Title

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ABSTRACT   Some paleonanthropologists invoke the competitive exclusion principle programmatically in support of a single-species (or lineage) hypothesis of hominid evolution. Others apparently accept the association between competitive exclusion and a single species view, and develop multi-species interpretations using only taxonomic concepts. This paper demonstrates that the competitive exclusion principle itself is too assumption-bound to be appropriate for analyzing questions of hominid coexistence. Especially, the principle does not establish the ecological validity of the single-species hypothesis. Contrary to its immediate appearances, the principle has developed historically and analytically to predict and explain the evolution and maintenance of diversity in communities. Used in this manner it constitutes an important basis for the study of hominid paleoecology. Niche concepts necessary to demonstrate this are introduced, and competition and other factors that may have influenced the realized niches of sympatric hominid species are discussed. Nearly all modifications of the competitive exclusion principle that make it more realistic also illuminate factors that generate stable coexistence among competing species. These factors and their organizing theory establish the relevance of a broad data base to the analysis of hominid paleoecology; they should help to guide research on the ecology of early homonid species and their interrelationships.

A pivotal issue in physical anthropology concerns the possible coexistence of multiple hominid species. This question has provoked much controversy, perhaps because its resolution affects topics from taxonomy and fossil interpretation to the construction and evaluation of models describing the evolution of traits unique to ourselves and our hominid ancestors. Despite central importance, physical anthropologists have spent relatively little time analyzing the ecological bases of this question. Most discussion has centered on its taxonomic implications. Anthropologists adopting quite divergent views on the question of single or multiple contemporaneous hominid species have apparently agreed that a simple application of the "competitive exclusion principle" (Hardin, 1960:1292) is the relevant ecological context of the debate. While single-or multi-species advocates disagree on whether the competitive exclusion principle is right or wrong, or applicable or not applicable, they have in common a highly restricted interpretation of its meaning.

In this paper I argue that ecological concepts of competition and interspecific relationships derived from the competitive exclusion principle are quite different from the lessons anthropologists have drawn from attention to the principle itself. The competitive exclusion principle does not provide ecological justification for the single-species hypothesis (cf. Wolpoff, 1971, 1976a). In addition, anthropologists who adopt multi-species interpretations using fossil evidence are often constrained by the conventional anthropological interpretation of the principle to ignore processes of interspecific competition. In doing so they miss the theory appropriate for analyzing this subject within an ecological framework, one to a large extent built on concepts that are extensions and ramifications of competitive exclusion. In short, competitive exclusion does not confirm the single-species hypothesis, but neither can it be overlooked in analysis of hominid paleoecology.

The plan of this discussion is as follows: After a brief note on terminology I review the diverse positions anthropologists have taken on the question of coexistence. I outline the use of competitive exclusion as it appears in Wolpoff's (1968, 1971, 1974) writings on the single-species hypothesis. Wolpoff's work takes a clear and consistent stand on this topic, and therefore provides a basis for raising questions about anthropological use of the concept. I then review the mathematical basis of the principle, with particular attention to assumptions, verbal interpretations, and tests of its validity. This discussion indicates that the principle itself is not particularly appropriate or useful for analysis of population interactions among related hominid species. Competition is, however, the starting point of concepts that are the relevant ecological context for this issue. These concepts—first, character displacement, niche, competition, and the other factors affecting the realized niche of a species; and second, limiting similarity, optimal foraging and niche differentiation—are examined, and their bearing on hominid paleoecology is outlined. In the aggregate these ideas present a rich framework for interpreting hominid evolution and ecology. With that I consider an important component of Wolpoff's position—the statement that culture is the hominid niche. I argue that this statement has no operational meaning in either of its key terms—culture and niche. Then, evidence from behavioral ecology and ethnographic analysis of foraging is cited to demonstrate how competition theory can be linked to ecological field studies. This section exemplifies the diverse types of indirect evidence important for investigation of hominid paleoecology.

The present paper carries this discussion through the first set of concepts, which augment competitive exclusion; a subsequent paper (Winterhalder, in preparation) will begin with the idea of limiting similarity.

Definition of several terms is important to what follows and is presented here: *sympatric* species are those with full or partial overlap of range. The spatially coincident distribution resulting from sympatry does not necessarily imply ecologically significant overlap of niche, or habitat (these terms are defined below). *Species* refers to a population of a species; *organism* to a member of such a population. Whatever the degree of higher taxonomic separation recognized, the processes important here occur between (and within) populations of distinct species. *Congeneric* refers to two or more species and carries an implication of similarity (e.g., competitors at a certain trophic level), whereas *interspecific* suggests greater functional or ecological differences (e.g., predator and prey). The *competitive exclusion principle* (hereafter CEP), also known as Gause's theorem or axiom, states that two species cannot stably occupy the same niche. Hardin (1960:1292) discusses the history and etymology of this term; it is defined fully below. The *single species hypothesis* (SSH) states that only one species of hominid has existed during any period. A weaker form states that two or more hominid species did not exist sympatrically. As used here, *coexistence* implies sympatry.

