Theory of Fitness in a Heterogeneous Environment. II. Developmental Flexibility and Niche Selection
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THEORY OF FITNESS IN A HETEROGENEOUS ENVIRONMENT II. DEVELOPMENTAL FLEXIBILITY AND NICHE SELECTION*

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The previous paper in this series (Levins, 1962) described a method for determining the optimal population structure of a species in terms of the statistical pattern of the environment. Three restrictive assumptions were made:

1. The phenotype is fixed independently of the environment;
2. Individuals are distributed at random among the niches;
3. The fitness of an individual depends on his own phenotype and the

environment, but not the composition of the population.

These restrictions will now be relaxed, and we will show the effects on our previous results of developmental flexibility, active niche selection, and interaction among different phenotypes. The final section discusses the conclusions of both papers and several approaches for testing the theory.

1. DEVELOPMENTAL FLEXIBILITY

The course of development of an individual is subject to long term, irreversible modification by the environment as well as to transitory fluctuations. The pattern of this long term modification may itself be subject to selection, so that the norm of reaction with regard to particular aspects of the environment may become an "optimal" norm of reaction. Three types of developmental flexibility will be considered: The phenotype may vary in a continuous way with the environment (Schmalhausen's dependent develop- ment, Schmalhausen, 1949). The phenotype may switch from one discrete state to another at some threshold value of the environmental factors (Schmal- hausen's regulative autonomous development). Or, there may be a stochastic switch mechanism in which a given genotype gives rise to two or more dis- crete classes

of phenotype in proportions that vary with some environmental factors.

An irreversible modification of development at any early stage will in gen- eral be advantageous only if the environmental factor evoking the modifica- tion is correlated with the environment at later stages when selection is operating. This may occur in several ways. The environmental stimulus may be an indicator of the niche the individual already occupies. For ex- ample, shade or moisture might indicate a forest niche. Or the environ- mental factor which serves as a cue may be pervasive over the whole region

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and yet be correlated with the proportions of various niches. For example, the photoperiod is an indicator of season and therefore is an indirect cue as to the likely proportions of available fruits. The factors of the environment which modify development need not be the same factors for which the modifications are adaptive.

The problem of finding the optimal norm of reaction has many complexities since there are many possible relations among the niche proportions, cue stimuli, and viabilities of phenotypes. Here we indicate an approach to these questions in some simplified situations.

The same adaptive functions can be studied here as were considered in previous sections with the difference that the probability that a given individual will ultimately be in niche 1 is now some function of the early en- vironment, e, of that individual and will be designated p_e. Similarly, the probability of ultimately being in niche 2 is $1 - p_e$. If e has a certain dis- tribution over the area of a population, the expected value or mean of p_e taken over all e will be denoted by p.

The first model to be considered is as follows: let the mean proportion of niche 1, p, be constant in

time but not in space and let the environmental cue e have the same distribution over the region in each generation. Then the fitness of the population is equal to the average of the fitnesses of individuals exposed to different values of e. This will be a maximum when it is maximum for each p_e. For each value of p_e the adaptive function is

$$A(W_1, W_2) = p_e W_1 + (1 - p_e)W_2.$$

Following the argument of 3.1, when the fitness set is convex the optimum phenotype for each p_e varies continuously with p_e so that the optimum norm of reaction is dependent development. When F is completely concave, the optimum norm is one which produces a single type of individual which is optimal for niche 1 or niche 2 depending on whether p_e is above or below some threshold value. Thus on a concave fitness set the optimum norm of reaction is a switch mechanism (regulative autonomous development).

In the second model we suppose that the environment consists entirely of niche 1 or of niche 2 with probabilities p_e, $1 - p_e$ respectively and that the environmental cue e is uniform over the region. Then, as in 3.2,

$$A(W_1, W_2) = W_1^{p_e} W_2^{1-p_e}.$$

If the fitness set is convex, the optimum norm of reaction is again de-pendent development, with

the phenotype varying continuously with p_e. If F is concave, the optimum is a mixture of types in proportions that depend on p_e, so that the optimum norm of reaction is a stochastic switch mechanism. Development can follow one of two channels, and the probability of taking a given channel depends on the environment.

