The Biological Aspects of Rare Plant Conservation
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Seven forms of rarity

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Summary

There are many ways in which a species can become rare and this path has profound evolutionary and ecological consequences. A theoretical framework of an eight-celled table is proposed for the different types of rarity depending on range, habitat specificity and local abundance. Seven forms of rarity are discussed with examples from the North American flora, in particular that of the narrow endemic. Studies of the competitive abilities of sparse and common prairie grasses provide insights into the biological nature of rarity and show that competitive abilities are more critical to persistence than to the regulation of abundance. Natural selection may operate to favor traits which offset the disadvantages of local small population size. We reach conclusions that are both unexpected and relevant to practical conservation philosophies.

Introduction

Perhaps the most common conclusion in this book is that there are many sorts of rare species. This fact is probably because species become rare by several pathways. If rarity has a variety of causes, then the evolutionary and ecological consequences of rarity may be equally diverse.

For instance, a species may be rare because it is especially subject to a density-dependent fungal pathogen, as it is the case with American Chestnut, *Castanea dentata* (Marsh.) Borkh. (Nelson, 1955). Let us contrast this case with one of rarity because of range contraction due to climatic change: *Pelliciera rhizophorae* Tr. & Planch., a mangrove usually placed in a monotypic family, the Pelliciaceae, close to the Theaceae, is now restricted to the Pacific coast from Costa Rica to Colombia, but occurred in Chiapas, southeast Mexico, in the Oligo-miocene (Langenheim *et al.*, 1967). In the case of the chestnut, the fungus has produced a major shift in life history, converting a large tree to a shrub. No such radical morphological or demographic changes accompany the contraction of range in *Pelliciera*. Its local densities remain high, and monospecific stands may still occur, albeit over a smaller area. For *Pelliciera*, we expect that island biogeographic or genetic consequences of drift will predominate; for *Castanea*,

the local consequences are ecological and epidemiologic. These two pathways to rarity show remarkably divergent responses. If we can dissect the varieties of rarity, our understanding of rare species may benefit from the provision of a basis for investigating causes and consequences of rarity.

Because authors are often concerned with consistent traits among special sorts of rare species (Griggs, 1940; Stebbins, 1942; Drury, 1974; Smith, 1976), the state of being rare seems rather monolithic from the literature. For instance, Griggs (1940) regards rare species, in his case geographic outliers of the Laurentian shield, as being competitively inferior. Drury (1974) views rare species as those where interbreeding among populations is severely restricted. A great amount of fascinating heterogeneity among rare species is unfortunately obscured by these generalities. In this paper I have two goals, first to construct a general scheme to characterize the varieties of rarity, and secondly, to show how natural selection operates on rare species (Rabinowitz, 1978; Rabinowitz and Rapp, in press).

This classification of rarity differs from the others in this book (see Ayensu Chapter 2), Good and Lavarack (Chapter 5) or Bratton and White (Chapter 39) for three fundamental reasons. First, the aim of drawing up a list of species is not imposed upon me, and so I need not employ the categories to fulfil a legal charge. Secondly, no specific taxa, geographical locality, or administrative units need be kept in mind. Thirdly, the endangered or threatened status of plants is not my central concern. These factors free me from the constraints of pragmatism, and this may contribute some clarity in exploring the biological consequences of rarity. Hopefully, the exercise will permit some new perspectives for people engaged in more practical concerns.

