Species at Risk: Research in Australia

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RARE SPECIES: PRECIOUS OR DROSS?

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This chapter addresses the problem of rareness, both in its biological and social contexts, with the aim of assessing whether rare species should be conserved. Indirectly, it suggests the factors which need to be taken into account if conservation of rare species is to be a goal. It analyses attitudes towards rarity, and examines the scientific value of studying rare species.

RARENESS IN COMMON USAGE

Rarity, like so many words in the language of biology, is derived from common usage where its meaning tends to be imprecise. Failure to appreciate the reasons for these imprecise meanings leads to difficulties when arguing the case for conservation of rare species. For instance, a connotation in which the term rareness is used in common usage implies that rare species are curiosities only of interest to specialised collectors; this implication is very pervasive, and those wishing to advance the conservation of rare species on biological grounds must be aware and take account of it when presenting their own case.

The state of being rare, in an object or a species, evokes human reactions which are important if conflicting attitudes towards the conservation of rare species are to be understood. Since the quality of being rare only requires that something else is common, it is a relative state that allows a value to be placed on it. This might be termed the sociological aspect of rarity. It is, firstly, a consequence of the human trait of gathering or collecting objects. In the endless list of objects which could be the subjects of collections, there is particular allure in collecting those which are difficult to acquire; generally the most difficult things to acquire are those which are rare, that is, the things that are uncommon. In this way all sorts of human or natural objects have come to be regarded as rare and hence material that it is desirable to collect.

The sociological aspect of rarity provided the original motive for the establishment of the collections that later became the large public museums, art galleries, and libraries of the western world. In part, the movement to establish reservations for the larger animals and plants whose status has been altered by human activities is of this sort. Examples are reserves established to protect some birds, the large cats, some ungulates, elephants, rhinoceros, and large parts of the tropical biota generally. Organisms in this class are "the rare and endangered species" of the conservation literature and of common speech.

In addition to emphasizing the desirability of rare species, the literature concerned with the "rare and endangered species" emphasises the role of humans in producing their condition and, also, upon the number of species that have become extinct through human activity. It emphasizes human responsibility and suggests that the rate of extinction should at least be reduced by a more thoughtful approach to human activities so that, by conservation, the persistence of "rare and endangered" species is no longer in jeopardy.

By contrast with these, understandably human, points of view, there is another - namely that there are more species extinct than currently living, and that irrespective of human activity, extinction is a normal biological process which cannot be halted. From such a view it is only a short step to conclude that rare species are heading for extinction anyway, and, therefore, that it is a waste of money to try and save them.

Rare species are also regarded by some as the non-useful antithesis of common species; it is pointed out that common species have large populations and, because of their abundance and ubiquity, perform most of the processes on which the ecological community depends.

The corollary of this is that the contribution of rare species to community dynamics is insignificant and can be readily dispensed with; that is, they are dross.

Among such contrasting viewpoints, what can reasonably be achieved by studying the biology of rare species? The nature of the information revealed by study is dependent on the hypotheses we hold about the significance of rare species in terms of uniqueness, relict nature or functional role in the dynamics of a community. It is in terms of the development of possible hypotheses that the study of rare species assumes scientific significance.

The four contrasting views of rare species, mentioned above, are very general. By contrast, a rigorous approach is required which will provide, in biological terms, hypotheses accounting for rareness, a coherent argument for the retention of rare species, and an indication whether it is possible to retain rare species. If we contrast this approach with one of the hypotheses mentioned above, namely that rare species are inevitably going to extinction and hence are not worth studying, it is obvious such a negative approach produces no new biological knowledge and no understanding of the nature and cause of rareness.

RARITY IN THE CONTEXT OF THE ECOSYSTEM

The study of species richness and its maintenance springs from the observation that tropical ecosystems are richer in species than those of higher latitudes. Study of this phenomenon has been stimulated by the development of indices which allow comparisons between ecosystems. It is characteristic of the numerous samples which are the basis of these studies that those taken from diverse environments have a few species or taxa represented by numerous individuals, whilst a large number of taxa are represented by only a few individuals.

