

1. THE IMPORTANCE OF EVOLUTIONARY IDEAS IN ECOLOGY— AND VICE VERSA

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INTRODUCTION

If anyone asked whether ecologists can do good work without any knowledge of evolution, the answer must surely be yes. Ecologists work mainly on situations existing at one particular moment of time or in one particular area. As a result it would appear that they can take the properties of a species as fixed and assume that evolution, which is all about changes in species and populations, has nothing to do with ecology. A perusal of any ecological journal would support this; not more than one article in twenty mentions evolution or overtly considers evolutionary processes—yet there is nothing scientifically inadequate about the rest.

Yet if we look more critically, it is patently wrong to descry evolution as a proper subject for ecologists, for three major reasons:

- (i) We all tacitly assume that what we examine ecologically is the product of evolution, and that as a result of natural selection it is adapted, more or less, to its environment, in the sense that it is fitted (*aptare*) to (*ad*) it.
- (ii) Species are clearly not fixed, but consist of a complex of different populations, often with extremely different ecological properties, which can change as a result of evolutionary processes in only a few generations.
- (iii) Ecologists themselves study life and death, and mechanisms of fitness, which are the stuff of evolution as we understand it.

So not only does evolutionary thinking form a conceptual background to ecology, but there is a two-way relationship between ecology and evolution, in that the findings of each is very relevant to the other. I shall endeavour to explore both sides of this relationship, using mainly plant examples, not because animal examples are not equally relevant but because of my own particular experience.

BIRTH, DEATH AND SURVIVAL

One of the first major steps towards an understanding of evolutionary processes and a retreat from special creation was unwittingly taken, of

course, by Malthus, a demographer. It was his obstinate arguments for the discrepancy between rates of increase of populations and the resources available to them that started the slow revolution in thinking about man's place in nature. His book, reprinted several times, forced people to think about the struggle for existence rather than to run away from the idea.

Now, demographic parameters are crucial objects of ecological study. Not only are we being given very detailed information about the apparent extravagances of nature in the processes of reproduction of species, but we are beginning see that this extravagance in plants particularly, can take place at many different places in the life cycle (Harper 1977; Begon & Mortimer 1981). Correlated with this, in accordance with Malthus, death takes its toll. It can be of whole individuals, and, in plants, not just in overcrowded young or at one particular period of 'old age', but progressively over several years. In *Plantago* (Sagar 1959) or *Anthoxanthum* (Antonovics 1972) it is better to talk of a half-life of 2 years because the depletion rate is so constant. Many plants spend a considerable portion of their life cycle as dormant seeds. Death works inexorably here too, as in many common annuals (Roberts 1964).

But death does not affect only whole individuals, or genets; it also affects single parts of an individual, or ramets. The ramets of *Ranunculus repens* have very similar patterns of survivorship to that of whole plants (Sarukhan & Harper 1973). So the quantity of a single individual which survives from one period to another can change considerably.

In the same manner, during growth the numbers of single parts of an individual can be altered. Growth is increase; but in different conditions the amount by which a plant may increase, and therefore contribute to the next generation, can vary dramatically, as is demonstrated by every experiment on plant density. Perhaps more importantly, the same can occur in conditions influenced by competition from other species; death does not necessarily occur, but large changes in growth and seed output are commonplace. Such differences of growth will be cumulative in vegetatively propagating plants, and we can observe differences in relative abundance becoming more and more pronounced with time even between genotypes (Hickey & McNeilly 1975). Differences between species, measured as Relative Replacement Rates (de Wit 1960; Van den Bergh 1968) can easily reach 5 or 10.

In perennial species, establishment of new seedlings can occur at the same time as older plants are dying. Since these two processes may compensate each other, the total population can appear static when, in fact, considerable change is occurring (Fig. 1.1). Rates of such turnover in perennial populations can often be as high as 100% per annum.

All this implies the possibility of natural selection, in which individuals

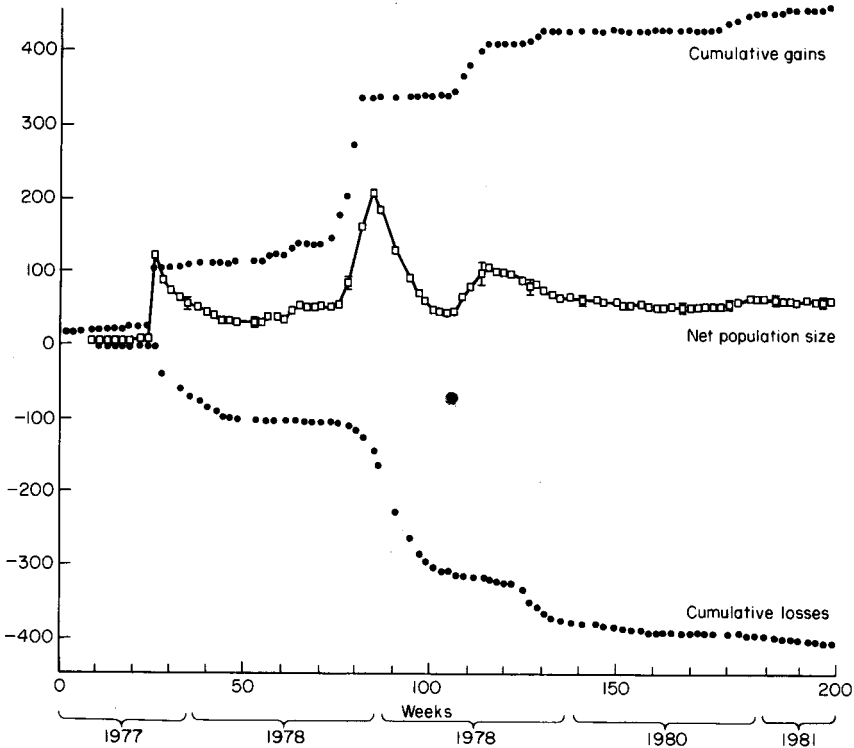


FIG. 1.1. The number of individuals, and the cumulative gains and losses, in a population of *Agrostis canina* on a copper mine at Glasdir, Dolgelley, Wales (data of S. Farrow, T. McNeilly and P.D. Putwain).

