Speciation environments and centres of diversity in southern Africa. I. Conceptual framework

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ABSTRACT

A knowledge of the nature and distribution of the environments where speciation (micro-evolution) is or has been rapid would help explain plant distributions and give insight into the mechanisms of plant evolution. Before southern African speciation environments can be identified and described, a number of basic theoretical concepts have to be clarified. In this paper the major taxonomic, systematic, floristic, ecological and evolutionary ideas pertinent to speciation environments are reviewed and discussed. Despite many publications about species concepts, species diversity, modes of speciation and the relationship between environments and genetic variability within taxa, it is still not possible to make predictions about the kinds of environments that favour speciation.

INTRODUCTION

A speciation environment is considered to be a place where speciation (micro-evolution) is particularly rapid, or has been so in the recent past. It would be informative to determine speciation environments for taxa and for regions, both to clarify species distribution patterns and to give insight into the mechanisms of micro-evolution. When seeking environments where taxa show evidence of proliferation and to correlate this proliferation with measurable environmental variables, it is necessary to link the disciplines of ecology, evolutionary biology, systematics and taxonomy. Such interdisciplinary work can be hazardous because the weaknesses of hypotheses and the assumptions on which they are based are often not explicit. In the sections which follow some of these troublesome concepts are discussed in order to show the contribution of each to our understanding of speciation environments.

TAXONOMY, SYSTEMATICS AND FLORISTICS

Chorologists, phytogeographers and community ecologists base much of their work on the names of taxa, but so far stability of names has not yet been attained, either because of differences in taxonomic treatment ('lumping' or 'splitting' of taxa) or because of changes made necessary by the rules of nomenclature. This is such a familiar problem that it will not be considered any further; it is enough to say that name changes alter one of the main elements used by other disciplines.

Related to the problem of name changes is the problem of species concepts. This has been the subject of many publications, such as the papers in Slobodichikoff (1976), but as Paterson (1981) has pointed out, there is still little agreement on what constitutes a species. Biological species are groups of individuals which exchange genetic material within the species but not with other species. They may be defined by reproductive isolation in the sense of Dobzhansky (1970) or Mayr (1970), or by the existence of specific mate recognition systems (Paterson, 1980). Taxonomic species are recognized on the basis of many features, but maintenance of genetic integrity is incidental and not central. The taxonomic species is the species concept of virtually all floras for the majority of species (Davis & Heywood, 1963, p. 94). In studies of speciation the plant groupings considered must have the potential to evolve, so the biological species and not the taxonomic species concept must be employed. Inferences about the species richness or degree of evolutionary activity in an area can only be based on enumeration of biological species. However, it is usually not possible to determine what proportion of a Flora is composed of non-biological species.

Species diversity is often used in phytogeography, ecology and evolutionary biology. Several aspects of diversity are distinguished:

1. Habitat diversity, which is subdivided into within-habitat (alpha) diversity and between-habitat (beta) diversity (MacArthur, 1965; Whittaker, 1972);

2. Species diversity, also called gamma diversity (Whittaker, 1972). Alpha and beta diversity are the measures most used by ecologists, while taxonomists, phytogeographers and evolutionists use gamma diversity as the measure of species richness in an area. Richerson & Lum (1980) point out that evenness of distribution in numbers of individuals among species is just as important a component of diversity as species richness because it is a measure of how evenly resources are partitioned among taxa and hence is an indicator of the degree of interaction between components of an ecosystem.