Ecosystems rich in species also occur outside the tropics. For instance, Lamont, Downes and Fox (1977) demonstrated an extraordinary species richness, comparable with tropical situations, in heathland in Western Australia; Hopkins and Hnatiuk (1981) in a nearby area recorded a much greater number of species, but only about 80 percent of the species were common to the two lists. George, Hopkins and Marchant (1979) showed by sampling quadrats from $1m^2$ to $1000m^2$ that a quadrat size of $250m^2$ was required before 95 percent of the total number of species present at the locality were included in the sample. These results provide extra-tropical examples of diversity and confirm quantitatively what every field naturalist knows - namely, that in one locality a few species are common and many are rare and only able to be located after extensive sampling.

RARE SPECIES IN A BIOLOGICAL CONTEXT

Biologists consider rare species from diverse points of view. On the one hand, those concerned with their conservation are obliged to catalogue those species which rank as being rare by some clearly understood definition (see e.g. Ovington 1978, Rye and Hopper 1981, Leigh, Briggs and Hartley 1981). Whilst such lists indicate what is at risk of becoming extinct and therefore in need of management, they do not indicate the causes of the observed rareness and cannot prescribe action for preservation of the rare species. On the other hand, geneticists such as Stebbins (1942) in his review of the reasons which had been proposed for the rareness of species, listed three possible causes:

1. those that were new species and had not yet had sufficient time to spread;
2. those that were senescent, i.e. conservative and unable to spread;
3. those that had few ecotypes will be rare or restricted in their range, whilst those with many ecotypes will be common and widespread.

Stebbins clearly regards the latter cause, i.e. genetic homogeneity, as the major cause of rareness. He further recognises two sorts of homogenetic species: firstly, those which were formerly more widely spread and are now restricted - his depleted species; and secondly, those whose range has never been more extensive - his insular species.

As a student of evolution, Mayr (1963) saw rare species as of two kinds: highly localised or highly specialised. Simpson (1944), looking at evolution from the point of view of a palaeontologist, however, saw rare species as (i) numerical relicts, i.e. survivors of a group once abundant; (ii) geographical relicts, now occupying smaller geographical ranges than their ancestors and earlier relatives; (iii) phylogenetic relicts, slowly-evolving groups surviving from remote times with little change; or (iv) as taxonomic relicts, groups much less varied than previously. These categories of rare species permit classification, but they give few clues as to the causes of rareness, for instance whether genetic homogeneity is the cause or the consequence of rareness.

Drury (1974), concerned with the management and re-establishment of small populations of rare species emphasised that in management, care should be taken to see that variability should be promoted whilst accepting that genetic diversity will be lacking. In contrast Andrewartha and Birch (1954) saw rareness in terms of the environmental factors which influence the components of the rate of increase, namely fecundity, speed of development, and duration of life. These authors laid great emphasis on the role of weather as it affects rareness, but also pointed out that any environmental factor can have an effect.

The foregoing may ascribe causes, but what, for instance, does 'too specialised' mean? Is it highly modified or adapted to a habitat or environment that is no longer widespread? And therefore is the rare species, in a sense, inappropriately adapted to the current circumstances? We infer status of rare species usually from present distribution, from historical changes in distribution or from knowledge of biology, life history or adaptations.

DISTRIBUTIONS

A simple classification of rare species based on distribution (Table 1) shows that rare species are not all distributed in a similar manner, and indeed if rareness is attributed to different causes it would be surprising if they did not display several kinds of distribution. Those distributions commonly recognised are:

1. Aggregated, areas of locally high density.
2. Disjunct, where a wider distribution has recently been broken, or local high density areas are connected by areas of low density.
3. Patchy, where there are discrete occurrences of higher density.
4. Fragmented, where the species does not occur where it might be expected.
5. Dispersed, a low frequency, widespread distribution.

Whilst such a classification does not add to an understanding of the causes of rarity, it does suggest that rare species should not all be thought of as equivalent.

TABLE 1. The categories of rare species which can be distinguished when distribution and density are simultaneously taken into account.

Density Distribution	High	Low
Widespread	Common	Rare
Restricted	Locally abundant but if local population small is considered rare	Rare

Dense local populations may be incipient species (in the sense of Stebbins 1942). On the other hand, if there are two local populations, widely separated, they are obviously relicts of an old, formerly more widespread species, i.e. they are geographical relicts (Simpson 1944).

ADAPTEDNESS

From Darwin to the present there has been frequent reference to the 'conditions of life' being suitable or unsuitable when discussing rare or abundant species. Just what the conditions of existence are cannot be inferred from simple correlations of abundance and environmental stresses. It is possible, however, to determine some of the conditions of life by either field or laboratory determinations of the stresses which an animal can tolerate. These studies are broadly classified as ecophysiological.