We now restrict ourselves to dependent development and examine the effect of developmental flexibility on the fitness set. It will be shown that the fitness set is made more convex.

Let the probability of an individual being in niche 1 be p_e and in niche 2 be $1 - p_e$ where p_e depends on the environmental factor e. As before, the average value of p_e taken over all e is p, the proportion of niche 1 in the re- gion. Since the optimum phenotypes in niches 1 and 2 are S_1 and S_2 respec- tively, we can define the average optimum phenotype, S_e, by

$$S_e = p_e S_1 + (1 - p_e) S_2.$$

The mean value of S_e taken over all e is then

$$\overline{S}_e = p S_1 + (1 - p) S_2.$$

If the early environment provides a clue as to the later environment, then the average value of S_e among those individuals that ultimately mature in niche 1 will be closer to S_1 than the average of S_e over the environments of individuals that are ultimately in niche 2. The mean value of S_e given that the later environment is niche 1 is

$$E\{S_e | \text{niche 1}\} = \overline{S}_e - (1 - p)k$$

and for niche 2,

$$E\{S_e | \text{niche 2}\} = \overline{S}_e + pk$$

where $S_1 < S_2$ and $k \geq 0$.

Hence the mean value of S_e is

$$E\{S_e\} = p[\bar{S}_e - (1-p)k] + (1-p)[\bar{S}_e + pk] = \bar{S}_e.$$

Since S_e is always between S_1 and S_2, $E\{S_e|\text{niche } 1\}$ is always between $E(S_e)$ and S_i. A larger k indicates that S_e is closer to S_i and that e is a better early indicator of later environment.

Let the phenotype y be influenced by the environment as follows:

$$y = y_0 + B(S_e - y_0)$$

where B is the coefficient of developmental flexibility and y_0 is the pheno- type when $B = 0$.

The absolute value of the deviation of the actual phenotype from the opti- mum in niche i is

$$|S_i - y_0 - B(S_e - y_0)|.$$

We always have $S_1 < S_e < S_2$. When $y_0 = S_i$, the absolute value of the deviation is $B|S_e - S_i|$ which is greater than zero if $B > 0$. Thus when $y_0 = S_i$ the organism's fitness in niche i is reduced by developmental flexibility. Therefore, the end points of the admissible boundary when developmental flexibility is allowed are the same as in the case when developmental flexi- bility is excluded, namely $y_0 = S_i$, $B = 0$.

On the other hand, when

$$y_0 = pS_1 + (1 - p)S_2$$

there are values of B which improve fitness simultaneously in both niches. Let the fitness of an individual in niche i be

$$W_i = W(S_i - y)$$

where $W(Z)$ is a bell-shaped curve with center at $Z = 0$. Then

$$W_1 = \underset{e}{E}W\{S_2 - y_0 - B(S_e - y_0)\} = \underset{e}{E}W\{(1 - p)(S_1 - S_2) - B(S_e - y_0)\} \text{ and}$$

$$W_2 = \underset{e}{E}\{W[S_2 - y_0 - B(S_e - y_0)]\} = \underset{e}{E}\{W[p(S_2 - S_1) - B(S_e - y_0)]\}$$ where the expectation is taken over all e. For small values of B, W_1 and W_2 can be approximated by

$$W_1 = W[(1 - p)(S_1 - S_2)] - B(S_e - y_0)W'[(1 - p)(S_1 - S_2)] \text{ and}$$

$$W_2 = W[p(S_2 - S_1)] - B(S_e - y_0)W'[p(S_2 - S_1)].$$ We now take the expected value over all e given niches 1 and 2 respectively.

$$W_1 = W[(1 - p)(S_1 - S_2)] - B[-(1 - p)k]W'[(1 - p)(S_1 - S_2)] \text{ and}$$

$$W_2 = W[p(S_2 - S_1)] - B\,p\,k\,W'[p(S_2 - S_1)].$$ From the shape of $W(Z)$ we know that $W'(Z) < 0$ when $Z > 0$ and $W'(Z) > 0$ when $Z < 0$. Thus, in both W_1 and W_2 the coefficient of B is positive. This means that a small positive value of B improves

fitness over what it would be for B = 0.

