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The Input from Population Genetics: “The New Ecological Genetics”¹

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Abstract. Recently there has been a growing interaction of genetical and ecological approaches to theoretical and natural populations. The relative ease with which plant populations can be studied demographically and experimentally suggests that plants will play a major role in developing this interaction. Already such studies have lead to a “new ecological genetics” that goes beyond earlier conceptualization of genetic differences among populations in the framework of experimental taxonomy. This new ecological genetics has developed a series of tenets that emphasize the importance of considering genetic and ecological factors in concert: 1) Explaining the abundance and distribution of organisms is basically the genetic problem of explaining limits to natural selection. 2) An understanding of community structure will come from consideration of how forces maintaining species diversity and genetic diversity interact. 3) Adaptation is operationally definable in terms of mortality and fecundity of individuals in populations. 4) Adaptation to new environments results in different genotypes with different life histories. 5) The distinction between “ecological time” and “evolutionary time” is artificial and misleading.

I formerly spoke to very many naturalists on the subject of evolution, and never once met with any sympathetic agreement. It is probable that some did then believe in evolution, but they were either silent, or expressed themselves so ambiguously that it was not easy to understand their meaning. Now things are wholly changed.

CHARLES DARWIN (“The Origin of Species,” 6th Ed., 1872).

Instead of thinking of ecological characteristics of species as constants, we have been forced by genetics to think of them as fluctuating between certain values or even drifting in time to different mean values. Likewise we have to think of a transect in the spatial distribution of the species as revealing a spectrum of values corresponding to a spatial genetic spectrum.

L. C. BIRCH (1960).

The interaction of genetics and plant ecology has a long history (reviews: Heslop-Harrison, 1964; Langlet, 1971). Following Darwin’s (1859) “Origin of Species” the surge of interest in phylogeny and in the inductive scientific

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method firmly wedded evolutionary studies with systematics (Allen, 1975) and as a result the impact of the early interaction of genetics and ecology was absorbed more by the newly emerging science of "experimental taxonomy" than by ecology. Ecology itself was preoccupied with nonoperational, semiphilosophical arguments about the individualistic *vs.* organismal nature of plant communities (MacIntosh, 1975); experimental studies seemed to carry little force and were seen as ineffectual reductionist approaches to larger questions. It is therefore only recently, with experimental approaches characteristic of physiological ecology (Mooney & Billings, 1961; Hiesey & Milner, 1965; Antonovics et al., 1967) or of plant-population ecology (Harper, 1967) that genetics has had an impact on plant ecology that is more than a parenthetical one. Indeed, in the past ten or 15 years there has been an exciting, accelerating trend towards the ever increasing interaction of population genetics and population ecology, a trend that promises to have a far-reaching impact on the broader areas of evolutionary biology and ecology.

The importance of considering ecological and genetic factors in concert was emphasized in a seminal paper by Birch (1960) but it was another ten years before explicit theoretical formulations relating the two areas were developed by Anderson and King (1970), Anderson (1971), and King and Anderson (1971). They showed that it was possible to study simultaneous changes in gene frequency and population size, using models that incorporated genetic differences in age-specific death rates, birth rates, and carrying capacities. Gene-frequency changes and population-size changes followed patterns quite different from those when the genetic or ecological parameters were considered separately. That the relationship between demography and genetics is indeed intimate was confirmed by the extensive theoretical analyses of Charlesworth (1970, 1971, 1972), Charlesworth and Giesel (1972*a,b*), and Giesel (1972).

These theoretical studies have been based mostly on results and concepts derived from investigations of animal populations. Their implications are, however, of paramount importance to the plant-population biologist. They provide him with a framework within which to integrate genetic and ecological approaches to plant populations and communities. They provide him with an alternative view of those numerous studies demonstrating "ecotypic variation," but which have till now been conceptualized in the context of "experimental taxonomy." Peter Raven, in this symposium, pointed out that this conceptualization may in fact not be very useful for the plant systematist. And indeed if as has been argued (Bradshaw, 1972), ecological and genetical processes are more closely intertwined in plants than animals, then these new approaches are particularly relevant to the student of plant populations.