of one sort replace those of another, or at least survive better than another. Demography is therefore the key to natural selection (Solbrig 1980). What can occur has been demonstrated by many artificial mixtures of selected genotypes (reviewed by Bradshaw 1972). Perhaps the most outstanding example is in mixtures of either *Lolium* or *Dactylis* cultivars sown as swards and given various treatments (Charles 1961). In all cases the mixtures changed their composition substantially, in different ways with different treatments, within a single generation, due to differential mortality, and expansion of the survivors. Any plant community is the result of such processes; pastures can reveal that it has happened by an examination of their genotypic structure (Fig. 1.2); far fewer genotypes remain than must have been present initially.

But selection is only effective as an evolutionary force if what survives is

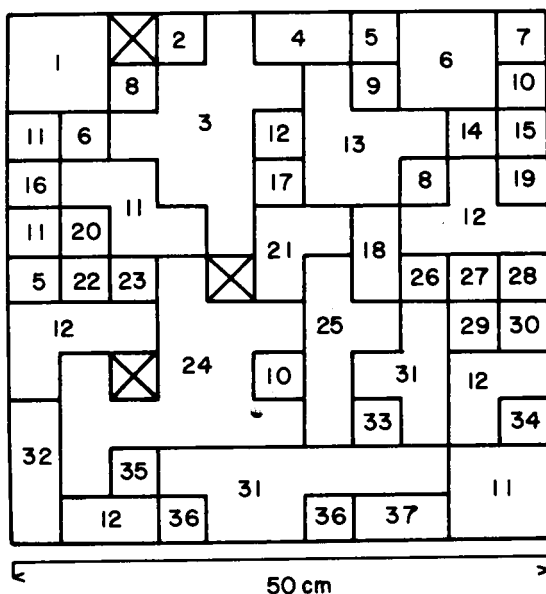


FIG. 1.2. The pattern of genotype distribution in a 9-year-old population of *Lolium perenne* in a grazed pasture (240 seeds originally sown in 50 × 50 cm area—genotypes identified by isozyme variation at PGI, GOT1 + 2, loci) (data of M. Roose and T. McNeilly).

genetically different from the original population mean. The degree of genetic change for a generation (ΔG_g) will depend on the selection differential (the difference between the phenotypes selected and the mean of the population ($P - \bar{P}$)) and the degree to which that difference is passed onto the next generation [the heritability (h^2)].

$$\Delta G_g = h^2(P - \bar{P})$$

This simple concept, well described in many places (e.g. Falconer 1981), is the key to understanding evolutionary change. Clearly if the individuals selected do not differ much from the mean or if their special characteristics are only poorly inherited, then evolutionary change will be limited. This was well understood, although perhaps oversimplified, by Fisher in his fundamental theorem of natural selection—the rate of increase in fitness of a population equals its genetic variance in fitness at the time.

HERITABILITY

We must therefore ask whether characters, especially those of ecological importance are heritable. Nearly all ecologically important characters are

TABLE 1.1. The various origins of variation in a character of a population, expressed as components of variance

 Components of variance (of a character in individuals of a population)

$$\begin{aligned} V_P &= V_G + V_E \\ &= V_A + V_D + V_I + V_E \end{aligned}$$

 where V_P = total variance between phenotypes

 V_G = variance due to genetic effects

 V_A = variance due to additive genetic effects

 V_D = variance due to dominance genetic effects

 V_I = variance due to interaction genetic effects

 V_E = variance due to environmental effects

continuously varying and so-called metric (see subsequent discussion by Lawrence in Chapter 2, p. 29). For these characters the variation must have several origins or components (Table 1.1). The degree of genetic determination of the character (or broad sense heritability) is given by a comparison of the total genetic variance with the total variance from all sources,

$$\text{degree of genetic determination (broad sense heritability)} = \frac{V_G}{V_P}.$$

The degree to which a character is transmitted to offspring is given by the additive genetic variance,

$$\text{degree of heritability (narrow sense heritability)} = \frac{V_A}{V_P}.$$

The broad sense heritability determines the outcome of selection on individuals. It will influence changes in genotype frequency in a population, since it measures the degree to which individuals are consistently different from one another. As such it is important, and can easily be measured if individual plants can be clonally replicated. Broad sense heritability is usually very high, e.g. > 0.85 for time of ear emergence in *Lolium* (Cooper 1959). But such differences, although important to the survival of the individual plants, may be due to various genetic and other effects which are not inherited, again very clearly shown in *Lolium* (Hayward 1970).

