

EVOLUTION IN
Changing
Environments

SOME THEORETICAL EXPLORATIONS

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MONOGRAPHS IN POPULATION BIOLOGY

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A third line of work is in the genetics of flexibility for different types of structures and processes. If the pattern of response is strategic, it would be selected separately for different aspects of the same organism instead of being controlled by some general "flexibility" factors, and may vary widely in the same character from group to group. The work of Bradshaw (1965) and his collaborators seems to support this view.

Finally, one could attempt to produce natural selection for an optimal strategy in laboratory populations. Since "strategy" is a phenotypic trait, there is no reason to doubt the possibility of such selection. The differentiation of the European corn borer (*Ostrinia nubilalis*) populations into distinct diapause races in the forty or so years since their introduction into North America encourages the belief that the selection may be strong enough to be rapidly effective. One such experiment would be to subject *Drosophila* larvae to a single day of high or low temperature in the last instar. The high-temperature treatment would be followed by selection of the first flies to emerge from the puparium. The low-temperature treatment would be followed by discarding the first flies and retaining the last group only. We would therefore expect natural selection for a pupal dormancy or pseudodiapause evoked by one day of later larval temperature. The next step from there would be to replace the temperature signal by light, or oil of wintergreen. We could then test the hypothesis of the arbitrary physical relation between the form of the signal and the evoked response, that almost any signal can be coupled to almost any responding system.

Beyond the specific experimental and observational testing of the theory, this approach directs attention toward the sufficient parameters of the environment, and would therefore direct biochematological work toward the definition and measurement of these evolutionarily significant characteristics of environment.

Finally, strategic analysis can be used to interpret the evolution of complex systems such as biochemical networks and behavioral modes, suggesting relevant measures and selection pressures.

CHAPTER THREE

The Theory of the Niche

The concept of the ecological niche has been used heuristically for a long time. Grinnell (1904) referred to the niches of birds to indicate that different species have different requirements. Elton (1927) used the niche mostly for defining a species' position in the trophic hierarchy. Biogeographers have long noted the apparent equivalence between organisms of different regions and corresponding numbers of species in corresponding formations. For instance, in Table 3.1 we show the percentages of bird species of the Maylayan and Australian rain forests in each level of the forest and for each food category. This correspondence suggests that the relative abundance of opportunities for species of each type, or the number niches, is the same in both forests. The notion of saturated environments versus those with empty niches has been used to compare insular and continental biotas. Finally, the classical experiments of Gause (1934) led to the exclusion principal: if two species coexist they must occupy different niches. But it was due to the work and inspiration of G. E. Hutchinson (1965) that progress has been made toward a rigorous theory of the niche.

A satisfactory theory of the niche must permit an accurate description of a species' niche, and must be able to use that description to answer the following questions:

1. What determines the degree of specialization of a species, or inversely, its niche breadth?
2. What determines the species diversity of a community in relation to area, climatic region, size of organism, trophic level, etc?
3. How similar can species be and yet coexist?
4. How do similar species divide the environment among them?

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TABLE 3.1. The subdivision of the rain forest habitat among bird species (from Harrison 1962)

	Per cent of 306 Maylayan birds (per cent of 117 Australian birds)				Total
	Herbi-vore	Carni-vore	Insecti-vore	Omnivore	
Air	0(0)	2(7)	4(5)	0(0)	6(12)
Upper canopy	13(9)	0(0)	5(1)	8(11)	26(21)
Middle zone	0(3)	4(5)	40(42)	10(7)	53(57)
Terrestrial	1(2)	0(0)	8(4)	6(4)	15(10)
Total	14(14)	6(12)	57(52)	24(22)	100(100)

5. How do species in the same community affect each others' evolution? When do species alter their niches?

There are a number of ways of representing the niche of a species in an abstract hyperplane. One method would be to let each axis represent an environmental factor such as temperature, size of food particle, etc. Then each point in the space represents a set of environmental components, and if the species can survive (or is found) in that environment the point is included in the niche. The niche is then a region of the environment space. This definition may be refined somewhat to indicate how well a species must do in a given environment for it to be included in the niche. In this representation, niche breadth appears as the area of the niche in the hyperplane.

Another representation increases the number of axes. Instead of a single temperature axis there are axes for minimum and maximum temperature (or for midpoint and range). Then the niche is reduced to a point. Here niches can no longer overlap, but similarity appears inversely as the geometric distance between points.

We prefer to define the niche as a fitness measure on an environment space. Figure 3.1 shows the temperature niche for two species of *Drosophila*.