However, regardless of the relative importance these developments have to studies of plants as opposed to animals, the role of botany in the future development of this area is likely to be considerable. In large measure this

is due to the many attributes of plants that make them particularly useful in experimental studies of population biology. Plant populations are semi-permanent and sessile: the fate of individuals can be followed, their abundance determined without complex mark-recapture techniques, and their environment can be more precisely defined than that of free-ranging animals. Plants have sexual reproductive structures that are well defined and often distinct from the vegetative parts: progeny number and reproductive effort can be readily estimated. Plants are easily propagated: large numbers can be grown under experimental conditions for studies of their genetics, physiology and experimental ecology. Seeds from one individual usually constitute a half-sib family: genetic components can therefore be estimated from field collections. Plants are often easily cloned (cf. Wu & Antonovics, 1975): this can aid genetic analysis and permit nondestructive sampling of individuals from field populations being studied demographically. Furthermore, field transplants of populations and families are possible, permitting comparison of life-history parameters under field conditions: many causes of mortality are not present in the laboratory. In summary the operationality that can be achieved with plants far surpasses that which is generally dreamed possible by the animal ecologist.

It must be mentioned that plant populations do have their limitations. Much of their biomass, their interactions, and a large proportion of the population (the seed pool) may be underground. There is considerable evidence from seed-dispersal distances and isozyme analysis that many plants living in close proximity are relatives; yet establishing these relationships precisely is difficult, much more so than in some higher animals where familial relationships are more obvious.

Two further attributes of plants, namely their vegetative spread and plasticity are often mentioned as difficulties in their population biology. Essentially the only disadvantage of an organism with vegetative reproduction is that it may hinder the identification of genetic individuals ("genets" *sensu* Harper & White, 1974). However, the demography of the individual physiological units (or "ramets") can be followed to provide meaningful information (e.g., Johnson & Cook, 1968). Moreover vegetative reproduction greatly facilitates sampling, estimation of genetic and environmental variance, and transplanting. The plasticity of plants, particularly in regard to overall size and its consequential effects on growth and survivorship, certainly invalidates the simple application of many animal-oriented models to plant populations since adjustment to density may be by change in size as well as change in numbers. Thus if we assume the Lotka-Volterra models, and apply them to plants on the assumption that r , the intrinsic rate of natural increase, stays at a high constant value equivalent to the reproductive output of many plants at low density, then with moderate carrying capacities the population overshoot is frequently so great as to result in the extinction of the population. This was also pointed out by Howard Levene in discussion during this symposium. Descriptions of density response in plants (e.g.,

De Wit, 1960; Harper & White, 1974) are well known, and could be incorporated into models of population regulation more applicable to plants. The plasticity of plants may have one further benefit. The emphasis on age as a major variable against which to measure demographic variables has its basis in the fact that in many animals it is a strong correlate of these parameters. In plants, however, size seems often to be more closely related than age to the survivorship and reproduction of an individual (Werner, 1975). In the first use of size-class modelling to study natural populations, Hartshorn (1975) stated "through the use of unequal stage (or size) groupings, the matrix [size-class transition] model should be applicable essentially to any plant population." By measuring populations on two successive years, it is possible to calculate the probability that a plant of a given size will be a particular size the next year (size-class transition probability), the probability that a plant of a given size will die and the probability of a recruit during that period reaching a particular size. In this way it is possible to assess population stability using measurements in two (or more) successive years, obviating the need for long-term study.

Finally, there is a dichotomy between approaches to plant and animal communities: the precise diets, foraging heights, activity times and so on of animals have few obvious counterparts in plants. Yet the precisely definable niche of many animals and the niche of a plant defined by its position on a multiple axis gradient are two ends of a continuum. The reconciliation of these outlooks is something to look forward to in the future as a period in ecology that will be immensely creative, but probably also one of considerable conflict.

