for their high incidences of endemics to serpentine: The Great Dyke of Zimbabwe has at least 20 species restricted to serpentine (111), while in New Caledonia 2 monotypic families, more than 30 genera and 900 species (60% of the island's flora), are restricted to serpentine outcrops (42). Examples from these two classic sites are *Dicoma niccolifera, Pearsonia metallifera,* and *Lotononis serpentinicola* from Zimbabwe; and *Geissois pruinosa, Sebertia acuminata,* and *Xylosma serpentinum* from New Caledonia. Several of these taxa are known to be accumulators of heavy metals in unusually high amounts (hyperaccumulators with > 1000 ppm).

Serpentine endemism in temperate areas is exemplified by the monotypic borage, *Halacsya sendteri* of Yugoslavia, and by the several species of the cruciferous genus *Streptanthus* (section *Euclisia*) of California. When the serpentine outcrop is highly local (i.e. "insular"), narrow endemism can be expected. Examples of the Californian local serpentine endemic include *Streptathus niger* of Tiburon Peninsula, *S. batrachopus* of Mount Tamalpais, and *Layia discoidea* at New Idria (45).

Denton's (17) study of *Sedum* (section *Gormania*) illustrates well the edaphic influence on narrow endemism. All taxa grow on rock outcrops in California and Oregon; some are restricted to ultramafic rocks—i.e. serpentinite and peridotite. Denton judged the most highly restricted entities to be relictual, based on their low (diploid) ploidal level, reproduction (self-compatibility and reduced cloning ability), and restriction to the most severe substrates. She challenges the notion that the highest concentrations of endemic taxa "are found in regions that are floristically rich and diverse and where extreme environmental gradients exist" (p. 151). While this relationship may hold for the broad region of the Klamath-Siskiyou mountain area, she found that it does not for local rock outcrop habitats: "The narrowest endemics of section *Gormania* are not found on richer or more diverse outcrops than the more widely distributed taxa" (p. 151).

Two spectacular cases of edaphic restriction in California are in *Streptanthus* (Cruciferae) and *Linum* (Linaceae). Of the 16 taxa in section *Euclisia (Streptanthus),* 14 are serpentine species, and 10 are narrow endemics (45, 46). Sharsmith's (86) monograph of *Hesperolinon* (sometimes treated as a section of

Linum) reveals that 8 of its 12 taxa are obligate or near-obligate serpentine endemics, some of which are quite local.

In a very real sense, the multitude of discontinuities created by geological processes is perhaps the ultimate cause of local rarity and narrow endemism. Given a regional climate, the fractionation of the landscape within that climatic zone by physical and chemical irregularities provides a host of discrete habitats. No doubt some landscape-making geological processes are the root cause of local to microclimate variations. Hence when microclimates foster a unique flora, the ultimate cause must be considered geological. In the absence of geomorphological processes that operate discontinuously in time and space, there would be no irregularity in land forms to produce local climates, and the world's landscapes would be pretty boring too. Humans also create geochemical discontinuities through toxic mine tailings that have provided the settings where local adaptation has been most clearly illuminated (9).

The edaphic specialist leads us to the distinction between two sorts of narrow endemics. Some are closely associated with some distinctive environmental feature that is usually edaphic—e.g. serpentine species and mangroves. In the absence of the feature—e.g. saline soils—the endemic is absent. Other endemics have ranges that simply occupy a tiny fraction of an extensive habitat. In many cases, the unoccupied portion of the habitat seems perfectly appropriate, and the absence of the species is particularly puzzling. Some species of *Astragalus* show this (4).

Plantago cordata and *Zizania texana,* both stream-dwelling endemics, provide good examples for comparison. Within an enormous range (from the Hudson River to northern Florida to Missouri to Ontario), *Plantago cordata* occurs only in scattered, isolated populations and is clearly a paleoendemic plant. Three dozen sites have been reported historically, and in some areas (Michigan and Virginia) the species now appears to be extinct. Meagher et al (61) showed that the heart-leaved plantain has considerable physiological plasticity and is capable of surviving under a variety of conditions. The sites where *P. cordata* occurs do not have any features that conspicuously distinguish them from nearby sites where the plant might grow but does not. These authors point to demographic features such as a low reproductive output and poor dispersal as the causes for the rarity.