A classification of rare species

To construct flexible categories for rarities, I distinguish three aspects of the situation of a species: geographic range, habitat specificity, and local population size, all of which have been introduced by previous contributors. Most of us would agree that each of these attributes is related to rarity in some way. For instance, illustrating with plants from America, *Andropogon gerardi* Vitman has a huge range – Florida to southern Quebec, westward to northern Mexico and Saskatchewan – whereas *A. niveus* Swallen is restricted to central Florida, and thus is more rare. With respect to habitat specificity, *Solidago canadensis* L. seems quite 'plastic' about where it grows – in thickets, roadsides, forest edges, clearings, prairies, fallow fields, varying soil types, moisture regimes and successional states. *Solidago bartramiana* Fern occurs only on slaty ledges, and *S. sempervirens* L. grows only in brackish conditions of coastal dunes; these two latter species, due to their habitat restriction from whatever causes, are validly regarded as rarer than *S. canadensis*. With respect to the third trait, local population size, *Festuca scabrella* Torr. and *F. idahoensis* Elmer are co-dominants with

Agropyron spicatum (Pursh) Scribn. & Sm. in the Palouse prairies of western North America, and thus their local abundances are large even though this type of grassland is quite limited in geographic extent. In contrast *Festuca paradoxa* Desv. is never dominant or really very common, and because of this 'chronic' local sparsity, we would consider it rarer than the other fescues, despite its more extensive range.

If each of these attributes is dichotomized, a $2 \times 2 \times 2$ or eight-celled block emerges (Figure 1). Although creating the hazard of false reification – that is, converting an idea into an object – such a simple scheme can aid in focusing our thoughts, and this is my intention. The patina – a gloss or incrustation conferred by age – of monolithic rarity may have hindered our understanding of an exceedingly heterogeneous assemblage of organisms. Since the products of rarity are diverse, the causes of rarity and the genetic and population consequences of rarity are undoubtedly equally multiple.

A second caution with such a scheme is that it is a typology of results (by intention) and not a typology of mechanisms or causes (Gould, 1977). Results of similar appearance may mask divergent processes; for instance geographically restricted species may be relictual (Cain, 1940; Ricklefs and Cox, 1978) or incipient (Lewis, 1966). In the absence of the relevant studies, the classification of processes resulting in rarity is a distant goal.

Seven of the eight cells contain rare species in some sense of the word. Only the upper left cell, species with wide ranges, several habitats, and locally high abundances, do not merit the designation. *Chenopodium album* L. is an example: it is circumtropical, nearly circumtemperate, and can occur in dense or sparse stands in weedy and non-weedy situations (Kapoor and Partap, 1979).

Directly beneath is probably the most ignored category of inconspicuous and unspectacular plants, sparse species – those with large ranges, several habitats, but consistently low populations. Such species are familiar (and pedestrian) to most botanists and especially to entomologists. In North America, *Dianthus armeria* L. is a familiar example. One is never really surprised to see Deptford Pink, but one would be quite startled to see it occupy 80 per cent of the biomass in a large field. Sparse plants are those, which, when one wants to show the species to a visitor, one can never locate a specimen! To me, they are the most curious form of rarity because they seem not to have a 'favored' habitat. They almost never appear on lists of 'threatened' or 'endangered' species. Sparse species of prairie grasses in Missouri are the topic of our current studies on the mechanisms of persistence (Rabinowitz, 1978; Rabinowitz and Rapp, in press).

Two of these cells appear to have very few residents, namely species of narrow geographic range but broad habitat specificity. Is this *modus operandi* unfeasible for some evolutionary or ecological reason or do ecologists simply pay little attention to such species? If the former is true, it is of great interest to know why such species either do not arise or have large probabilities of extinction. For instance, demographic stochasticity, which is a process in small populations analagous to

GEOGRAPHIC RANGE	Large		Small	
HABITAT SPECIFICITY	Wide	Narrow	Wide	Narrow
LOCAL POPULATION SIZE				
Large, dominant somewhere	Locally abundant over a large range in several habitats	Locally abundant over a large range in a specific habitat	Locally abundant in several habitats but restricted geographically	Locally abundant in a specific habitat but restricted geographically
Small, non-dominant	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

Figure 1 A typology of rare species based on three characteristics; geographic range, habitat specificity, and local population size