Such studies (see Keast 1981 for review papers) fall into one or other of the following:

1. Physiological responses to field-induced stresses, e.g. heat, water shortage, electrolyte loading or inadequate diet.
2. The physiological response to stresses administered in the laboratory which are believed to be a realistic representation of field conditions. Such studies have encompassed regulation of body temperature under heat or cold stress, water deprivation or nitrogen balance.
3. The physiological mechanism of response to field or laboratory conditions presumed to mimic field situations, e.g. in vertebrates the role of endocrine glands in initiating and sustaining the animal's response.

Only a few species have been examined in this way and none has been subject to a complete ecophysiological analysis. Some of the species studied are common and widespread; others, particularly marsupials, have been unable to maintain their former abundance or distribution in an environment developed for agriculture and pastures. Yet it is clear from the results of ecophysiological analyses that all species have well-developed behavioural and physiological capacities to handle environmental stresses imposed by heat, water deprivation, electrolyte loading and low quality diet, which are adequate for survival provided that the environment is so structured that the organism has the scope to use both its evolved behaviour and physiological traits for survival. Nevertheless, despite this capacity, many species have changed status either in the geologically recent past (Lundelius 1957, Baynes 1980) or in the historical past, and must now be considered rare: that is, despite their clear adaptation, they are reduced in numbers. Andrewartha and Birch (1954) discussed this phenomenon in terms of the factors which affect the rate of increase "r". The foregoing suggests that adaptive physiological responses cannot account for the occurrence of rare species. None of the proposed classifications or suggested causes takes into account the observations referred to earlier that in most situations rareness is very frequent, and it is the less abundant species that make up the biological diversity exhibited there.

DYNAMICS OF ECOSYSTEMS

An understanding of diversity and how it is maintained is essential to understand rare species and their biological significance. In order to gain this understanding it is necessary to recognize the dynamic state of any local biological assemblage. Environments change seasonally. The seasonal effects on recruitment and persistence of both plants and animals have been described by Andrewartha and Birch (1954) and by Hopkins and Hnatiuk (1981). Generally we know so little about the requirements of specific organisms that we cannot see what the effects of particular environmental influences are.

Thus many influences may contribute to rareness or abundance of a species, and from the simple observation of abundance alone one is quite unable to infer a plausible cause of rarity. But the likely factors in the dynamic situation that contribute to variations in the rate of increase cannot be ignored. They include:

1. Fluctuations - either climatic oscillations leading to relict distributions outside the principal range of the species, or variations in intensity of seasons.

2. Predation during establishment phase (Whelan and Main 1979).

3. Intra-specific competition leading to small populations.

4. Environmental conditions for regeneration - production of propagules, recruitment and establishment.

5. Disturbance - such as drought, fire and storms.

6. Physiological tolerance. When fluctuations favour one and then another species, it is clear that both will co-exist (i.e. no competitive exclusion), but without such oscillations one species will soon become dominant, i.e. diverse assemblages are a manifestation of oscillation in conditions.

Regardless of these factors that influence the conditions of existence, the function of the ecosystem (that is, the roles performed, as distinct from the composition in terms of individuals and taxonomic groups) depends on the fixation of nitrogen, the abstraction of minerals, the retention or delayed loss of nutrients in short supply, maintenance of lags and feedback loops in the system, and the redistribution of nutrients that are tending to accumulate in sinks (the role of animals).

Certainly in an extant ecosystem it is the common species that perform the bulk of the above. However, given that the physical and biological components of the environment have changed in the past and may change again in the future, it follows that the status of currently abundant and rare species may be reversed.

Such an extant ecosystem could be likened to a palimpsest over-written many times after imperfect erasures. I have pointed out elsewhere (Main 1981a) that each ecosystem commonly persists if inputs of essential nutrients equal outputs of losses from the system. Moreover, leakage from a system represents an unexploited resource and, given time, a specialist capable of exploiting the resource will evolve or invade. Thus a stable ecosystem requires nitrogen fixation, mineral abstraction and retention of both nitrogen and minerals in order to persist. Species presently rare but once common in former ecosystems would have performed these functions, depending on their physiological capacity and the inherent instability of long- and short-term climate and seasonality. At present, the relicts in an ecosystem remain as insurance policies. Should the climate revert to something like former conditions, then selection would assemble a new ecosystem or restructure the present one so that the vital functions or roles continue to be performed.

