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Resource Partitioning Among Competing Species—A Coevolutionary Approach

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A reasonably general theory for predicting the outcome of coevolution among interacting species is developed. It is applied to a model for resource partitioning among competing species.

Current theory for resource partitioning is based on derivations of a "limiting similarity"—i.e., a limit to how similar competitors can be to one another consistent with coexistence. This theory presumes there is a mechanism, perhaps invasion and extinction, which causes competitors to attain the limiting similarity. The view taken in this paper is that partitioning is an evolutionary compromise between pressures for character displacement and disadvantages inherent in the shift to different resource types.

A set of principles is offered for the evolution of the parameters in ecological models. (1) For single population models natural selection causes the parameters ultimately to assume those values which produce the highest equilibrium population size. (2) For models of interacting populations, but without interspecific frequency-dependence, natural selection causes the parameters to assume values which produce either the highest or lowest equilibrium population size for any species depending on the sign of the "feedback" in the community obtained by deleting that species. (3) For models of interacting populations with interspecific frequency dependence natural selection leads to parameter values which produce intermediate equilibrium population sizes. A function called the conditional equilibrium population size is introduced. Provided (a) the mean fitness is a maximum in each species at a stable coevolutionary equilibrium and (b) there is negative density-dependence in each species then natural selection causes the parameters to assume values which produce the highest conditional equilibrium population size for each species.

These coevolutionary principles, applied to a model for resource partitioning, entail that the niche separation between species relative to given niche widths, increases with the variety of available resources and decreases with the number of competing populations. Also, the evolution of character displacement between two species does not proceed far enough to maximize the equilibrium population sizes of the species involved. These results imply that the relationship between the niche overlap (of nearest neighbors) and species diversity is qualitatively different depending on whether the variety of resources at any place covaries with the species diversity there. Without covariation niche

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overlap increases with species diversity; with covariation overlap may decrease with species diversity. This study provides the beginning of a theory for the convergent evolution of community structure.

INTRODUCTION

Resource partitioning among competing species is one of the most intriguing phenomena of population biology. It underlies the well-known morphological patterns of character displacement (Brown and Wilson, 1956) and of size differences among species like Darwin's finches (Lack, 1947). And, the manner of resource partitioning explains the species diversity pattern of many groups (MacArthur, 1965). This central place of resource partitioning in both evolution and ecology has led to its study from many points of view, both empirical and mathematical.

The mathematical models to explain resource partitioning all offer derivations of a "limiting similarity," that is, some limit to how similar competing species can be to one another consistent with continued coexistence. Various mathematical criteria lead to limiting similarities: positivity of the equilibrium population sizes (MacArthur and Levins, 1967; Roughgarden, 1974; Roughgarden and Feldman, 1975) and persistence in a stochastic environment (May and MacArthur, 1972). Regardless of mathematical details, all these models predict some minimum amount by which species must differ in their resource use. The obvious question then is, do resource partitioning patterns really represent a collection of species which differ by the minimum possible amount? What mechanism would cause competitors to differ by the minimum possible amount; and if no mechanism is found, what would explain the partitioning patterns which *are* observed?

The mechanism invoked to produce competitors separated by the limiting similarity is invasion from a source region (or equivalently, invasion from a recently speciated geographical isolate) coupled with extinction (MacArthur, 1972; May and MacArthur, 1972). If, for some reason, a location contains competitors separated by more than the limiting similarity, then invasion will occur and fill in the gap. And conversely, if, for some reason, a location contains competitors more similar than the limiting similarity then extinction will result. In May and MacArthur's (1972) theory especially, existence of a limiting similarity is based on population extinction induced by environmental fluctuation.

It is simply not obvious that many cases of resource partitioning involve the maintenance of limiting similarities by a process of invasion and extinction. First, many situations are not at saturation with respect to further invasion. As is well known, islands are often depauperate and introductions pose a hazard.

Indeed even island endemics are sometimes successfully introduced to other nearby islands. (For examples among West Indian *Anolis* lizards see Lazell, 1972.) Second, extinction may not be a particularly common process, in spite of its demonstration in certain situations (Simberloff and Wilson, 1969; Diamond, 1973). The striking endemism of island radiations suggests a long persistence time for the populations involved, and Williams (1969), for example, can find virtually no evidence of extinctions in the island biogeography of West Indian Anoles. Thus although an invasion-extinction process might conceivably lead to resource partitioning where limiting similarities are attained, the evidence for sufficiently frequent invasion and extinction seems lacking, especially in groups which are poor dispersers relative to birds and insects.

Nonetheless, bona fide repeatable patterns do occur in the resource partitioning among island competitors even though the invasion-extinction mechanism for achieving the limiting similarities seems absent. In *Anolis* lizards for example, Schoener (1969) has shown that all Lesser Antillean islands with one anole species have average adult male jaw sizes around 10 mm and almost all islands with two species have one species with jaws of about 7 mm and another species with jaws of about 15 mm. The repeatability of the pattern is dramatic. These considerations suggest a need for a theoretical approach to resource partitioning which is not based on limiting similarity arguments.

An alternative approach is to consider partitioning as the result of a coevolutionary process. In general terms, there is a selection pressure for character displacement to avoid interspecific competition. But, by definition, displacement involves a shift to different resources and it is often reasonable to assume there is some disadvantage to shifting resources. For example, displacement in size requires a shift to increased use of smaller or larger prey. But smaller insects have more indigestable exoskeletal material per unit weight, while larger insects tend to be comparatively rare. Thus there may be some disadvantage to displacement, and we might conjecture that partitioning represents an evolutionary compromise between the pressure to displace and the disadvantage to displacing. Moreover, with three or more species, still another factor is that displacing to avoid one species may increase competition with another. In a coevolutionary approach, the resource partitioning pattern represents the evolutionary compromise among all these factors.

To develop a coevolutionary theory of resource partitioning two steps are involved. First, the issue of the coevolution of resource partitioning is a special case of the general topic of coevolution. The theory for coevolution is little developed and we cannot call upon existing machinery to apply here. Instead we must develop some basic (though simple) principles to predict the evolutionary equilibrium attained in any coevolutionary process. This work actually occupies most of the paper and is also explored through a series of mathematical appendices. The second step is to apply these principles about coevolution to the

problem of resource partitioning. The mathematics for this step also appear in an appendix.

The Theory of Coevolution

Coevolution may be defined as evolution where the fitness of each phenotype in a species depends on the population size of that species and on both the population sizes and gene frequencies of other species. The topic of coevolution lies between population genetics and ecology. It can be approached from two points of view. From the point of view of population genetics the problem is to classify the evolutionary possibilities (polymorphism, fixation, cycling, etc., in each species) on the basis of the selection pressures on the various genotypes in the system.

From an ecological point of view the problem is quite different. As an ecologist, one inherits many models for population growth and interaction; the Lotka–Volterra competition equations and various predator-prey models are familiar examples. In these ecological models the variables are population sizes and the parameters in these models specify the nature and strength of the interactions within and between species. Let $m = (m_1, m_2, \ldots)$ denote the parameters in an ecological model. Then typically ecological models are solved for the stable equilibrium abundances $(\hat{N}_1(m), \hat{N}_2(m), \ldots)$, provided a stable equilibrium exists, and various topics of ecological interest (coexistence of competitors, relative abundance of predator and prey, etc.) are addressed using this equilibrium solution. In this ecological context, interest in coevolution concerns the evolution of the parameters, m. The parameters for population interactions presumably are not arbitrary, they are set by natural selection. So, from an ecological point of view, the key questions concerning coevolution are: (1) How does natural selection on the m's influence the equilibrium population sizes, $\hat{N}_i(m)$? and (2) Suppose there is a well-defined set of possible m's which is evolutionarily available to a species, then which particular value of m will obtain at the evolutionary equilibrium?

We might hope that both questions can be answered similtaneously with the following sort of principle: suppose evolution within species-s equilibrates at the parameter value m^* which maximizes the equilibrium population size of species-s. If such a principle were true then the answer to the first question would be that natural selection in species-s on the parameter m, leads to the highest equilibrium population size of species-s. The answer to the second question would be that at evolutionary equilibrium $m = m^*$, i.e., m evolves to that value which corresponds to the maximum equilibrium population size of species-s. Obviously any approach of this sort will require very careful development. There are many variables involved, both population sizes and gene frequencies in all the species, and the coupling between these variables

may lead to nonobvious complications. In the following pages we develop this kind of idea in more detail.

Density-Dependent Evolution in a Single Species

Consider a single species with genetic variation for the parameters in a population growth model. Specifically, suppose there is a genetic system of one locus with two alleles, A_1 and A_2. Let p be the frequency of A_1, and N the population size. The (absolute) selective values of the phenotype corresponding to each genotype (W_{ij} corresponds to A_iA_j) are all functions of N. The equations governing this system are

$$N_{t+1} = \overline{W}Nt, \tag{1a}$$

$$p_{t+1} = [p_tW_{11} + (1 - p_t)\, W_{12}]\, p_t/\overline{W}, \tag{1b}$$

where

$$\overline{W} = p^2W_{11} + 2p(1 - p)\, W_{12} + (1 - p)^2\, W_{22}\,. \tag{1c}$$

Let us focus attention on Eq. (1a). This is the equation for the population dynamics part of the model. We can regard this equation as containing a set of parameters which are themselves functions of p, the gene frequency. To make this idea clearer consider an example. Suppose the fitness are linear functions of density

$$W_{ij} = 1 + m_{1,ij} - m_{2,ij}N. \tag{2a}$$

Then $\overline{W}$ is given by

$$\overline{W} = 1 + m_1 - m_2N, \tag{2b}$$

where

$$m_i = m_i(p) = p^2m_{i,11} + 2p(1 - p)\, m_{i,12} + (1 - p)^2\, m_{i,22}\,. \tag{2c}$$

In this context we can consider the set of possible m's which is evolutionarily available to the species as being defined by $m_1(p)$ and $m_2(p)$. By definition, all evolutionarily available values of the parameters in our population dynamic model are generated by letting p vary between 0 and 1. Furthermore, we can inquire about how the equilibrium population size predicted by the population dynamic equation depends on the parameters, and then in turn on p. The equilibrium population size for any parameter values is found by setting $\overline{W} = 1$, yielding, in our example,

$$\hat{N}(m_1\,, m_2) = m_1/m_2\,. \tag{2d}$$

Because the parameters are themselves functions of p we can write this as

$$\hat{N}(p) = \hat{N}(m_1(p), m_2(p)) = m_1(p)/m_2(p). \tag{2e}$$

In this context we can answer our two basic questions about coevolution *by reference to the gene frequency at its evolutionary equilibrium.* Let the equilibrium gene frequency be $\hat{p}$. Then, at equilibrium, natural selection will have caused the parameters of the population dynamic model to equal $m_1(\hat{p})$, and $m_2(\hat{p})$, and the population size at equilibrium will be $\hat{N}(m_1(\hat{p}), m_2(\hat{p}))$. In this way we can study how natural selection influences the parameters of a population dynamic model and the equilibrium population sizes which are attained as a result.

By placing the problem of the evolution of ecological parameters in this particular population genetic context we can justify the following principle.

PRINCIPLE 1. *Natural selection causes the parameters of a single species population dynamic model eventually to assume those values which produce the largest equilibrium population size.*

I stress that this principle refers only to the final outcome of the evolutionary process. During the approach to the evolutionary equilibrium the parameters are continually changing and they may not approach their equilibrium values monotonically. Also the population size may not approach its equilibrium value monotonically because of overshoots.

To illustrate this principle let us return to the example of linear fitness functions in Eq. (2). By convention we identify $m_{1,ij}$ as r_{ij} and $m_{2,ij}$ as r_{ij}/K_{ij}, where r_{ij} and K_{ij} are the intrinsic rates of increase and carrying capacities associated with each genotype (Roughgarden, 1971). Figure 1 illustrates, as a dashed line, the function $\hat{N}(p)$ in a particular example. This function represents the equilibrium population size predicted by the population dynamic model (1a) for all the evolutionarily available values of the parameters. Notice that a certain p produces parameter values which lead to the highest possible equilibrium population size. The figure also illustrates trajectories for the simultaneous change in p and N which were obtained by iterating Eq. (1) from various initial conditions. Notice that all the trajectories converge to the highest point on the $\hat{N}(p)$ curve. Thus, at equilibrium, the parameters in the population dynamic model, $m_1(p)$ and $m_2(p)$, have evolved those values which produce the highest equilibrium population size.