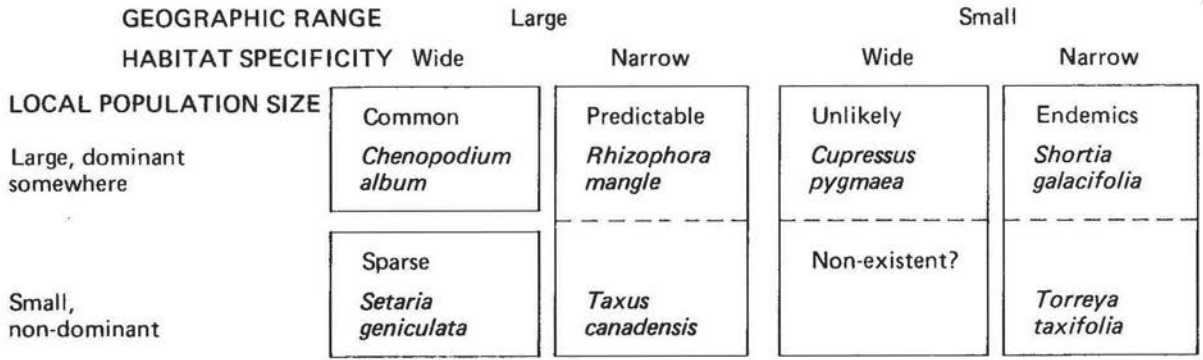

Figure 2 Summary and illustrations of species for the typology of rare species shown in Figure 1

genetic drift and which results in fluctuating population numbers, due to small sample phenomena (May, 1973; Mertz *et al.*, 1976), may cause local extinction. These deletions of populations may reduce the variety of habitats occupied and, in essence, convert a perhaps unstable species into one in the categories on the right in Figure 1, namely an endemic. Examples of such unusual species are *Cupressus pygmaea* (Lemmon) Sarg., a dwarf conifer found on coastal terraces of Mendocino County, California (Westman, 1975; Westman and Whittaker, 1975) and *Fuchsia procumbens* R. Cunn. ex. A. Cunn., a New Zealand plant (Given, Chapter 4), with small range but several habitats.

Species which have wide ranges but are associated with particular habitats are generally quite predictable in their occurrence (especially if you are a good systematist). If one is in a bog, on the strand, or on serpentine soils, one can generally find the plants peculiar to these places with relative confidence. In Caribbean Panama, on calm marine shorelines, for instance, one is very likely to find *Rhizophora mangle* L. and other mangroves, which are characteristically abundant where they occur. These species tend to be precarious as a result of habitat destruction. Mangrove swamps often are endangered because they are a habitat that many people find objectionable for a variety of reasons, usually that the trees are between them and the sea. In contrast to mangroves, which are nearly always locally common, Dr Given (Chapter 4) has given us the example of *Lepidium oleraceum* Forst.f., Cook's scurvygrass, once collected for vitamin C and now found on coastal rocks in several scattered sites around New Zealand but in locally very low densities.

Species with both narrow geographic range and narrow habitat specificity are the classic rarities in the sense of restricted endemics, often endangered or threatened. These rare endemic plants are often showy or newsworthy in some way. *Shortia galacifolia* T. & G., an attractive member of the Diapensiaceae, is endemic to several escarpment gorges of the Appalachian mountains and has endeared itself to the attentions of botanists for over a century (Gray, 1878; Ross, 1936; Davies, 1955, 1960; Rhoades 1966; and Vivian, 1967).

On an autecological level, such species receive a lot of attention. Terrell *et al.* (1978), for instance, have recently provided an excellent comparative study of the endemic aquatic *Zizania texana* Hitchc. and the widespread *Z. aquatica* L. *Zizania texana* lives on only 2.4 km of the upper San Marcos River in Texas in unusual alkaline conditions where water temperatures vary only 5°C annually, in contrast to the more varying conditions of *Z. aquatica* (see also Lucas and Synge, 1978).