Seen in this light, climatic and environmental changes can be viewed on a scale in which amplitude and duration vary. Major changes of the past were of great magnitude and long duration whilst more recent and familiar differences are between seasons, drought, fire and storms. It is the major changes which lead to ecosystem restructuring. The minor oscillations lead to local extinctions, heterogeneity or patchiness in the distribution, and maintain the biota in a constant flux. If the idea of the palimpsest is adopted, climatic change might lead to a species-rich and diverse biota and ecosystems, whilst oscillations and drought may lead to extinctions and species-poor simplification of ecosystems. Clearly the extinctions, over-writing, and ecosystem changes can be complex, but it is possible to suggest how changes might occur (see Table 2).

In Table 2 I have assumed that an ecosystem is likely to represent a palimpsest and have set up a series of sub-hypotheses which predict the characteristics of, on the one hand, the rare species which will be found there and, on the other, the ecosystem in which it occurs. The table is deficient in that it does not include the life history characteristics of an organism in relation to the tabulated perturbations. The chance that a plant will persist is much greater than that of an animal because it can have perennating organs, such as underground tubers, rhizomes or lignotubers or dormant propagules which effectively lengthen each generation. Animals have none of these characteristics and rely on colonisation by new individuals of habitats which in the past have been unsuitable but are now favourable. The testing of the sub-hypotheses of Table 2 in field cases of rareness is the only way possible to distinguish the type and causes of rareness. NB

The role of predators in the abundance of prey species cannot be overlooked: its effectiveness is the basis of biological control. The decline of Opuntia after the introduction of Cactoblastis, and of rabbits after myxomatosis, are well known Australian examples. The abundance of many pests introduced to Australia which lack controls in the form of predators, parasites and disease also attests to the efficacy of this method of population control.

Viewed in the above way, study of rare species is the converse of the study of diversity; it is almost the consequence of there being species richness. However, unlike the designation of diversity by means of a mathematical value, the present approach interprets rareness and diversity in terms of a dynamic reaction between selection, ecophysiological capacities of organisms, and environmental events which continuously renew patchiness of the environment, with persistence being mediated by an ecosystem composed of species which produce the necessary loops and feedbacks to maintain the flow of nutrients within it.

Table 2. Possible interactions of environmental factors and their likely effects on ecosystems and rareness.

Effect on ecosystems	Climate: Stable	Climate: Changing – Change within climatic zone *or*	Climate: Changing – Across climatic boundaries	New land surface	Disturbance e.g. fire, storms, erosion	Variability in seasonality	Predator
Climate – Stable		Species of former climatic regime disadvantaged, now rare possibly passing to extinction	Rareness due to range changes common	In late seres odd pioneer species may occur as rarities	Usually disturbance-intolerant species escaping by chance	Unadapted species escaping seasonality in minor restricted habitats	Rare species resulting from predation are diffusely or widely spread
Climate – Changing – Change within climatic zone	Reorganise and restructure ecosystem		Species favoured by former climate now rare, plus rare colonising species	Rare species are forms characteristic of interrupted or reversed seres	Usually disturbance (e.g. fire) intolerant relicts of former climate	Unadapted species of former climatic regime now in minor favoured habitats	Formerly common and widespread species may become rare if change favours predator
Climate – Changing – Across climatic boundaries	Intermingling of biotic elements	Range extension of those elements favoured by change		Related to interrupted seres and distance from old and new climatic boundaries	Commonly disturbance-intolerant relicts towards edge of range	Many different origins, e.g. 1) relicts of former climate; 2) near edge of old and new ranges; 3) competitively inferior species	Rareness due to predation unusual
New land surface	Seral changes of succession	Succession interrupted regardless of direction of change	Succession interrupted except in minor favoured localities		Disturbance-sensitive species escaping by chance	Colonisers characterised by being disadvantaged but not eliminated	Rareness due to predation unusual
Disturbance, e.g. fire, storms, erosion	From survivors and pioneer migrants	Limited to biota tolerant of both disturbance and changed climate	Simplified depending on area of disturbance; relicts do not re-establish	Disclimax, revert to earlier seres; retarded succession, disturbance-tolerant pioneers		Species disadvantaged but eliminated	Rare species become very rare if disadvantaged and taken as prey
Variability in seasonality	Dominated by long-lived species recruiting in good seasons or species with physiological and other adaptations	Dominated by tolerant species	Very heterogeneous	Succession retarded by seasonal failure of recruitment	Dominated by tolerant, fugitive or nomadic species		Maintains rarities if takes commonest prey
Predator	If diet unspecialised, increases diversity	If diet unspecialised, maintains diversity	Little influence on diversity	Only specialised predators and little influence on diversity	Reduces diversity if attacks species disfavoured by disturbance	Increases diversity if takes commonest prey	