Species diversity has bearing on photogeography because high diversity for an area will be the result of one or all of the following: rapid speciation with correspondingly low extinction rates; high immigration rates; large pools, or several different pools, from which elements of a flora have been drawn; and the type of environment which encourages diversity. As Gentry (1981) points out, a high concentration of species in an area can be due to gamma, alpha or beta diversity, or to combinations of these. If concentration is a result of high gamma diversity then local endemism is likely to be important; if due to high alpha diversity, it

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means that the plant communities are richer in numbers of species than the same communities elsewhere; and if due to beta diversity, then many different communities, each having a distinctive species complement, are 'packed' into the area. It is therefore important that the type of diversity is specified when discussing environments, selection pressures, species interactions, etc. Areas of maximum diversity, either alpha, beta or gamma, are not necessarily evolutionary cradles. Speciation is only one of a number of mechanisms leading to high levels of diversity, and some kinds of speciation may reduce alpha or gamma diversity.

Furthermore, despite the large theoretical and applied literature on the subject, the mechanisms underlying differences in diversity are still imperfectly known. Richerson & Lum (1980) show that it is not yet possible to predict even whether environmental stability or instability is most likely to be correlated with maximum gamma diversity for an area.

ECOLOGY

In finding an environment in which speciation has been rapid we hope to find the mechanisms (selective pressures) that have encouraged micro-evolution in taxa or habitats. Many of these selective pressures are ecological, and may be grouped into abiotic environmental differences; biotic interactions such as competition, predation/parasitism, symbiosis and mimicry; or factors related to levels of complexity of the biocoenosis such as stability and resilience. In some cases the assumptions underlying these ecological concepts are imprecise or only partly tested, yet the concepts are taken as proven by workers in other fields.

1. *Abiotic environmental differences*

Different abiotic environments will exert different selection pressures on organisms, but general principles describing the direction and magnitude of selection of different environments have not been formulated. For example, it is not possible to predict the effect of environmental stability on gamma diversity (Richerson & Lum, 1980) or intraspecific genetic heterogeneity (Hamrick *et al.*, 1976).

2. *Biotic interactions: competition*

Competition is the biotic interaction most often considered as a selective force (*e.g.*, 'survival of the fittest'). There is a large amount of literature on the effects of intra- and interspecific competition. Gause (1934), Beals (1968), Bartholomew (1970), Levin & Anderson (1970), Horn & MacArthur (1972), Miles (1974), Schaffer (1977), Waser (1978) and Berendse (1979, 1981) give a representative sample of the range of situations and effects of competitive interactions. Evolutionarily, and in some cases even ecologically, competition is not as clearly effective as the competitive exclusion principle (Hardin, 1960) or the phenomenon of character displacement (Brown & Wilson, 1956) suggest. In fact, certain

authors seriously question both the role of competition in determining the coexistence or extinction of populations (*e.g.*, Elton (1958) for the replacement of red squirrels by grey squirrels in Britain), and the role of reinforcement in speciation (see Paterson (1978) for examples). Competitive interactions can be quite complex. Leeuck & Rice (1976) showed that *Aristida oligantha* is able to dominate old field seral stages for extended periods because of the negative effects of its rhizophore bacteria upon nitrogen fixing bacteria associated with species of later seral stages. In this case a superficially simple case of competition is really the result of a number of kinds of interactions. The effects of competition, and of other kinds of interactions, must be critically appraised for each situation. As Janzen's data (Janzen 1969, 1971) and hypotheses (*e.g.*, Janzen 1976, 1977) show, it is far easier to pose questions about the effects of interactions than to illustrate their action as selective forces.

3. *Stability and resilience of communities*

The ecosystem concepts of stability and resilience are sometimes misapplied, and since stability is often considered to be central to diversity, there is a need for clarification. Stability is the property allowing an ecosystem to resist small disturbances and promoting the recovery of the system if disturbances occur. (Holling, 1973). As Walker (1980) and Walker *et al.* (1981) have pointed out, stable systems have low variability, and if they do change much they will not return to their former equilibrium states. Stable systems provide environments that show little change through time. By contrast, resilient systems may be changed considerably by disturbances yet still return to their equilibrium states (Holling, 1973; Walker, 1980). Resilient systems show high variability, are often unstable, and hence provide temporally heterogenous environments. Our knowledge of the relationships between stability, resilience and species diversity is still imperfect, and their importance to speciation cannot be predicted.

