

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 bioclimatological 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.

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)				
	Herbi-vore	Carni-vore	Insecti-vore	Omni-vore	Total
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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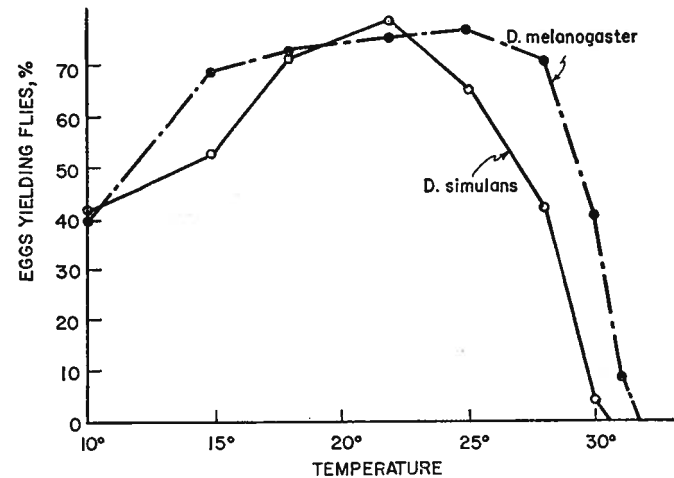


FIGURE 3.1. The temperature/emergence relation for two species of *Drosophila*. Clearly *D. melanogaster* has a broader temperature niche than *D. simulans*. (After Tantawy and Mallah, 1961.)

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 Tantawy'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.

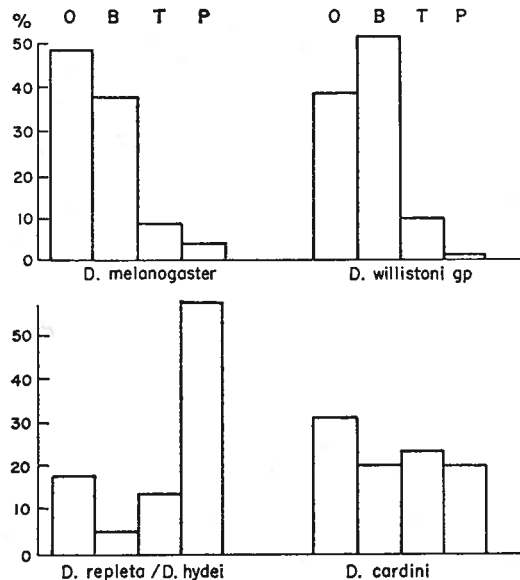


FIGURE 3.2. Food preference histograms for four species of *Drosophila*. O, orange; B, banana; T, tomato; P, potato. (From Martinez Pico et al., 1965.)

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. repleta*. 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

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
Maximum	14	13
<i>D. melanogaster</i>	2.4	3.5
<i>D. willistoni</i>	5.3	7.5
<i>D. latifasciaeformis</i>	7.0	8.5
<i>D. Dunni</i>	5.4	5.2
<i>D. ananassae</i>	5.4	4.0
<i>All flies</i>	6.1	8.5

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-

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

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

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	M	L
AA'	$2x(1-x)$	$(M+L)/2 + h$	$(M+L)/2 + h$
A'A'	$(1-x)^2$	L	M

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

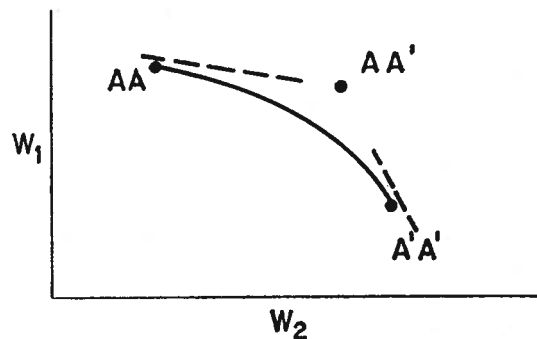


FIGURE 3.3. Model for selection in two environments. The equilibrium population is the point of tangency of the fitness set (solid curve) with the Adaptive Function $A = pW_1 + (1 - p)W_2$ (the broken lines).