THE STUDY OF RARE SPECIES

I have suggested in this chapter that a rich biota may represent a palimpsest in which each over-writing represents a mixing of old and new biotas into another (new) ecosystem. If this chapter were only to consider the common concept of rareness or merely define the kinds of rare species that can be found, it would do a disservice to the problems posed by rareness in the context of the current desire to conserve species and representative habitats. Simply by creating reservations surrounded by settled country, one may make even common species rare, which then require the same sort of understanding for their conservation, as one needs for rare species in a natural and undisturbed setting. This approach has difficulties. Rare species need study before they can be conserved, but their study poses problems because: (i) they are difficult to find in numbers, (ii) it is undesirable to take any or many for study and therefore get statistically adequate samples, (iii) it is uncertain that populations will persist long enough to obtain answers, and (iv) it is uncertain that even when the biology is known, the species will be able to be conserved.

On the other hand, because common species on reserves may become rare, there is a need to understand how species presently rare maintain their populations. Aspects particularly relevant to this topic include (i) population structure, especially the significance of cyclic changes in the structure or abundance, (ii) breeding system, (iii) gene flow with respect to aggregated or dispersed distribution, (iv) genetic diversity within the population, and (v) likely causes of rareness, e.g. predators, parasites, diseases, genetic uniformity and physiological specialisation.

In considering the foregoing practical aspects of study of rare species, it should not be overlooked that if rare species result from environmental changes, then they may be viewed as the key to studying past conditions and, when the conditions which favour a higher rate of increase in them are understood, the measure of how species diversity and complexity make for robustness of the ecosystem within the range of perturbations experienced in nature and imposed by humans will become interpretable.

RESERVE SIZE

In determining the appropriate size of a reservation there are numerous problems. Main and Yadav (1972), after studying the macropods retained on offshore islands on the Western Australian coast, pointed out that Barrow Island (ca. 20,000 ha) retained all the macropods of the adjacent mainland except the red kangaroo (*Macropus rufus*), and so appeared to indicate the minimum size of any adequate reservation for retaining a representative assemblage of macropod marsupials. Frankel and Soulé (1981) suggest that much larger areas are required if it is desired to retain populations of large, sparsely-distributed species with a sufficient gene pool for natural evolutionary processes to operate. There has been considerable debate as to whether it is better to opt for a single large reservation or to have several smaller ones (Frankel and Soulé 1981). In terms of the practicability of obtaining reservations, the theoretical advantages of each of the above cases have little impact. The land use planner seeks to have the smallest possible size for reservations or to have none at all so that useful activities can be maximised. Under these circumstances it is of the utmost practical importance to be able to indicate a size such as Barrow Island (20,000 ha) which is manifestly too small to represent the topographic diversity to retain a fully representative suite of large macropod marsupials. Nevertheless, as pointed out by Main (1979, p.86), the aims of conservation are twofold: firstly, to retain representatives of taxonomically or biogeographically interesting biota, and secondly, to retain representatives of evolved communities.

These two aims require different but related management procedures and different criteria for selection. Prior to European settlement of Australia it would have been possible to select the location and size of reservations in accordance with theory. At the present time we are left with little choice: the area where rare forms occur is available for reservation or it is not. Should the habitat be available but of inadequate size in terms of a theoretically ideal area, the locality is reserved in the clear knowledge that it will require considerable biological knowledge and close management for the successful retention of the conserved forms. The conservation of representative communities or ecosystems is a different issue insofar as adequate size is clearly essential. No amount of management can substitute for the area needed for the natural regeneration of communities to take place. Should an inadequate area be reserved, then clearly the community will become simplified by the loss of some, especially the rarer, of the species originally included.

The foregoing is a serious problem, particularly when the choice of areas available for reservation is restricted and the time during which choice can be made is short. I have inferred elsewhere (Main 1979) that on the plateau of Western Australia, small reservations might be adequate because of the complex soil types which occur there.