This principle is justified by a theorem about density-dependent natural selection which is proved in Appendix I. The theorem is based on the work of Anderson (1971) and MacArthur (1962). Interested readers are urged to consult Appendix I for various technical aspects of density-dependent selection. The results apply specifically to density-dependent as distinct from frequency-dependent selection. Although the model is structurally stable to the addition of a small amount of frequency-dependence, a large amount of frequency-dependence would invalidate the approach. Also, if genetic variation in the

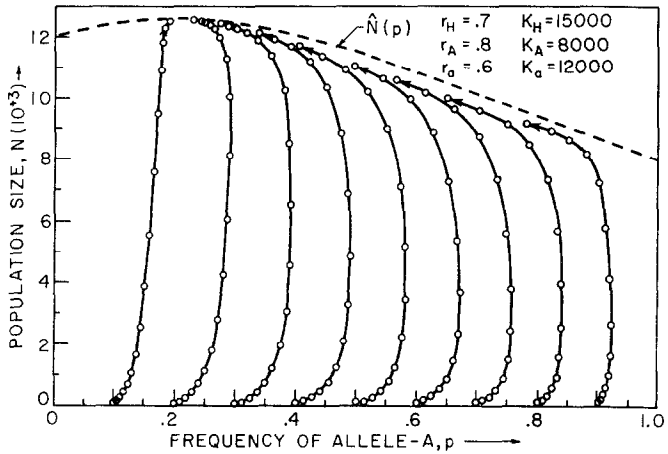

FIG. 1. Illustration of Principle 1. In this example the heterozygote has the largest carrying capacity and a polymorphism results. The figure illustrates various trajectories. In each the population begins at a low population size and a given allele frequency, and through time the population grows and the allele frequency changes. All trajectories converge to the highest point of the $\hat{N}(p)$ curve. In this sense density-dependent selection causes the parameters in the population dynamic model to assume those values which lead to the highest equilibrium population size.

parameters of a population dynamic model is assigned to certain more complex genetic systems then the principle above will be misleading in certain cases. For a recent review and new results on the fundamental theorem and other topics concerning multilocus genetic models see Karlin (1975).

COEVOLUTION WITHOUT INTERSPECIFIC FREQUENCY DEPENDENCE

Let us now turn to ecological models for several interacting species. These models may be solved for the stable equilibrium abundances $(\hat{N}_1(m), \hat{N}_2(m),...)$, provided a stable equilibrium exists. The equilibrium abundance of each species is a function of the parameters in the model $m = (m_1, m_2, ...)$. Again we address the following two questions: (1) How does evolution of the parameters m influence the equilibrium population sizes attained as a result, and (2) Provided there is a well-defined set of evolutionarily available parameter values, which particular value will obtain at the evolutionary equilibrium?

The way to answer these questions depends critically on whether genetic variation in a parameter leads to interspecific frequency-dependence. Technically, we define the *absence* of interspecific frequency dependence as the condition where $\partial \bar{W}_s / \partial p_u \equiv 0$ for $s \neq u$, i.e., the mean fitness in species-s is

independent of the gene frequency in other species. To understand this condition in more biological terms let us consider a familiar predator–prey model where V is the prey abundance and P is the predator abundance,

$$\begin{aligned} V_{t+1} &= [1 + r - rV_t/K - aP_t]V_t\,, \\ P_{t+1} &= [1 + abV_t - e]P_t\,. \end{aligned} \tag{3a}$$

In this model the prey grow logistically with parameters r and K, the quantity aV is the number of prey caught per predator per time interval (i.e., the so-called functional response), b is the predator's conversion parameter, and e is the predator death rate. This model leads to a stable equilibrium $(\hat{V}, \hat{P})$ under easily determined conditions. We are interested in the evolution of all the parameters in the model above. But there are many ways to proceed. Suppose, for example, that there is genetic variation in r and K in the prey and variation in b and e in the predator. We should then consider the fitnesses

$$\begin{aligned} W_{V,ij} &= 1 + r_{ij} - r_{ij}V/K_{ij} - aP, \\ W_{P,ij} &= 1 + ab_{ij}V - e_{ij}\,. \end{aligned} \tag{3b}$$

These fitnesses do *not* produce interspecific frequency dependence. On the other hand, suppose there is also variation in both predator and prey for the parameter a. Let $a_{ij,kl}$ be the capture rate of predator genotype kl against prey genotype ij. Then we must consider fitnesses of the form

$$\begin{aligned} W_{V,ij} &= 1 + r_{ij} - r_{ij}V/K_{ij} - [p_2{}^2a_{ij,11} + 2p_2(1 - p_2)\,a_{ij,12} \\ &\qquad + (1 - p_2)^2\,a_{ij,22}]P, \\ W_{P,kl} &= 1 + [p_1{}^2a_{11,kl} + 2p_1(1 - p_1)\,a_{12,kl} + (1 - p_1)^2\,a_{22,kl}]\,b_{kl}V - e_{kl}\,. \end{aligned} \tag{3c}$$

Where p_1 and p_2 are the gene frequencies in the prey and predator respectively. These fitness functions *do* involve interspecific frequency dependence because the fitness of each type depends on the gene frequency in another species. Genetic variation in either or both species for a parameter like a in the model above automatically involves interspecific frequency-dependent selection. Variation in parameters like r, K, b, and e may or may not involve interspecific frequency-dependent selection; if so it must be by explicit assumption. For example, we might stipulate that any prey phenotype with a high r and K must also be more susceptible to predation (high a). But coupling r and K to a would introduce interspecific frequency-dependence. In this way some care must be exercised when discussing the evolution of parameters in models of interacting populations—genetic variation in some parameters necessarily involves interspecific frequency-dependence while genetic variation in other parameters does

not. In the following paragraphs we pursue the situation without interspecific frequency-dependence, and then turn to the situation where it is present.

We consider a set of S different interacting species, each with genetic variation at one locus with two alleles, but without interspecific frequency-dependence,

$$N_{s,t+1} = \bar{W}_s N_{s,t} \qquad (s = 1, 2, \ldots, S), \tag{4a}$$

$$p_{s,t+1} = [p_{s,t} W_{s,11} + (1 - p_{s,t}) W_{s,12}] p_{s,t} / \bar{W}_s , \tag{4b}$$

where

$$\bar{W}_s = p_s^2 W_{s,11} + 2p_s(1 - p_s) W_{s,12} + (1 - p_s)^2 W_{s,22} . \tag{4c}$$

As before we focus attention on the equations for the population-dynamic part of the model, (4a). We can regard these equations as containing parameters, $m = (m_1, m_2, \ldots)$ which are themselves functions of the gene frequencies $(p_1, p_2, \ldots, p_S)$. We can solve for the equilibrium population sizes in terms of these parameters by setting $\bar{W}_s = 1$ for all s, and then in turn see how the equilibrium population sizes depend on the gene frequencies. And as before, if we can solve for the equilibrium gene frequencies $(\hat{p}_1, \hat{p}_2, \ldots, \hat{p}_S)$ then we can determine the parameter values and population sizes at the evolutionary equilibrium.

In the example of the predator–prey model without interspecific frequency dependence we have

$$\begin{aligned} \bar{W}_V &= 1 + m_1 - m_2 V - m_3 P, \\ \bar{W}_P &= 1 + m_4 V - m_5 , \end{aligned} \tag{5a}$$

where

$$\begin{aligned} m_1 &= m_1(p_1) = p_1^2 r_{11} + 2p_1(1 - p_1) r_{12} + (1 - p_1)^2 r_{22} , \\ m_2 &= m_2(p_1) = p_1^2 r_{11}/K_{11} + 2p_1(1 - p_1) r_{12}/K_{12} + (1 - p_1)^2 V_{22}/K_{22} , \\ m_3 &= a, \\ m_4 &= m_4(p_2) = p_2^2 a b_{11} + 2p_2(1 - p_2) a b_{12} + (1 - p_2)^2 a b_{22} , \\ m_5 &= m_5(p_2) = p_2^2 e_{11} + 2p_2(1 - p_2) e_{12} + (1 - p_2)^2 e_{22} . \end{aligned} \tag{5b}$$

The equilibrium population sizes for the two species in terms of these parameters are

$$\begin{aligned} \hat{V}(m_1 \cdots m_5) &= m_5/m_4 , \\ \hat{P}(m_1 \cdots m_5) &= (m_1 m_4 - m_2 m_5)/(m_3 m_4). \end{aligned} \tag{5c}$$

$\hat{V}$ and $\hat{P}$ are, in principle, functions of p_1 and p_2 because these parameters are functions of p_1 and p_2. (However, $\hat{V}$ does not in fact depend on p_1.) m_1 and m_2

are functions of p_1 while m_4 and m_5 are functions of p_2. Hence evolution within the prey will determine the values assumed by the parameters m_1 and m_2, while the predator's evolution will determine m_4 and m_5.

More generally, if some parameter, say m_i is a function of p_s then we say the parameter m_i is under the *evolutionary control* of species-s. All evolutionarily available values of m_i are obtained by letting p_s vary between 0 and 1. From the assumption that there is no interspecific frequency-dependence it follows that each parameter is a function of no more than one gene frequency. Hence we can classify every parameter in the ecological model as being under the evolutionary control of one particular species in the system (or not subject to evolution at all as with parameter m_3 above).

The outcome of coevolution for any given species will be seen to depend on the ecological milieu in which it is embedded. To make this idea more precise we use the concept of the "feedback" of an ecological network as introduced by Levins (1974). Suppose we are given a set of variables, say $N_1, \ldots, N_S$, together with dynamical equations for these variables. The dynamical equations give dN_i/dt or ΔN_i depending on whether the system is specified in continuous or discrete time. We can form a matrix of the effect of each species on the dynamics of one another by tabulating the quantities $\partial(\Delta N_i)/\partial N_j$ for all i and j. Let the dimension of the matrix be $S \times S$. Then Levins defines the *feedback* of this system as $(-1)^{S-1}$ times the determinant of this matrix. For example, in the simple case of only one species the matrix consists of one element $\partial(\Delta N)/\partial N$. Therefore this quantity is Levin's measure of the "feedback" in a system of one species. Recall that a necessary condition for stable equilibrium in a single-population model is negative density dependence, i.e., in Levin's terminology there must be negative feedback. This idea can be generalized to assert that a necessary condition for stability of a dynamical system is that the sum of the feedback of all subsystems at any given level must be negative. These words simply offer a restatement of well-known stability criteria, but they allow a more physical interpretation of these criteria than otherwise possible.