Closely related to stability, resilience and spatial heterogeneity is the question of intraspecific genetic variability. Reviews such as those by Hamrick *et al.* (1976) and Hedrick *et al.* (1979) and research papers such as those of Antonovics (1968), Tigerstadt (1973), Babbel & Selander (1974) and Bosbach & Hurka (1981) show that there is still much to learn. For example, marginal populations are frequently phenotypically less variable than those from the centre of a species range (Soule, 1973), but a number of contradictions to this conclusion have been reported [*e.g.*, Tigerstadt (1973) and Bosbach & Hurka (1981)]. These conflicting data suggest that the underlying principles are still not understood.

EVOLUTIONARY THEORY

There are numerous hypotheses for the mechanisms leading to speciation but, as Paterson (1981) points out, only a few are supported by data. There is also little information about the evolutionary behaviour of a taxon in response to

different ecological situations, or about the selective effects of the same ecological conditions on different taxa. Genetic variability within a species or population is the basis for micro-evolution under differential selection pressure, and it would be helpful to be able to predict localities where genetic variability is likely to be high. Unfortunately, as increasing numbers of taxa are studied, it is clear that the kinds of genotypes that 'fit' particular environments cannot be postulated (Bosbach & Hurka, 1981).

Stebbins's (1974) concept of canalization of genotypes as a result of their evolutionary history has received too little attention. Both Stebbins (1974) and Riedl (1977) indicate the possible importance of the degree of canalization of the genotype and the existence, degree and nature of within-genotype hierarchies on subsequent genetic ability, but these hypotheses have not yet been tested by experiments.

Modes and concepts of speciation

Speciation is a primary process leading to patterns of plant distribution and is central to taxonomy and evolutionary study. Underlying its significance, Clayton & Cope (1980) list the introduction of species and the origin of new species as one of the major sources of discrepancy between boundaries of phytochoria and phytogeographical formations.

Evolutionary biologists, taxonomists, phytogeographers and chorologists are interested in the process and outcome of the splitting of populations into taxa or reproductively separate lineages. This phenomenon is called cladogenesis by Dobzhansky (1937), true speciation by Mayr (1963) and primary speciation by Grant (1971). It is contrasted with the process in which a species changes through time but does not split, which Dobzhansky (1937) called anagenesis and Mayr (1963) called phyletic speciation. Phyletic speciation may be the result of mutations (autogenous) or introgression (allogenous), the latter being equivalent to Grant's (1971) secondary speciation.

Whenever true speciation is discussed, only the biological concept of species can be considered. This means that only sexually reproducing organisms can be accepted as species. Zoologists are therefore seldom faced with situations where agamospermy is facultative, which is the case for a considerable number of plant species (see for example Gustafsson 1946 & 1947; Brown & Emery, 1958; Asker, 1979), or where cleistogamy and chasmogamy occur together (*e.g.*, Maheshwari & Baldev, 1958; Schemske, 1978). This means that while the agomospheric plants are reproducing asexually they cannot be considered as part of a species population. However, under these conditions, the argument that new genotypes will be 'swamped by pollen from more numerous individuals', made so strongly by Levin (1975) and Paterson (1981), probably does not hold. As Tothill (1966) has indicated for *Heteropogon contortus*, frequent agamospermic reproduction together with sexual reproduction is a powerful mechanism allowing differentiation of gene pools even in the face of strong pollen flow. All of the above means that botanists must be wary of accepting evolutionary models that do not recognize that the flexibility of the reproductive biology of many advanced plants is far greater than that found in most animals.