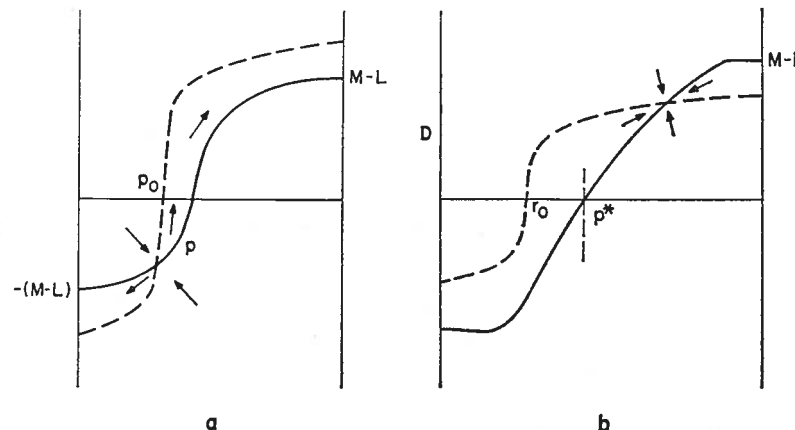


FIGURE 3.4a and b. The coevolution of habitat preference and niche breadth. *D* (the difference between fitness in environments I and II) evolves toward the solid line, while p^* , the effective frequency of habitat I, is a consequence of behavior and evolves toward the broken line. p_0 is the proportion 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.

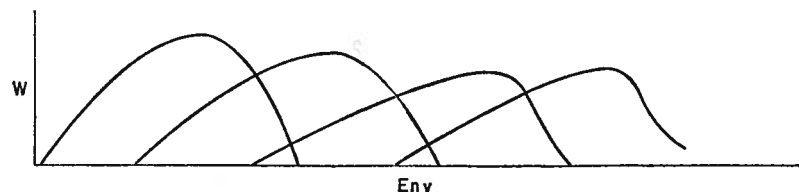


FIGURE 3.5. A one-dimensional array of niches.

This has the consequence that each species competes primarily with its two neighbors and hardly at all with the others. If two factors are distinguished, as in Harrison's classification of rain forest birds, competition is spread more evenly among several species which overlap in different directions. Thus niche dimensionality refers not to the number of biologically relevant factors in the environment, which may be virtually unlimited, but to the number of factors which serve to separate species.

No formal conventions have yet been adopted for measuring niche dimension. However we can already ask how many niche dimensions there are in a community and their relative importance.

MacArthur (1958) has analyzed the bird environment in terms of vegetation profile. He found that the relative density of vegetation at three levels corresponding to the herbaceous and low shrub, middle, and upper levels of the forest is sufficient to predict the occurrence of warbler species within the deciduous forest of the northeastern United States.

Our experiments with *Drosophila* were mostly limited to the species attracted to fruit bait on the ground, thus excluding the pollen and fungus feeders. We found differences among species in food preference, microhabitat within the forest, sites within a region, time of day, and season. We approached the dimensionality by way of a measure of community diversity

$$D = -\sum f_i \log f_i, \quad (3.5)$$

where f_i is the relative abundance of species i . When several

TABLE 3.5. Contributions of niche components to diversity. Diversity measures given as logarithms to base 10

	Texas*	Puerto Rico	Brazil†	Belém (Brazil)
Within trap		.28		
Among microhabitats		.25		
Total with collection	.53	.53	.67	.56
Seasonal	.22	.16	.12	.03
Total within site	.75	.69	.79	.59
Among sites in zone	.25	.22	.10	
Among zones				
Total	1.00	.91		

Note: The among zones and sites figure for "Texas" comes from the whole southwestern United States.

* From Patterson (1943).

† From Dobzhansky and Pavan (1950).

collections are made the total community diversity is equal to the average diversity within collections plus the diversity due to differences among collections. Therefore by using different seasons, baits, or sites as "collections" we can measure the relative importance of niche components along different dimensions. The food component is an overestimate, since it was based on setting out traps of different kinds of bait in equal numbers. In nature the non-uniform distribution of foods would reduce their contribution to diversity. The diurnal component of diversity does not directly separate species, since flies can come to the same bait at different hours. However it is an indirect indication of different microhabitat preferences. The niche components for our Puerto Rican *Drosophila* are shown in Table 3.5 along with comparable data from Brazil and the United States. We note that total diversity is roughly comparable for all regions but that the seasonal component of diversity falls from 30% of the total at Austin, Texas, to 22% in Puerto Rico, to 16% for all Brazilian collections, and to 3% for Belém. This gives a more meaningful measure of environmental variability for flies than would the meteorological data alone.