We have found that the following measures are a set of sufficient parameters for the theory of the niche and community:

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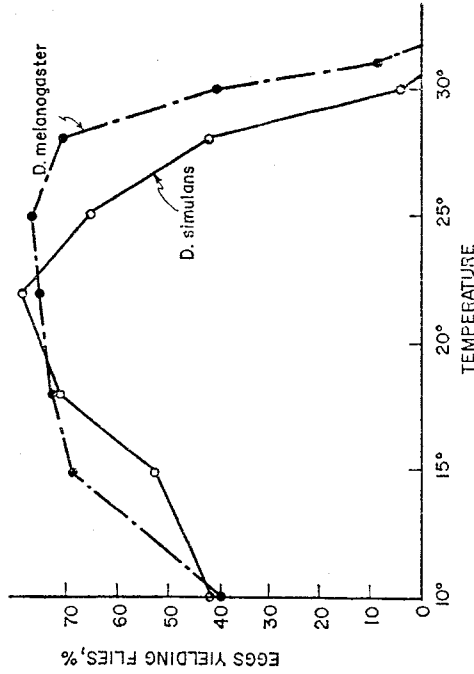


FIGURE 3.1. The temperature/emergence relation for two species of *Drosophila*. Clearly *D. melanogaster* has a broader temperature niche than *D. simulans*. (After Tantaawy and Malah, 1961.)

1. niche breadth;
2. niche dimension;
3. niche overlap;
4. community diversity.

NICHE BREADTH

Data on niche breadth come from three sources:

1. Survival experiments such as those of Tantaawy's in Figure 3.1. Since fitness requires not only survival but also successful reproduction, this is clearly not a complete fitness measure but is an important component. In the figure it is seen that *D. simulans* has a narrower, higher, more specialized temperature niche than *D. melanogaster*. Any measure of spread could be used to quantify niche breadth.

2. Habitat or food selectivity in multiple choice experiments. For example, Martinez et al. (1965) set out several different kinds of bait (banana, tomato, potato, and oranges) in *Drosophila* traps less than ten feet apart. Thus any fly caught on any bait could have reached any of the others.

patchy environment indicates a broad niche, and extreme clustering suggests a narrow niche provided we can exclude a clustering tendency *per se* and the persistence of progeny at the site of their birth. When the patches are small enough compared to the mobility of the species, the potential niche is measured.

Maldonado and Levins (in preparation) studied the microhabitat niche of *Drosophila* by setting out 20 traps with the same banana bait in a small area and classifying the species taken in each trap separately. Some of their results are shown in Table 3.2.

TABLE 3.2. Microhabitat niche breadths for *Drosophila*. $B = 1/\sum p_i^2$

	Collection 5		Collection 6	
	14	13	13	8.5
Maximum	2.4	3.5	7.5	8.5
<i>D. melanogaster</i>	5.3	7.5	5.2	4.0
<i>D. willistoni</i>	7.0	8.5	5.4	6.1
<i>D. latifasciataeformis</i>	5.4	5.2	4.0	8.5
<i>D. Dummi</i>	5.4	4.0		
<i>D. ananassae</i>	6.1	8.5		
All flies				

Two measures of niche breadth have been proposed:

$$\log B = -\sum p_i \log p_i \quad (3.1)$$

and

$$1/B = \sum p_i^2 \quad (3.2)$$

In both measures, p_i is the proportion of the species which is found in environment i , which selects environment i , or in the case of a viability measure

$$p_i = v_i / \sum_i v_i \quad (3.3)$$

where v_i is the viability in environment i .

There is no very strong reason to prefer one measure over the other as yet. Both give niche breadths equal to N for N equally used resources or for uniform utilization over an interval of length N and no utilization outside. And both measures are similar, as is shown in Table 3.3. Finally, since the number of environmental classes is arbitrary, the meas-

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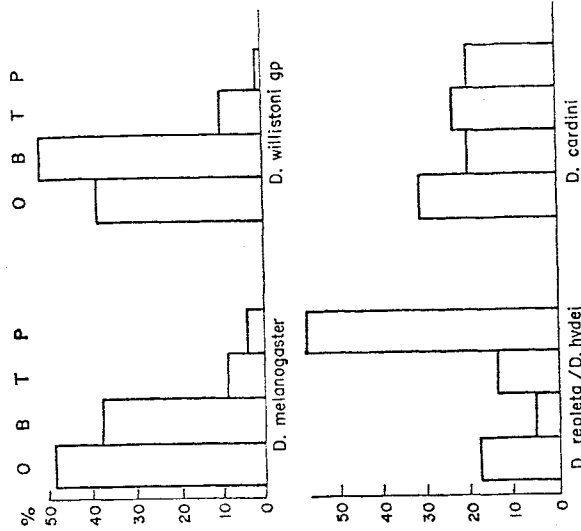


FIGURE 3.2. Food preference histograms for four species of *Drosophila*. O, orange; B, banana; T, tomato; P, potato. (From Martinez Pico et al., 1965.)