For all y_0 such that

$$\overline{S}_e - (1 - p)k \leq y_0 \leq \overline{S}_e + p\,k$$

fitness is improved in both niches by developmental flexibility. Thus, the fitness set bulges out for these values of y_0, and F becomes more convex.

2. NICHE SELECTION

It is, of course, unrealistic to assume a random distribution of individuals among the niches. In nature there is a wide range of selectivity, from com- plete restriction to a single food plant or host through graded preferences to a widely polyphagous condition. Temperature and light preferences are widespread, perhaps universal. Therefore, the proportion of individuals in a given niche will be greater than the frequency of the niche if that niche is preferred, and less than the niche frequency if it is the less desired niche.

It is clear that absolute preference for the niche in which the type does best would give maximal fitness if that niche is readily available, but could result in extinction of the species if that niche is sometimes absent. Thus it would seem that an optimal mode of behavior would be one in which the individual searches for the preferred niche for a given period of time, and if

it has not found it then accepts some other mode. However, such an instan- taneous change in behavior after some critical interval has elapsed is unrealistic. Therefore, we assume that niche preference is initially absolute and decreases exponentially with the passing of time.

Let p be the frequency of the preferred niche and $1 - p$ the frequency of the less preferred niche. Let the probability of finding some niche in the interval $(t, t + dt)$ be rdt. If it is the preferred niche, it will always be ac- cepted. If it is the less desired niche, it will be accepted with the proba- bility $1 - e^{-\lambda t}$ where λ is a measure of the rate at which selectivity de- creases. Then the probability of no niche being accepted in the interval $(t, t + dt)$ given that no choice has been made previously is

$$1 - r[1 - (1 - p)e^{-\lambda t}]dt.$$

Let q_t be the probability that no choice has been made up to time t. Then from the above it follows that

$$q_{t+dt} = q_t[1 - r(1 - (1 - p)e^{-\lambda t})dt]$$

and

$$q_{t+dt} - q_t = -rq_t[1 - (1 - p)e^{-\lambda t}]dt.$$

As dt approaches zero, we obtain the differential

equation

$$\frac{dq}{dt} = -rq[1 - (1 - p)e^{-\lambda t}]$$

which has the solution

$$q_t = q_0 e^{\frac{r(1-p)}{\lambda}(1-e^{-\lambda t})-rt}$$

where $q_0 = 1$.

The probability that a niche is accepted in the interval $(t, t + dt)$ is

$$q_t r[1 - (1 - p) e^{-\lambda t}] dt.$$

If a niche is chosen in that interval, the probability that it will be the preferred niche is

$$\frac{p}{p + (1 - p) e^{-\lambda t}}.$$

Thus, the total probability that niche 1 (the preferred niche) is chosen in interval $(t, t + dt)$ is $prq_t dt$. The proportion of individuals in niche 1 is then the integral, p^*, of $prq_t dt$ over all t. Hence,

$$p^* = pr \int_0^\infty e^{\frac{r(1-p)}{\lambda}(1-e^{-\lambda t})-t} \, dt.$$

With the substitution $rt = u$, we have

$$p^* = p \int_0^\infty e^{\frac{r(1-p)}{\lambda}\left(1-e^{-\frac{\lambda u}{r}}\right)-\frac{u}{r}} du.$$

Thus, the effect of niche selection is to replace p in the adaptive function by p*. We see from the expression for p* that p* is greater than p since

$$\int_0^\infty e^{-u} du = 1$$

and

$$e^{\frac{r(1-p)}{\lambda}\left(1-e^{-\frac{\lambda u}{r}}\right)} > 1.$$

Further, the variance of p* is less than the variance of p. This follows from an examination of the ratio of any two values of p, p_1 and p_2, and the corresponding ratio of the P*'s.