The relatively small contribution of geographic sites is striking. This is perhaps a result peculiar to small animals. Within a forest there is considerable variation in temperature and humidity from one cubic centimeter to another. Almost all the range of environments that can be found among forests at all elevations in Puerto Rico can occur somewhere within the same forest. Similarly, the diversity found at Austin alone is only increased by one-third when we include the whole southwest. This would of course not be true for species with very narrow food preferences such as *Drosophila carcinophila*, which breeds on the gills of land crabs in the Caribbean, or *D. peninsularis*, which is mostly a littoral species in areas with cactus.

We expect the situation to be different with regard to larger animals. The variation from one quarter acre to another is not as great as that from cubic centimeter to cubic centimeter, and will therefore include a smaller part of the total variation over a geographic range. For the trees of the forest, zonation is also quite prominent.

Thus we expect the comparative study of niche dimensions to be an important part of community ecology.

NICHE OVERLAP

At issue here is the amount of competition or of ecological similarity among species. One measure would be some geometric distance, such as

$$d_{i,j} = \sum_h (p_{ih} - p_{jh})^2 \tag{3.6}$$

where p_{ih} is the niche measure of species i in environment h . However not all biological differences reduce competition. Different birds may capture the same insects in flight or on a tree; fruit flies may use the same fruit at different hours. The p_{ih} must be limited to components of competition. In a coarse-grained environment, where individuals spend their whole lives in the same patch, viability in each patch type separately affects the competition, but in a fine-grained environment this will not be true.

The above measure has been used (Martinez et al., 1965)

TABLE 3.6. Maximum number of species for which the expected value of the community is positive

Average α	Covariance (α_{ij} with α_{ji})									
	.005	.01	.015	.02	.025	.03	.05	.075	.1	.3
.1	34	27	19	15	13	11	8	6	5	3
.2	24	22	16	13	11	10	7	6	4	
.3	21	18	13	11	9	8	6	5	4	
.4	17	14	11	9	7	7	5	4	4	
.5	14	11	8	7	6	5	4	3	3	
.6	12	8	—	5	5	5	3	3	3	

for food differences. However we prefer to measure niche overlap by the coefficient α_{ij} used by Gause. He started from the Volterra equations for increase of species x and y :

$$dx/dt = rx(K - x - \alpha y)/K \tag{3.7}$$

and

$$dy/dt = ry(K - \beta x - y)/K. \tag{3.8}$$

The coefficients α and β measure the reduction in the rate of increase of x caused by an individual of y compared to the effect of an individual of x , and vice versa. Since this competition depends on the probability that individuals of the two species meet (in the sense of seeking food in the same habitat, or pursuing the same kind of prey) a good approximation for α_{ij} is

$$\alpha_{ij} = \sum_h p_{ih}p_{jh} / \sum_h p_{ih}^2 \tag{3.9}$$

which is

$$\alpha_{ij} = \sum_h p_{ih}p_{jh}(B_i), \tag{3.10}$$

where B_i is the niche breadth. Thus α_{ij} is similar to a regression coefficient of one species' use of environment on that of the other. We see that because of the factor B_i , α_{ij} will not equal α_{ji} unless their niche breadths are equal. There is the unexpected result that α_{ij} can exceed one even without special mechanisms, such as environmental poisoning. A broad-niched species spread out over many environments will have a lower rate of encounter between members than would a more specialized species. Suppose for example that

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TABLE 3.7. Coefficients of competition between species. First number is microhabitat α ; number in parentheses is seasonal α . From unpublished studies at Mayagüez, Puerto Rico

Species	mel	lat	will	Dun	ana
<i>D. melanogaster</i>	1(1)	.30(.61)	.42(.76)	.61(.55)	.16(.75)
<i>D. latifasciiformis</i>	.72(.70)	1(1)	.92(.79)	.72(.48)	.60(.50)
<i>D. willistoni</i> sp.	.88(.95)	.81(.85)	1(1)	.96(.57)	.47(.59)
<i>D. Dunni</i>	.90(.34)	.44(.26)	.67(.29)	1(1)	.38(.63)
<i>D. ananassae</i>	.18(.60)	.28(.35)	.25(.38)	.29(.81)	1(1)

one species uses environments *A* and *B* with frequencies 2/3 and 1/3, and that the second species is limited to the first environment. The probability of encounters between members of the first species is $(2/3)^2 + (1/3)^2$ or 5/9, the encounters of the second species with itself have a relative frequency of 1, and the encounters between species occur only in habitat *A* at the rate of $1 \times 2/3 = 6/9$. Therefore $\alpha_{12} = 6/5$ and $\alpha_{21} = 2/3$. This does not mean however that species 2 will exclude species 1, because the broad-niched species may have a greater *K*.