In contrast, *Zizania texana* has only a single population on the San Marcos River in Texas, 640 km from the nearest congener *(Z. aquatica)* in Louisiana, and it is probably a neoendemic (103). The site is distinctive for its water chemistry and its equitable environmental conditions; a spring from a limestone source produces neutral to alkaline water with high flow rates and creates a thermal regime varying only 5° C annually. Thus the habitat of this extreme endemic is itself rare, and we do not need to invoke additional factors to explain why *Z. texana* lives nowhere else.

Rarity Resulting from Organism Interactions

RARITY AND COEVOLUTION Synergisms and antagonisms of all sorts between species may result in the genesis of a rare member of any given interactive syndrome. In the following interactions, one of the coevolved pair of organisms might be rare: host-pathogen, two symbionts, two commensals, herbivore-herb, pollinator-plant, host-epiphyte, host-parasite (both flowering plants), and others. At least one member of a synergistic pair is most likely to be rare when the relationship is new. A case in point is the putative hybrid species, *Penstemon spectabilis,* whose origin Straw (98) postulated as follows: The F_1 hybrid between *P. centranthifolius* and *P. grinnellii* was transformed into a species only when an insect vector different from either pollinator of the parent species mediated homogamous matings of the hybrid entity. At an early stage of this speciational event, the new taxon must have been rare.

Another situation where rarity is promoted and even maintained by biotic interaction could well be the host plant–pathogen syndrome. Several years ago, Gillett (27) proposed that pest pressure by bacteria and fungi as well as by invertebrates like insects and roundworms can account for "the apparently pointless multiplicity of species in areas where it has had time to operate" (p. 40). Gillett's paper, written well before the current boom in coevolutionary studies, provided a theoretical, and largely untested, basis for explaining the high incidence of both speciation *and* rarity in some parts of the world—e.g. the tropics, South Africa. Whenever a pest or pathogen finds a suitable host, the host may escape by evolving an ability to resist or avoid it, this in time may warrant its recognition as a distinct taxon. In such situations, not only is the initial divergent population rare, but it may never survive pest pressure to become common.

The same model may be invoked for other adverse interactions, such as herbivory and competitive, or even allelopathic, inhibition. Though current evidence is still meager, we see this as a potential explanation of initial or ongoing endemism that arises out of different kinds of coevolutionary relationships.

SYNECOLOGICAL FACTORS PROMOTING RARITY Endemic taxa are rarely if ever found as isolated individuals or as monocultures in nature. The rare, local endemic coexists with other organisms. Sometimes the community can be as unique as the rare taxon itself—e.g. *Lobelia elgonensis* is restricted to the distinctive alpine flora of central Africa; *Arctostaphylos myrtifolia* occurs with other acid heath flora only on azonal soils derived from Eocene laterites and acid sericitic schist at Ione, California; *Becium homblei* is an endemic of serpentine communities on the ultramafic Great Dyke in Zimbabwe. In other

instances, an endemic is simply a unique member of a common or widespread community type. *Poa pachypholis* occurs only at Ilwaco, Washington, but it is found in the common grass-forb-seacliff community of the north Pacific Coast. *Tauschia stricklandii* grows only at one place in Mount Rainier National Park and at one other site in Washington, but it is a member of the widespread mountain meadow community of the Pacific Northwest.

Considering plants as members of biotic communities poses special questions. Do rare taxa tend to occur more often in unusual or unique communities, rather than in common ones? Does a system of interacting organisms influence the population size and dynamics of rare taxa? How is plant succession related to rarity?