For this reason the true (or narrow sense) heritability is needed. This can be measured in a number of ways (Falconer 1981; Lawrence in Chapter 2, p. 29), of which the regression of offspring on parents is the most obvious, but not necessarily any simpler than other methods, such as the variation between sibs or half-sibs produced by pair crosses or a polycross. Common sense must indicate to ecologists that characters are inherited, since offspring

TABLE 1.2. Narrow sense heritabilities of some ecologically important characters in plants

Plants	Characters	Heritability	References
<i>Lolium perenne</i>	Date of ear emergence	0.87 (parent/offspring)	(Cooper 1959)
	Rate of leaf appearance	0.73 (pair crosses)	(Cooper & Edwards 1961)
	Rates of photosynthesis		
	(high light)	0.30	} (diallel) (Wilson & Cooper 1969)
	(low light)	0.14	
	Mesophyll cell thickness	0.33	
	Leaf length	0.42	
<i>Dactylis glomerata</i>	Yield		
	(spring)	0.67	} (polycross) (Stratton <i>et al.</i> 1979)
	(autumn)	0.04	
	Digestibility		
	(spring)	0.62	
	(autumn)	0.49	
<i>Oryza sativa</i>	Competitive ability (panicle number)	0.12 (F_3 families)	(Sakai 1961)
<i>Agrostis tenuis</i>	Tolerance to copper	0.70 (diallel)	(Gartside & McNeilly 1974)
<i>Geranium carolinianum</i>	Resistance to SO_2	0.50 (parent/offspring)	(Taylor 1978)
<i>Linum usitatissimum</i>	Plasticity to density		
	(height)	0.74	} (F_3 families) (Khan <i>et al.</i> 1976)
	(capsule number)	0.66	

always resemble parents. But the essence of a heritability test is to find out how far different parents give rise to different progenies, each similar to their parents, or how far the progeny of one set of parents resemble each other and are different from progeny of other parents.

In fact, heritabilities of ecologically important characters can be quite high (Table 1.2). The same range of heritabilities can be found for characters in animals. However in all cases heritabilities tend to be lower for fitness characters. When heritabilities are high for a given selection differential, progress under selection can be considerable, and, in the appropriate material, progress can be maintained for many generations, as shown by the famous Illinois corn experiment (Woodworth, Leng & Jugenheimer 1952), in which the selected lines transgressed completely the limits of the original population.

However, when heritabilities are low, little progress under selection may be possible. This is shown by a comparison of selection for egg number ($h^2 = 0.25$) and egg weight ($h^2 = 0.75$) in chickens (Lerner 1958).

For characters determined by a single gene, the concept of heritability does not apply and high selection pressures inevitably have radical effects on gene frequency (e.g. Shorrocks 1978).

NATURAL SELECTION AND EVOLUTIONARY CHANGE

High birth and death rates combined with high heritability of ecologically important characters imply that evolution should be happening everywhere, and at appreciable rates, just as it can in experimental material. Yet in practice this hardly seems true. In natural situations, change in important characters such as in horses' teeth (Simpson 1953) or many other examples, appears to occur only over geologic time.

Nevertheless, over the past few decades we have uncovered a few examples where rapid change has occurred. Metal tolerance for instance seems able to evolve in only one or two generations (Wu, Bradshaw & Thurman 1975). Sulphur dioxide tolerance in plants and industrial melanism in insects have obviously evolved since industrialization (Taylor & Murdy 1975; Bishop & Cook 1980). Similarly the population differentiation in snails and grass species in response to man-made variations of habitats (Cain & Sheppard 1954; Bradshaw 1959) must have come about in the last few hundred years. Yet for most characters in most species there is little change in either time or space.

Why should so many characters in so many species be so stable? It cannot any longer be because we have not looked for evolutionary change. Nor can it be because there are no opportunities. On the waste heaps of metal mines, for instance, there is still plenty of open space available for colonization by, more, tolerant species than those which exist at the present. Similarly, until the appearance of the new amphidiploid grass species, *Spartina anglica*, estuarine saltings have been available for angiosperm colonists ever since angiosperms first appeared in the Mesozoic. And in habitats already colonized there are still opportunities for new, more competitive species, as is demonstrated by every successful alien.

GENOSTASIS AND EVOLUTIONARY PLATEAUS

If birth and death rates can be so high and therefore generate high potential selection pressures, it follows from simple theory that natural selection may exhaust the variation available to it. In long-term selection experiments, limits to selection and selection plateaus are well known for many different characters in different organisms (Lerner 1958; Robertson 1955). These

can be due to complex causes, such as epistasis in which genes do not act additively, co-adapted gene complexes in which genes have been selected to act together, pleiotropy in which there are subsidiary effects of genes which are disadvantageous, or linkage in which the genes concerned are linked to other genes which are disadvantageous (for discussion cf. Antonovics 1976 and Falconer 1981). All of these effects can cause the otherwise advantageous effects of genes, and therefore the influence of selection, to be nullified.

It is possible that species or populations have become adapted to a particular environment in such a way that any deviations in their characteristics, no matter what direction, lead to loss of adaptation. Under such conditions, stabilizing selection operates, eliminating the deviants and maintaining the population as it is in perpetuity. However it must be remembered that in such situations the possibility of evolution to become *more* adapted to the existing situation must still exist. There can be no reason why, for instance, even a turtle cannot become a better turtle by evolving mechanisms for more efficient food conversion, or for faster swimming at no other cost. The occurrence of stabilizing selection is direct evidence of some other restrictions to evolution.

We therefore come to an alternative possibility commonly overlooked. Lack of genetic change in situations of potentially high selective pressure can be due to lack of appropriate variation. Selection can only act on herit-

TABLE 1.3. Examples of the different sources of ecological adaptation in plant breeding programmes

Sources	Adaptations
From original gene pools	
Potato	Blight resistance within <i>S. tuberosum</i>
Alfalfa	Spotted aphid resistance
Sugar beet	Sugar content
Rye	Reduced height
From other gene pools—other cultivars	
Barley	Yellow dwarf resistance from Abyssinian cultivars
Wheat	Dwarfing genes from Japanese cultivars
Grapes	Root aphid resistance from American material
Cotton	Blackarm resistance from African cultivars
From other gene pools—other species	
Oats	Mildew resistance from <i>A. ludoviciana</i>
Bread wheat	Stem rust resistance from <i>T. dicoccum</i>
Bread what	Eye spot resistance from <i>Aegilops ventricosa</i>
Rice	Grassy stunt resistance from <i>O. nivara</i>
Delphinium	Red flower colour from <i>D. cardinale</i>
Potato	Blight resistance from <i>S. demissum</i>

able variation; if the appropriate variation is not present then evolutionary change is not possible. It is of no significance if other, inappropriate, variation occurs. This situation is familiar to every plant breeder, who may be lucky in finding the character he wishes within his starting material, but may also be unlucky and have to look for it in other, often distantly related, material (Table 1.3). Yet we usually forget that this must be common in more normal evolution.