The coefficient of competition α can be measured with respect to any aspect of the environment separately, and the over-all α will then be a product of the individual ones. Once we have defined α we can raise questions about its statistical distribution. What is the average level of competition (how closely are niches packed), how variable is α , how does this differ in young and mature communities, etc.? In Table 3.7 we show some α 's obtained from Puerto Rican *Drosophila*.

The logistic equations 3.7, 3.8 have been criticized from a number of points of view. However the use of the bracketed term in the equation to define the equilibrium conditions does not depend on the validity of the equations for describing the rate of change toward equilibrium. Nor does it matter that the α_{ij} may vary with population density.

THE COMMUNITY MATRIX

The simultaneous equations

$$dx_i/dt = r_i x_i (K_i - x_i - \sum \alpha_{ij} x_j) / K_i \quad (3.11)$$

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can give an equilibrium community when

$$K_i = x_i + \sum \alpha_{ij} x_j \quad (3.12)$$

for all *i*. These equations can be expressed as a single matrix equation

$$AX = K, \quad (3.12)$$

where *X* is the column vector $\begin{pmatrix} x_1 \\ x_2 \\ x_3 \\ \vdots \\ \vdots \\ \vdots \end{pmatrix}$,

K is the vector of the *K_i*, and *A* is the community matrix

$$A = \begin{vmatrix} 1 & \alpha_{12} & \alpha_{13} & \cdots & \\ \alpha_{21} & 1 & \alpha_{23} & \cdots & \\ \alpha_{31} & \alpha_{32} & 1 & \cdots & \\ \cdot & & & & 1 \end{vmatrix}$$

whose elements α_{ij} are the competition coefficients. Even without the solving of equations the matrix gives much information about the community. For competitors the α 's are positive, while for predator-prey pairs α_{ij} and α_{ji} have opposite sign. For competitive α 's, the average value indicates how closely species are packed. If the niche is one-dimensional, each species can have only a few positive α 's and the others will be near zero. As the dimensionality of the niche increases the variance of the α 's can be reduced. Thus the variance of the α 's is an indicator of dimensionality. For competitors, $\alpha_{ij} = \alpha_{ji}$ when the niches are equal in breadth. Then the pairs of symmetrically arranged terms have a correlation of +1. As the niche breadths become more variable, this correlation decreases, and it is also reduced by predator-prey pairs.

With the descriptive parameters of the niche defined and the community matrix described, we can use them to study the original questions.

The simultaneous equations 3.12 could be solved to get the relative abundances if we knew the α_{ij} and the *K_i*. We

have suggested how to measure the α_{ij} , but K_i is less directly observable, since it is the maximum population attainable in the absence of competitors. Therefore we reversed the procedure, and used the known x_i and the calculated α 's to find K_i . This was done for microhabitat separation in our Puerto Rican *Drosophila*. In Table 3.8 we show the frequencies of

TABLE 3.8. Carrying capacity K and relative niche breadth B/\bar{B} . From unpublished data, collections at Mayagüez, Puerto Rico, 12/26/65. \bar{B} is the breadth for all flies combined.

Species	Frequency	K	B/\bar{B}	$K/(B/\bar{B})$
<i>D. melanogaster</i>	.03	.41	.42	.98
<i>D. willistoni</i> group	.54	.89	.87	1.02
<i>D. latifasciaeformis</i>	.32	.92	1.00	.92
<i>D. Dunni</i>	.01	.62	.61	1.02
<i>D. ananassae</i>	.08	.27	.47	.62
<i>D. tripunctata</i> species	.02	.35	.44	.79

species, their niche breadths B relative to the breadth for all flies, \bar{B} , the estimated K , and the ratio of K to B/\bar{B} . The uniformity of this ratio suggests the hypothesis for more general testing of whether the carrying capacity K is proportional to the niche breadth B .

There is no *a priori* reason to expect this result. It means that the species do not differ very much in the average efficiency with which they utilize their resources but only in how wide a range of microhabitats they can use. Another surprising result is the suggestion that in spite of seasonal changes in relative abundance of the species, at each moment the community is in equilibrium for the current environment but this equilibrium changes with the changes in the resources, keeping the community close to a moving equilibrium. Thus the community matrix approach helps to determine if we have in fact identified the important environmental factors and to determine if the community is near equilibrium.