$$\frac{P_1^*}{} = P_1 \frac{\int_0^\infty e^{\frac{(1-p_1)}{\lambda}\left(1-e^{-\frac{\lambda u}{r}}\right)-\frac{u}{r}} du}{}$$

$$P_2{}^* \qquad p_2 \qquad \int_0^\infty e^{\frac{(1-p_2)}{\lambda}\left(1-e^{-\frac{\lambda u}{r}}\right)-\frac{u}{r}} \, du.$$

Let $p_1 > p_2$. Then

$$e \int_0^\infty e^{\frac{(1-p_1)}{\lambda}\left(1-e^{-\frac{\lambda u}{r}}\right)-\frac{u}{r}} \, du < \int_0^\infty e^{\frac{(1-p_2)}{\lambda}\left(1-e^{-\frac{\lambda u}{r}}\right)-\frac{u}{r}} \, du.$$

Therefore, the ratios of the p*'s are closer to unity than the ratio of the p's; there is less spread in the distribution of p*, and the variance is smaller. Thus, niche selection reduces the effective variance of the environment, so that on a concave fitness set a population with niche selection is less likely to have a polymorphic optimum.

This result depends on the special assumption that all individuals prefer the same niche, and that within a niche fitness is independent of population density. If we relax these assumptions and suppose instead that fitness declines with population density, that niche preference is modified by density, and that each phenotype in the population selects preferentially that niche in which it would be more fit, we would be led to the opposite conclusion. For then phenotypes which are

adapted to usually rare niches can be kept in the population without much loss of fitness, and the population will be more evenly spread over its environment.

3. INTERACTIONS BETWEEN INDIVIDUALS

A mixed population can be represented by a point on the straight line join- ing the representations of the separate types only if the different types do not interact to effect each other's fitness. There is a growing body of evidence (for example, Levene, Pavlovsky and Dobzhansky, 1954; Lewontin, 1955; and Sakai, 1955) that such interactions may be important.

In the absence of a general quantitative description of these mutual interaction effects, we will take for illustration the simplest model, quadratic interaction. Let the fitness of a given type in a given niche vary with the proportion of individuals of other phenotypes. If there are two types in the proportions q, $1 - q$, the fitness of type 1 in niche i will be $w_{i1}* = w_{i1}[1 + a(1 - q)]$ and the fitness of type 2 in niche i will be $w_{i2}* = w_{i2}[1 + bq]$ where w_{i1} and w_{i2} are the fitnesses of the two types when alone, $w_{i1}*$ and $w_{i2}*$ are their fitnesses when both are present, and a and b are measures of the interaction effects. Then the fitness of the mixed population in niche i is

$$qw_{i1}{}^* + (1 - q)w_{i2}{}^* = qw_{i1} + (1 - q)w_{i2} + q(1 - q)[aw_{i1} + bw_{i2}].$$

The fitness of a mixed population is represented by a point on a parabolic arc joining the fitness points of the separate types. In such a situation the expanded fitness set F' is not the smallest convex set that contains F. However, if we redefine "straight line" to be the arc of the interaction curve, in this case parabolic, the previous theory holds.

The well known result follows that, if interaction is positive, F' can more readily contain points outside of F, giving polymorphic optima, whereas negative interaction makes monomorphic optima more likely.

CONCLUSIONS AND DISCUSSION

The fitness of a species over its whole distribution can be resolved into the contributions of several adaptive systems. First, there is the fitness of individual members of the species. This in turn can be separated into ' 'physiological' ' homeostasis and developmental flexibility. The former in- cludes the tolerance of the organism for non-optimal conditions and its ca- pacity for rapid

reversible changes in internal state corresponding to transitory fluctuations in the environment. The latter refers to irreversible de- velopmental modifications of an adaptive character.

The distinction between physiological homeostasis and developmental flexibility is an arbitrary one which must be defined operationally for each experimental situation. Suppose that the life span of an organism is divided into two periods which we designate early and late. Let groups of individuals be subjected to various combinations of early and late environments at two intensities, arbitrarily designated +1 and −1, and let the fitness of each group be measured (for example, by the average number of seed set per seed sown). Suppose the results are those shown in table 1.