This situation appears to be a dominant factor in the evolution of metal tolerance. Evolution of tolerance in individual species appears to be related to the occurrence of variability in metal tolerance in the normal populations of those species (Gartside & McNeilly 1974). This relationship has been examined by a new sensitive culture technique and appears to hold widely (Table 1.4). It would appear usually to be a property of the whole species. But there is no reason why, in cases where there is no gene exchange, it should not be a property of individual populations. In small populations, whether by drift or founder effects, there is the possibility of gene fixation and exclusion of particular genes, as in the absence of genes for copper tolerance in

TABLE 1.4. The percentage of copper tolerant individuals found in normal populations of various grass species, in relation to the presence of the species on copper polluted waste and whether the plants collected were tolerant of copper (data of C. Ingram)

Species	Percentage of occurrence of tolerant individuals	Presence of species on mines		Tolerance of collected adult plants
		On waste	Margins	
<i>Holcus lanatus</i>	0.16	+	+	+
<i>Agrostis tenuis</i>	0.13	+	+	+
<i>Festuca ovina</i>	0.07	—	+	—
<i>Dactylis glomerata</i>	0.05	+	+	+
<i>Deschampsia flexuosa</i>	0.03	+	+	+
<i>Anthoxanthum odoratum</i>	0.02	—	+	—
<i>Festuca rubra</i>	0.01	+	+	+
<i>Lolium perenne</i>	0.005	—	+	—
<i>Poa pratensis</i>	0.0	—	+	—
<i>Poa trivialis</i>	0.0	—	+	—
<i>Phleum pratense</i>	0.0	—	+	—
<i>Cynosurus cristatus</i>	0.0	—	+	—
<i>Alopecurus pratensis</i>	0.0	—	+	—
<i>Bromus mollis</i>	0.0	—	+	—
<i>Arrhenatherum elatius</i>	0.0	—	+	—

a modern cultivar of *Agrostis tenuis* (Humphreys & Bradshaw 1976).

Lack of variability for resistance has recently become apparent in disease outbreaks, and has led to catastrophes. The effect of the introduction of chestnut blight into North America from China has been to cause the total elimination of the American chestnut (*Castanea dentata*), which apparently possesses no variability whatever for resistance. The same must be true for foliose lichens and SO_2 : they disappear completely in areas of high SO_2 . But interestingly this then gives rise to evolution of melanism in moths, which do possess appropriate variability in pigmentation.

When there is lack of variability for a character, either because there was little initially or because natural selection has fixed the additive variation previously present, heritabilities will be low, because V_A is small compared with V_p . This is characteristic of many fitness characters, presumably because of the prior effects of natural selection; but it also appears in artificial selection experiments as additive variation is exhausted and only epistatic non-additive variation is left (Lerner 1958).

Situations in which evolution is limited by lack of appropriate genetic variation, are obviously widespread and indeed almost universal. The condition, which can be called *genostasis*, requires much wider recognition than it has previously been accorded. It may, or may not, be related to the *stasis* suggested in current discussions on long-term evolution involving punctuated equilibria (Eldredge & Gould 1972, Grant 1982). From the point of present-day evolution and ecology it is certainly crucial to appreciate when genostasis may, or may not, be occurring.

VARIATION AND EVOLUTIONARY CHANGE

When variation is available there is no doubt that evolution can occur, often very rapidly. Despite Haldane's (1957) dilemma about the cost of natural selection, if we assume the usual situation in which populations are controlled in some density-dependent manner, then the increase in numbers of individuals possessing an advantageous gene can be purely at the expense of those not possessing it (Sved 1968).

Evolution is likely to be most rapid in those situations in which selection has not already acted, because in relation to the particular selection pressure, there can be a store of hidden unselected variability. The extent of this hidden variability can be seen when a population is subject to a new environment; although in the old environment it can be very uniform, in the new it can be very variable, as in *Lolium rigidum* exposed to the unusual conditions (for it) of continuous light and warmth (Cooper 1954). The best examples of rapid

TABLE 1.5. Examples of evolution of resistance in weeds which have been exposed to triazine herbicides

Have evolved resistance*	Have not evolved resistance
<i>Amaranthus retroflexus</i>	<i>Agropyron repens</i>
<i>A. powellii</i>	<i>Anagallis arvensis</i>
<i>A. hybridus</i>	<i>Capsella bursapastoris</i>
<i>Brassica campestris</i>	<i>Sonchus arvensis</i>
<i>Chenopodium album</i>	<i>S. oleracea</i>
<i>C. strictum</i>	<i>Stellaria media</i>
<i>Senecio vulgaris</i>	<i>Taraxacum officinale</i>
<i>Solanum nigrum</i>	<i>Thlaspi arvense</i>

*From Bandeen, Stephenson & Cowett 1982; Gressel *et al.* 1982.

evolution, including those already mentioned, do in fact come, for both plants and animals, from new man-made situations such as those arising from the use of pesticides and herbicides and from industrial pollution (Bishop & Cook 1981 Bradshaw & McNeilly 1981, LeBaron & Gressel 1982).