Truly narrow endemics (i.e. extremely local rarities) are most often members of distinctive communities, or at least of singular habitats. This assertion is impossible to verify on a global basis, but some statistics from regional floras do provide corroboration. We have used inventory catalogs of rare and endangered plants in some states of the western United States to generate the data in Table 3. Since the areal extent of unique habitats is at least an order of magnitude less than the area of common habitats, these species' counts reflect an underlying asymmetry in the distribution of endemics. Of course, while unique habitats delimit endemics, the small size of an endemic's range per se may also limit the number of available habitats.

The process of compiling ecological life histories has favored common species. For years, the *Journal of Ecology* has published detailed accounts of the attributes of selected taxa in the British flora. Often included in the species portraits are synecological data: community status, competitive ability, interactions with other organisms, etc. Rarely has the series included narrow endemics. Occasionally, an intensive study of a rare taxon takes on some of the features of an ecological life history; examples include *Lobelia gattingeri* (6),

Table 3 Occurrence of endemics[a] in unique or common habitats, based on data from inventories of rare and endangered taxa.

Location of Inventory (Reference)	Taxon in unique habitat		Taxon in common habitat		Uncertain		Total (Number)
	Number	%	Number	%	Number	%	
California (90)	560	49	388	34	185	16	1133
Oregon (87)	139	49	111	39	34	12	284
Washington (108)	65	47	74	53	0	0	139
Yukon Territory (18)	5	38	8	62	0	0	13

[a]Disjuncts or peripherals omitted.

Pedicularis furbishiae (56), *Silene diclinis* (69), and *Ranunculus ophioglossoides* (19).

Pedicularis furbishiae, consisting of around 600 known individual plants, occupies a precarious habitat along the St. John River in northern Maine. It prefers a calcareous substrate situated in the transient river terraces between the water's edge and the adjacent spruce forests. Its constant association with *Alnus crispa* suggests a host-parasite relationship, which has not yet been confirmed. None of the associated plant species is narrowly restricted to the *Pedicularis furbishiae* localities. Moreover, the transient river terrace habitat is more widespread than the lousewort populations. Neither unique pollinators nor highly local habitat conditions explain its narrow range, and the cause of the restriction is not yet known. *Silene diclinis*, equally rare in southeastern Spain (ca. 600 individuals), occupies a similarly transient habitat—old cultivated orchards of olive and carob on limestone (69). Yet there is nothing to suggest that the habitat is unique either in terms of its associated flora and fauna or in its physical features. It has been suggested, without direct evidence, that both rarities are glacial relicts.

These two examples suggest that there is a common denominator in the synecology of certain rarities. Their occupation of transient or unstable habitats marks them as successional taxa, whose existence could be obliterated when vegetation "matures" (34). As long as the successional stage persists, the rarity's habitat is preserved. Of course, this explanation does not address the issue of how the narrow endemic originated; it simply accounts for its perpetuation.

Quite another view of the successional position of rare plants is espoused by Mahler (57). His brief note merits quoting in toto: "Species occurring in the lower seral stages of plant succession are not apt to become extinct. However, endemic species of rare occurrence in the climax stage of the site . . . are the taxa most susceptible to reduction in population numbers and with catastrophic events or man's activity are apt to become extinct." Mahler (personal communication) believes rare plants of specialized climax habitats are more likely to go extinct if the habitats are narrowly limited in extent.

Rarities also may occupy extensive, stable, climax-forest situations. Their present range restriction may be due either to the past history of the area or to the destruction of their specialized habitat within the climax forest. The well-documented case of the semiaquatic *Plantago cordata* shows how change in a habitat, in this case produced by human activity, can reduce the population size of the entity (61). This highly specialized plantain has not been able to adapt to the shifting man-made habitats now available to it.

The rich species diversity so often found in tropical forests is enmeshed with notions of rarity. At lowland sites, the number of tree species can be remarkably large,—e.g. 502 woody species in a 2000 m^2 area in a central Amazonian forest

(Klinge cited in 47). Furthermore, in any such sample, a small number of individuals often is taken as a sign that the taxon is rare. Representation of a species may be less than one individual per hectare (47). Kubitzki (47) takes issue with the assumption that low population densities in the tropics signify rarity: "Since the tropical lowland forests often encompass huge areas, a low population density does not necessarily imply rarity in the sense of a low global abundancy." Hubbell (41) has shown that the shapes of dominance-diversity curves are similar in tropical and temperate zones. This result indicates, not that the proportion of rare species in tropical forests is higher, but simply that there are more species.