We can now assert a principle for the evolution of the parameters in an ecological model for interacting populations:

PRINCIPLE 2. *Consider the evolution of the parameters in an ecological model of S interacting populations and assume that there is no interspecific frequency dependence.*

A. *Suppose there is negative feedback in the ecological system of $S - 1$ species which is obtained by deleting species-s. Then natural selection within species-s causes the parameters under the evolutionary control of species-s eventually to assume those values which produce the largest equilibrium population size for species-s, with respect to variation of those parameters.*

B. *Suppose there is positive feedback in the ecological system of* $S - 1$ *species obtained by deleting species-s. Then natural selection within species-s causes the parameters under the evolutionary control of species-s eventually to assume those values which produce the smallest equilibrium population size for species-s, with respect to variation of those parameters.*

C. *Suppose there is (identically) zero feedback in the ecological system of* $S - 1$ *species obtained by deleting species-s. Then natural selection within species-s on the parameters under the evolutionary control of species-s has no influence on the equilibrium population size of species-s.*

D. *A stable community does contain some species which satisfy condition A above.*

We can apply this principle to many ecological models. As our first example let us return to the predator-prey model without interspecific frequency dependence. Condition A of this principle applies to the predator population. At the co-evolutionary equilibrium, natural selection within the predator population will have caused the parameters b and e to have those values which produce the highest equilibrium predator abundance, $\hat{P}$. Condition A applies to the predator because the ecological system obtained by deleting the predator consists of the prey population. The prey population contains negative feedback because of the negative density dependence inherent in the logistic equation. In contrast, condition C applies to the prey population. The ecological system obtained by deleting the prey consists of the predator population. The predator population contains no density dependence at all and therefore the feedback in this system is identically zero. Therefore natural selection on the parameters under the evolutionary control of the prey, r and K, does not influence the equilibrium prey abundance $\hat{V}$. This result is directly verified by checking that $\hat{V}$ is not a function of p_1, as noted earlier. Condition C asserts only that $\hat{V}$ is not affected by the evolution in the prey; it does not tell us what values the prey parameters will have at equilibrium. This question is answered by Principle 3 to be presented later.

As a further example of the application of this principle we illustrate a case where evolution leads to the smallest equilibrium population size. Consider the following model.

$$\begin{aligned} N_{1,t+1} &= [1 + r - rN_{1,t}/K + \alpha_{12} rN_{2,t}/K]\, N_{1,t}\,, \\ N_{2,t+1} &= [1 + r - \alpha_{21} rN_{1,t}/K + rN_{2,t}/K]\, N_{2,t} \qquad (r, K_1, \alpha_{12}, \alpha_{21} > 0). \end{aligned} \tag{6a}$$

Species-2 has a positive effect on *both* its own population growth and the growth of species-1. Species-2 might be viewed as a pioneer species which stabilizes the habitat or soil for itself and other species. Species-1 however exerts a negative effect on both its own population growth and the growth of

species-2. Species-1 might be viewed as a typical competitor. It can be verified that there is a stable positive equilibrium $(\hat{N}_1, \hat{N}_2)$ in this model if and only if

$$\begin{gathered} \alpha_{12} > 1, \\ 2 - \alpha_{12} < \alpha_{21} < 1, \\ \alpha_{12}\alpha_{21} > 1, \\ r < 4(\alpha_{12}\alpha_{21} - 1)/[(\alpha_{12} - \alpha_{21}) - 2 + Q^{1/2}], \\ Q = (\alpha_{12} - \alpha_{21})^2 - 4\alpha_{12}(\alpha_{12} - 1)\,\alpha_{21}(1 - \alpha_{21}). \end{gathered} \tag{6b}$$

Species-1 satisfies condition B in the principle above because when species-1 is deleted we are left with a system possessing positive feedback. Therefore by condition B natural selection within species-1 will cause the parameters under its evolutionary control to assume values which produce the lowest $\hat{N}_1$. To see what this means let us inspect the fitnesses within species-1 more closely.

$$W_{1,ij} = 1 + r - rN_1/K + \alpha_{1ij,2}rN_2/K. \tag{6c}$$

The W's for the genotypes within species-1 differ only in the parameter α_{12}. There is selection in favor of increasing α_{12} because increasing α_{12} leads to a higher fitness. But the equilibrium population size is given by

$$\hat{N}_1 = K(\alpha_{12} - 1)/(\alpha_{12}\alpha_{21} - 1), \tag{6d}$$

and it is readily seen that $\partial\hat{N}_1/\partial\alpha_{12} < 0$. Thus selection within species-1 will tend to raise α_{12} but this leads to a reduction in $\hat{N}_1$. In contrast, species-2 satisfies condition A and natural selection causes the parameters under the evolutionary control of species-2 to assume values which maximize $\hat{N}_2$. Notice by condition D of the principle above that every stable community must contain at least one species for which natural selection on its parameters maximizes its equilibrium population size. Moreover it is not uncommon for all species to satisfy condition A.

Principle 2 as stated above is justified by a theorem about density-dependent natural selection in interacting populations which is proved in Appendix II. This theorem relies, as before, on the absence of intra- and interspecific frequency-dependence and on a genetic system in which classical density-independent selection leads to a stable equilibrium where the mean fitness is maximized. Coevolution between two competitors without interspecific frequency-dependence has been solved in detail by Leon (1974).

Coevolution With Interspecific Frequency-Dependence

The inclusion of interspecific frequency dependence in the system substantially charges the preceding results. In general terms both the location of any coevolutionary equilibrium point and its stability are influenced by interspecific frequency-dependence.

To illustrate the problems involved, let us begin with a simple example. Consider two competing species and fitnesses of the form

$$\begin{aligned} \overline{W}_1 &= 1 + r - rN_1/K - (p_1^2\alpha_{11,2} + 2p_1(1-p_1)\alpha_{12,2} + (1-p_1)^2\alpha_{22,2})rN_2/K, \\ W_2 &= 1 + r - rN_2/K - (p_1^2\alpha_{2,11} + 2p_1(1-p_1)\alpha_{2,12} + (1-p_1)^2\alpha_{2,22})rN_1/K. \end{aligned} \tag{7a}$$

$\overline{W}_1$ is the mean fitness in species-1. $\alpha_{ij,2}$ is the competition coefficient representing the effect of an individual of species-2 against an individual of type ij in species-1 and $\alpha_{2,ij}$ is the effect of type ij in species-1 against an individual in species-2. We assume there is no genetic variation within species-2; only species-1 is evolving. Hence W_2 is the fitness of any individual in species-2 as well as the mean fitness in species-2. There is interspecific frequency-dependence in this system because $\partial W_2/\partial p_1 \neq 0$. In this system both α_{12} and α_{21} are under the evolutionary control of species-1. By principle 2, we expect that natural selection causes α_{12} and α_{21} to assume those values which lead to the highest equilibrium population size for species-1, $\hat{N}_1$. But this is false. A simple illustration is provided by the "case of the nasty competitor." Let

$$\begin{aligned} &\alpha_{11,2} = \alpha_{12,2} = \alpha_{22,2} = \alpha, \\ &\alpha_{2,11} > \alpha_{2,12} > \alpha_{2,22}. \end{aligned} \tag{7b}$$

Type A_1A_1 in species-1 is perfectly nasty; he interferes with members of species-2 more than any other type but receives absolutely no benefit in return nor incurs any cost to himself—the lack of any benefit or cost to the nastiness is reflected in his having the same r, K, and α_{12} as every other genotype. We can see without any calculations that the equilibrium population size of species-1 would be maximized with the fixation of the A_1 allele. With A_1 fixed α_{21} has its highest value resulting in the lowest $\hat{N}_2$ and hence the highest $\hat{N}_1$. But clearly A_1 will *not* be fixed by natural selection. There is no differential fitness within species-1 because all types have the same r, K and α_{12}. In fact, the trait of pure interspecific nastiness is selectively neutral. Therefore some new principle is required to cover the evolution of ecological parameters in the presence of interspecific frequency-dependence.

To state this principle we must introduce a new, though simple, quantity. We define the *conditional equilibrium population size of species-s*, $\tilde{N}_s$, as the equilibrium abundance of species-s based on assuming the other species are constants, not variables, in the system. $\tilde{N}_s$ is simply obtained by setting $\overline{W}_s = 1$ and solving for N_s as a function of the parameters in the system *and* the abundances of the other species in the system. For example the conditional equilibrium population size for the prey in Eq. (5) is obtained by setting $\overline{W}_V = 1$ and solving for V,

$$\tilde{V}(m_1, m_2, m_3, P) = (m_1 - m_3P)/m_2. \tag{8a}$$

Similarly the condition equilibrium population size of species-1 in the second example (i.e., the species who evolved a minimum population size) is

$$\tilde{N}_1(K, \alpha_{12}, N_2) = K + \alpha_{12}N_2 . \tag{8b}$$

And our most recent example, a population with genetic variation for the competition coefficients, is

$$\tilde{N}_1(K, \alpha_{12}, N_2) = K - \alpha_{12}N_2 . \tag{8c}$$

In every case, the conditional equilibrium population size is obtained from solving a *single* equation, $\overline{W}_s = 1$, for N_s. $\tilde{N}_s$ is therefore a function of the parameters in $\overline{W}_s$ as well as of the population sizes of any species with which it interacts.

Interspecific frequency-dependence implies that some parameters will be under the joint evolutionary control of several species. Usually a parameter like the predation coefficient, a, in the predator–prey model above is under the joint control of two species, although it is possible to conceive of parameters being under the control of more than two species. Again we impose a 1 locus-2 allele scheme of genetic variation for the parameters. Then we can define the evolutionarily available values of a parameter as those values obtained by letting the gene frequencies vary between 0 and 1. Specifically in the case of a parameter under the control of two species, we write $m_i(p_1, p_2)$. The values of m_i which are evolutionarily available to species-1 are themselves a function of p_2 and are obtained by letting p_1 vary between 0 and 1 for any given p_2; and similarly for species-2. In this context we assert

PRINCIPLE 3. *Consider the evolution of the parameters in an ecological model of S interacting populations. There may be interspecific frequency-dependence.*

A. *Suppose there is density-dependence (positive or negative) in species-s. At any coevolutionary equilibrium (stable or unstable) the parameters under the evolutionary control of species-s, including parameters whose control is shared with other species, have values which produce a critical point to the conditional equilibrium population size of species-s,* $\tilde{N}_s$, *with respect to variation of those parameters. It is understood here that* $\tilde{N}_s$ *is evaluated at* $N_i = \tilde{N}_i(m)$, *i.e., the population sizes used to evaluate* $\tilde{N}_s$ *must be equilibrium abundances. (A critical point means the derivative is zero.)*

B. *Suppose the density-dependence is negative (positive) in species-s. The mean fitness is maximized at the coevolutionary equilibrium in species-s if and only if the conditional equilibrium population size,* $\tilde{N}_s$, *is maximized (minimized) with respect to variation of the parameters under the evolutionary control of species-s.*

C. *It is generally neither necessary nor sufficient for a stable coevolutionary*

equilibrium with interspecific frequency-dependence that the mean fitness be maximized within each of the species. Whether the mean fitness is maximized within one or more of the species at a stable equilibrium must be checked in each model.

Observe that this principle can be used to find the location of any coevolutionary equilibrium point, but asserts nothing about the stability of the equilibrium. However we can say that any equilibrium point, whether stable or not, which corresponds to the mean fitness being maximized in some species also corresponds to a maximum or minimum of the conditional equilibrium population size of that species depending on the sign of its density-dependence. This principle subsumes Principle 2 as a special case. If there happens to be no interspecific frequency-dependence then, as shown in Appendix II, stable equilibria do correspond with fitness being maximized in each species. Hence in this case stable coevolutionary equilibria correspond with the evolution of parameter values which maximize or minimize $\tilde{N}_s$ depending on the sign of the density-dependence in species-s.

In general terms the biological importance of a principle that the conditional equilibrium population size, $\tilde{N}_s$, is maximized at the evolutionary equilibrium is that this principle enables one to compute optimum strategies while excluding any "feedback" from the ecological system which results after the evolution of the strategy. Such subsequent feedback may be beneficial or injurious to a species, but in either event it is irrelevant to determining which strategy is "chosen" by natural selection.

We can reconsider our previous examples in light of Principle 3. (1) Consider the predator–prey model (5). Evolution within the prey does not influence the equilibrium population size, $\hat{V}$. However, evolution within the prey does maximize the conditional equilibrium prey population size $\tilde{V}$. (2) In the model of Eq. (6) species-1 evolved a minimum equilibrium population size $\tilde{N}_1$. However, this corresponds to maximizing the conditional equilibrium population size of species-1, $\tilde{N}_1$.

When there is interspecific frequency-dependence the issue of stability must be settled case by case. For example it can be shown that if species-1 has genetic variation and species-2 does not, and if $\bar{W}_1$ is of the form

$$\bar{W}_1 = f(N_1, N_2) + g(p_1)\, h(N_1, N_2), \tag{9}$$

then the mean fitness within species-1 must be maximized at any stable equilibrium. This form covers the example of competition introduced in Eq. (7). $\tilde{N}_1$ in the case of the "nasty competitor" ceases to be a function of p_1, bearing out the point that pure interspecific nastiness is selectively neutral.