Other material will be in a genostatic condition, which will only be relieved by mutation giving real novelties, or by hybridization or gene flow giving new gene pools, as in *Drosophila* (Lewontin & Birch 1966). The most spectacular present-day examples of the relief of a genostatic condition with startling evolutionary and ecological consequences must surely be the appearance of *Spartina anglica* from the introduction of the alien *S. alterniflora* (Marchant 1968). If we understood the genetic situation more clearly it is possible that the present havoc in Europe from Dutch elm disease (*Ceratocystis ulmi*) after its re-introduction from America has the same cause—the acquisition of virulence genes in America.

Certainly it is possible to mimic such startling evolutionary changes. In this country resistance to the widely used triazine herbicides has been absent from common weed populations until recently, and still does not occur in many species (Table 1.5). Yet if genes for resistance to triazines are introduced into a susceptible population, the change in frequency of resistant genotypes is remarkably fast (Fig. 1.3).

Yet for reasons already given, such rapid change is the exception rather than the rule. Genostasis is the common condition. Does this suggest that evolutionary and ecological time scales are really very different (Begon & Mortimer 1981) and that the disciplines can have little to do with each other?

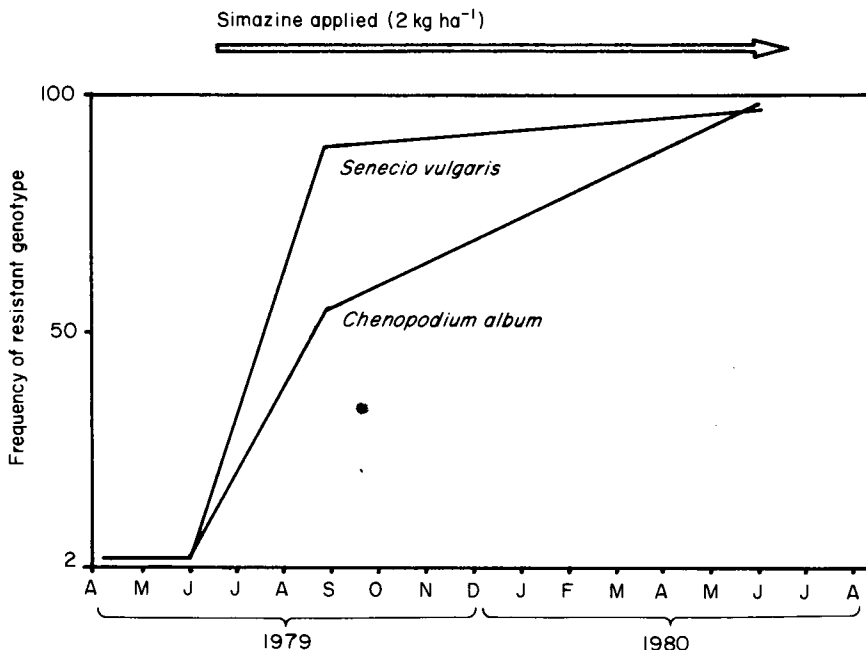


FIG. 1.3. The change of frequency of resistant genotypes in populations of *Senecio vulgaris* and *Chenopodium album* exposed to simazine, into which 2% of a resistant genotype was introduced (data of K.R. Scott and P.D. Putwain)

POPULATION DIFFERENTIATION AND ECOLOGICAL AMPLITUDE

Despite the normal differences in time scale it must be remembered that we will always be dealing with material which could, in the past, have suffered evolutionary change because of past, if not present, variability. In fact, the sorting, and favouring process caused by natural selection seems always to have proceeded some distance in all species. Population differentiation within species is universal. Sometimes, as in *Achillea* (Clausen, Keck & Heisey 1948), the amount of evolutionary adjustment is so considerable that the extreme populations of the same species cannot survive in each other's habitat. The differences, as in calcium response in *Festuca ovina* (Snaydon & Bradshaw 1961), can be so great that populations behave as differently as ecologically distinct species.

Any character can be affected. There are excellent examples of population differences in response to climate, for example in *Potentilla* (Clausen,

Keck & Heisey 1940) and in different prairie grasses (McMillan, 1959) and to soil, for example in *Trifolium repens* (Snaydon & Bradshaw 1962) and in *Dactylis glomerata* (Crossley & Bradshaw 1968). But we now realize that life history parameters can be affected, for example in *Poa annua* (Law, Bradshaw & Putwain 1977) and in *Taraxacum* (Gadgil & Solbrig 1972). Even phenotypic plasticity can be affected by natural selection, for example in *Linum usitatissimum* (Khan, Antonovics & Bradshaw 1976) (where heritabilities have been determined), in *Capsella bursa-pastoris* (Sørensen 1954) and in *Ranunculus flammula* (Cook & Johnson 1968), so that sensitivity to environmental factors is itself under evolutionary control. The physiological processes which underlie population differences are themselves becoming understood, for instance climatic response in *Solidago virgaurea* (Bjorkman & Holmgren, 1963) and zinc tolerance in grasses (Brookes, Collins & Thurman 1981). A good review of the evidence is provided by Heslop-Harrison (1964).

At the same time it has become realized that these differences can occur very locally, well within the confines of what ecologists might treat as a single habitat, as in the cliff populations of *Agrostis stolonifera* (Aston & Bradshaw 1966), or vernal pool populations of *Veronica peregrina* (Linhart 1974). The balance between the opposing forces of gene flow and selection appears weighted in favour of selection (Jain & Bradshaw 1966), as any ecologist might have suspected.