TABLE 1

			+1	Late −1
Early	+1		1.6	1.4
	−1		.6	.4

In this table, fitness $(W) = 1 + .5E + .1L$.

These data were obtained from the model which expresses fitness by

$$W = 1 + .5E + .1L$$

where E and L stand for early and late environments respectively. The co-efficients of E and L indicate how sensitive the organism is to environmental differences at the corresponding stages of development, and thereby measure inversely the physiological homeostasis of the organism in the two stages. Now consider the hypothetical data in table 2.

TABLE 2

			Late	
			+1	−1
Early	+1		1.7	.5
	−1		.5	1.3

In this table, fitness $(W) = 1 + .1E + .1L + .5E \times L$.

These data were obtained from the expression

$$W = 1 + .1E + .1L + .5E \times L$$

where E and L are again the early and late environments. The coefficients of E and L inversely measure the physiological homeostasis in the two stages. The coefficient of E × L measures the increment in fitness when the early and late environments are the same. Therefore, it can be inter- preted as a measure of the long lasting modification of development in the early stage in the direction of improved survival in that environment at the expense of reduced survival in the opposite environment, that is as developmental flexibility.

A second adaptive system is based on static polymorphism, the exist- ence of a permanent and stable diversity within populations, in which each of the types is superior to all the others in some environmental phase or niche. This is a sort of insurance in the face of random fluctuations in the environment. However, it was shown that static polymorphism can only be advantageous when the difference between the different niches exceeds some minimal value which measures individual

tolerance or homeostasis.

A third adaptive system is the geographic differentiation into local races, subspecies, ecotypes, or clines.

Finally, there is the genetic flexibility of the species — its ability to respond to the selection pressures of a changing environment. This component of fitness will be considered in a separate paper.

The relative importance of these components of fitness depends on many factors — conflicting selection pressures, populations size, past history, available cytological mechanisms, etc. In the study just referred to we con- sidered the selection pressures acting on the components of some of these adaptive systems. It was found that the optimum adaptive system depends on the pattern of heterogeneity of the environment in space and time. The optimum was defined in such a way that interpopulation selection would be directed toward the optimum. Intrapopulation selection may reinforce inter- population selection or act against it. However, if the fitness of individual types does not depend on the frequencies within the population, we might expect that intrapopulation selection would generally also tend to the same optimum.

The structure of actual populations may differ from the theoretical optima for a number of reasons. If the assumptions of the model can be applied

reasonably to a given population, departures from the predicted might be ascribed to the effects of other factors than those considered here — antagonistic selection, migration, population size, etc. Or it may be that the population is not yet in equilibrium with its environment, that its present properties are more determined by past history than by present conditions.

Thus, the correspondence between the predicted (optimal) population characteristics and those observed in nature will be only statistical. It would be possible to summarize our results by listing "tendencies." For example, species occupying more heterogeneous environments "tend" to be more polymorphic than species living in more uniform environments. Such an approach would result in a series of generalizations analogous to the familiar eco-geographic laws.

However, we prefer a different interpretation. There are two kinds of generalizations in evolutionary theory — statements about causes of evolu- tion and statements about frequent results, or tendencies. An identified causal factor is assumed to be present whether or not its effect is obvious, whereas a tendency is sometimes expressed and sometimes not. For example, we could talk about a tendency for unsupported

objects to move toward the center of the earth, or we could discuss gravitational attraction. In the former case, each bird, airplane, or rocket is an "exception" to the tendency. In the latter case we claim that gravity is just as relevant for ob- jects moving in the wrong direction, and that a knowledge of the magnitude and direction of the gravitational attraction helps identify and measure the opposing forces.

The state of a species or population at any time is one of tenuous equilibrium among opposing factors or of transition from one equilibrium to another. Its evolution can be studied by identifying and measuring these factors, the vectors acting on a population. Then the correspondence be-

tween the predicted and observed situations becomes one of the ways of measuring the importance of a particular factor, and any correlations de-rived from the data must be subordinated to the dynamics of change. Otherwise statements about the results of evolution are too readily converted into statements about causes, as in the claim by one eminent biologist that the evolution of the brain in a given phylogeny was "guided by the law of increasing size."