Because of these many technical advantages of plants for population and genetic studies, it is clear that many old concepts will be revised and that new ideas will develop. Already the interaction of population genetics and ecology has led to the emergence of a new kind of thinking, a "new ecological genetics." This "new ecological genetics" is based on a series of tenets, the generality and usefulness of which remain in need of assessment, but which form a new basis from which to view the natural world. I want to summarize these tenets, and to provide evidence for their validity.

1. *The ecological amplitude of a species (both within and among communities) has a genetic component. Explaining the abundance and distribution of organisms is basically a genetic problem.*

The major message of the early ecological geneticists was that the ecological range of a species has a strong genetic component. They showed that genetic differentiation was often an absolute prerequisite for range extension since frequently there was mortality of races transplanted into the habitats of other races. Many of their studies are now classical examples in the evolutionary literature. In spite of this, ecologists have considered physiological tolerances to both climatic and biotic factors as *explanations* of limits to species distributions. But in fact the physiological tolerances

are a *result* of the limits and not their cause: the limits themselves are either lack of genetic variance for those tolerances or "constraints" on existing genetic variance. These constraints may be gene flow from different populations, negative correlations among fitness components, or coevolutionary changes by competitors and predators. The subject of the nature of limits to species distribution is a neglected area and in great need of study (for discussion: Grant, 1974; Antonovics, 1976*a*). It still has to be recognized that genetic differentiation within a species is the rule rather than the exception; perhaps of more interest are situations where such differentiation is demonstrably absent (e.g., Palmer, 1972).

These general principles apply to not only the distribution of a species over different habitats, but to the abundance of a species in a community. There is now a growing body of evidence that different members of a single population may be differently adapted to different segments of a particular community. Such exact microdifferentiation has been shown in *Avena barbata* (Hamrick & Allard, 1972) and *Veronica peregrina* (Linhart, 1974) growing in highly localized moisture gradients, in *Taraxacum officinale* in undisturbed and disturbed sites (Solbrig & Simpson, 1974), and among individuals of *Trifolium repens* sampled from one field in relation to associated grass species (Turkington, 1975).

Watson (1974), in a study of *Plantago lanceolata* in a 1×5 m segment of pasture, showed that individuals could be roughly divided according to growth habit into three phenotypic classes, namely prostrate, intermediate, and upright. Growth habit was shown to be significantly correlated with the height of vegetation surrounding each individual ($r = 0.31$, $p < .001$). From detailed vegetation maps, the expected numbers of plantains of each growth habit associated with neighboring species were calculated. The results showed that prostrate plantains were significantly positively associated with *Hieracium pilosella*, a prostrate rosette form. Intermediate phenotypes were positively associated with *Galium verum* and *Trifolium repens*. The upright group of plantains was negatively associated with species of low height and occurred in expected frequency among taller species. In June 1969, after the growth habit of each plantain had been noted, the individuals in one half of this area were removed and cloned in the greenhouse by propagating small, excised side shoots produced following removal of the apical rosette. They were planted out in standard garden conditions in September 1969 in a randomized, replicated design. Measurements of the plants in June and September 1970 (i.e., after ca. one year's growth under standard conditions) showed that the original growth habit in the field was significantly correlated with growth habit under standard conditions ($r = .40$, $r = .37$, $p < .001$, for June and September measurements). The differences in growth habit are therefore in all likelihood genetically determined. These results strongly suggest that the ability of *P. lanceolata* to grow in the presence of a range of species of varying heights may be to a large degree dependent on the range of genotypes that it produces.

These results, together with those of other workers mentioned previously, argue strongly for the importance of a genetic component in "niche width," even in a single community. The relative roles of genetic and phenotypic components in niche width have been considered from several general standpoints (Bradshaw, 1965; Levins, 1968) and in the context of specific theoretical models (Roughgarden, 1972; Emlen, 1976). But the relative contribution of phenotypic plasticity and genetic variation to the total phenotypic variance, and their relative contribution to variance in fitness remains in need of detailed quantification in natural populations. The fact that niche width has a genetic component also supports the argument that genetic variance and outbreeding are not just a *sine qua non* of long-term evolutionary progress but are of immediate and direct ecological importance in the survival of the offspring of an individual (Williams, 1975).