Rather than introduce further examples we illustrate Principle 3 by applying it to the original problem of the evolution of resource partitioning. Principle 3 is justified by the theorem in Appendix III.

Coevolution of Resource Partitioning Patterns

Resource partitioning is the differential use of resources by competing populations. Typically, the competing species are identified, resource categories distinguished, and the frequency of use by each population of each resource category observed. Resource partitioning is thus documented with frequency distributions representing the resource use by each of the competing populations.

Certain descriptive indices are computed from the frequency distributions describing the resource use. A location parameter describes the "niche position." A dispersion parameter describes the "niche width" or breadth. Common dispersion measures are the Shannon–Weaver index, the variance, etc. The "niche overlap" between any pair of species is measured by various overlap indices. The "niche separation" between any pair is often measurable as some distance between the niche positions of the members of the pair. For any choice of descriptive statistics there are certain necessary interrelationships which follow from the definitions. For example, with fixed niche positions, the overlap between a pair is an increasing function of the niche widths, etc.

An easily visualized case is one in which the resource categories are prey-size categories. Many competing populations of vertebrates partition with respect to the size of prey. Examples are widespread among birds (Cody, 1974), lizards (Schoener and Gorman, 1968), fish (Randall, 1967), etc. If the partitioning is with respect to some "axis" like prey size then the frequency distributions may have the general appearance of normal or log-normal curves, and the ordinary mean and standard deviation are good measures of niche position and niche width. Similarly the niche separation is simply the difference between the means of each population.

The purpose of a mathematical model in this context is to predict the niche separations. As mentioned in the introduction, current theory predicts the minimum niche separation consistent with coexistence, i.e., the so-called "limiting similarity." Instead let us predict the niche separations on the basis of the coevolutionary principles introduced above.

The model as formulated below is the standard setup for resource partitioning theory. (1) The competition model is the Lotka–Volterra competition system. The parameters in this model are the competition coefficients α_{ij} and the carrying capacities, K_i. These parameters are interpreted in terms of the niche positions, widths, and separations as follows. It is assumed that species may have different nich positions but they all have the same niche width. (2) We assume that the competition coefficient between two species is a function of their niche separation. Let the niche position of species-i be x_i. Then it is assumed that $\alpha_{i,j} = \alpha(x_i - x_j)$. The competition function $\alpha(d)$, where d denotes the niche separation between two species, satisfies $\alpha(0) = 1$, $\alpha(d) > 0$, $\alpha(d) < (>) 0$ for $d > (<) 0$, and $\alpha(d) \to 0$ as $d \to \pm\infty$. (For attempts at empirical estimates

of $\alpha(d)$ see Roughgarden, 1972; Schoener, 1976.) Moreover we assume, with earlier workers, that reciprocal competition coefficients are equal and therefore $\alpha(d)$ is symmetric about zero. Typically it is assumed that $\alpha(d) = \exp[-(d/\sigma_\alpha)^2]$. The width of the competition function is measured by the standard deviation of $\alpha(d)$. (To calculate this $\alpha(d)$ must first be normalized to unit area.) The standard deviation of $\alpha(d)$, denoted σ_α, is a quantity which is very closely related to the niche width. The niche width is defined as the standard deviation of the resource utilization curve of a species and is denoted by w. σ_α must be a monotonic increasing function of w because the range over which the competition operates is determined by the range over which species take resources. Indeed, with the overlap index proposed by MacArthur and Levins (1967) it turns out that $\sigma_\alpha = (2)^{1/2}w$. I will use this convention for Fig. 2 (see later) in order to make the results directly comparable with existing literature on resource partitioning. So, to summarize, we assume the competition coefficients are given by a competition function, $\alpha(d)$, where d is the niche separation between two species, and where the width of the competition function is directly proportional to the niche width of the competing species. (3) We assume the carrying capacity of species-i is a function of its niche position, $K_i = K(x_i)$. $K(x)$ is called the carrying capacity function. The standard deviation of $K(x)$ (again provided $K(x)$ is first normalized to unit area) is denoted σ_k and is a measure of the variety of available resources. Thus the model consists of a set of species with niche positions, x_i, and a common niche width, w. Both the competition between species and the carrying capacity of each species are inferred from the set of x_i and w. The parameter σ_k specifies the variety of available resources in the environment while $\sigma_\alpha = (2)^{1/2}w$ specifies the variety of resources used by each species.

As many have pointed out there are limitations in this standard formulation of resource partitioning theory. The assumption of equal niche widths is dubious as is the assumption that all species share a common $K(x)$ function. This formulation is an idealization of the phenomenon of resource partitioning. It is not intended to offer numerically accurate predictions. The protocol for solving problems about resource partitioning is legitimately illustrated in this context and many qualitative conclusions are undoubtedly robust.

Apart from limitations inherent in the formulation of resource partitioning theory an additional limitation to the study here is the assumption that the niche positions may evolve while the niche widths are fixed. There are two reasons why I feel this is justifiable as a first step. (1) The niche width of a species is due to two components, one reflecting the presence of different kinds of individuals within a population (the so-called between-phenotype component, BPC) and the other reflecting the average range of resources used by the different kinds of individuals (the so-called within-phenotype component, WPC). Theory about the evolution of the BPC appears in Roughgarden (1972). That for the

WPC takes the form of models for optimum foraging strategies (see Schoener, 1971). An evolutionary theory for the niche width of a population must combine the theories for these different components. Developing this combined theory is a difficult task and I believe warrants a separate treatment. However, if it is assumed that the BPC is small enough to be ignored then perhaps progress can be made. In any event, considering the niche width as evolving jointly with the niche positions introduces many new considerations and is not a simple extension of this paper. (2) My data on the BPC of *Anolis* lizards (Roughgarden, 1974) show that this component of the niche width is quite constant within a lineage even though there may be shifts in niche position. The data suggest that the phenotype variance in a character like jaw length or bill length is evolutionarily conservative relative to the mean for such characters. Obviously the next step should be to consider the joint evolution of niche positions and niche widths; these remarks are simply intended to justify our *beginning* with the evolution of the niche positions while regarding the niche widths as fixed.

Two Competitors

Consider first the evolution of the resource partitioning between two competitors. The competition equations with parameters written in terms of the niche positions are

$$\begin{aligned} N_{1,t+1} &= [1 + r_1 - r_1 N_{1,t}/K(x_1) - \alpha(x_1 - x_2)\, r_1 N_{2,t}/K(x_1)]\, N_{1,t}\,, \\ N_{2,t+1} &= [1 + r_2 - \alpha(x_2 - x_1)\, r_2 N_{1,t}/K(x_2) - r_2 N_{2,t}/K(x_2)]\, N_{2,t}\,. \end{aligned} \tag{10}$$

The carrying capacity of species-1, $K(x_1)$, is under the evolutionary control of species-1, and similarly for species-2; and the competition coefficients, $\alpha(x_1 - x_2)$ and $\alpha(x_2 - x_1)$, are each under the joint evolutionary control of both species. By definition, all values of K which are evolutionarily available to species-1 are given by the values of the function $K(x_1)$ as x_1 is allowed to vary between $-\infty$ and ∞. The problem then is find the values of x_1 and x_2 which obtain at the coevolutionary equilibrium for these species.

This coevolutionary problem is clearly one where there is inherent interspecific frequency-dependence. Hence we cannot apply Principle 2; the niche positions at evolutionary equilibrium are *not* those which maximize the equilibrium population sizes of the species. Instead, we apply Principle 3 and *assume* that an equilibrium in which the average fitness in each species is a local maximum is stable. If so, by Principle 3 the populations assume niche positions,

x_1, x_2, which maximize the conditional equilibrium population sizes of the species. Specifically we have

$$\tilde{N}_1(x_1, x_2, N_2) = K(x_1) - \alpha(x_1 - x_2)N_2, \tag{11a}$$

$$\tilde{N}_2(x_1, x_2, N_1) = K(x_2) - \alpha(x_2 - x_1)N_1. \tag{11b}$$

By Principle 3 at the coevolutionary equilibrium $\tilde{N}_1$ is maximized with respect to x_1 and $\tilde{N}_2$ with respect to x_2, provided $\tilde{N}_1$ and $\tilde{N}_2$ are evaluated at $N_i = \hat{N}_i(x_1, x_2)$. So differentiating (11a) with respect to x_1 and (11b) with respect to x_2, and then substituting $N_i = \hat{N}_i$ yields a pair of simultaneous equations for x_1 and x_2. The solutions to these equations, $\hat{x}_1$ and $\hat{x}_2$, are the niche positions which should obtain at the coevolutionary equilibrium according to Principle 3.

Further analysis appears in Appendix IV. If $K(x)$ and $\alpha(d)$ are symmetric functions then there is a simple technique for the solution. With symmetry the optimum niche locations for the species are on opposite sides of the peak in the carrying capacity function. The optimum niche locations can then be labelled as $-\hat{x}$ and $\hat{x}$ where, by convention, we locate the origin of the resource axis below the peak of $K(x)$. The niche separation at the evolutionary equilibrium, $\hat{d}$, then equals $2\hat{x}$. Moreover, if $K(x)$ and $\alpha(d)$ are not only symmetric but also of the same functional form then the niche locations, $\hat{x}$, can be obtained explicitly. The earlier literature has dwelled on the case where both $K(x)$ and $\alpha(d)$ are Gaussian.

In the Gaussian case the equilibrium niche locations from Principle 3 are

$$x^* = (\ln[-1 + 2\sigma_k^{*2}]/2)^{1/2}, \tag{12}$$

where $x^* = \hat{x}/\sigma_\alpha$ and $\sigma_k{}^* = \sigma_k/\sigma_\alpha$. By dividing every quantity by σ_α the units are scaled to remove the effect of differing niche widths. Thus two wide niche species which are far apart are equivalent to two narrow nich species closer together. This formula is plotted in Fig. 2 as explained later. Notice that the niche separation is rather insensitive to $\sigma_k{}^2$, the measure of the variety of available resources.

The niche positions which maximize the equilibrium population sizes, $\hat{N}_1$ and $\hat{N}_2$, are different from (12) above. Specifically in the Gaussian case.

$$x^* = (\ln[-1 + 4\sigma_k^{*2}]/2)^{1/2}. \tag{13}$$

The niche separation which maximizes the population sizes of the competing species is wider than that which evolves by natural selection according to Principle 3. Thus the evolution of character displacement does not proceed far enough. Somewhat more displacement than that achieved by natural selection would yield larger population sizes for the populations involved.

Three Competitors

To find the niche positions for each of three competing species at the coevolutionary equilibrium we again appeal to Principle 3. The conditional equilibrium population size for each species is of the form

$$\tilde{N}_1(x_1, x_2, x_3, N_2, N_3) = K(x_1) - \alpha(x_1 - x_2)N_2 - \alpha(x_1 - x_3)N_3, \quad (14)$$

and similarly for $\tilde{N}_2$ and $\tilde{N}_3$. Then, as before, each $\tilde{N}_i$ is differentiated with respect to x_i, set equal to zero, and then evaluated at $N_i = \hat{N}_i$. This procedure yields three simultaneous polynomials for the three niche positions. Even in the symmetric case I have found no simple solution for these equations. However, to illustrate their solution I have taken the example of Gaussian $K(x)$ and $\alpha(d)$. The optimum niche positions will be arranged as $-\hat{x}$, 0, and $\hat{x}$ so that one will occupy the center and the other two will be in the tails of the resource spectrum. The equation for $\hat{x}$ was solved numerically.