At a more abstract level the community matrix leads to some results about the limit to the number of coexisting

species. In order for a community to be stable the determinant of its matrix must be positive. Furthermore, the symmetrized determinant whose element $\alpha_{ij}^* = \alpha_{ji}^* = (\alpha_{ij} + \alpha_{ji})/2$ must be positive, and so must each subdeterminant formed by striking out a row and the corresponding column. Therefore we can investigate the average value of these determinants in terms of the statistical distribution of the α . In Appendix I (at the end of this chapter) we derive the recurrence relation for the expected value D_n of a determinant of rank n (n rows and columns). The result is the pair of equations

$$D_n = D_{n-1} - (n-1)\bar{\alpha}^2 T_{n-1} - (n-1) \text{cov}(\alpha_{ij}, \alpha_{ji}) D_{n-2} \quad (3.13)$$

$$T_n = D_{n-1} - (n-1)\bar{\alpha} T_{n-1} \quad (3.14)$$

where the initial values $D_0, D_1 = 1$. We see that the covariance term enters in such a way as to reduce D_n . Thus a community in which niches are equally broad can hold fewer species than one with high dimension (uniform α 's, low variance) and non-uniform niche breadths. We suspect that as a community matures the variance of the α 's decreases and more species could be accommodated. Thus a waif fauna of diverse origins should reach a demographic equilibrium with fewer species than old faunae hold. Recent work by Wilson and Taylor on Pacific ants (1967) seems to support this idea.

In the next section we will use the equations 3.13, 3.14 to estimate the number of species which can coexist in a community given their general similarity and heterogeneity.

THE NUMBER OF SPECIES IN A COMMUNITY

Gause's analysis of competition for a part of species lead to the conclusion that for equal K 's, any $\alpha < 1$ permits coexistence. This was interpreted to mean that the two species must use the environment in different ways and therefore that there must be at least two distinguishable resources to support two species.

This can be extended to the more general theorem: The number of species cannot exceed the number of distinct

resources. In Appendix II (at the end of this chapter) we offer two proofs of this. The first uses the simultaneous equations (3.12) and our definition of α_{ij} . It therefore assumes the α 's are constant. They can of course vary with population density and also with the abundance of resources. To demonstrate that the result is robust, that it does not depend on these simplifications, we also give an alternative proof in which the amounts of resource may change as a result of being utilized. This alters the degree of competition, but not the final conclusion.

For the purposes of this theorem, a community such as Harrison's birds which divides the habitat by food type and height in the canopy would have as many resources as there are combinations of layer and food. But immediately a difficulty arises: how similar can resources be and still count as distinct resources? How can a continuum of resource (temperature range of habitat, height, food particles size) be divided into discrete resources?

First, we note that the equilibrium depends on the superiority of each species in part of the resource space. If two resources are so similar that the same species is superior in both, only one species will persist. A more detailed analysis can proceed as follows (after MacArthur and Levins, 1967):

On a continuum of one dimension, let the niches of an array of species be as in Figure 3.5. If there are only two species and the K 's are equal, there is no limit to the similarity of two species short of complete identity. Now consider three species. The middle one competes to the extent α with the other two, while the outside species compete to the extent β . If the middle species is absent, the other two reach equilibrium at $x_1 = x_3 = K/(1 + \beta)$.

Then species 2 can increase only if

$$K - \alpha \frac{K}{1 + \beta} - \frac{\alpha K}{1 + \beta} > 0.$$

Thus it is required that

$$\alpha < (1 + \beta)/2.$$

If the outside species do not overlap at all, α must be less

than $1/2$, and the sum of the α 's less than 1. The competition between species 1 and 3 reduces their ability to compete with species 2, so that α can be somewhat greater. If the niche has a normal shape $\exp(-x^2/2\sigma^2)$, two species whose preferred environments differ by M will compete to the extent $\alpha = \exp(-M^2/2\sigma^2)$. Then the maximum α allowable between adjacent species is about 0.54 instead of 0.50 for a rectangular niche. From this we find the closest M , which is proportional to σ . Therefore, the number of species which can coexist is equal to the total range of resources divided by a multiple of the niche breadth. This is an upper limit, since inequalities in the K 's and variability of the α_{ij} will reduce the number of species. For instance, a rare resource which is too similar to an abundant resource cannot support a different species.

As the dimensionality of the niche increases, each species has more immediate neighbors in niche space. But these neighbors also compete with each other. At the extreme when the number of species equals the number of dimensions plus one, all of the α 's can be equal and any $\alpha < 1$ permits a demographic equilibrium.