Some of their results are shown in Figure 3.2. A species such as *D. cardini*, which is attracted to each bait with almost equal frequency, would be said to have a broad niche for food as compared to *D. replata*. Of course the baits offered did not span the whole range of *Drosophila* food, but it did include fruits differing in acidity, starchiness, and sugar content. All the flies were drawn from the same population, and since we did not observe evidence of aggressive exclusion of flies, the distributions are assumed to indicate true preferences and hence to correspond to the pre-competitive or potential niches.

3. Actual distributions of species over environments. (a) Environmental factor identifiable. We can use the frequency distribution of tidal organisms over levels across a beach, plant species vs. altitude, or flies against season of the year. (b) The environmental factor not identifiable but known to vary. Then the uniformity of a distribution over a presumed

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TABLE 3.3. Two measures of seasonal niche breadth for *Drosophila*. * Measure 1 = $1/\sum p_i^2$; measure 2 = $\exp(-\sum p_i \log p_i)$; maximum value is 25. Data for Austin, Texas, from Patterson, 1943

Species	B1	B2
All		
<i>D. melanogaster + simulans</i>	11.14	14.27
<i>D. hydei</i>	9.58	12.06
<i>D. mulleri + aldrichi</i>	3.64	6.24
<i>D. macrospina</i>	4.23	6.92
<i>D. longicornis</i>	8.30	10.71
<i>D. affinis + algonquin</i>	4.39	6.95
<i>D. hematofila</i>	9.81	12.58
<i>D. putrida</i>	3.51	5.16
<i>D. pseudoobscura</i>	3.52	6.16
<i>D. melanica</i>	4.65	6.51
<i>D. busckii</i>	10.35	13.07
<i>D. meridiana</i>	3.21	4.51
<i>D. immigrans</i>	3.06	3.69
<i>D. robusta</i>	1.70	1.84
<i>D. tripunctata</i>	2.53	3.44
	6.72	9.35
Average	4.08	5.35
Correlation		.98

* Species with fewer than 100 flies omitted.

ure B should be divided by the maximum number, which is the number of classes, to give comparable measures of niche breadth.

Once we have a measure of niche breadth we can ask whether the abundant species tend to have broader niches than the rare ones, whether climax species have narrower niches than colonizing species. We can also compare niche breadths for the biotac of different regions, zones, trophic levels, or taxonomic groups. For the Puerto Rican *Drosophila* we have found that the abundant species are usually the ones which are broad-niched.

Immediately the question arises, how can we tell if we are measuring the relevant factors so that the calculated niche breadths have real meaning. We will show below that the niche description leads to predictions of numbers of species and other community properties which enable us to check its completeness.

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In the previous chapter we reached several conclusions about niche breadth. Qualitatively they all suggested that a broad niche is optimal in an environment which is uncertain. This uncertainty may derive from temporal variation in the environment from generation to generation, from a coarse-grained patchiness which is uncertain for each individual, or from a low density of usable resources or habitats (low productivity of the environment for the species in question). In a stable environment, fitness will be spread out only over environments which are so similar as to give a convex fitness set.

One difficulty with the theory is that while the species is allowed to adapt to a pattern of environmental heterogeneity that pattern is taken as given. Yet we know that habitat or food preferences may reduce the effective environmental heterogeneity. The amount of niche reduction by behavioral preferences depends on the viability niche breadth and on the productivity. We showed in Chapter 2 that fitness, \bar{W} , was given by

$$\bar{W} = [M - (M - L)\theta q / (p + \theta q)] [1 - \exp(-\lambda(p + \theta q)t)], \quad (3.4)$$

where M is the fitness in the better habitat, L is fitness in the poorer habitat, p and q are the relative frequencies of the two habitats (or resources), θ (between zero and one) is the probability of accepting the less favored environment, λ is a measure of the probability of encountering a unit of either habitat per unit time, and t is the available time. We saw that for a fixed p, λ, t the optimum value of θ may be zero when $M - L$ is very large and the optimal θ is one when $M = L$ (or when $M - L$ is small enough). But for a population $M - L$ depends on the gene frequency. In Table 3.4 we show a model of a one-locus, two-allele system with symmetric effects. This is also shown in Figure 3.3. We took $h > 0$ in order to have a convex fitness set.