The results appear in Fig. 2 and are expressed in terms of the niche separation relative to the niche width to facilitate comparison with other work in the literature. The niche width w is defined as $\sigma_\alpha/(2)^{1/2}$, thereby following a convention which is exact if the MacArthur–Levins overlap formula correctly predicts the competition coefficients from overlap data. The niche separation, d, is simply $\hat{x}$ with three competitors, and $2\hat{x}$ with two competitors. The figure illustrates intuitive results. (1) For a given variety of resources, σ_k^2, the equilibrium separation is less with three species than with two. In other words, for a given σ_k^2, the "packing" becomes tighter as the species diversity increases. (2) For a given number of species, the separation increases with the variety of resources σ_k^2. But notice the "slow" dependence of d upon σ_k^2 as mentioned earlier.

These results are intuitive and appear as conjectures in ecological lore. This

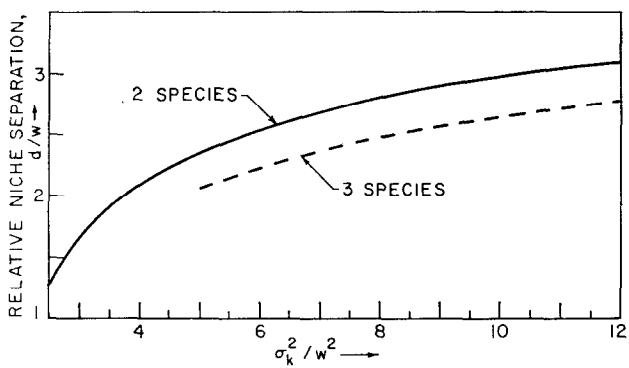

Fig. 2. Niche separation which results from coevolution as a function of the variance of available resources on an island, and of the number of competitors. The curve for two species is from Eq. (12) and that for three species was obtained numerically from Eq. (14).

is the first time they have derived from a model in which the coevolutionary process is specified. However, in the lore, statements about "species packing" often confound niche width effects with the packing per se. It is often asserted that packing is closer in species-rich locations where the evidence is solely differences between species means. But for many possible reasons, niches may be narrower in species-rich regions producing smaller differences between species even for the same degree of packing. The prediction developed above are independent of the niche width because of the scaling in terms of w, and refer to the packing itself.

Discussion

There are many studies of the relationship between species number and either niche overlap or niche separation. These studies involve finding locations which differ in species number and then comparing the resource partitioning patterns among the locations. The coevolutionary model here implies that the *qualitative outcome* of such studies depends on whether the locations chosen for the study vary only in species diversity or covary in both species diversity and in the variety of available resources.

Consider a set of locations each with the *same variety of resources but with differing species numbers*. From Fig. 2, for a fixed variety of resources, the separation decreases and the overlap increases as the number of species increases. So d/w, the niche separation distance between nearest neighbors should show a significant negative correlation with S, the species number. Next, consider a set of locations where *species diversity is correlated with the diversity of resources*. By assumption, locations with a larger species number have a larger underlying variety of resources. The relationship between d/w and S for these locations depends on two counteracting factors. In Fig. 2 increasing species diversity, S, reduces the optimum d/w while increasing σ_k^2 raises it. So if the locations are such that S covaries with σ_k^2 the coevolutionary model entails an absence of any conspicuous negative correlation between d/w and S. In fact, depending on the numerical relationships involved, a slight positive correlation between d/w and S is possible. For example, in Fig. 2 if the locations with two species possess σ_k^2/w^2 between 3 and 5 while locations with three species possess σ_k^2/w^2 between 5 and 10 then the average d/w is slightly higher in the locations with three species than with two. In examples of this sort d/w would show a positive correlation with S, which is opposite to the overall result which arises if σ_k^2 does not covary with S.

I suggest that island studies differ from continental studies in the extent to which S covaries with σ_k^2. Often, islands differ in species diversity because of differing proximities to a source region. Remote islands may have a depauperate fauna either because of a lower steady state rate of immigration leading to a lower

equilibrium species diversity in the sense of MacArthur and Wilson (1967), or may lack groups or species which are poor dispersers and which never colonize over water. In either event, there need be no correlation between S and σ_k^2. In contrast, at locations within a continent, there probably is a strong correlation between S and σ_k^2. Since there is no shortage of species to colonize any location the number who become established should be correlated with the variety of resources in the location. If this suggestion is correct then the relation between d/w and S should be quite different among islands as compared to that among locations within a continent.

In a recent study Pianka (1973, 1974) has discovered that niche overlap decreases as species diversity increases, based on locations within continents. Pianka, following MacArthur (1972) and May and MacArthur (1972) interprets this in terms of "diffuse competition." An alternative explanation suggested by the coevolutionary model involves the covariation of S with σ_k^2 as discussed above.

Another application of this coevolutionary approach is to the question of convergent community evolution. Recent studies, e.g., Pianka (1973) and Cody (1974), have documented the niche structure of similar communities from different continents. For birds, these studies generally show a broad outline of parallel niche structure with many identifiable ecological equivalents in both continents, but also a disturbingly large amount of differences between continents. For lizards there seem to be more differences than similarities. These facts invite two explanations. First, the regions being compared are not really identical, rainfall and temperature patterns differ, etc., and thus the evolution of identical community structure is not expected. Second, perhaps there are multiple evolutionarily stable outcomes from the coevolution of community structure. The mathematical machinery developed here is relevant to the second explanation. The coevolutionary theory predicts the existence of multiple evolutionary equilibria if several solutions exist which are local maxima to the conditional equilibrium population sizes. In the cases examined there was in fact only one solution; so in these simple cases coevolution leads to only one scheme of niche relationships. The application of this mathematical machinery to more complex interactions and more species will provide the first theory on the issue of a convergent evolution of community structure.

APPENDIX I: Density-Dependent Selection in a Single Population

I. *The Basic Model*

Consider one locus with two alleles, A_1 and A_2 . p is the frequency of A_1 and N is the population size. $W_{ij}(N)$ is the (absolute) selective value of genotype A_iA_j ; it is a function only of N and is strictly positive.

The basic model is

$$p_{t+1} = [p_t W_{11}(N_t) + (1 - p_t)\, W_{12}(N_t)]\, p_t / \overline{W}(p_t, N_t), \tag{1a}$$

$$N_{t+1} = \overline{W}(p_t, N_t)\, N_t, \tag{1b}$$

where

$$\overline{W}(p, N) = p^2 W_{11}(N) + 2p(1 - p)\, W_{12}(N) + (1 - p)^2\, W_{22}(N). \tag{1c}$$

Because the $W_{ij}(N)$ are functions only of N and not of p we can also write (1a) as

$$p_{t+1} = p_t(1 - p_t)[\partial \overline{W}(p_t, N_t)/\partial p_t]/[2\overline{W}(p_t, N_t)] + p_t. \tag{1d}$$

Equilibrium points of this system satisfy

$$\partial \overline{W}(p, N)/\partial p = 0 \qquad \text{and} \qquad \overline{W}(p, N) = 1. \tag{1e}$$

II. *The Implicit Definition of the Curve,* $\hat{N}(p)$

We impose a monotonicity condition on the fitness functions

Condition 1.

$$\begin{aligned} &\text{(a)} \quad W_{ij}(0) > 1; \\ &\text{(b)} \quad W'_{ij}(N) < 0 \qquad \text{for all } N; \\ &\text{(c)} \quad W_{ij}(N) \to 0 \qquad \text{as } N \to \infty. \end{aligned} \tag{2}$$

This condition implies several results:

1. Consider the function $\overline{W}$ with *fixed* p but with N as a variable. We denote this function as $\overline{W}_p(N)$ to emphasize that p is a parameter. $\overline{W}_p(N)$ is a monotone function of N for any p,

$$\begin{aligned} \overline{W}_p(0) &> 1, \\ \overline{W}_p'(N) &< 0. \end{aligned} \tag{3}$$

2. The above result implies that for any p there is a unique N (which depends on p) such that $\overline{W}_p(N) = 1$.

3. Then by the implicit function theorem we can regard the equation

$$\overline{W}(p, N) - 1 = 0 \tag{4}$$

as implicitly defining N as a function of p. We denote the function so defined as $\hat{N}(p)$. Differentiating implicitly and solving for $\hat{N}'(p)$ we obtain

$$\hat{N}'(p) = -(\partial \overline{W}/\partial p)/(\partial \overline{W}/\partial N). \tag{5}$$

By Condition 1, $\partial \overline{W}/\partial N \neq 0$ and therefore $\hat{N}(p)$ is a differentiable function of p.

III. *The Role of the Curve $\hat{N}(p)$ When p is Held Fixed*

We impose conditions in the strength of the density-dependence.

Condition 2. Along the curve $\hat{N}(p)$ the inequality below is satisfied.

$$-N\overline{W}_p'(N) < 2.$$

Condition 3. For all N the inequality below is satisfied.

$$-NW_{ij}'(N) < 2.$$

Condition 3 implies Condition 2. Condition 3 says that fitness functions must become flat as N becomes large, and that their slopes can never be too high. Although Condition 3 seems strong it is satisfied in surprisingly many choices of exponential and hyperbolic fitness functions. However, Condition 2, which is weaker, is all that is needed in the proofs.

Now consider the population dynamics which results if p is held fixed. That is, consider the transformation

$$N_{t+1} = \overline{W}_p(N)\, N_t\,. \tag{6}$$

We note two results.

1. Given Condition 1, $N = \hat{N}(p)$ is the unique positive equilibrium point of the transformation (6).

2. Given Condition 1, $N = \hat{N}(p)$ is a locally *stable* equilibrium point of the transformation (6) for any p if and only if Condition 2 is satisfied. This result is proved by requiring that

$$-1 < dN_{t+1}/dN_t < 1, \tag{7}$$

where the derivative is evaluated at $N_t = \hat{N}(p)$. The right-hand inequality is satisfied given Condition 1 and the left-hand inequality is identical to Condition 2.

In general terms we see that with monotone fitness functions and if the density-dependence is not too strong then the curve $\hat{N}(p)$ gives the stable equilibrium population size attained with any fixed p. Thus if evolution is prevented from occurring (i.e., p is fixed) the equilibrium population size which is attained is some point on the curve $\hat{N}(p)$. We will now show that if evolution *is* allowed to occur (p is allowed to vary) then the equilibrium is at a maximum of N along this curve, $\hat{N}(p)$. Thus evolution will generally yield an equilibrium population size higher than that which occurs if evolution is prevented.

IV. *The Role of the Curve, $\hat{N}(p)$, When Both N and p Vary*

Consider the transformation equations, (1), for N_{t+1} and p_{t+1}. Both N and p are variables; neither is fixed. We note several results:

1. If Condition 1 is satisfied then any equilibrium, (p^*, N^*), of Eqs. (1) must be on the $\hat{N}(p)$ curve. Any equilibrium point (p^*, N^*) must satisfy

$$\overline{W}(p^*, N^*) = 1. \tag{8}$$

Any point satisfying this equation lies in the $\hat{N}(p)$ curve.

2. If Condition 1 is satisfied, the point (p^*, N^*) is an equilibrium of the equations (1) if and only if p^* is a critical point of the function $\hat{N}(p)$ and $N^* = \hat{N}(p^*)$. To show this we note that equilibria of system (1) must satisfy

$$\partial\overline{W}/\partial p = 0, \tag{9}$$

where the derivative is evaluated at a point on the $N(p)$ curve. By the implicit function theorem

$$\partial\overline{W}/\partial p = -(\partial\overline{W}/\partial N)\,\hat{N}'(p). \tag{10}$$

Therefore $\partial\overline{W}/\partial p = 0$ if and only if $\hat{N}'(p) = 0$ since $\partial\overline{W}/\partial N \neq 0$ by Condition 1. Therefore, the equilibrium conditions for system (1), Eqs. (8) and (9), are satisfied at some point if and only if that point is either a local minimum or maximum of N along the $\hat{N}(p)$ curve.