Populations also differentiate in relation to changes occurring in time, in relation to successional changes. This is very clear from recent work on *Spartina patens* (Silander & Antonovics (1979) and on *Poa annua* and other species (Law 1979). Some species, at least, can climb their own seres.

So a species cannot be understood by the ecological behaviour of one of its populations, but by the behaviour of the sum (not the mean) of all its populations. This becomes very apparent from transplant experiments where extreme populations of a single species cannot survive in each other's habitat, whether over large geographical distances, e.g. *Achillea* (Clausen, Keck & Heisey 1948) or small, e.g. *Agrostis tenuis* (Bradshaw 1960). The ability to colonize a habitat may often be related more to evolutionary capability than anything else. There is no doubt, for instance, that only a few species can colonize metal-contaminated habitats (Bradshaw 1975) (Table 1.6), despite the fact that a wide range of species have had the opportunity to do so. This can be related to the evidence already given in Table 1.4. Ecological amplitude on a local or a wide scale has therefore a strong evolutionary component. It must be related to genetical rather than physiological flexibility.

TABLE 1.6. Species to be found in mown grassland in copper-contaminated and uncontaminated areas at Prescott, Lancs. (Bradshaw 1975, updated)

Copper in soil (ppm)	Species found	
< 2000 <i>Adjacent to refinery</i>	<i>Agrostis stolonifera</i>	<i>Festuca rubra</i>
	<i>A. tenuis</i>	<i>Agropyron repens</i>
		<i>Holcus lanatus</i>
< 500 <i>Away from refinery</i>	<i>Ranunculus repens</i>	<i>Achillea millefolium</i>
	<i>R. bulbosus</i>	<i>Hypochaeris radicata</i>
	<i>Cerastium vulgatum</i>	<i>Leontodon autumnale</i>
	<i>Trifolium repens</i>	<i>Luzula campestris</i>
	<i>T. pratense</i>	<i>Lolium perenne</i>
	<i>Taraxacum officinale</i>	<i>Poa annua</i>
	<i>Rumex obtusifolius</i>	<i>P. pratensis</i>
	<i>Prunella vulgaris</i>	<i>P. trivialis</i>
	<i>Plantago lanceolata</i>	<i>Dactylis glomerata</i>
	<i>Bellis perennis</i>	<i>Cynosurus cristatus</i>
		<i>Hordeum murinum</i>

THE NATURE OF SELECTION

While the findings of evolution can be applied to ecology, the reverse is also important. As evolutionary theory has developed there has been a notable lack of critical ecological thinking on the nature of selection and its effects. The effects of selection on continuous variation have been separated by Mather (1953) into three types: directional, stabilizing and disruptive. These at first sight seem fairly straightforward, yet examined ecologically, they perhaps have complexities.

Directional selection

Situations in which individuals at one end of a continuous range of variation are disfavoured, are basically simple and lead to normal types of evolutionary progression. Yet precise analysis of many situations has shown that the coefficients of selection generated can be immensely variable, for instance, in barley mixtures, for the variety Vaughn, 0.22–1.59 (Allard, Harding & Wehrhan 1966). So in practice evolutionary changes can be reversed from one generation to another, very apparent when the changes in gene frequency in composite cross populations of barley are followed over a number of years (Suneson & Stevens 1953). Any simple ecological experience should lead us to expect this; annual variations in climatic conditions alone can have startling effects on populations. But an examination of the precise ecological

causes of such *fluctuating selection* would provide us with a much better understanding of the nature of this important aspect of selection (Felsenstein 1976).

When directional selection for one character is occurring certain genes are increasing in frequency. There is no reason why these genes should not (a) have direct effects on other characters by pleiotropy, (b) be closely linked to other genes whose frequency and therefore effects will also change, and (c) be acting on a physiological or growth system with limits, so that changes in one aspect of the system are accompanied by reciprocal or compensatory effects in another aspect. All this gives rise to *correlated response*, which is well known to plant breeders. It can cause trivial effects, e.g. changes in panicle characters in *Lolium perenne* when flowering time is being selected, due to linkage (Cooper 1960), or major effects, e.g. changes in frequency of the genes for cyanogenesis in legume species related to temperature rather than to the presence of predators, because of the pleiotropic effects of the genes on cold tolerance (Jones 1973).

It is difficult to envisage that any single gene can act in isolation from other genes; since most characters are complex many genes are usually involved together. This can lead to *co-adaptation* within gene complexes. The result is that where there is a simple geographical gradient in selection, one balanced conservative gene complex will persist over a large section of that gradient until it is suddenly replaced by another. As a result sudden changes in a character can occur without obvious relationship to similar changes in the environment. These *area effects*, reported particularly in snails *Partula* (Clarke 1968) and *Cepaea* (Cain & Currey 1963), inevitably complicate the simple effects of directional selection.

Stabilizing selection

There has been wide acceptance of the idea that individuals which deviate most, for any character, from the mean of population are likely to be less fit. It is a concept that seems ecologically very reasonable, and evidence for it continues to appear, whether for chaeta number in *Drosophila* (Kearsey & Barnes 1970), flowering time in *Phleum* (Charles 1964) or response to soil nutrients in *Dactylis* (Crossley & Bradshaw 1968).

Yet surprisingly little work has been done by ecologists to confirm that extreme individuals are usually less fit and to show the processes which lead to this. Indeed, what has for so long been considered the most effective evidence, the recovery of individuals of *Passer domesticus* knocked down by a storm, does not on re-examination now seem to be clear cut (Johnson,

Niles & Rohwer 1972). There is certainly more work needed on the fitness of the extreme.