The extreme of a restricted rare species is one that is known to have existed, but has been subsequently lost. The intuitive notion of a rare organism is one that is difficult to find, and the most endangered that a species can become is to be declared extinct! Lost species hold a particular fascination, rather like ships lost at sea. A fine example is *Betula uber* (Ashe) Fernald, Ashe's Birch or Virginia Round-leaf Birch, mentioned by Ayensu (Chapter 2), first collected in 1914 from

Smyth County, Virginia. The only other collection, near the first locality, was a single undated specimen rediscovered in 1973 (Mazzeo, 1974). After numerous searches, Johnson (1954) asserted:

> The only conclusion that seems warranted at this time from these several failures to rediscover this birch is that it probably no longer exists as an individual and very likely never did so in the form of a population. Ashe's birch has probably died or been destroyed in the process of urbanization of the community in which he found it 40 years ago. It is probable that this birch variety was founded solely on an aberrant individual and certainly does not appear to deserve further consideration as a species.

Sixty-one years after the original collection, the plant was rediscovered in 1975 by Douglas Ogle, who found the tree by employing an 'if I were a horse' strategy (Preston, 1976). Reasoning that when Ashe collected, the present paved roads did not exist, Ogle searched along traces of logging roads shown him by an elderly resident. The tree is extant in a population of 12 mature trees, some of which were reproductive, one sapling, and 21 seedlings (Ogle and Mazzeo, 1976). *Betula uber* is so rare that it was lost for over 60 years and is an example of the tenacity of botanists, who continued to hunt for living representatives for over half a century, against all reasonable likelihood of its continued existence. Its rediscovery was reported in *The New Yorker* magazine (Kinkead, 1976).

This eight-celled scheme does not include the category of 'pseudo-rare' organisms about which, perhaps, the most sound data exist and which tells us the most about the biological processes occurring in small populations. Species on the margins as opposed to the central portions of their ranges have been an active aspect of evolutionary studies (Stebbins, 1974), especially for *Drosophila* (Lewontin, 1974). In plants, for example, marginal and central populations of *Paeonia californica* Nutt. ex. T. & G. (Stebbins and Ellerton, 1939; Walters, 1942; Grant, 1956, 1975) and more recently of *Hordeum jubatum* L. (Schumaker and Babble, 1980) were compared to assess the relative effects of reproductive isolation, genetic drift, and selection on genetic structure. Ecophysiological and reproductive studies on marginal populations shed light on mechanisms determining or controlling range as shown, for example, by Pigott's studies on *Tilia platyphyllos* Scop. in Britain (Chapter 25). These studies on marginal rarity have the major advantage that they have an automatic control. Monitoring rare species (for instance, Bradshaw's long term assessments of the Teesdale rarities) tells us a lot about the characteristics of these taxa. However, in the absence of comparative data for related common taxa, essentially control species, we cannot judge whether the traits of rare plants are unique to them or are some random sample of plant traits in general and unrelated to the rare state.

Perhaps the least information is available on the fine scale causes of changes in abundance within what seems on casual view to be a homogeneous and

appropriate site. Changes of orders of magnitude in population sizes occur on the scale of meters without striking underlying heterogeneity, and this garden-variety variance in density is very puzzling. Greig-Smith and Sagar (Chapter 32) investigated the causes of local rarity in *Carlina vulgaris* L. in a dune site where the plant was locally common very close by. Excluding both the absence of disturbance to produce new sites for establishment and also nutrient deficiencies of the substrate, they found that augmentation by sowing fruits increased local populations and that the likely source of propagule depletion was mammal predation on seeds.

Competitive abilities of sparse species

One aspect of our study of sparse prairie grasses in Missouri is illustrative of the difficulties in dissecting causes versus consequences of rarity. In order to examine the common assumption that rare species are inferior competitors (McNaughton and Wolf, 1970; Schlesinger 1978; Grime, 1979), we established de Wit competition experiments from seed in the glasshouse from May to September (see Harper, 1977, for a general explanation of de Wit plots and Rabinowitz in review for experimental details and a more thorough analysis of the data).