2. *Forces maintaining species diversity and genetic diversity are similar. An understanding of community structure will come from considering how these kinds of diversity interact.*

Models showing maintenance of genetic polymorphism can frequently be applied to noninterbreeding populations. For example, competition (Schutz & Usanis, 1969; Cockerham and Burrows, 1971; Antonovics, 1976) or predator-mediated frequency dependent selection (Allen, 1976) and multiple niche selection (Christensen & Feldman, 1975; Levin, 1974) will maintain genetic as well as species diversity. Indeed models of selection in the haploid state on single genes are equivalent models of selection among noninterbreeding species. There are added forces that can maintain genetic but not ecological diversity. Mechanisms involving the diploid state (e.g., selection in opposite directions in haploids and diploids), heterozygosity (e.g., heterozygous advantage), or situations unique to multilocus models (e.g., epistatic interactions, linkage) are all uniquely genetical. Furthermore the pressure of "invasion" by new genes or gene combinations by mutation, recombination and migration is greater than the "invasion" by new species from adjacent areas. It is nevertheless pertinent to ask to what extent such forces act similarly within and between species or to what extent a decrease in species diversity is accompanied by a corresponding increase in genetic diversity of the component species. In depauperate island communities evolutionary diversification has been commonly noted. And in an overall summary of isozyme studies, Powell (1975) detected a lower, but nonsignificant, heterozygosity in vertebrates and invertebrates from "tropical life-zones" than in those from "temperate life-zones." Clearly genetic diversity and species diversity are related phenomena and should not be treated as entirely separate phenomena.

The fact that niche width within and between communities has a genetic component implies that measures of species diversity and community distance using taxonomic criteria will underestimate effective diversity or distance. The categories used by the ecologist are categories created by the taxonomists for different needs and with different philosophies. For exam-

ple, if populations of a single species taken from two communities show genetic differences in some physiological parameter, then this may be poor grounds for taxonomic subdivision, but it may be very important in interpretations of community constancy, since similar taxonomy may not reflect similar evolutionary responses to environmental conditions. It seems that much ecological thinking is still a generation behind that of the systematist, in that it remains locked into a typological view of the species. The current "individualistic" view of communities, first championed by Gleason (see MacIntosh, 1975), has embedded in it a view of a species that is remarkably typological: the "individualistic species" is almost synonymous in usage with "typological species."

The consequences of escaping from such thinking is to view communities as consisting of evolving components, rather than collections of types plucked out by the abiotic and biotic pressures of the environment (cf. Harper, 1967; Pickett, 1976). This view may lead to fresh questions. To what extent are different members of a plant community coevolved? Should species that undergo extensive genetic differentiation be given the same weight in ordination studies as highly invariant species? Are the long-standing coevolved responses to natural perturbation different in essence from changes in secondary succession resulting from man-made disturbances? These are but some of the questions now being asked. The answers are at times dramatic. For example, in the few cases where competitive relationships have been analyzed between populations of two species from the same community, and compared with competitive relationships of those species from different communities, coevolution has been readily detected (Allard & Adams, 1968; Snaydon, 1976; Turkington, 1975).

3. *Darwinian fitness can be measured in terms of mortality and fecundity of individuals within populations. Adaptation is a dynamic process, operationally definable and not just a "matching" of the individual to the environment.*

Ever since the theory of evolution by natural selection was proposed, and particularly since it was popularized by the aphorism "survival of the fittest," critics of the theory have argued (e.g., Peters, 1976) that it is an untestable tautology, the proof of which is based on circular arguments or a *posteriori* reasoning. However, as soon as we merge the genetic and ecological views of life and death processes (e.g., Fisher, 1958) these criticisms perforce evaporate. The success of an individual, or of a set of phenotypes, can be defined in terms of that individual's contribution to future generations. This contribution can be measured *a priori* (i.e., not just by observation of future generations) by making a series of estimates the most important of which are the life-history parameters of age-specific birth and death rates and the rate of population increase. Other parameters such as seed quality, or coefficient of relationship to competitors, are undoubtedly important, but techniques for their measurement or their theoretical roles are less well defined.