If we are able to measure the α 's, the community matrix approach of the previous section enables us to ask the slightly different question: how many species of roughly the kinds we have observed, i.e., drawn from the same universe of species with α taken from the same distribution, can coexist. Given the average, variance, and covariances of the α 's, we can iterate equations 3.13, 3.14 to find the expected value D_n of the determinant of the community matrix. The greatest value of n for which D_n remains positive is our best prediction as to the numbers of species in the community. In Table 3.6 we have calculated D_n for different *Drosophila* communities. The results are of the right qualitative level, suggesting that these communities are more or less saturated.

So far we have limited the discussion to demographic equilibrium. Two other types of equilibrium must be considered. First, if a community is able to reach demographic equilibrium with N species present but if there are more than

N different competitors available, it is possible for there to be several alternative stable communities existing in different patches of the same environment. Then each community will be subject to occasional invasions, and we have to ask under what circumstances will a stable community be resistant to invasion? In the second model of the appendix, it is seen that if a pair of resources supporting two species is similar enough, species intermediate between the two (less specialized with respect to these resources) can out-compete the pair of them. "Similar enough" in this context means that, for a normal shaped niche the resources differ by less than 2σ on the environmental axis. Thus, although species can coexist on resources 2σ apart they are replaceable, and invasion phenomena will result in communities with species $2-5\sigma$ apart.

Finally we note briefly that there is also an evolutionary equilibrium brought about by the coevolution of species.

Brown and Wilson (1956) introduced the concept of character displacement to indicate an increase in the difference between two species in their region of contact as a response to selection for reduced competition. Where species compete for foods of different sizes, the size of a bird's bill or legs, or of a mammal's linear dimensions, may be an appropriate measure of displacement. This approach has been taken by Schoener (1965) and others.

But character displacement is only a special case of coevolution. A somewhat more general treatment can be given using a fitness set argument. For a given species, let the two axes represent the coefficients of competition α_1 and α_2 with two competitors on opposite sides along a single niche dimension. We will assume that the shape of the niche is fixed but that its peak can occur at any point. Thus each point in the fitness set corresponds to the center of a niche. Fitness is maximized for the components in question when total competition, $\alpha_1 X_1 + \alpha_2 X_2$ is minimized. Here X_1 and X_2 are the relative abundances of competitors 1 and 2.

In Figure 3.6 we show the optima. In 3.6a, the fitness set is concave. This means that species 1 and 2 are further apart than 2σ . Then the optimum strategy for an incoming

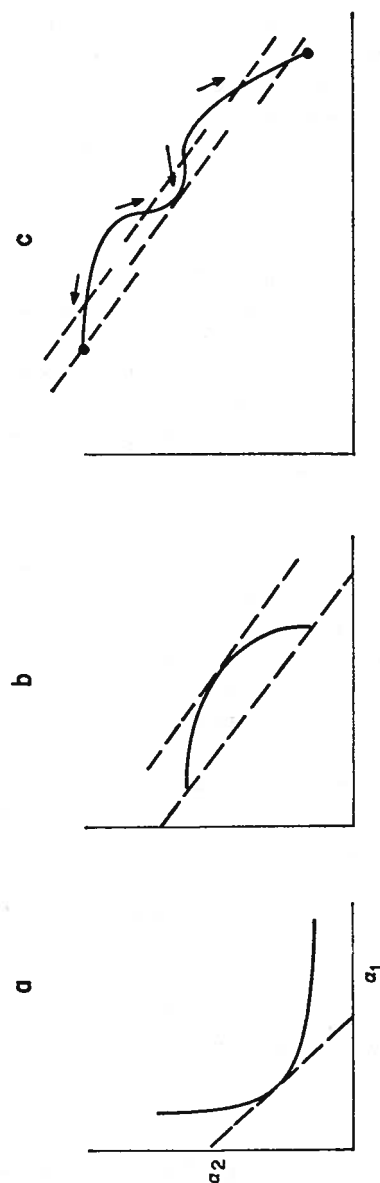


FIGURE 3.6. The evolution of an introduced species. In 3.6a, the optimum position for the new species is intermediate between those already present. In 3.6b, the invader will converge toward one of the species already present. In 3.6c, the outcome will depend on the initial position of the new species' niche.

species would be to occupy an intermediate position. If species 1 and 2 are equally abundant, it would be the midpoint. In 3.6b, species 1 and 2 are closer than 2σ , so that the fitness set is convex. Here fitness is maximized by approaching and displacing either species 1 or 2, depending on where the species starts from.