We claim that in this study the direction of a particular component of se-lection has been identified. The next step, the determination of whether it is of sufficient magnitude to exert a noticeable influence on evolution, is an experimental problem.

There are three principal experimental approaches for testing the theory:

1. The study of the responses of experimental populations to different patterns of environmental heterogeneity;

2. The comparison of the structures of natural populations of the same or related species;

3. The statistical analysis of the adaptive systems

for a large number of taxonomic groups.

Experimental Populations

If the fitness of each phenotype is independent of the composition of the population and if the density of the population does not greatly affect the relative fitnesses, it seems reasonable to expect that intrapopulation selection will move in the same direction as the theory predicts for interpopulation selection. Then it might be possible to observe the formation of optimal population structures. In order to set up such experiments, it is necessary to obtain the fitness set for a given population and a pair of defined niches. This could be done by dividing the progeny of single pairs into two batches raised under the two environments. The fitness of each group could be estimated using such information as the percentage reaching maturity, average number of eggs produced, etc. The data for the two batches together define a single point in the fitness space, and the array of all such points for many single pairs would constitute the fitness set. Alternatively, one might prefer to consider the fitness set for particular chromosomes extracted from the population and compared to some standard chromosome.

A convex fitness set is readily attainable by

taking the two environments close enough together. A concave fitness set might be more difficult to find. However, it is suggested that we could produce a concave fitness set as follows: An initial population is divided into two lines, designated High and Low. They are selected for survival in increasingly extreme conditions in opposite directions, such as high and low temperature. As the two niches diverge, the initially convex fitness set will become concave when each line can grow in an environment lethal to the other, if not before then.

At different stages in the divergence, experimental populations can be established using founders from both the High and Low lines, and exposing them to the appropriate environmental pattern.

In the early stages of divergence, when the fitness set is convex, we would expect the equilibrium population to have a unimodal distribution whose fitness in each niche will be intermediate between those of the founding populations.

In the later stages of divergence, after a concave fitness set has been attained, the equilibrium population will depend on the environmental pattern. If both environments are always available to the population in about constant proportions, the optimum population will be adapted to one of the two niches and should soon be equal in fitness in this niche to the founding population raised in that environment. An alternative optimum would consist of the formation of two populations each adapted to one of the niches. That is, an isolating mechanism might arise giving in affect two populations. If the

two environments alternate about once per generation, the expected result would be a polymorphic population which would show a bimodal distribution of fitnesses in each niche, and the sensitivity of the whole population to selection in either niche would gradually decline.

The "equilibrium" we are discussing here is not the initial equilibrium reached after some 10 to 50 generations when different karyotypes of Drosophila of the same geographic origin are introduced into a population cage. It would involve a more radical reconstruction of the genetic system through the selection of many modifiers. Heterosis may arise where initially there was none, or heterosis may break down. Perhaps several hundred generations may be required before an "optimum" equilibrium is established, and even then its maintenance may be accompanied by genic and chromosomal turn over.

Comparisons within species or groups of species

Two theoretical models for the distribution of polymorphism within a species are of current interest. Da Cunha and Dobzhansky (1954) suggest that the amount of polymorphism is correlated with the number of niches available. This is based on

the demonstration by Levene (1953) that when more than one niche is available, the necessary conditions for stable polymorphism are less stringent. Thus this theory is concerned with stability rather than optimality. The data for *Drosophila robusta*, *D. willistoni*, and a number of other species support the hypothesis, but the cosmopolitan species show very little polymorphism and in *D. pseudoobscura* the data are ambiguous.

Carson (1955) seems to accept the argument that niche diversity makes polymorphism more likely. However, since his interest is species formation he emphasizes the distinction between central (multi-niche) and marginal (few niche) populations.

Both of these approaches and our own make similar predictions in expect- ing polymorphism and environmental heterogeneity to go together. They

differ, however, in the measurements of polymorphism and of environmental heterogeneity, and also seem to disagree in several predictions.