The literature on cladogenesis is extensive and only some of the proposed models will be discussed here, to show the difficulties that arise in trying to use these models for interpretation. More complete treatments of cladogenesis are to be found in Grant (1971), Mayr (1963) and White (1968). The commonest form of speciation apparently occurs when populations become spatially isolated and then differentiate as a result of genetic rearrangements. If the differentiation is sufficiently great that the segregates are reproductively isolated if (or when) they become sympatric once more, then speciation has taken place. This is the classic 'species pump' hypothesis of Valentine (1967), and is the only mode of speciation which Paterson (1981) recognized as being supported by observed critical facts. The process is called allopatric speciation and its importance has been shown by many studies.

Sympatric speciation, where fragmentation of a gene pool occurs without spatial separation, was shown to be theoretically possible as long as there are different niches available and the selective advantages are high for different genomes in different niches (Maynard Smith, 1966). Bush (1969, 1974) has advocated sympatric speciation as the mode whereby sibling of fruit flies have evolved, but Paterson (1981) argues that the case presented by Bush is inconclusive. Paterson's own argument against sympatric speciation by the formation of alloploids is, however, also invalid because of his assumptions about plant reproductive strategies. Sympatric speciation is therefore seen as a mode supported by little evidence, which might be more applicable to plants than to animals.

Two refinements of the concept of sympatric speciation are parapatric and stasipatric speciation. In parapatry, differentiation occurs between populations in the same geographical region, but in different habitats or niches. Lewis & Raven (1958) reported sympatric speciation in diploid species of *Clarkia* in response to edaphic factors, and Gentry (1981) has reported micro-evolution in response to edaphic factors in *Passiflora*. It is possible that high beta diversity is an indicator that parapatric speciation has taken place, but data are few at this stage and no conclusion can be drawn. In stasipatry, White (1968) states that chromosomal rearrangements occur within the range of the species, and as a result of the superior performance of the new genome, spread through the range of the parental species. Lewis (1966) pointed out that rapid chromosome reorganization in marginal populations is a frequent mode of plant speciation, and as we discuss elsewhere (Gibbs Russell & Robinson, in press), we believe that stasipatric and perhaps parapatric speciation is of considerable importance to the development of the African flora.

Paterson (1981) warns of the difficulties of most of the models of speciation but, as Jameson (1977) has stressed, it is unlikely that a single model will

hold for all situations. Since the mode (or modes) of speciation will determine where differentiation will be rapid and the kind of taxa that are likely to be evolving rapidly, it is too early to assume that there is only one model of speciation, particularly for plant taxa which show great flexibility in their reproductive biology.

The kind of speciation referred to by Grant, Dobzhansky, Mayr and others deal primarily with changes through time, but do not consider the phytochoria where they occur. Data from the eastern Cape (Gibbs Russell & Robinson, 1981) suggest that the type of speciation may be linked to the phytochorion and hence that it may be necessary to take account of where speciation occurs relative to the area of major adaptive radiation of a taxon. As a result we feel it is necessary to introduce terms linking the process of speciation to the phytochorion where it is taking place.

a. phytochorial sympatry: speciation in the phytochorion where major adaptive radiation of the group occurred.

b. phytochorial allopatry: speciation in a phytochorion other than the one where major adaptive radiation of the group occurred.

A mode of speciation which has received too little attention is that of allogenous phyletic speciation. Here, new species are formed as a result of introgression from other taxa. In some cases this may lead to a reduction in species numbers if species boundaries are sufficiently blurred, and may result from migration of a derived species back into the range of a parental or sibling species. In southern Africa, where much of the flora is derived from tropical taxa, it is possible to envisage evolution taking place in a series of steps. Allopatric, parapatric or stasipatric could lead to the evolution of derived species in phytochorial allopatry, or to narrowly endemic species in phytochorial sympatry. Allogenous phyletic speciation may then occur as derived genetic segregates, which have become differentiated to some extent, exchange genes with parental, sibling or other species.