However, if the niche is multidimensional, convergence on a single axis or on several axes need not result in displacement. We could obtain clusters of very similar species in apparent violation of Gause's principle and our intuitions about natural selection.

If the niche curves are of normal shape, the fitness set will not be pure concave. Rather it will look like that in Figure 3.6c. Depending on the initial condition of the incoming species, it may approach one of the previously existing species or occupy an intermediate range.

Thus the coevolution will tend to pack species in their niche space. If the niche space is one-dimensional, the limiting packing will be to a closeness of about 2σ . For a higher dimension, with competition spread more evenly, packing may be somewhat closer. But all of our analyses agree that the number of species will depend on the range of environment divided by niche breadth.

The analysis of adaptive strategies in Chapter 2 showed that a species loses fitness in a heterogeneous environment. It would be better off specialized, but the uncertainty of the environment forces niche expansion. Thus we can assert roughly that the number of species which can be maintained in a community is proportional to the uncertainty of the environment. This may account for increase in numbers of species in areas of stable environment and high productivity, such as Hawaii and the tropical forests.

The approach outlined in this chapter leads to a number of qualitative predictions which are testable in the field. For instance, the number of species should be greater in regions of environment stability, smaller in groups with good homeostasis, smaller in new-equilibrium faunae than in old ones. It would also be used for more quantitative predictions relating the number of species to the average and variance

of α 's and even to get relative abundances from niche breadth and α 's.

Several types of laboratory experiments suggest themselves. In *Drosophila*, a heterogeneous environment can be provided in population cages with food cups of different kinds. We could make one kind of cup easily identifiable (say by a textural or olfactory signal), and unfavorable in varying degrees (say with DDT, or simply by removing a given proportion of the pupae that emerge). Flies are collected as they hatch, released into the cage for a short time to lay eggs, and the cage is then cleaned by a vacuum cleaner or given a heat shock that removes adults but won't kill eggs. The time available is the equivalent of productivity, and the difference between the viability in the two environments is the other essential parameter. This system should result in the evolution of optimal niche breadth and specialization.

Or a community could be simulated using several types of habitat and species. The α 's could be calculated first, and the equilibrium populations predicted. But these will also evolve in the course of the experiment.

Beyond question of specific prediction, this approach emphasizes the sufficient parameters niche breadth, dimension, overlap, and community diversity as objects of study. We would want to know their statistical distribution in nature, and differences between types of animals or habitats in their means and variances.

A number of theoretical questions have scarcely been investigated. For example, we don't have any useful theory as yet relating the community matrix to the relative abundance of constituent species. Another series of problems relates to ecological engineering: given a matrix, how can a minimum alteration be applied to get maximum effect, either toward eliminating a species or toward stabilizing the community.

The equations that led to the community matrix may be adequate for the equilibrium condition, but the logistic is very poor as a description of the dynamics of a community. It may be, as Kerner (1957) and Leigh (1965) believe, that

the unrealistic aspects of the Volterra equations have opposite effects, and that the behavior of the whole system may not be too far from that described by their statistical mechanical approach. But that is still open to question.

APPENDICES TO CHAPTER THREE

Appendix I. The Expected Value of the Determinant of the Community Matrix

Consider the $n \times n$ matrix whose elements are α_{ij} , the coefficients of competition of species j on species i :

$$M = \begin{pmatrix} 1 & \alpha_{12} & \alpha_{13} & \cdots & \alpha_{1n} \\ \alpha_{21} & 1 & \alpha_{23} & \cdots & \\ \cdot & & & & \\ \cdot & & & & \\ \alpha_{n1} & & & & 1 \end{pmatrix}$$

The determinant of this matrix can be expanded by minors of the first row and first column to give

$$D_n = D_{n-1} + \sum_{i,j} (-1)^{i+j+1} \alpha_{i1} \alpha_{1j} A_{11ij}$$

where A_{11ij} is the $(n-2) \times (n-2)$ determinant formed by deleting rows 1 and i and columns 1 and j of the original determinant. Now define T_n as the same determinant with the first column replaced by 1's, and expand in the same way:

$$T_n = D_{n-1} + \sum_{i,j} (-1)^{i+j+1} \alpha_{1j} A_{11ij}$$

We now assume that all the α_{ij} are statistically independent except that α_{ij} may be correlated with α_{ji} . With this assumption, the expected values of D_n and T_n are