Disruptive selection

Perhaps it is here that the ecologist has the most scope for providing understanding. The problem is that the subject is complex at the outset because several different processes are involved (Clarke 1979). However, in all the cases to be considered it is genotypes which are different that are favoured. From this it follows that genotypes which are rare must be favoured. This means that frequency-dependent fitness and disruptive selection co-occur and are two aspects of the same selective situation.

Evidence for selection by predators against the commonest, *apostatic* selection, shows that it is of widespread occurrence (Clarke 1969). Wherever it occurs it will inevitably lead to the maintenance of variation and, in an extreme form, balanced polymorphism in prey populations. The detailed ecological and behavioural evidence which is available, such as for fish/corixids (Popham 1942) and passerine birds/artificial baits (Allen 1975), illustrates exactly the important contribution that ecologists can make. It is important to realize that the principle has important applications to the evolution of plant diversity, as suggested by Gillett (1962), Janzen (1970) and others. It may perhaps apply in grazing situations, e.g. sheep/*Trifolium repens* (Cahn & Harper 1976). It may also cause diversity in predators (Paulson 1973).

Parasitism can have similar effects. There is no space to discuss the recent developments in our thinking, since these have been well reviewed (Taylor & Muller 1976) in a series of contributions all of which show the importance of an ecological approach.

When two genotypes are competing for similar resources we are now well aware that they will more escape each other's competitive effects the more different they are in their requirements. The results will be a stable mixture. This ecological concept of *annidation* or *niche diversity*, elegantly developed for interaction between plant species by de Wit (1960) and others (Harper 1977), has scarcely been applied to evolutionary situations except, notably, by Antonovics (1978). Yet it is completely applicable to interactions between genotypes within species. Very clear annidation has been shown between genotypes of *Linum* which would lead to stable polymorphisms (Khan, Putwain & Bradshaw 1975). Since in every population there is liable to be competition between the genotypes that compose it, it should follow that evolution of annidation and stable diversity as a consequence, without loss of population fitness, should be commonplace. It will be difficult to

detect in outbreeding populations because of the individuality of single genotypes, which explains perhaps why it has not been demonstrated so far. But the very elegant demonstration of the evolution of a stable polymorphism due to annidation in a hybrid bulk population of *Hordeum* (Allard & Adams 1969) (which is inbreeding) should have aroused much more interest than

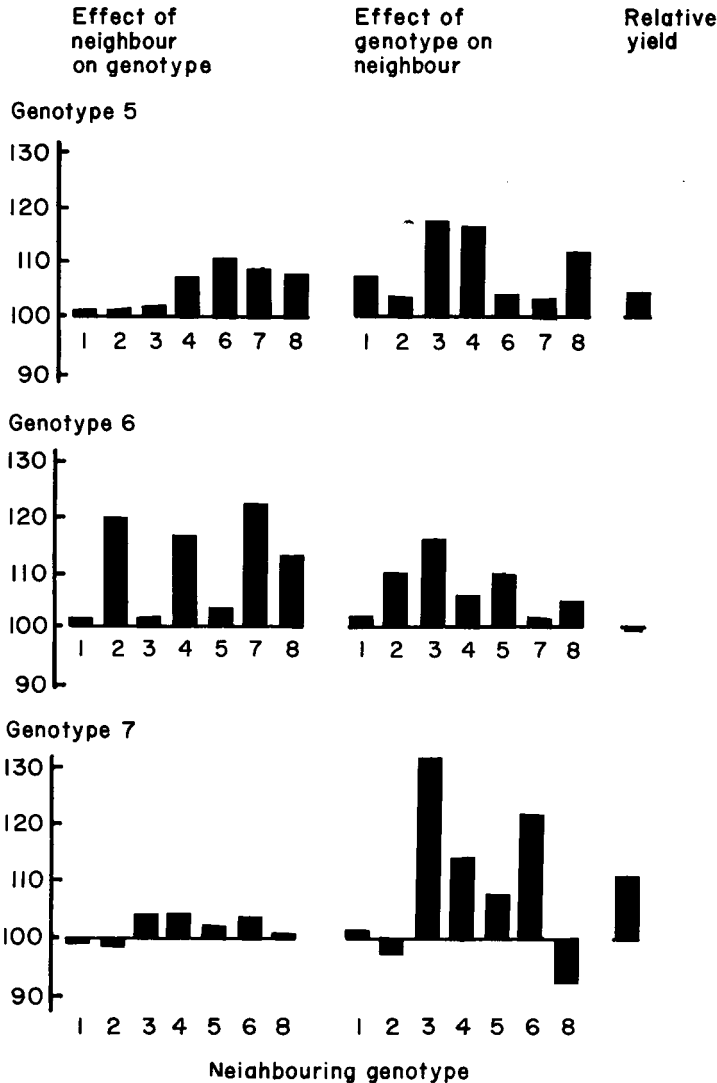


FIG. 1.4. Examples of the positive interactions, in pair mixtures, found between eight genotypes abstracted from a stable polymorphic bulk-hybrid population of *Hordeum sativum* (Allard & Adams 1969).

it has done so far, especially since the authors demonstrate that the selective forces involved can be powerful in their effects (Fig. 1.4).

Facilitation, when genotypes influence each other in a positive fashion (in contrast to annihilation where there is merely the reduction of the negative effects of competition (Khan *et al.* 1975) will have similar evolutionary effects. Although the term is widely used, unequivocal examples of facilitation are rare. For this reason perhaps, and also for the more cogent reason that true facilitation is a much more complex process, there appear to be no examples so far of it contributing to evolutionary processes in populations. But this does not mean that we should not look for them.