3. If both Condition 1 and Condition 2 are satisfied then a point (p^*, N^*) is a locally stable equilibrium of the system (1) if and only if N^* is a local *maximum* of N along the $\hat{N}(p)$ curve and $N^* = \hat{N}(p^*)$. The local stability of an equilibrium is determined by the eigenvalues of the matrix

$$\begin{pmatrix} \partial N_{t+1}/\partial N_t & \partial N_{t+1}/\partial p_t \\ \partial p_{t+1}/\partial N_t & \partial p_{t+1}/\partial p_t \end{pmatrix}, \tag{11}$$

where the elements are evaluated at equilibrium point. The upper right element is

$$\partial N_{t+1}/\partial p_t = N_t \partial\overline{W}/\partial p_t = 0 \tag{12}$$

at equilibrium. Therefore the eigenvalues of the matrix are

$$\begin{aligned} \lambda_1 &= \partial N_{t+1}/\partial N_t\,, \\ \lambda_2 &= \partial p_{t+1}/\partial p_t\,. \end{aligned} \tag{13}$$

Given Condition 2, we have shown that $-1 < \partial N_{t+1}/\partial N_t < 1$ at any point along the $\hat{N}(p)$ curve and therefore at (p^*, N^*) in particular. Hence given Condition 2, $-1 < \lambda_1 < 1$. λ_2 is given explicitly by

$$\lambda_2 = \frac{p(1-p)}{2\overline{W}}\,\frac{\partial^2\overline{W}}{\partial p^2} + 1. \tag{14}$$

At equilibrium, $-1 < \lambda_2 < 1$ (in fact $0 < \lambda_2 < 1$) if and only if $\partial^2\overline{W}/\partial p^2 < 0$. Moreover, $\partial^2\overline{W}/\partial p^2$ is related to $N''(p)$ as

$$\partial^2\overline{W}/\partial p^2 = (-\partial\overline{W}/\partial N)\, N''(p). \tag{15}$$

This relation is obtained by differentiating (10) with respect to p and noting that $\hat{N}'(p) = 0$ at equilibrium. Since $\partial\overline{W}/\partial N < 0$ by condition 1, it follows that $\partial^2\overline{W}/\partial p^2 < 0$ if $N''(p) < 0$ at this point. Thus, given Conditions 1 and 2, local maxima of N along the curve $\hat{N}(p)$ correspond with stable equilibria for density-dependent evolution.

V. *Summary*

The results above can be summarized in the following theorem:

THEOREM 1. *Suppose the fitness functions, $W_{ij}(N)$, are strictly monotone decreasing with $W_{ij}(0) > 1$, and $W_{ij}(N) \to 0$ as $N \to \infty$; and suppose, for any fixed p, that $N = \hat{N}(p)$ is the stable equilibrium of the transformation $N_{t+1} = \overline{W}_p(N_t)N_t$. Under these conditions the point (p^*, N^*) is a locally stable equilibrium of the transformation* (1) *in which both N and p vary if and only if $N^* = \hat{N}(p^*)$ and N^* is a local maximum of N along the curve $\hat{N}(p)$. To find equilibria, solve for p^* in the equation $\hat{N}'(p^*) = 0$ and then set $N^* = \hat{N}(p^*)$. This point is stable if and only if $N''(p^*) < 0$.*

This theorem is the only analog of the fundamental theorem of natural selection which is currently known for density-dependent selection. It was first proved by Anderson (1971) for the case of linear fitness functions. The theorem is far weaker than the theorem of Kingman (1961) which shows that $\overline{W}(p)$ is a function of state which monotonically increases through time (a Liapunov function). In contrast, the $\hat{N}(p)$ function discussed above is not a function of state at all; it is simply a curve in the p-N plane. The $\hat{N}(p)$ curve represents all the possible equilibrium population sizes which result with different fixed gene frequencies. The theorem asserts that evolution leads to an equilibrium gene frequency which is associated with a local maximum of the possible equilibrium population sizes.

APPENDIX II. COEVOLUTION AMONG INTERACTING POPULATIONS: NO INTERSPECIFIC FREQUENCY-DEPENDENCE

I. *Basic Model*

Consider S populations each with genetic variation at one locus with two alleles. Let the alleles in species-s ($s = 1, 2, \ldots, S$) be $A_{s,1}$ and $A_{s,2}$. Let $N_{s,t}$

and $p_{s,t}$ be the abundance and frequency of $A_{s,1}$ in species-s, respectively. Let $W_{s,ij}$ be the selective value of genotype $A_{s,i}A_{s,j}$ in species-s. $W_{s,ij}$ satisfies

(a) $W_{s,ij} > 0$.

(b) $W_{s,ij}$ may be a function of N_s; typically $W_{s,ij}$ is a decreasing function of N_s indicating intraspecific competition (negative density-dependence).

(c) $W_{s,ij}$ may be function of any N_u ($u \neq s$); it will be a decreasing function of N_u if species-u is a competitor or predator of species-s; it will be an increasing function if species-u is a prey or mutualist of species-s.

(d) $W_{s,ij}$ is *not* a function of any p_s ($s = 1, 2,..., S$). There is neither intraspecific nor interspecific frequency-dependence.

The basic equations are

$$p_{s,t+1} = p_{s,t}(1 - p_{s,t})(\partial \bar{W}_s/\partial p_{s,t})/(2\bar{W}_s) + p_{s,t}, \tag{1a}$$

$$N_{s,t+1} = \bar{W}_s N_{s,t} \qquad (s = 1, 2,..., S). \tag{1b}$$

where

$$\bar{W}_s = p_{s,t}^2 W_{s,11} + 2p_{s,t}(1 - p_{s,t})\, W_{s,12} + (1 - p_{s,t})^2\, W_{s,22}\,. \tag{1c}$$

An equilibrium point ($\hat{p}_1$, $\hat{p}_2$,..., $\hat{p}_s$, $\hat{N}_1$, $\hat{N}_2$,..., $\hat{N}_s$) satisfies

$$\begin{aligned} \partial \bar{W}_s/\partial p_s &= 0 \\ \bar{W}_s &= 1 \qquad (s = 1, 2,..., S). \end{aligned} \tag{2}$$

II. *The Functions $\hat{N}_s$ Obtained When the p's Are Held Fixed*

Consider a purely population dynamic model which results if all the gene frequencies are held fixed. Let us denote $\bar{W}_{s,p}$ ($N_1 \cdots N_S$) as the mean fitness in species-s provided all the p's are held fixed. Then a purely population-dynamic model is given by

$$N_{s,t+1} = \bar{W}_{s,p}(N_1 \cdots N_S)\, N_{s,t} \qquad (s = 1, 2,..., S). \tag{3}$$

We will *assume* that this population dynamic model is well-behaved in a certain sense before proceeding with the discussion of evolution.

Assume, for every set of fixed gene frequencies ($p_1 \cdots p_S$), *there is a unique positive and locally stable equilibrium* ($\hat{N}_1$, $\hat{N}_2$,..., $\hat{N}_S$) *for the purely population dynamic model* (3).

Whether this assumption is met usually must be established by detailed reference to the fitness functions used in any particular case. If this assumption is not met with certain $W_{s,ij}$ then a population genetic model for coevolution using these $W_{s,ij}$ will show bizarre behavior. Such behavior would not be a result of coevolution *per se* because it can be traced directly to the underlying

population dynamic model within which the coevolution is embedded. In contrast, we will see later that coevolution *with* interspecific frequency-dependence can destabilize a system in which the population dynamics itself is very well behaved.

We now characterize the $\hat{N}_s$ as functions of the p_s:

1. The equilibrium point, for any species, $\hat{N}_s$, is a function of the p's and is implicitly defined by the relation

$$\bar{W}_s(p_1, p_2, \ldots, p_S, N_1, N_2, \ldots, N_S) = 1 \qquad (s = 1, 2, \ldots, S). \tag{4}$$

The derivatives of $\hat{N}_s$ with respect to any p are obtained by differentiating (4) implicitly. We focus attention in $\partial\hat{N}_s/\partial p_s$:

$$\frac{\partial \hat{N}_s}{\partial p_s} = \frac{\partial \bar{W}_s}{\partial p_s}\left[\frac{-\det_{ss}(\partial \bar{W}_i/\partial N_j)}{\det(\partial \bar{W}_i/\partial N_j)}\right], \tag{5}$$

where the matrix $(\partial \bar{W}_i/\partial N_j)$ is

$$(\partial \bar{W}_i/\partial N_j) = \begin{pmatrix} \partial \bar{W}_1/\partial N_1 & \cdots & \partial \bar{W}_1/\partial N_S \\ \vdots & & \vdots \\ \partial \bar{W}_S/\partial N_1 & \cdots & \partial \bar{W}_S/\partial N_S \end{pmatrix}. \tag{6}$$

The symbol $\det(\partial \bar{W}_i/\partial N_j)$ means the determinant of the matrix $(\partial \bar{W}_i/\partial N_j)$ and the symbol $\det_{ss}(\partial \bar{W}_i/\partial N_j)$ means the principal minor of order $S - 1$ of the ssth element, i.e., the determinant of the matrix obtained by striking out the sth row and sth column.

2. The assumption that $(\hat{N}_1, \ldots, \hat{N}_S)$ is a locally stable equilibrium point for any set of fixed p's means that the matrix

$$\left(\frac{\partial N_{i,t+1}}{\partial N_{j,t}}\right) = \begin{pmatrix} N_1\left(\frac{\partial \bar{W}_1}{\partial N_1}\right) + 1 & \cdots & N_1 \frac{\partial \bar{W}_1}{\partial N_s} \\ \vdots & & \vdots \\ N_s\left(\frac{\partial \bar{W}_s}{\partial N_s}\right) & \cdots & N_s\left(\frac{\partial \bar{W}_s}{\partial N_s}\right) + 1 \end{pmatrix}_{\{N_i = \hat{N}_i\}} \tag{7}$$

has eigenvalues, λ^*, satisfying $|\lambda^*| < 1$ for any set of p's. Let the characteristic equation for this matrix be denoted $h(\lambda)$. We will show that this assumption implies

$$\begin{aligned} &\text{a.} \quad \det(\partial \bar{W}_i/\partial N_j) > 0 && \text{for } S \text{ even,} \\ &\qquad\;\; \det(\partial \bar{W}_i/\partial N_j) < 0 && \text{for } S \text{ odd.} \\ &\text{b.} \quad \textstyle\sum \det_{ss}(\partial \bar{W}_i/\partial N_j) < 0 && \text{for } S \text{ even,} \\ &\qquad\;\; \textstyle\sum \det_{ss}(\partial \bar{W}_i/\partial N_j) > 0 && \text{for } S \text{ odd.} \end{aligned} \tag{8}$$

To prove these results consider the matrix

$$\begin{pmatrix} N_1 \dfrac{\partial \overline{W}_1}{\partial N_1} & \cdots & N_1 \dfrac{\partial \overline{W}_1}{\partial N_S} \\ \vdots & & \vdots \\ N_s \dfrac{\partial \overline{W}_S}{\partial N_1} & \cdots & N_s \dfrac{\partial \overline{W}_S}{\partial N_S} \end{pmatrix}. \tag{9}$$

Let the characteristic equation of this matrix be denoted as $g(\lambda)$. Then

$$g(\lambda) \equiv h(\lambda + 1). \tag{10}$$

By assumptions roots λ^* of $h(\lambda)$ satisfy $|\lambda^*| < 1$. Therefore it is necessary that the real part of every root of $g(\lambda)$ be less than zero. Roots of $g(\lambda)$ satisfy

$$\begin{aligned} &\lambda^S - c_1\lambda^{S-1} + \cdots - c_{S-1}\lambda + c_S = 0 \qquad (S \text{ even}), \\ &\lambda^S - c_1\lambda^{S-1} + \cdots + c_{S-1}\lambda - c_S = 0 \qquad (S \text{ odd}), \end{aligned} \tag{11}$$

where c_i is the sum of all principal minors of order i. A necessary condition that roots λ^* of $g(\lambda)$ satisfy $\mathrm{Re}(\lambda^*) < 0$ is that all coefficients of λ in (11) be positive. Therefore, the assumption that the purely population dynamic system (3) has a unique positive locally stable equilibria implies the inequalities in (8). In particular $\det(\partial \overline{W}_i/\partial N_j) \neq 0$.