> 'They are in fact archipelagos of different soil types interdigitating and if the animal species are adapted to the habitats present on these different soil types, they are occurring in less extensive environments than one would assume from the vast expanse of the state. The diversity that can be sustained over a long period of time is that which can coexist in the small refuges that are left when drought or fire or both reduce the effective area of the soil type and habitat' (Main 1979, p.83).

In two papers on the lizards and mammals included in reserves of the wheatbelt area of Western Australia, Kitchener et al. (1980a, 1980b) found that, contrary to expectation, these reserves contained faunal diversity comparable to continental islands of equivalent size and concluded that past events such as postulated by Main (1979) had contributed to the observed results. Whilst Kitchener et al. (1980b) concluded that a reservation of about 40,000 ha is needed in order to conserve a regional assemblage of mammals, their results show that much smaller reservations will conserve significant assemblages of rare species. Moreover, included in many of these reserves, especially those associated with granite rocks, are fragmented populations of showy red-flowered shrubs with good nectar flows which have been interpreted as being adapted to attracting migratory nectar-feeding birds (Main 1981b). Thus small reserves such as the above not only retain terrestrial vertebrate assemblages but also serve a vital function in maintaining the populations of much wider-ranging species.

The size of reserves needed for invertebrates has yet to be established but B.Y. Main (pers. comm.) informs me that for the terrestrial and rather sedentary Mygalomorphae even small areas can retain great diversity, for example, the North Bungulla Nature Reserve No. 17732 in Western Australia, an area of 104 ha, contains 11 species in 8 genera. Moreover, similar species richness is usual for equivalent sized areas with the same range of soil types and vegetation. The problem of management of such reservations will be to provide the diversity of disturbance required to maintain the various patches that now exist and that form the basis of the observed diversity.

DISCUSSION

In the previous sections, the point of view that rare species are worth preserving, i.e. are precious, has been advanced. I suggested that a classification of rare species on the criteria listed above, is a static rather than a dynamic concept. We can classify and place species in categories but have no theory as to how the species function in an ecosystem. Classification alone does not acknowledge that any ecosystem is a dynamic entity which has not always been composed of the same dominant species. These facts must be taken into account if rare species are to be conserved.

I have contrasted two extreme concepts when considering rare species. The first is that of the practical person who either views them as biological elements on the way to extinction or useless items sought by dilettante collectors; either way that person sees no value in them. The second view presented is that rare species are precious because they are biologically important either as a record of the past, or as alternative components of the ecosystem, or else as insurance policies so that roles will be fulfilled even though changes occur.

The retention of rare species is a matter of stewardship. Their retention gives the ecosystem the possibility of flexibility to respond to environmental change in the future, thereby enabling roles to be filled from the indigenous organisms.

Different prior ecosystems are best indicated by the fossil record containing pollen and other plant traces and the fossil remains of animals. Rare species that are relicts are important because they enable us to look towards the past and interpret it. They are thus in their own right valuable elements for study; without them, study of the past becomes much more difficult, since interpretation of the biological significance of fossil occurrences depends on some knowledge of an organism which is assumed to be closely related or similar in function to those represented by the fossils.

Rare species on small reserves may be the only way to retain relicts for study - are they any more discardable than the relicts of our cultural rise contained in museums? Moreover, retention in reserves of whatever size is the only way that we can demonstrate to the population at large (those to whom rareness has the connotation of common usage) that their land and its biota has a history which showed that the environment did fluctuate in the past, and that the present droughts and catastrophes mirror past occurrences and will be repeated in the future, thus indicating that the present land must be treated with respect.

Examples suggest that whilst climates change, sometimes in complicated ways, involving both temperature and precipitation, the changes are never so drastic that some ecosystems cannot occupy the environment. Moreover, these different ecosystems contain relict species of the replaced ecosystem. Given the magnitude and frequency of climatic changes in the past, any extant ecosystems may contain remnants and relict species of many of the former ecosystems that occurred in the locality. The relicts will generally be rare species occupying habitats favoured either by topography or aspect.

Thus it has been suggested that rarity may be caused by many factors which have in common that they affect "r", the rate of increase (Andrewartha and Birch 1954). From this conclusion it may be inferred that causes of rareness are to be found in the biology and life history of the rare species. The question of how they persist in the face of a low rate of increase is related to the conditions which lead to successful recruitment, and especially whether they are episodic or local, what role chance plays in episodes of recruitment, and the nature of the exponential decay of the population in less propitious seasons following a successful episode of recruitment. Finally, the genetic composition and diversity of the population is important in relation to breeding patterns and possible gene flow.