We find the paradoxical result that the sparse species are very nearly uniformly superior competitors to the common grasses. This result is seen in the bottom four graphs (Figure 3) which show the average total yield of a sparse grass on the left of each diagram and the average total yield of a common grass on the right. For the sparse grasses, yield falls above that expected on the basis of the monocultural yield (the dashed line descending to the right). In contrast, for the common grasses, the yields fall below expectation (dashed lines descending to the left). Thus, the convex curves of yield demonstrate the superior competitive abilities of the sparse species.

As a consequence of the superior competitive abilities, however, individuals of the sparse species grow largest when planted in low proportion with a common grass in high proportion (Figure 4). Presumably, this results because the presence of the common grass is more like empty space to a sparse individual than is the presence of other sparse individuals. The two top diagrams (Figure 4) show the dry weight of an individual of a sparse species versus its proportion in a mixture. The identity of the competing species is shown beside each line. For instance, in the upper left diagram, individuals of the sparse species *Festuca paradoxa* are largest when planted as 10 per cent in a mixture with the common grass *Andropogon gerardi* planted as 90 per cent. Individuals of *Sphenopholis obtusata* (upper right diagram) also grow largest when planted in low proportion with either of the common grasses. Contrariwise, the individuals of the common species grow largest when in monoculture or in the presence of other common species (Figure 4, the bottom two diagrams). Thus, an initially paradoxical result is reinterpreted into the Panglossian ('the best of all possible worlds') result (Gould