3. The inequalities (8) above state that the sum of the principal minors of order $S - 1$ for the matrix $(\partial \overline{W}_i/\partial N_j)$ are of opposite sign to the determinant of the matrix. Therefore some principal minors may be of the same sign as the determinant but they can not *all* be of the same sign. Instead, most or all principal minors are typically of opposite sign to the determinant. For example with two species the principal minor of the element of $\partial \overline{W}_1/\partial N_1$ is simply $\partial \overline{W}_2/\partial N_2$, and vice versa. The determinant is positive (since S is even). Therefore the presence of intraspecific competition within both species ensures that both principal minors are of opposite sign to the determinant. Typical models for competition, predator–prey, mutualism, etc., would all include negative intraspecific density-dependence. Nonetheless, the possibility of models in which the principal minor is the same sign as the determinant should not be overlooked.

III. *Coevolution*

Now consider the model in which both the population sizes and gene frequencies change according to Eqs. (1). We can characterize the equilibrium behavior of this coevolutionary model in terms of the functions N_s introduced above.

1. Consider the space of dimension $2S$ with axes $p_1, p_2, \ldots, p_S$, and $N_1, N_2, \ldots, N_S$. There is a hyperplane of dimension S in this space given by

$$\gamma(p) = (p_1, p_2, \ldots, p_S, \hat{N}_1(p), \hat{N}_2(p), \ldots, \hat{N}_S(p)), \tag{12}$$

where p is shorthand for "$p_1, p_2, \ldots, p_S$." Clearly any equilibrium point $(p_1^*, p_2^*, \ldots, N_1^*, \ldots)$ for Eqs. (1) lies on this hyperplane, $\gamma(p)$.

2. Suppose for every s, $\det_{ss}(\partial \overline{W}_i/\partial N_j) \neq 0$. Then a point $(p_1^*, p_2^*, \ldots, N_1^*, N_2^*)$ is an equilibrium point of Eqs. (1) if and only if for every s,

$$\begin{aligned} &\partial \hat{N}_s(p^*)/\partial p_s = 0 \qquad (s = 1, 2, \ldots, S), \\ &N_s^* = \hat{N}_s(p^*). \end{aligned} \tag{13}$$

This result obtains because any equilibrium must satisfy $\partial \overline{W}_s/\partial p_s = 0$ for all s. By Eq. (5) $\partial \hat{N}_s/\partial_s = 0$ if and only if $\partial \overline{W}_s/\partial p_s =$ provided $\det_{ss}(\partial \overline{W}_i/\partial N_j) \neq 0$.

3. Given the assumption that every point on $\gamma(p)$ is a stable equilibrium of the purely population dynamic model, then an equilibrium point $(p_1^*, p_2^*, \ldots, N_1^*, N_2^*, \ldots)$ of Eqs. (1) is locally stable if and only if

$$\partial^2 \overline{W}_s(p^*, N^*)/\partial p_s^2 < 0 \qquad (s = 1, 2, \ldots, S). \tag{14}$$

This is to say that provided the population dynamic part of the model is well behaved then an equilibrium point is stable if and only if,(for every s, the mean fitness of species-s is a local maximum with respect to variation of p_s.

This result is proved by examining the eigenvalues of the $2S \times 2S$ square matrix

$$\begin{pmatrix} \partial p_{1,t+1}/\partial p_{1,t} & \cdots & \partial p_{1,t+1}/\partial N_{S,t} \\ \vdots & & \vdots \\ \partial N_{S,t+1}/\partial p_{1,t} & \cdots & \partial N_{S,t+1}/\partial N_{S,t} \end{pmatrix}. \tag{15}$$

Consider the first S columns. Specifically, consider column s where $1 \leqslant s \leqslant S$. One entry is $\partial N_{s,t+1}/\partial p_s = N \partial \overline{W}_s/\partial p_s = 0$ at equilibrium. With one exception all other entries in this column are also zero because of the assumption that $\overline{W}_s$ is not a function of p_u where $u \neq s$. The only nonzero entry in the column is $\partial p_{s,t+1}/\partial p_s$ which is on the main diagonal. Therefore the eigenvalues of matrix (15) are

$$\lambda_s^* = \partial p_{s,t+1}/\partial p_{s,t} \qquad (s = 1, 2, \ldots, S), \tag{16}$$

together with the S eigenvalues of the matrix characterizing the purely population dynamic model, e.g., the eigenvalues of matrix (7). By assumption the eigenvalues of matrix (7) satisfy $|\lambda^*| < 1$ for any p, and therefore for p^* in particular. The eigenvalues given in (6) are real and between -1 and 1 (actually

between 0 and 1) if and only if $\partial^2 \overline{W}_s / \partial p_s^2 < 0$, that is, if and only if p_s^* maximizes $\overline{W}_s$.

4. Although the mean fitness of species-s is maximized with respect to p_s at a stable equilibrium the population size of species-s is *not* necessarily also maximized. Whether it is or not depends on whether the $\det_{ss}(\partial \overline{W}_i / \partial N_j)$ is of opposite sign to $\det(\partial \overline{W}_i / \partial N_j)$. To obtain this result first note that at equilibrium

$$\partial \hat{N}_i(p) / \partial p_j = 0 \qquad (i, j = 1, 2, \ldots, S). \tag{17}$$

In Eq. (13) we stress that $\partial \hat{N}_i / \partial p_i = 0$ at equilibrium but it can also be verified that the derivatives with respect to the other p's are also zero equilibrium. So, twice differentiating implicitly in $\overline{W}_s = 1$ and taking account of (17) leads to

$$\frac{\partial^2 \hat{N}_s}{\partial p_s^2} = \frac{\partial^2 \overline{W}_s}{\partial p_s^2} \left[\frac{-\det_{ss}(\partial \overline{W}_i / \partial N_j)}{\det(\partial \overline{W}_i / \partial N_j)} \right]. \tag{18}$$

Therefore, provided $\det_{ss}(\partial \overline{W}_i / \partial N_j) \neq 0$ we see that $\hat{N}_s$ is maximized with respect to p_s whenever the principal minor is of opposite sign to the determinant, and is minimized whenever the principal minor is the same sign as the determinant.

As mentioned before, in most applications all the principal minors of order $S - 1$ in the matrix $(\partial \overline{W}_i / \partial N_j)$ will be of opposite sign to the determinant. If so, at equilibrium each population size $\hat{N}_s$ is at a local maximum with respect to the corresponding p_s. However, it is possible for some species, but not all, to have principal minors which are the same sign as the determinant. For these species each equilibrium population size, $\hat{N}_s$, is a local minimum with respect to the corresponding p_s.

IV. *Summary*

The results above may be summarized as follows:

THEOREM 2. *Consider S species each with genetic variation at one locus with two alleles. The fitness of any genotype in any species may be a function of any population size, N_s, $(s = 1, 2, \ldots, S)$. The fitness of any genotype may* not *be a function of the allele frequency in any species, p_s $(s = 1, 2, \ldots, S)$.*

Suppose there is a unique locally stable equilibrium, $(\hat{N}_1(p), \hat{N}_2(p), \ldots, \hat{N}_s(p))$ in the purely population dynamic model for any fixed p.

$$N_{s,t+1} = \overline{W}_{s,p}(N_1, N_2, \ldots, N_s) N_{s,t} \qquad (s = 1, 2, \ldots, S),$$

where p is shorthand for "$p_1, p_2, \ldots, p_s$." Then the point $(p_1^*, p_2^*, \ldots, N_1^*, N_2^*)$ is a locally stable equilibrium for the coevolution model in which both the p_s and N_s

vary, provided at this point $\det_{ss}(\partial \overline{W}_i/\partial N_j) \neq 0$ *for* $s = 1, 2, \ldots, S$, *if and only if, for each* s, *the appropriate condition below is satisfied*:

a. $\det_{ss}(\partial \overline{W}_i/\partial N_j) \det(\partial \overline{W}_i/\partial N_j) < 0$:

$$\begin{aligned} \partial \hat{N}_s(p^*)/\partial p_s &= 0, \\ \partial^2 \hat{N}_s(p^*)/\partial p_s^2 &< 0, \\ N_s^* &= \hat{N}_s(p^*), \end{aligned}$$

i.e., $\hat{N}_s$ *is a local maximum with respect to* p_s.

b. $\det_{ss}(\partial \overline{W}_i/\partial N_j) \det(\partial \overline{W}_i/\partial N_j) > 0$:

$$\begin{aligned} \partial \hat{N}_s(p^*)/\partial p_s &= 0, \\ \partial^2 \hat{N}_s(p^*)/\partial p_s^2 &> 0, \\ N_s^* &= \hat{N}_s(p^*), \end{aligned}$$

i.e., $\tilde{N}_s$ *is a local minimum with respect to* p_s.

Moreover, if S *is even (odd) then* $\det(\partial \overline{W}_i/\partial p_j) > (<)\ 0$, *and not all* $\det_{ss}(\partial \overline{W}_i/\partial N_j)$ *can be the same sign as* $\det(\partial \overline{W}_i/\partial N_j)$.

APPENDIX III. Coevolution among Interacting Populations: With Interspecific Frequency-Dependence

I. *The Model*

The model is the same as in Appendix II with the following exceptions:

a. $W_{s,ij}$ must be a monotonic function of N_s, specifically $\partial W_{s,ij}/\partial N_s \neq 0$.

b. $W_{s,ij}$ may be a function of any p_u $(u \neq s)$. There is interspecific but not intraspecific frequency-dependence.

Again the equilibria satisfy

$$\begin{aligned} \partial \overline{W}_s/\partial p_s &= 0, \\ \overline{W}_s &= 1 \qquad (s = 1, 2, \ldots, S). \end{aligned} \tag{1}$$

The presence of interspecific frequency-dependence influences both the position and stability of any equilibrium. In this appendix we develop a criterion relating the *position* of the equilibrium to the equilibrium population size, but there proves to be no simple criterion to indicate the stability of the equilibrium.

II. *The* $\hat{N}_s$ *and* $\tilde{N}_s$ *Functions*

As before we assume that the population dynamics are well behaved for fixed p. Specifically we assume that $(\hat{N}_1(p) \cdots \hat{N}_S(p))$ is a unique stable equilibrium

point for fixed p ($p \equiv (p_1 \cdots p_S)$) of the purely population dynamic model. As before the $\hat{N}_s(p)$ are defined implicitly by the *system* of equations.

$$\overline{W}_s(p_1 \cdots p_s, N_1(p) \cdots N_s(p)) = 1 \qquad (s = 1, 2,..., S). \tag{2}$$

Remember that each $\hat{N}_s(p)$ is a function of S variables, namely $p_1, p_2, ..., p_S$.

We introduce another set of function, $\tilde{N}_s(p_1 \cdots p_s, N_1 \cdots N_{u \neq s} \cdots N_S)$. Each is a function of $2S - 1$ variables: the S gene frequencies and the $S - 1$ other population sizes. Each $\tilde{N}_s$ is defined implicitly by the *single* equation.

$$\overline{W}_s(p_1 \cdots {}_S, N_1, N_2, ..., N_s \cdots N_S) = 1. \tag{3}$$

By the implicit function theorem the derivatives of $\tilde{N}_s$ are of the form

$$\partial \tilde{N}_s / \partial p_s = (\partial \overline{W}_s / \partial p_s)/(-\partial \overline{W}_s / \partial N_s). \tag{4}$$

III. *Coevolution*

Consider the model in which both gene frequencies and population vary through time.

1. As before, any equilibrium point ($p_1^* \cdots p_s^*, N_1^* \cdots N_s^*$) lies on the hyperplane $\gamma(p)$ defined by

$$\gamma(p_1 \cdots p_S) = (p_1 \cdots p_S, \hat{N}_1(p) \cdots \hat{N}_S(p)) \tag{5}$$

where p denotes ($p_1 \cdots p_S$).