The Habitat Attributes of Rare Taxa

Conservationists who want to protect an endangered endemic species usually emphasize the need to preserve its habitat. This idea is based on the presumption that the vitality of an endemic is dependent on its continued occupancy of a convivial habitat. This notion has not been tested explicitly, though perhaps the reintroduction of a rare taxon into its natural habitat may be construed as an unintentional test. We must ask therefore: What attributes of an endemic's habitat are crucial for its survival? To what degree can the habitat be modified and still host the rarity?

One approach to the problem of how to characterize a habitat for an endemic is to ask what it takes to provide the *lebensraum* for a narrow endemic. The first requirement surely must be knowledge of its tolerance ranges. What does it require in the way of climate (i.e. temperature, light, and water), edaphic conditions, and interactions with other organisms? Since all organisms need some particular mix of these ingredients, the rare plant would seem to require some unique qualitative and quantitative combination of these same elements. In addition, the areal extent of the habitat where these unique requirements are met is likely to be abruptly discontinuous with neighboring areas where the same factors may be present in different proportions or with distinct absolute values. In other words, the habitat of the rarity is expected to be sharply discontinuous with neighboring habitats of contrasting attributes.

For endemics associated with particular habitats, it is surprising that little evidence supports the view that they have narrowed tolerances or that, equivalently, rare species have small niches. Arboreta demonstrate that trees, both endemic and widespread, are capable of growing in habitats and conditions well beyond those in which they naturally occur. Mangroves and other halophytes do not require salt water (3), nor do serpentine plants require magnesium (107). These plants clearly possess the capacity to tolerate conditions that are toxic to, and thus exclude, other species. But the converse need not be true: Species with these unusual capacities are not intolerant of more common environments. Mangroves can grow in the absence of a tidal influx,

but in nature they simply do not. Why these endemics do not grow in more ordinary habitats is a puzzle; their absence is usually attributed to competition from other vegetation or to the high cost of maintaining their special abilities. Understanding the exclusion of endemics from more common habitats is an area that needs further investigation.

The size of the endemic's area, its ecogeographic isolation, its temporal duration (steady state or seral), and its intrinsic attributes are essential features of its generalized habitat and they determine the endemic's fitness within it. A complete roster of information on a plant's habitat and inherent fitness is never available for a rare taxon, and it is uncertain whether we would really understand the endemic even if we had this information. But perhaps there is a way around the impasse of our gaps in information. The bioassay method, used so successfully in other areas of applied biology, could be utilized as a surrogate test of a species' capacities; the rare taxon itself becomes the bioassay unit. The success or failure of introducing (or reintroducing) the rare plant both into its preferred habitat and into a less convivial habitat, as a control, then measures the fit between the organism and its habitat (10).

THE POPULATION BIOLOGY OF RARE TAXA

Plant demography over the last decade has developed into a sophisticated discipline with a substantial body of data (36, 88). Although we are gaining information on the life histories of endemics from numerous studies (e.g. see 5–7 for *Lobelia gattergeri, Leavenworthia exigua* var. *laciniata,* and *L. stylosa;* 70, 71 for *Plantago* spp.), none of the demographic studies on endemics have been as thorough or complete as Sarukhan's classic works (80–82) on *Ranunculus.* Our current knowledge of the demography of endemics does not permit us to answer questions such as whether survivorship, dispersal, pollination, seedling establishment, or other properties differ systematically from plants with a small range compared to those with a larger one.