$$E(D_n) = E(D_{n-1}) + \bar{\alpha}^2(n-1)^2 E\{(-1)^{i+j+1} A_{11ij}\} - (n-1) \text{cov}(\alpha_{ij}, \alpha_{ji}) E(D_{n-2})$$

$$E(T_n) = E(D_{n-1}) + \bar{\alpha}(n-1)^2 E\{(-1)^{i+j+1} A_{11ij}\}$$

Now remove a species from the community. Since the order-

ing of species is arbitrary, we can remove the first species. T_{n-1} is formed by replacing the second column by 1's:

$$T_{n-1} = \begin{pmatrix} 1 & \alpha_{23} & \alpha_{24} & \cdots & \alpha_{2n} \\ 1 & 1 & \alpha_{34} & \cdots & \\ \cdot & & & & \\ \cdot & & & & \\ \cdot & & & & \\ 1 & & & & 1 \end{pmatrix}$$

This can be expanded by the minors of elements of the column of 1's:

$$T_{n-1} = \sum_j (-1)^{i+j} A_{112j}$$

This has the expected value,

$$E(T_{n-1}) = E\left\{ \sum_{j=2}^n (-1) A_{112j} \right\}$$

But since the ordering of species is arbitrary,

$$E(A_{112j}) = E(A_{11ij})$$

and

$$E(T_{n-1}) = -(n-1) E\{(-1)^{j+i} A_{11ij}\}$$

Substituting this value in the equations for D_n and T_n , and dropping the E symbol, we have the final result

$$D_n = D_{n-1} - (n-1) \bar{\alpha}^2 T_{n-1} - (n-1) \text{cov}(\alpha_{ij}, \alpha_{ji}) D_{n-2}$$

$$T_n = D_{n-1} - (n-1) \alpha T_{n-1}$$

When there is no covariance, this reduces to

$$D_n = D_{n-1} - (n-1) \alpha^2 T_{n-1}$$

for which we have the explicit solution

$$D_n = (1 - \alpha)^{n-1} \{1 + (n-1)\alpha\}$$

$$T_n = (1 - \alpha)^{n-1}$$

Appendix II. Proof That the Number of Species Cannot Exceed the Number of Resources

Proof 1: Consider the set of simultaneous equations

$$x_i' = r_i x_i \left(K_i - \sum_j \alpha_{ij} x_j \right) / K_i$$

If there is an equilibrium community other than all $x_i = 0$, the determinant of the matrix A whose elements are α_{ij} must be different from zero, which requires that the matrix be of rank n for n species. But by the definition of α_{ij} ,

$$A = BPP^T$$

where:

$$B = \begin{Bmatrix} \sum p_{1h}^2 & 0 & 0 & 0 \\ 0 & \sum p_{2h}^2 & & 0 \\ 0 & & & \sum p_{nh}^2 \end{Bmatrix}$$

$$P = \begin{Bmatrix} p_{11} & p_{12} & \dots & p_{1k} \\ \cdot & p_{22} & \dots & \cdot \\ \cdot & & & \cdot \\ \cdot & & & \cdot \\ p_{n1} & & & p_{nk} \end{Bmatrix}$$

and P^T is the transpose of P , with elements $p_{hj}^T = p_{jh}$. Here p_{ih} is the proportion of resource h (or habitat h) among the resources used by species i . Thus B is of rank $n \times n$, P is an $n \times k$ matrix when there are n species and k resources, and P^T is $k \times n$. Hence if $k < n$, A is of rank k and there can be no stable community.

Proof 2:

Let there be k resources R_h , $h = 1 \dots k$, and n species utilizing these resources. Suppose that species i can increase as long as $\sum_h C_{ih} R_h > T_i$ where the C_{ih} are inverse measures of the effectiveness of utilization of resource h by species i and T_i is some threshold. On a graph whose coordinates are the resource levels R_h , each species can increase as long as the point (R_1, R_2, \dots, R_k) representing the combination

of resources present lies above the plane $\sum_h C_{ih} R_h = T_i$.

Where the resources are represented by a point on the plane, the species is in equilibrium, and where m planes intersect we have the set of possible resource combinations that can just support m species. Finally the intersection of k such planes defines a single point at which k species can be in equilibrium with k resources. It is infinitely unlikely that $n > k$ planes intersect at a point in k space. The $(k + 1)$ st species will intersect with any $k - 1$ others at a point either closer to the origin or further away than the intersection of the first k . This defines an alternative community which will either replace or be replaced by the first one.