2. In addition to lying on $\gamma(p)$ an equilibrium point ($p_1^* \cdots p_S^*, N_1^* \cdots N_S^*$) satisfies, for each s,

$$\partial \tilde{N}_s / \partial p_s = 0. \tag{6}$$

It follows directly from Eq. (4) that $\partial \overline{W}_s / \partial p_s = 0$ is equivalent to $\partial \tilde{N}_s / \partial p_s = 0$ provided $\partial \overline{W}_s / \partial N_s \neq 0$. Thus a point is an equilibrium point if and only if it it is on the $\gamma(p)$ hyperplane and the slope of $\tilde{N}_s$ with respect to p_s is zero.

3. The mean fitness within species-s is at a local maximum at equilibrium if and only if $\tilde{N}_s(p^*, N^*)$ is at a local maximum with respect to p_s, provided $\partial \overline{W}_s / \partial N_s < 0$. Conversely, the mean fitness is at a maximum at equilibrium if and only if $\tilde{N}_s(p^*, N^*)$ is a local minimum with respect to p_s, provided $\partial \overline{W}_s / \partial N_s > 0$. This result follows directly from the equation,

$$\partial^2 \tilde{N}_s / \partial p_s^2 = (\partial^2 \overline{W}_s / \partial p_s^2)/(-\partial \overline{W}_s / \partial N_s) \tag{7}$$

4. The condition that the mean fitness at equilibrium in species-s is a local maximum with respect to p_s is, in general, neither necessary nor sufficient

for the stability of the equilibrium even if the pure population dynamic model is well behaved. Hence whether $\tilde{N}_s$ is a maximum or minimum with respect to p_s is also neither necessary nor sufficient for stability.

5. However, there are classes of simple examples where the condition that $\bar{W}_s$ be a local maximum with respect to p_s at equilibrium is necessary for stability and classes of examples where it is both necessary and sufficient for stability. But such results require detailed reference to the fitness functions.

IV. *Summary*

THEOREM 3. *Consider S species, each with genetic variation at one locus with two alleles. The fitness of any genotype in species-s* must *be a monotonic function of N_s and may be a function of any other population size as well. The fitness must not be a function of p_s but may be a function of the gene frequency in any other species.*

Suppose there is a unique locally stable equilibrium $(\hat{N}_1(p), \hat{N}_2(p),..., \hat{N}_S(p))$ *in the purely population dynamic model for any fixed p, where p is shorthand for "$p_1, p_2,..., p_S$." Suppose also there is a function for each s, defined implicitly by* $\bar{W}_s(p_1 \cdots p_S, N_1 \cdots N_S) = 1$. *The function so defined is denoted* $\tilde{N}_s(p_1 \cdots p_s, N_1 \cdots N_{u\neq s} \cdots N_S)$; *it is a function of* $2S - 1$ *variables. Then,*

1. *A point* $(p_1^* \cdots p_s^*, N_1^* \cdots N_S^*)$ *is an equilibrium of the coevolution model if and only if this point satisfies, for each s,*

$$\begin{aligned} &\partial\tilde{N}_s(p^*, N^*)/\partial p_s = 0, \\ &N_s^* = \hat{N}_s(p^*). \end{aligned} \tag{1}$$

2. *Suppose* (p^*, N^*) *is an equilibrium point. This point represents a local maximum of $\bar{W}_s$ with respect to p_s if and only if, in addition to* (1) *above, the appropriate condition below is satisfied*:

a. $\partial\bar{W}_s/\partial N_s < 0$:

$$\partial^2\tilde{N}_s(p^*, N^*)/\partial p_s^2 < 0$$

($\tilde{N}_s$ is maximized with respect to p_s),

b. $\partial\bar{W}_s/\partial N_s > 0$:

$$\partial^2\tilde{N}_s(p^*, N^*)/\partial p_s^2 > 0$$

($\tilde{N}_s$ is minimized with respect to p_s).

Remark. The theorem above presents a criterion for locating the equilibrium point in terms of the $\tilde{N}_s$ functions. Moreover, the theorem presents a criterion also in terms of the $\tilde{N}_s$ functions which indicates whether any equilibrium is associated with a local maximum of the mean fitness in each species. The

theorem does not assert conditions for the stability of an equilibrium. In particular, it may neither be necessary nor sufficient for stability that the mean fitness is at a local maximum within all the species.

APPENDIX IV. Application of Principle 3 to Resource Partitioning Two Competitors

The conditional $\tilde{N}$'s are

$$\tilde{N}_1(x_1, x_2, N_2) = K(x_1) - \alpha(x_1 - x_2)N_2,$$
$$\tilde{N}_2(x_2, x_1, N_1) = K(x_2) - \alpha(x_2 - x_1)N_1.$$

The equilibrium x_1 and x_2 then satisfy

$$dK(x_1)/dx_1 - N_2\, \partial\alpha(x_1 - x_2)/\partial x_1 = 0,$$
$$dK(x_2)/dx_2 - N_1\, \partial\alpha(x_2 - x_1)/\partial x_2 = 0,$$

where

$$N_1 = [K(x_1) - \alpha(x_1 - x_2)\, K(x_2)]/[1 - \alpha(x_1 - x_2)\, \alpha(x_2 - x_1)],$$
$$N_2 = [K(x_2) - \alpha(x_2 - x_1)\, K(x_1)]/[1 - \alpha(x_1 - x_2)\, \alpha(x_2 - x_1)].$$

With symmetry and assuming niche locations at $-x$ and x the equation for x becomes

$$dK(x)/dx - [K(x)/(1 + \alpha(2x))]\, \partial\alpha(x_1 - x_2)/\partial x_1 \,|_{-x_1=x_2=x} = 0.$$

A general class of symmetric functions for $K(x)$ and $\alpha(d)$ is of the form

$$f(x) = a \exp[-c(|\, x\, |/\sigma)^n],$$

where

$$c = [\Gamma(3/n)/\Gamma(1/n)]^{1/2}, \qquad a = c/[2\sigma\Gamma(1/n + 1)].$$

This function has unit area. σ is the standard deviation and n controls the kurtosis. If $n = 2$ the function is Gaussian. If $n < 2$ the function has a shape peak and thick tails; $n = 1$ for example, represents back to back exponential curves. If $n > 2$ the function has a broad peak with thin tails. a and c are normalization constants which ensure consistency in the parameterization. When $f(x)$ represents $K(x)$ the constant, a, always divides out; and when $f(x)$ represents $\alpha(d)$ there is no constant, a, because $\alpha(0)$ must equal 1. So the only constant of any importance is c and it is determined only by n and not by σ. Using this general class of functions the equation for x becomes

$$\frac{\alpha(2x)}{1 + \alpha(2x)} = \left[\frac{c_k n_k \sigma_\alpha^{n_\alpha}}{c_\alpha n_\alpha \sigma_k^{n_k} 2^{n_\alpha - 1}}\right] x^{n_k - n_\alpha}.$$

The niche location, x, is at the intersection of the right hand side (RHS) with the left hand side (LHS). The LHS is a curve decreasing monotonically from 1/2 to zero as $x \to \infty$. The LHS is a simple power of x provided $n_k \neq n_\alpha$ otherwise it is a constant. Clearly if $n_k \neq n_\alpha$ there is always exactly one solution since the RHS increases monotonically from the origin. If $n_k = n_\alpha$ there is exactly one solution provided $(\sigma_k/\sigma_\alpha)^n > 2^{2-n}$. If $n_k = n_\alpha = n$, the solution is

$$\frac{\hat{x}}{\sigma_\alpha} = \left(\frac{1}{2^n c} \ln \left[\frac{1}{2}\left(\frac{2\sigma_k}{\sigma_\alpha}\right)^n - 1\right]\right)^{1/n}.$$

If $n = 2$ this reduces to the all-Gaussian example quoted in the text. Note the weak dependence in σ_k for any n.

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References

Anderson, W. W. 1971. Genetic equilibrium and population growth under density-regulated selection, *Amer. Natur.* **105**, 489–498.

Brown, W. L., and Wilson, E. O. 1956. Character displacement, *Syst. Zool.* **5**, 49–64.

Cody, M. L. 1974. "Competition and the Structure of Bird Communities," Princeton Univ. Press, Princeton, N.J.

Diamond, J. 1973. Distributional ecology of New Guinea birds, *Science* **179**, 759–769.

Karlin, S. 1975. General two locus selection models: Some objectives, results and interpretations, *Theor. Pop. Biol.* **7**, 364–398.

Kingman, J. F. C. 1961. A matrix inequality, *Quart. J. Math.* **12**, 78–80.

Lack, D. 1947. "Darwin's Finches," Cambridge Univ. Press, New York.

Lazell, J. 1972. The *Anoles* (Saurea, Iguanidae) of the Lesser Antilles, *Bull. Mus. Comp. Zool. Harvard Univ.* **143**, 1–115.

Leon, J. A. 1974. Selection in contexts of interspecific competition, *Amer. Natur.* **108**, 739–757.

Levins, R. 1974. The qualitative analysis of partially specific systems in mathematical analysis of fundamental biological phenomena, *Ann. N.Y. Acad. Sci.* **231**, 123–138.

MacArthur, R. 1962. Some generalized theorems of natural selection, *Proc. Nat. Acad. Sci. U.S.A.* **48**, 1893–1897.

MacArthur, R. H. 1965. Patterns of species diversity, *Biol. Rev.* **40**, 510–533.

MacArthur, R. 1972. "Geographical Ecology," Harper and Row, New York.

MacArthur, R. H., and Levins, R. 1967. The limiting similarity, convergence and divergence of coexisting species, *Amer. Natur.* **101**, 377–385.

MacArthur, R. H., and Wilson, E. O. 1967. "The Theory of Island Biogeography," Princeton Univ. Press, Princeton, N.J.

MAY, R. M., AND MACARTHUR, R. H. 1972. Niche overlap as a function of environmental variability, *Proc. Nat. Acad. Sci. U.S.A.* **69**, 1109–1113.

PIANKA, E. R. 1973. The structure of lizard communities, *Ann. Rev. Ecol. Syst.* **4**, 53–74.

PIANKA, E. R. 1974. Niche overlap and diffuse competition, *Proc. Nat. Acad. of Sci. U.S.A.* **71**, 2141–2145.

RANDALL, J. E. 1967. Food habits of reef fishes of the West Indies (Proceedings of the International Conference on the Tropical Ocean, 1965), *Studies in Ttopical Ocean Miami* **5**, 665–847.

ROUGHGARDEN, J. D. 1971. Density-dependent natural selection, *Ecology* **52**, 453–468.

ROUGHGARDEN, J. D. 1972. Evolution of niche width, *Amer. Natur.* **106**, 683–718.

ROUGHGARDEN, J. D. 1974. Species packing and the competition function with illustrations from coral reef fish, *Theor. Pop. Biol.* **5**, 163–186.

ROUGHGARDEN, J. D. 1974. Niche width: Biogeographic patterns among *Anolis* lizard populations, *Amer. Natur.* **108**, 429–442.

ROUGHGARDEN, J. D., AND FELDMAN, M. 1975. Species packing and predation pressure, *Ecology* **56**, 489–492.

SCHOENER, T. W. 1969. Size patterns in West Indian *Anolis* lizards. I. Size and species diversity, *Syst. Zool.* **18**, 386–401.

SCHOENER, T. W. 1971. Theory of feeding strategies. *Ann. Rev. Ecol. Syst.* **2**, 369–404.

SCHOENER, T. W. 1976. Competition, *in* "The Biology of the Reptilia" (Gans and Tinkle, Eds.), in press.

SCHOENER, T. W., AND GORMAN, G. 1968. Some niche differences in three Lesser Antillean lizards of the genus *Anolis*, *Ecology* **49**, 819–830.

SIMBERLOFF, D. S., AND WILSON, E. O. 1969. Experimental zoogeography of islands: The colonization of empty islands, *Ecology* **50**, 228–295.

WILLIAMS, E. E. 1969. The ecology of colonization as seen in the zoogeography of anoline lizards on small islands, *Quart. Rev. Biol.* **44**, 345–389.