Carson measures polymorphism by the proportion of the genotype in which inversions block free recombination. His theory refers specifically to cytological polymorphism. Dobzhansky et al. measure polymorphism by hetero- zygosity — the number of inversion heterozygotes per individual or the num- ber of distinct inversions in the population. We are concerned only with polymorphism for niche adaptations. The only types we wish to recognize are those which are fitter than every other type in at least one niche and which therefore are represented on the admissible boundary of the fitnes s set. Thus the Lancetilla population of *D. tropicalis*, in which more than 70 per cent of the flies are heterozygous for an inversion, is highly poly- morphic from Dobzhansky's viewpoint. However, it is by no means certain that the three karyotypes represent adaptations to different niches. The heterozygote may be superior to both homozygotes in all environments encountered by the population. On the other hand, populations which are cyto- logically

homozygous may be polymorphic with respect to many genes of ecological significance. Thus, although we have spoken of polymorphism, our theory is concerned only with ecological polymorphism, the coexistence of two or more phenotypes each adapted in one or more niches.

A proper test of the theory would require identification of the environmental factors to which the polymorphs are adapted. In the absence of specific information on this point, the number of inversion types in a popu- lation (rather than the proportion of heterozygotes) can be taken as a very rough guess as to the number of ecotypes.

For Carson's purposes the location of a population or its relative abun- dance is sufficient indication of environmental heterogeneity. Da Cunha and Dobzhansky use a quasiquantitative scale devised by Dansereau (1952) which includes both spatial and temporal heterogeneity. However, in our theory, these two aspects of the environment have very different signifi- cance. Ecological polymorphism is optimal only when the environment undergoes changes of sufficient magnitude so that the fitness set of the population with respect to the two extreme environments is concave, or when two niches which are themselves sufficiently distinct occur in chang- ing proportions

in such a way that each niche is the predominant one part of the time. Spatial heterogeneity contributes to polymorphism only indirectly. If there are more niches, one might suppose that some of these are likely to be sufficiently far apart to give a concave fitness set. Further, an abundance of different vegetation types, each with its own fruiting season, gives rise to a great temporal heterogeneity in the available food for Droso- phila even when the climate is rather uniform, as along the Amazon.

I have recalculated the data of Da Cunha and Dobzhansky (1953) and Da Cunha, Burla and Dobzhansky (1950) in the following way: the total number of chromosome inversions reported for each locality was found. The localities were divided according to temporal heterogeneity (seasonal changes). The average number of chromosome types for the uniform locali-

ties was 19.2 and for the seasonal ones 27.2. Thus, it is apparent that much of the variation in chromosomal polymorphism among the localities can be ascribed to temporal heterogeneity of the environment although this appears as only a 0 or 1 on the scale that goes from 5.5 to 12.

Since Da Cunha et al. are interested in the stability rather than the optimality of polymorphism, the likelihood of polymorphism should not be increased in their view by a concave fitness set. On the contrary, it would seem as if a convex fitness set is more likely to give stability. For example, let the niche optima be s, −s and let the three genotypes (or inversion types) have phenotypes

$$
\begin{array}{ll}
AA & a \\
AA' & 0 \\
A'A' & -a
\end{array}
$$

Assume further that the two niches are equally frequent. Then each homozygote has a mean

$\frac{1}{2} [\mathbb{W}(s + a) + \mathbb{W}(s - a)]$ which is less than $\mathbb{W}(s)$,

the fit-ness of the heterozygote (when F is convex). When the fitness is concave, the mean fitness of the heterozygote is less than that of the homozygotes although the harmonic mean may still be more than that of the homozygotes and polymorphism might be stable.

Thus, a comparison of successful species in the same region would (on the Da Cunha–Dobzhansky theory) reveal a position or zero correlation between individual homeostasis and polymorphism, whereas we would expect a negative correlation since good homeostasis is more likely to give a convex fitness set and therefore a monomorphic optimum. In particular, we expect that *D. willistoni,* since it is highly polymorphic, will prove to have relatively poor individual homeostasis compared to the cosmopolitan species and to its own siblings.