Proposed speciation environments

The environment in which speciation takes place is as important as the mode of speciation. Such areas will not necessarily have high alpha, beta or gamma diversity. Phyletic speciation, while changing the nature of taxa of an area through time, does not result in an increase in the numbers of species, and allogenous phyletic speciation may even reduce gamma diversity. By contrast, Gibbs Russell & Robinson (1981) show that high gamma diversity can result simply from close juxtaposition of a number of phytochorial elements with apparently low speciation rates. If speciation environments could be recognized, either in general or for specific taxa, our understanding of the mechanisms of micro-evolution would be advanced and predictions about man's impact on the flora of the future may possibly be made. A number of types of environments have been suggested as particularly conducive to micro-evolution.

(a) *Tropical environments*

The high gamma diversity found in many tropical regions has long been taken to indicate that this was the type of environment where speciation was most rapid. Countering this, Stebbins (1974) suggested that tropical areas, specifically the forests, are museums. Both viewpoints are probably too narrow, and at least some plant groups are evolving rapidly in tropical forest environments. Evolution here is often in response to biotic factors (*e.g.*, pollinators in the orchids). Simpson (1977) pointed out that there is no reason to suppose that tropical forests provide less opportunity for species proliferation than do other environments. From the general point of view, the significance of tropical environments is that climatic conditions are stable and favourable for a wide range of plants.

(b) *Fluctuating environments, often ecotones*

Environmental fluctuations can isolate populations and thereby accelerate allopatric speciation by the 'species pump' mode of Valentine (1967). Peripheral populations may become isolated, or populations may be established beyond the optimum range during exceptionally favourable periods. When conditions become severe these populations may be isolated and differentiate. Both Stebbins (1972, 1974) and Valentine (1967) take instability as the key environmental feature encouraging species formation.

(c) *Arid regions*

The hypothesis that arid regions are centres of speciation, strongly advocated by Stebbins (1952), Raven (1964) and Axelrod (1972) is really a variant of fluctuating environments as a stimulus to speciation since arid areas are usually characterized by fluctuations of climate.

(d) *Fine-scale spatial heterogeneity*

Topographic, edaphic or other environmental heterogeneity is generally assumed to encourage fragmentation by providing isolated microhabitats close together. The work of Lewis & Raven (1958) on *Clarkia* and of Gentry (1981) on *Passiflora* are examples of this. From these studies it seems that edaphic heterogeneity alone may promote speciation in stable environments.

The variety of environments that have been suggested as favourable for speciation shows that it is still not possible to state unequivocally that a single kind of environment promotes gene pool fragmentation. Spatial heterogeneity, instability and the complexity of biotic interactions all seem significant for some groups or in some areas. The difficulty of making predictions about speciation environments is increased because there are no clear-cut relationships between stable or resilient ecosystems, particular environments and rates of speciation.

CONCLUSION

Many of the concepts that have a bearing on speciation and speciation environments have their

own internal uncertainties. It is therefore difficult to combine them to make interpretations, establish tests of hypotheses or derive general principles. Nevertheless, we believe that attempting to define speciation environments provides a useful change of perspective in studying the mechanisms of evolution of the southern African flora, and hence of explaining patterns of distribution of taxa.

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Kennis van die aard en verspreiding van omgewings waar spesiasie (mikro-ewolusie) vinnig plaasvind of plaasgevind het kan nuttig wees om die verspreiding van plante te verduidelik en kan insig gee in die meganismes van plantewolusie. Voordat die Suider-Afrikaanse spesiasie omgewings geïdentifiseer en beskryf kan word, moet 'n aantal basiese begrippe opgeklaar word. In hierdie artikel word die vernaamste taksonomiese, ekologiese en ewolusionêre begrippe wat betrekking het op die spesiale omgewings hersien en bespreek. Daar word aangetoon dat ten spyte van baie publikasies oor spesies begrippe, spesiesdiversiteit, maniere van spesiasie en die verwantskap tussen die omgewing en intra-takson genetiese variasie, nie een van die begrippe verfynd is tot op die punt waar voorspellings gemaak kan word nie.

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