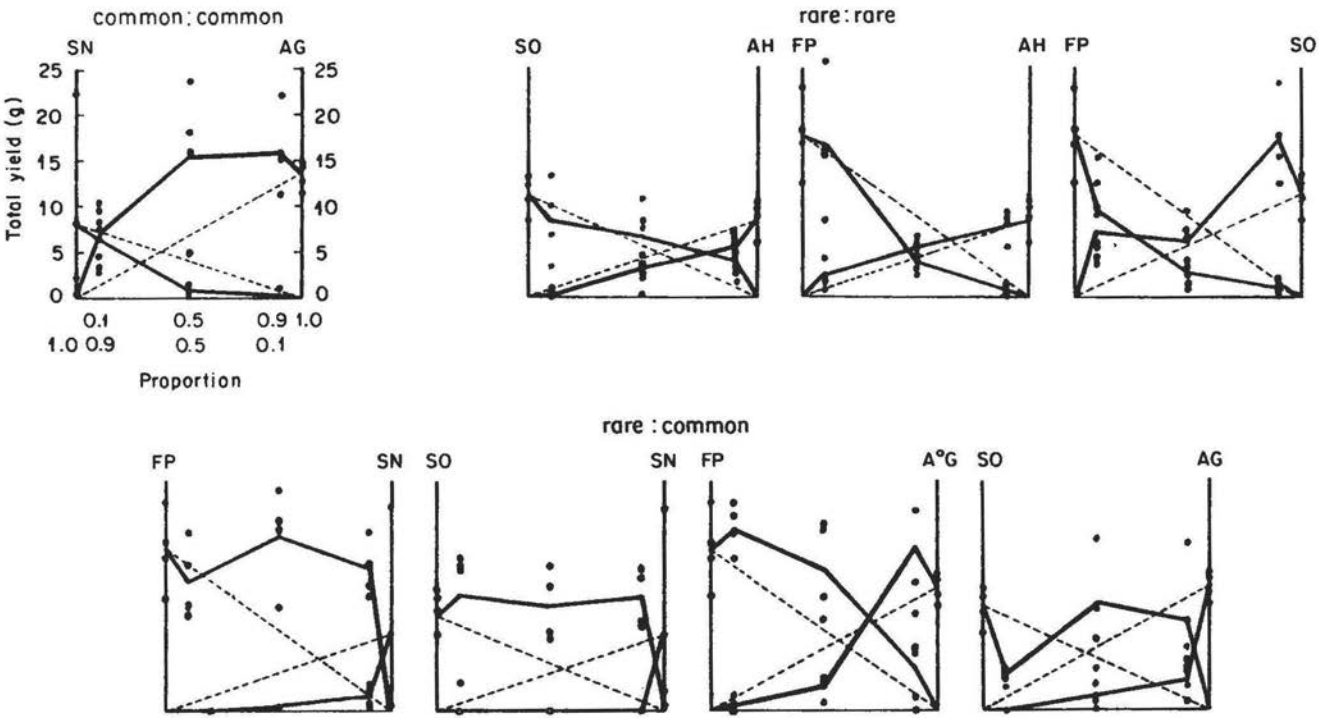

Figure 3 De Wit plots of the total yield from pairwise competition experiments with rare and common species of prairie grasses. Symbols: for common grasses, SN = *Sorghastrum nutans* (L.) Nash, AG = *Andropogon gerardi* Vitman; for sparse grasses, SO = *Sphenopholis obtusata* (Michx.) Scribn., AH = *Agrostis hiemalis* (Walt.) B.S.P., and FP = *Festuca paradoxa* Desv.

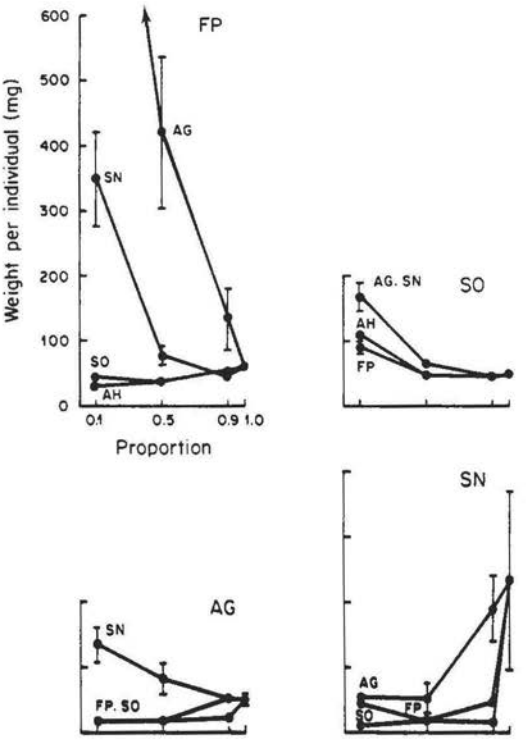

Figure 4 Size of individuals grown in different proportion and with different competitors for rare and common species of prairie grasses. The symbols are the same as for Figure 3. Sparse species are in the top row, common species in the bottom row

and Lewontin, 1979) – that sparse species grow best when sparse, and common species grow best when common.

Natural selection and sparse species

Natural selection cannot, clearly, select for rarity, and it is impossible for rarity to be an adaptive strategy. An individual may be at an advantage because it is rare, for instance, if its herbivores or pathogens cannot find it. Rausher (1980) provides an interesting example for the locally rare *Aristolochia serpentaria* L. and its herbivore *Battus philenor*. As a consequence of the advantage, the individual will reproduce more, become locally more common, and therefore automatically loses the advantage. Thus it is quixotic to say that an organism is adapted to be rare.

But one can assert that an organism may be adapted to the condition or situation of being rare. If an organism is rare for whatever reason (for instance, the fungal pathogen *Endothia parasitica* which infects chestnuts), there are additional disadvantages customarily associated with small population size, for instance being a long way from potential mates. Natural selection can act to favor traits which offset the disadvantages of small local population size, no matter what its cause, and thus render local extinction less likely.

The competitive abilities of the sparse species are best viewed in this light. Since the sparse grasses are competitively superior, the competitive abilities (at least in the short term) cannot be the cause of the sparsity. But given that the species are sparse, the trait that they grow best when surrounded by many individuals of common species is clearly advantageous and will function to render persistence more likely. The competitive abilities are best understood as having nothing to do with the regulation of population size but as a mechanism that offsets a major disadvantage of rarity.

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