In Western Australia the presence of rare species is closely correlated with diversity and abundance (Hopper, Campbell and Moran 1982). From the hypothesis developed, diversity and rare species should be highest across zones of climatic transition, in areas of newly exposed land where pronounced variations in conditions caused by seasons, drought, fire and storms occur.

The areas of high species diversity studied by Lamont et al. (1977) and Hopkins and Hnatiuk (1981) lie across an old shoreline (Baxter 1972) at a latitude that is markedly affected by the expansion and contraction of the typical Mediterranean climate of south-western Australia (Wyroll 1979). George et al. (1979) mention a further area on the south coast lying east of the boundary of the reliable Mediterranean climate of the south-west where it crosses an old emergent Tertiary shoreline (see also Hopper et al. 1982).

On the plateau of Western Australia species richness of plants and invertebrates, e.g. mygalomorphs and frogs, appears to be coincident with the past contact of the western extension of the central arid area and the more reliable climate of the south-west (Bowler et al. 1976).

The southwest of Western Australia is subject to drought, fire, summer rain from tropical cyclones as well as the infrequent tornadic windstorm (Southern 1979). As such there would be ample cause for the initiation and maintenance of the observed diversity and frequency of rare species.

The central desert area studied by Pianka (1981) has an extraordinary diversity of lizards which may be related both to the vegetational diversity of the area but also to the biology of <u>Triodia</u>. The latter is a plant regenerated by fire (Winkworth 1967) which undergoes a very marked sequence of individual stages of growth and senescence as it develops through the small tussock stage of young plants to the large rounded tussock of mature stages followed by the death and degeneration of the central tillers leaving a ring of living material. The heterogeneity of the desert region resulting from differences in soil, aspect, fire history, time since last fire, and seasonal conditions pertaining following fire, e.g. summer cyclonic or winter rains, all appear to be components influencing the observed diversity in ways which are related to the biology of individual species of lizards.

Clearly, the kinds of rare species conceived by Mayr (1963), Simpson (1944) and Stebbins (1942) are to be found, but not all rare species will be of the kinds listed by them. There will be many species which are rare because at the time of observation the physical and biological conditions of the environment are such that "r" is depressed and in these cases the interpretation of Andrewartha and Birch (1954) is valid. It is important that the significance of the large number of possible causes for the depression of "r" is appreciated, and it is in this light that Table 2 and the sub-hypotheses arising should be considered.

In a broader context, the diversity within and organisation of these communities composed of long-lived shrubs and generally shorter-lived animals would appear to be analogous to coral communities in the marine environment, with the long-lived coral colonies the analogues of the shrubs of the terrestrial situation, especially with respect to longevity and the structure they provide. It is therefore of interest that the diversity within coral ecosystems has been explained by hypotheses which emphasise the stability of the environment as the cause and the contrary argument that the diversity is engendered by the environmental instability with its attendant mortality and consequent space and opportunities for colonisation. Bradbury (1977) sees merit in both of these hypotheses and develops a hypothesis which sees the roles served by organisms in the community as basic.

In simple communities there are few or single species filling each role. In diverse communities there are many organisms capable of performing each role. The many species ensure that the roles are always performed under any prevailing conditions (Bradbury 1977). In this regard Bradbury's interpretation is not unlike that advanced by Main (1981a) to account for community structure in terrestrial situations in Western Australia.

Connell (1978) has discussed diversity in tropical rainforest and coral reefs in terms of disturbance, a proposition also advanced by Webb and Tracey (1981) for the rainforests of Queensland. Loucks (1970), from studies of Wisconsin forests, hypothesised that evolution of diversity of species in ecosystems is an adaptation to a repeated pattern of changing environments initiated by random processes such as fires. Bormann and Likens (1979) considered both fire and wind as ~~agents of~~ disturbance leading to a shifting-mosaic steady state in northern hardwood forests of the United States. Results of all these studies suggest that a static concept of ecosystems must give way to an appreciation of the role of disturbance in maintaining diversity: the rarities observed are significant for the role they fulfil when disturbance and change occur, and in this sense they are precious. Without them we would have environments reduced in diversity and made up entirely of 'weedy' or 'pest' species.

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