Phenotypes can be grouped by their genetic constitution or by other criteria such as whether they originate by seed or as vegetative offshoots. Their genetic constitution can be determined using isozyme analysis, or by nondestructive sampling and growth of individuals under standard conditions. In experimental transplants, individuals can be classified both by family and by population of origin. It is thereby possible to test directly the adaptive significance of particular traits or particular character complexes. As a result one can view adaptation as an operationally definable concept and test directly the contribution of different characters to the overall fitness of the organism. We need not be confined to the dangerous procedure of assessing whether a trait is adaptive or not by seeing if it fits our biological intuition of what would be "good" for the individual in a particular environment.

4. *Genetic adjustment to environmentally induced changes in fecundity and mortality may be by direct response in the affected age-specific parameter or by compensatory change in other parts of the life history. Adaptation to new environments will result in different genotypes with different life histories.*

When a population is subjected to changes in fecundity or mortality as a result of a changed environment, it is likely that different genotypes will respond differently to these changes. By definition, those genotypes with life histories that maximize their contribution to future generations will spread in the population. These "successful" genotypes may be of two kinds: there may be in the population genotypes associated with life histories which are immune to the new environmental stress, and there may be those associated with life histories that compensate for the environmental stress. This distinction is best illustrated by an example. Imagine a population of perennials that is not frost tolerant, migrating into an area where frost is prevalent. The population may have genetic variance of two types (to speak teleologically, it has two options). There may be genetic variance for frost resistance, or there may be genetic variance for devoting more resources to reproduction in the first year and less to growth and survival in subsequent years. Selection may therefore be for frost resistance and maintenance of the perennial habit; or it may be for the development of the annual habit and a change in the life-history of the organism. It is interesting to note that in this example the two "options" are in fact mutually exclusive in that selection for frost tolerance would be relatively ineffective in an annual. This example is clearly oversimplified to illustrate how both direct response to a life-history shift and indirect compensatory change in other life-history parameters can be adaptive. The subject has been treated rigorously from a theoretical standpoint by Emlen (1970), who has predicted specific life-history responses for different age-specific shifts in mortality and fecundity.

In natural populations, the genetic changes may be complex and inter-

twined. For example, genetic changes in the affected life-history parameter may result in correlated effects on other life-history components, and compensatory changes in life history may result in overt genetic shifts in morphology and physiology since obviously a life history is the cumulative result of tangible birth and death processes of the plant. Fortunately, this complexity can probably be unravelled. For example, it may seem rather specious to talk of the plant changing its life history by, among other things, "shifting its resource allocation." However, this process need not require organizational changes in, say, phloem structure or sink-source relationships within the plant. As Primack (1976) has pointed out in species of *Plantago*, earliness of flowering is strongly correlated with reproductive effort, and changing sensitivity to photoperiodic induction may be a mechanism of life-history adjustment in this genus.

5. *The distinction between "ecological time" and "evolutionary time" is artificial and misleading. Changes of both kinds may be on any time scale: frequently genetic and ecological changes are simultaneous.*

It has become commonplace in the literature (Slobodkin, 1967) and in informal, but often earnest, conversation to make a distinction between "evolutionary time" and "ecological time." These terms carry the implication that evolutionary changes are long-term, or at least slower, than ecological changes. We can question this assumption since by definition genetic change manifests itself through demographic processes and, conversely, ecological change results in life-history shifts that in all likelihood will be genotype dependent. Evolutionary and ecological change are therefore inseparable. We can also question the assumption of a difference between the rates of evolutionary and ecological processes from the viewpoint of our general knowledge of these processes. Examples of rapid evolutionary change are now almost too numerous to review (e.g., Antonovics, 1975; Berry, 1972; Dyer, 1968; Wu & Antonovics, 1975). This evolutionary change can be of a kind that leads to rapid speciation, not just in plants where the processes of polyploidy and related phenomena are well known, but also in animals (Bush, 1975; Dobzhansky, 1972; White, 1968). Very often ecological consequences of these evolutionary changes are much more long-term. For example, the highly successful allopolyploid *Spartina townsendii* arose fairly suddenly in the south of England in the late nineteenth century as a result of chromosome doubling in a hybrid between *S. maritima* and *S. alterniflora* (Marchant, 1967); but its ecological effects are likely to be protracted either directly in terms of its own increases in numbers or indirectly in terms of its effects on the overall ecology of estuarine mud flats.