As seen from the figure, the equilibrium gene frequency will be zero if p is small enough and one if p is close enough to one. For the population as a whole, the difference in fitness between the two environments is $M - L$ when the

TABLE 3.4. Model of fitness in two environments

Genotype	Frequency	Fitness in environment	
		I	II
AA	x^2	$\frac{M}{(M+L)/2 + h}$	$\frac{L}{(M+L)/2 + h}$
AA'	$2x(1-x)$		
A'A'	$(1-x)^2$		

gene frequency of A is zero, $-(M - L)$ when the frequency is one, and zero at some intermediate gene frequency (here at 1/2, due to the symmetry).

In Figures 3.4a,b we represent this fitness difference D of the equilibrium population as a function of $p^* = p/(p + \theta q)$, the effective frequency of environment I.

Since D is the result of natural selection, we claim that for each p^* , D approaches the solid curve. In terms of gene frequency x , $D = (2x - 1)(M - L)$.

But for each D there is some optimum θ which determines an optimum p^* . For $D = 0$, the optimum θ is one and $p^* = p$. For some D sufficiently large, the optimum θ falls below one and can decrease to zero. Thus p^* will evolve toward the broken line in Figures 3.3a,b. The joint evolution of D and p^* (that is, of viability niche breadth and habitat

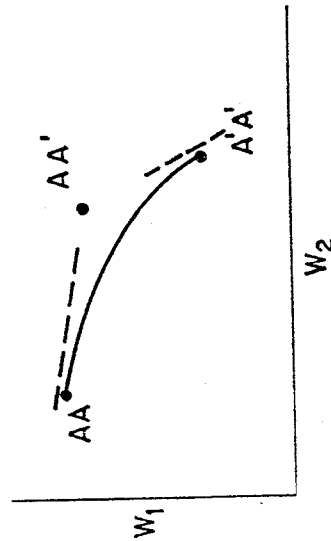


FIGURE 3.3. Model for selection in two environments. The equilibrium population is the point of tangency of the fitness set (solid curve) with the Adaptive Function $A = pW_1 + (1 - p)W_2$ (the broken lines).

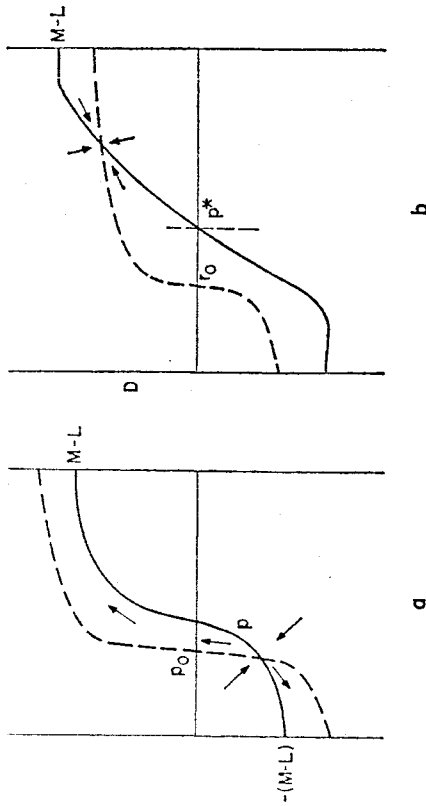


FIGURE 3.4a and b. The coevolution of habitat preference and niche breadth. D (the difference between fitness in environments I and II) evolves toward the solid line, while p^* , the effective frequency of habitat I, is a consequence of behavior and evolves toward the broken line. p_0 is the proportion of habitat I in the environment. In 3.4a the result is a stable equilibrium, in 3.4b there are two alternative specialized modes of adaptation.

selection) is shown by the arrows in the figures. If productivity is sufficiently low even the maximum D (at $x = 0,1$) may be insufficient to favor habitat selectivity. Then there is a stable equilibrium at $p^* = p$ and D less than $M - L$. But if productivity is high enough so that habitat specialization is favored at $D = \mp(M - L)$, there is an unstable equilibrium and two stable states corresponding to full specialization to the two alternative environments. Finally, asymmetry in the model may result in an unstable equilibrium separating one specialized and one unspecialized equilibrium. Here past history as well as the ecological situation determines the outcome.

NICHE DIMENSION

If species divide their habitat among themselves on the basis of a single factor such as temperature, their niches can be represented along a single dimension as in Figure 3.5.