Two studies on rarity, neither of which concerns an endemic, provide models for future work on endemism, both because they yield interesting results and because they illustrate divergent approaches. Wells (110) observed the development, phenology, mortality, and reproduction of the widespread orchids *Spiranthes spiralis, Aceras anthropophorum,* and *Herminium monorchis* in Bedfordshire chalk grassland in England. He showed how changes in management, such as brush clearing and grazing that occurred more than a decade prior to the emergence of the orchids from their belowground mycorrhizome phase, affected their population recruitment and current dynamics. Sophisticated observational studies and field natural histories such as Wells' work are critically important to achieving the conservation management of endemics.

How local population size is regulated for endemics and why we see many

plants in one m^2 and none in the adjoining m^2 are among the most puzzling ecological phenomena for all sorts of plants. *Carlina vulgaris* is widespread and often common. On Anglesey dunes in Wales, Greig-Smith & Sagar (32) investigated patches where *C. vulgaris* had small populations in order to explore the factors that restricted its local increase. Through a series of experiments in removal, nutrient enrichment, seed sowing, and caging, they inferred that competition from neighbors and low fertility were responsible for local rarity. Sowing additional fruits did increase population size, and predation by small mammals on seed heads limited propagule production. Thus work on plants that are not generally rare can tell us a great deal about dynamic processes in small populations. Applied to endemics an experimental approach such as Greig-Smith & Sagar's would provide much useful information.

SOME CASE HISTORIES

Recognition that some rare taxa are in danger of extinction has provoked intensive studies of the biology of particular rarities. These efforts often are stimulated by governmental orders that certain rare taxa be preserved in their natural habitats. Ecological life-history profiles, with data on demographics, habitat status and potential vitality of the plants, have been compiled for several such taxa. Most such studies are not usually published in accessible journal form but rather, appear as mimeographed status reports to the contracting agency. We have had access to a number of these reports through the kindness of various regional offices of the Rare and Endangered Species Program, US Fish and Wildlife Service. We now examine some of those rarities for which fairly complete status reports have been compiled.

1. *Astragalus phoenix* Barneby—Ash Meadows milk vetch (Leguminosae). This edaphic endemic closely matches the *Mentzelia* case (see below) in its narrow restriction to flats, washes, and knolls of calcareous alkaline soils at Ash Meadows, Nevada (75). Its present population is probably less than 600 individuals, mostly mature (three or more years old). Reproduction is sparse; parent plants produce few pods, and these are entrapped by the parent plant. Seed production, though low, is assured by effective self-pollination. The major impediment to survival—let alone spread—of *A. phoenix* is disturbance of the substrate. Plants do not establish on sites where the distinctive soil crust is broken.

2. *Betula uber* (Ashe) Fernald—Virginia Round-Leaf Birch (Betulaceae). By 1980 a single population of 20 individuals was all that remained of this highly publicized rarity of Smyth County, Virginia (84). Despite its near extinction, implementation of a recovery plan (1982) may foster its survival. So few individuals survive that research on the biology of *B. uber* must be limited to nondestructive sampling and to propagules in cultivation. From 1975 to

1980, half of the remaining individuals (trees, saplings, and seedlings) had been eliminated by natural and human causes. No new recruits have been observed, and the remaining 20 plants are of reduced vigor. Suppression by the overstory and repeated sampling by those studying the restricted endemic appear to account for the reduced vigor. Reproductive output is presumed to be extremely low. Deliberate sowings of seed collected in the wild yielded ca. 1% germination, and of 300 seedlings, only 3 were judged *B. uber;* the rest were similar to the sympatric and widespread *B. lenta*.

There appears to be nothing exceptional in the habitat of *B. uber* to account for its restriction. Its association on disturbed alluvial flats with the successional *B. lenta* suggests that the habitat is transient. Moreover, its co-occurrence with *B. lenta* and *B. alleghaniensis* suggests a hybrid origin for the rarity.

Given its sympatry and resemblance to *B. lenta* (series Costatae, dark-barked tree birches), is *B. uber* a good species? A morphometric analysis (85) supported its specific status as well as its affinity to *B. lenta*. But even if it were reduced to infraspecific status (or considered conspecific with the variable *B. lenta*), the uniqueness of the population would persist. Harper (37) reminds us that rare gene pools may escape taxonomic recognition and still be worthy of preservation.