The final possible cause of disruptive selection is *variation of environment in space* on a very localized scale—a phenomenon well known to all ecologists. Such variation grades into directional selection in different habitats when the spatial scale is large and into annihilation when the spatial scale is so small that the different environments cannot be disentangled from each other. Different closely adjacent habitats are well known to be able to cause the evolutionary differentiation of distinct populations (Jain & Bradshaw 1966) despite the fact that the populations are parapatric (adjacent and able to exchange genes). The scale on which such differentiation can occur is measurable in terms of metres, e.g. in *Liatris* (Schaal 1975) or even centimetres, e.g. in *Anthoxanthum* (Snaydon & Davies 1976). In this latter experiment, where the environmental differences are due to the soil effects of the Park Grass Experiment, transplant experiments have shown that the differences in half-life between alien and native material are at least 50% (Davies & Snaydon 1976).

Localized environmental variation, over the scale of metres or fraction of a metre, can be caused by many different factors, microclimate, edaphic or biotic. They are commonplace in all habitats. As a result we have the possibility of relatively permanent, spatially fixed, very local differences in the environment experienced by a single interbreeding population of individuals, a truly multiple-niche situation, which can exert powerful disruptive, or frequent dependent, selection in a form which satisfies the conditions necessary for stable polymorphism. Yet despite this, cases in which disruptive selection due to localized environmental variation occurs have not yet been clearly established. The existence of genotypes within *Trifolium repens* showing differences in adaptation to different grass species (Turkington & Harper 1979) seem to be an example. There are, clearly, differences in performance of clones of *Agrostis stolonifera* transplanted into different areas of an old meadow (Table 1.7), but just how far local variation in environment (of what ever cause) has clearly selected different genotypes is not yet clear. It is only detailed transplant work of this sort in perennial species which is

TABLE 1.7. Specific genotype adaptation in a perennial grass in different permanent pastures in Cheshire shown by a transplant experiment with *Agrostis stolonifera*. Clones from three fields were reciprocally transplanted into three randomly chosen quadrats in three areas of each field. The table shows an analysis of variance of tiller numbers (natural logarithm) present 10 weeks after planting of single tillers. Variance ratios showing superscripts are quasi-*F* ratios (data of D.A. Weir and A.M. Mortimer)

Sources of variation	DF	MS	VR
Fields (F)	2	325.41	23.42' ***
Populations (P)	2	49.49	3.23' NS
Clones in P (C in P)	9	14.11	2.10 *
Areas in F (A in F)	6	25.03	4.21' **
Quadrats in (A in F)	18	2.99	< 1 NS
F × P	4	10.57	1.28 NS
F × (C in P)	18	11.28	1.24 NS
P × (A in P)	12	11.94	2.31' **
P × (Q in A in P)	36	3.97	< 1 NS
(C in P) × (A in F)	54	5.09	< 1 NS
(C in P) × (Q in A in F)	162	9.06	1.35 *
Error	308	6.71	
Total	631		

likely to elucidate a selective process which *a priori* would seem probably widespread.

THE EVOLUTIONARY ENDPOINT—ADAPTATION?

Ecologists look at characters; geneticists look at genes. Nevertheless, no matter which approach, we all tend to expect that the outcome of evolution is adaptation. But such a conclusion is simplistic and even naive. What we should only expect is that the outcome is material which is selected and more adapted than the material which preceded it. Evolution is merely a replacement system using what is better, in terms of fitness, than the rest.

In the final state, the material must have some fitness or it would not survive. So in a sense the material is adapted, better than what was there before, but certainly not in a state of grace. Evolution has to make do with what is already present and whatever new material is to hand. It is essentially a tinkering process (Jacob 1977). As a result, as we have seen, fitness can be limited by (a) genostasis—lack of variability; (b) pleiotropy and linkage—deleterious side effects; (c) phenotypic plasticity—variability hidden from selection; and (d) ancestry—limits set by the past.

Not only must we take a pluralistic approach to the agents of evolutionary

change, as Gould & Lewontin (1979) have suggested, but also realize that the limitations set by the supply of appropriate variability are overriding.

These limitations can occur on a small or on a vast scale. Land plants would have had a very different scale of success if they had been able to produce a membrane which restricted the diffusion of water but not of CO_2 . In grass breeding, subtle internal resource limitations, for which there seems no available genetic variability by which they can be overcome, control the improvement of leaf-area production in *Lolium* (Edwards & Cooper 1963). Ancestry can have effects which are obvious, such as no trees in the Gramineae, or subtle, such as the way defense to particular groups of insects is limited to certain families of Angiosperms (Erhlich & Raven 1964). Species can get trapped geographically, such as the Monterey pine (Cain 1944), or have lost particular genes in an evolutionary migration, such as is suggested for certain alpine Eurasiatic plants (Turesson 1931). Finally we must remember the Red Queen hypothesis (Van Valen 1973)—everything else is evolving so that any one species must itself evolve to stand still.

So we will always be dealing with imperfect organisms, certainly not showing perfect adaptation—fitting to (the present). It may indeed be better to think of them as showing “abaptation” (Harper 1982)—fitting from (the past).

CONCLUSION

In their review of genetics and ecology, Sammeta & Levins (1970) said that ‘the integration of population genetics and ecology with other disciplines into a coherent evolutionary biology of populations has barely begun’. Everything the ecologist looks at is the result of evolution. We are coming to realize that species are at times both less immutable *and* at other times more immutable and capricious than we previously suspected. Ecologists cannot afford any longer to take a simplistic view of the species they work with.

At the same time nearly everything the ecologist looks at can lead to evolution. Ecology is crucial to understanding evolutionary mechanisms. But whether or not evolution will occur depends on the heritability of characters and the availability of variation.

So future progress in understanding evolution depends every much on a pluralism of approaches and a community of effort between ecologists and geneticists.

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