It could be argued that it is far easier to change the numbers of individuals in a population than to change their genetics. But this is arguing very much from a perspective where the recent impact of man has thoroughly disturbed populations, and where his technology is increasingly capable of destroying them. Even then the counter arguments are powerful. If we

could readily control populations, there would be no need for huge herbicide, pesticide, and other control programs. And if man puts in similar effort into recreating genotypes (as is the case with plant breeders), then large genetic changes can be achieved rapidly.

From a long-term, geological time-scale perspective, evolutionary and ecological changes may have very different rates. Ecological rates are often slower than evolutionary ones. That various regions of the world frequently have communities that are very different in terms of their species composition but very similar in terms of their "niche structure" has long been obvious to naturalists (Darwin used this as one of his major arguments for evolutionary change), but only recently is it being quantitatively and formally documented. Different species play very similar roles, almost as if the ecology and community composition is in some way fixed but the taxonomic, and hence evolutionary composition, very variable (Mooney & Dunn, 1970; Pianka, 1973). Clearly if one interprets ecological constancy over geological time in terms of taxonomic composition one is by definition making ecological change as rapid as evolutionary change; ecological change may in fact be much slower.

Finally it is worth emphasizing that a large number of studies have demonstrated that genetic change can be substantial within a single generation (Ford, 1975). Genetic changes occur during seed multiplication and establishment of pasture crops (Crossley & Bradshaw, 1968; Snaydon, 1976); genetic changes occur during self thinning in mixtures of *Plantago lanceolata* populations (Antonovics, 1976b), and they also occur progressively in experimental populations of perennials (Hickey & McNeilly, 1975). Obviously these rapid changes represent the action of strong selection pressures. Such selection pressures are only likely to be common in nonequilibrium, seminatural situations. But these observations argue strongly for the all pervasiveness and continuous action of selection maintaining specific adaptations in stable populations, for strong selective forces when biotic and abiotic environmental conditions change in time or space, and for dynamic evolutionary processes at ecotones.

CONCLUSION

This paper has been written from an obviously biased perspective: it may seem that I have overstated the input that population genetics is having on plant-population biology but it would not come as a surprise to me if the case has been understated. The whole area is, to aptly express it, very much at a crossroads where directions and emphases are uncertain. It is clear that out of the range of genetic variation present in a community, the between-species component is greater than the within-species component. I therefore do not wish to discount ecological studies that have looked at species composition and interactions without regard to the intraspecific variation. These studies will continue to form the mainstay of ecological generalizations and predictions. However, if we are to analyze the processes

occurring in ecosystems at the population level, and such analysis seems an essential part of understanding ecological and evolutionary causation, we ignore at our peril the input from population genetics. Increasingly "the new ecological genetics" is asking questions about what were once thought to be long-term evolutionary processes answerable only by comparative systematics, in terms of present-day processes that are operationally testable. Plants, because of their experimental advantages, will have an important part to play in this trend.

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WILDFLOWERS OF THE SOUTHEASTERN UNITED STATES. *Wilbur H. Duncan and Leonard E. Foot*. vii + 296 pages. University of Georgia Press, Athens. 1975. \$12.00.

An attractive book with 485 color photographs of wildflowers (most herbaceous) of the southeastern United States. There are no keys, but each species figured is briefly discussed. Introduced plants as well as natives are included. The photographs range from excellent to adequate. Apparently the book was subsidized and consequently the price is moderate.