3. *Hudsonia montana* Nutt.—Mountain Golden Heather (Cistaceae). The status report (63) on this rare North Carolina plant is a model of its kind, for conservation purposes. It contains the best biological information available for the taxon and provides us with a well-documented case history. The plant is restricted to quartzite ledges of the Table Rock area, Burke County, North Carolina. The habitat, unique and local within the southern Appalachian Mountains, is described as "an open heath–bald vegetation type, with scattered shrubs (mostly Ericaceae), few herbs or forbs and much bare ground" (63, p. 291). *H. montana* is restricted to the more open areas of the ledges by competition (overtopping and shading) from other shrubs in the adjacent areas.

The four known populations in the Table Rock area consist of 100–200 individuals, from mature clones (4–8 dm in diameter) to juvenile plants and seedlings. Mature clones are much more common than juveniles or seedlings; nothing is known of the plants "stored" in the seed bank, though four-year-old seed could be germinated. Reproduction is both sexual (selfing and outcrossing) and vegetative (rooting at the edge of a growing clump). The clonal mode predominates. Seed is dispersed locally (precinctively).

H. montana appears to be relictual, surviving in restricted sites where its locally xeric habitat may persist. Barring changes to the surrounding terrain, and with Federal protection, this remarkable rarity should persist indefinitely as a narrow edaphic endemic.

4. *Lupinus padre-crowleyi* C. P. Smith—DeDecker's lupin syn. *L. dedeckerae* (Fabaceae). This rare and distinct Mono Basin (California) lupin

appears to be a newly evolved entity (102). Its small but vigorous populations are not confined to exceptional edaphic habitats and are associated with both common as well as locally rare species of the region. Changes in late Pleistocene climate following hybridization may have left the new entity stranded following retreat of one of its parents. Height-class distribution for 8 subpopulations reveals that the normal-to-left–skewed cohorts contain young recruits. Thus the total population size of the species (100,000± individuals) appears to be large enough, with vigorous replacement, to avoid extinction. The plastic breeding system (insect pollination plus self-compatibility) of this wholly sexual species supplies sufficient seed for continuity, if seed-to-established-plant conversion is successful. Thus, barring natural or human disturbance, *L. padre-crowleyi* should expand its range into nearby compatible habitats.

5. *Mentzelia leucophylla* Brandegee—Ash Meadows stick-leaf (Loasaceae). This is one of several plant and animal taxa narrowly confined to the local spring-fed "oasis" in the desert, Ash Meadows, Nye County, Nevada (76). "Ash Meadows is an extensive lowland plains area of the Amargosa Valley (around 75 sq. mi.), which is the more or less dissected remnants of a large Pleistocene playa that extended well into California. Hence the soils are extremely fine textured (silts and clays) and have slow internal drainage, and the water table is near the surface in much of the area . . . The soils are light colored and have a high salt content; many are heavily salt encrusted at the surface" (8). The present population of the plant is estimated to be less than 100 individuals, occupying an area less than one mile square. *M. leucophylla* is presumed to be a biennial, though individuals may flower the first year; nonbolting rosettes also are present. Reproduction is presumed to be by seed from outcrossed individuals. The taxon may be genuinely evanescent—doomed to extinction after its short life span. It is thought to have arisen after the pluvial lake of 10,000 years BP disappeared. *M. leucophylla* is a polyploid (n = 18), exceptional in its group for having a base number of 9, rather than 11, the usual base number among its congeners. It is very sensitive to disturbance and also is subject to decimation in drought years. Should the climate change, survival of the species would be further impaired. *M. leucophylla* is thus a relictual, highly local, edaphic endemic, whose survival is made precarious by continuing climatic deterioration, aggravated by human disturbance.