A second discrepancy between our view and that of Carson as well as Da Cunha et al. concerns submarginal populations. Toward the ecological extreme of a species' distribution, the number of niches utilized presumably decreases. But relatively minor environmental differences between niches may become more important when some pervasive factor is extreme and homeostasis possibly weakened. Thus, the fitness set may

become more concave toward the margins, giving rise to submarginal polymorphism and race formation.

A final prediction concerns race formation. Discrete races would be expected when the fitness set is concave and the local optimum is monomorphic. Thus, subdominant species with little polymorphism should show greater differences between geographic populations than more polymorphic domi- nants. A dominant species with low polymorphism (convex fitness set) should show continuous variation along an environmental gradient.

Statistical Analysis of a Biota

The plants and animals which live together in the same region do not necessarily experience the same kind of environmental heterogeneity. For example, the meadow environment is more variable than the forest and less variable than disturbed ground. The average conditions over a longer life span have a smaller variance than over a short life span. The seed of climax forest trees usually fall near the parent and are more likely to grow under similar conditions than would the seed of weeds. Thus, from the general ecology of a species it is possible to derive a quasi quantitative measure of environmental heterogeneity.

For plants, an index of temporal heterogeneity can be established as follows, where positive scores indicate more variability:

1. Habitat: -1 for forest 0 for meadow or savanna 1 for disturbed ground.

2. Successional position: -1 for climax 0 for subclimax 1 for

colonizers and weeds.

3. Seed dispersal: − 1 for poor dispersal   1 for good dispersal.

4. Life span: −.1 for perennials   0 for annuals   1 for ephemerals.

Similarly the effective spatial heterogeneity of a population's environment depends on the area covered by the panmictic unit, the occurrence of microniches large enough for an individual to grow in, and the number of niches occupied. Thus, an index can be constructed in which positive values indicate more spatial heterogeneity.

1. Occurrence: − 1 for rare or specialized   1 for ubiquitous

2. Size: − 1 for large trees   0 for shrubs   1 for small herbs, lianas, and epiphytes.

3. Pollination (indicating size of panmictic population):

− 1 for selfers   0 for bee pollination   1 for pollination by wind or less specialized insects.

The optimum structure also depends on individual homeostasis. This might be measured directly by transplantation experiments or could be inferred to some extent from habitat.

Such a study might be most effective using pairs of related but ecologically distinct families such as Malvaceae-Bombacaceae, Solanaceae-Scrophulariaceae, etc.

Over a geographic gradient in the environment of the region studied, we would anticipate the following sort of results:

1. The annual weed mode of adaptation: high individual homeostasis; ran- dom genetic differences between populations of the same area; little genetic differentiation along the transect; each species occurs over a wide ecologi-

cal range; little response to selection for adaptation to particular microniches (often associated with polyploidy). Genera may be large but without division into coenospecies.

2. Forest herbs, shrubby weeds, secondary growths, subclimax: intermediate.

3. Climax vegetation, especially forest trees: lower individual homeostasis; adaptive genetic differentiation along a transect; each species confined to narrow range of ecological zones. Little adaptive polymorphism within populations; allopatric races or coenospecies; freer response to selection. Caution must be observed in avoiding the circular reasoning of defining the ecological zones by their unique climax vegetation and then discovering that these trees are confined to one zone.

Similar indices could be worked out for animals. A summary of the general results is given in Table 3.

TABLE 3

Difference small between niche optima

Difference large between niche optima
as compared to individual homeostasis

as compared to individual homeostasis

	Environment heterogeneous in space	Environment heterogeneous in time	
Optimum phenotype	Specialized to one or the other niche (specialized to one niche)	Intermediate between optima in the two niches	Optimum phenotype for more frequent niche (specialized to one niche)
Optimum population structure	Polymorphic mixture of specialized types in each niche	Monomorphic of moderate fitness	Monomorphic, specialized types
Pattern along geographic gradient	Cline in proportions of same polymorphic types in niche frequency	Continuous cline in phenotype	Discrete races separated at some critical value of niche frequency

SUMMARY OF SYMBOLS

A summary of symbols may be found in the preceding paper of this series (Levins, 1962).

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