6. *Shortia galacifolia* T. & G.—Oconee Bells (Diapensiaceae). This clump-forming herbaceous perennial, a plant of great ornamental horticultural value, is endemic to small portions of the southern Appalachian Mountains of the eastern United States. It is restricted to rhododendron thickets or to mixed (cove) hardwood stands, often in close proximity to watercourses. The status report (1) is based on 1979 field studies of 20 historic sites. The report lists three major habitat types (Angiosperm forest, mixed forest and shrub), which can be

found in a wide range of topographies (mountains, hills, and ridges; scarps, bluffs, cliffs, and escarpments; valleys, gorges, and channels; plains and flats; ravines) and on a wide variety of metamorphic substrates. The species successional status "ranges from mid/transient to late/climax stages." Eleven localities were censused, using the clump or colony (from a few cm^2 to many m^2 in size) as the population unit. At 7 localities, the sample consisted of all the population units, 2–125 in number; some localities showed a range of cover classes but 6 localities had none (i.e. they were all of one class?). Population areas for the 11 localities ranged in size from 1 m^2 to 1730 m^2, with 5 localities of less than 10 m^2 in area. While the large size of some clumps are the result of clonal increase via underground stems, some sexual reproduction does occur. In some sites very young seedlings can be found on late-stage, decaying logs. *Shortia galacifolia* has lost territory largely due to human interventions—sites inundated by dams, disturbed by logging and collecting for garden use, and other habitat intrusions. The only natural disturbance making inroads on population size is recurrent stream bank slippage. With sufficient habitat protection, Oconee Bells should be able to maintain itself in the discrete sites in perpetuity.

7. *Silene polypetala* (Walt.) Fernald & Schubert—Fringed campion (Caryophyllaceae). Ever since its discovery in the late eighteenth century (15), this distinctive silene appears to have continued as a rare, local endemic. Presently it is confined to two disjunct regions of the southeastern United States: west central Georgia and the southwestern Georgia–Florida border area. The habitat for the more northern localities (Talbot and Crow counties, Georgia) is "rich deciduous woods on river banks and on hardwood bottom lands near the Flint River" (15). The more southerly populations are in deep calcareous ravines along Lake Seminole and the Apalachicola River. Both localities support mixed communities of hardwood tree species, with a shrub understory. Population sizes range from 25 to 250 individuals, and one population consists of several hundred individuals. All populations were deemed vigorous, when seen in flower. No seedlings were observed; individuals in some populations are propagated by the layering of decumbent stems. *S. polypetala* is rare presumably because of its close tracking of a unique habitat—forested ravines and hardwood bottoms bordering certain rivers in the southern United States. Though other eastern North American silenes are known from woodland habitats (*S. virginica, S. ovata,* and *S. rotundifolia*), the very distinct *S. polypetala* appears to be the most mesic taxon of them all. Its origin and relationships are obscure; with two other eastern North American taxa, it is linked with species in western United States—*S. laciniata* and *S. parishii* (40). Crosses of *S. polypetala* with several eastern North American silenes yielded vigorous but wholly sterile F^1 hybrids (44).

RARITY AND CONSERVATION

The conservation of narrow endemics that are threatened or endangered has become a major concern shared by governments, conservation organizations, and individuals. An axiom for preservation is "Know thy organism." An oft-repeated justification for preserving rare populations is the argument for the conservation of gene pools—i.e. the unique genetic resources of rare organisms may be useful in breeding programs. Two recent works (26, 83) address the relationship of genetics and evolution to conservation. At symposia on rare plant conservation, detailed protocols on the information-gathering process are provided that could yield valuable biological information (64, 68, 100). Papers by Henefin et al (39), Morse (63), and others (64) provide procedures for studying the biological attributes of rare taxa. Morse's (63) account of *Hudsonia montana* is a good example of a biological life history of a rare taxon. Because we are convinced that biology as a whole will be enriched by the study of rare organisms, we encourage the biological community to undertake more extensive research on the genetic, demographic, reproductive, and habitat characteristics of rare plant populations. More comparative studies to contrast the biologies of rare taxa with those of related common ones would be particularly valuable.

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