<div align="center">ANTHROPOLOGICAL USES OF COMPETITIVE EXCLUSION</div>

<div align="center">*Historical aspects*</div>

Wolpoff (1971: 601) attributes the earliest suggestion that the CEP be applied to hominid taxonomy to Mayr (1950): "As early as 1950, Ernst Mayr suggested applying the competitive exclusion principle to early hominid evolution. As a result, the single

species hypothesis emerged." An examination of Mayr's argument can illuminate difficulties in anthropological uses of the CEP-SSH relationship.

Mayr (1950) argued strongly that the prevailing procedure of assigning each hominid fossil specimen to a distinct species was not justified in light of population biology or taxonomic procedure. He stated that the fossil evidence justified recognition of only three species of one genus of hominid (*Homo transvaalensis, H. erectus*, and *H. sapiens* was his terminology). The apparent temporal separation and evident morphological succession of these forms indicated to him "that never more than one species of man existed on the earth at any one time." He went on to ask, "What is the cause for this puzzling trait of the hominid stock to stop speciating in spite of its eminent evolutionary success?" (1950: 116). In answer he reasoned that "man's great ecological diversity" and "Gause's rule" could provide the explanation. In effect, Mayr documented fossil evidence in favor of the SSH and then cited the CEP as an ecological explanation.

By 1963 Mayr had reversed his opinion, accepting that in at least two instances the evidence indicated contemporaneous species of hominids, *Australopithecus* and *Paranthropus* (or alternatively *Australopithecus africanus* and *A. robustus*) in South Africa, and *Zinjanthropus* and a more *Homo*-like form ("co-*Zinjanthropus*") in East Africa. Again, it was his interpretation of the fossil evidence that dictated how he used the CEP. In this case it affirmed that "The coexisting types were, so far as known, rather distinct from each other" (1963a: 340). In both instances Mayr argued from his taxonomic assessment to explanations based on the CEP.

The question of the priority or greater reliability of the two sides of the relationship between the CEP and taxonomic judgment divides human paleontologists. Contemporary proponents of a SSH give the CEP priority in their taxonomic interpretations of the large variability characterizing the fossil evidence of a given time horizon (e.g., Wolpoff 1971: 608). Two related arguments are used to preserve the CEP-derived SSH. Brace (1973) believes that the variability represents strong sexual dimorphism within a single species. In contrast, Wolpoff (1968, 1971, 1974) takes the position that it represents subspecific or polytypic variation. Both Brace (1973; see also Brace et al., 1973) and Wolpoff (1971) assign all fossil hominid specimens from the late Pliocene to the Recent to a single evolving lineage.

Other hominid paleontologists come closer to Mayr's form of reasoning; ecological rationales are mustered for taxonomic judgments based primarily on fossil evidence. Robinson (1954, 1963a, b, 1972) proposed the earliest and most thorough of the multi-species interpretations. Robinson separated fossils representing robust australopithecine species (*Paranthropus sp.*) and gracile forms (*Australopithecus sp.* and later (1972) *Homo africanus*) at the generic level. He offered a dietary hypothesis based on dental and cranial traits for their ecological divergence. According to Robinson the larger form was a vegetarian specialized on tough plant foods of low nutritive value, was the phylogenetically older (stem) of the related genera, and was only partially effective as a biped. In contrast, the smaller form was omnivorous, phylogenetically younger, antecedent to *Homo,* and fully biped. Robinson envisioned the two forms as divergent phyletic lines that coexisted stably for long periods (e.g., 1963a: 394). In earlier papers he stated that both probably used tools, although *Paranthropus* was less adept (1963a: 389–399), and that both were characterized by a primitive form of culture (1963b: 598). By 1972 Robinson had revised this opinion, stating that *Paranthropus* was "not actively culture-bearing" (1972: 252). Robinson's hypothesis holds that the gracile form *(H. africanus)* evolved more advanced cultural abilities as climatic dessication during the late Pliocene selected it toward a more omnivorous diet in a savanna habitat and toward dependence on greater degrees of intelligence and tool manufacture (1963a: 411).

While much of Wolpoff's work (1968, 1971, 1974, 1976a,b) is a critique of Robinson's evidence, this two-species interpretation continues to receive support. Du Brul (1977), for instance, finds convergences between the dental anatomy and oral mechanics of samples representing the two australopithecine forms and two species of bear (*Ursus horribilis,* the grizzly bear, and *Ailuropoda,* the giant panda, with known and distinct dietary habits. Hall (1977) has used an analysis of the paleobiology and systematics

of two closely related canids (*Canis lupus,* the wolf, and *Canis latrans,* the coyote) to suggest that two australopithecine forms (*Australopithecus robustus* and *A. africanus*) could have coexisted as ecologically distinct and phylogenetically differentiated species.

Other authors have proposed coexistence of two or more hominid species using taxonomic criteria and fossil evidence, although proposals differ in the samples used, the taxonomic groupings recognized, and the time periods covered. Campbell (1974: 195) states that only populations designated "Homo habilis" and *Australopithecus boisei* from East Africa meet the minimal conditions of morphologically distinct species. Pilbeam and Zwell (1973: 78) suggest two hominid lineages in Africa from 2.5 to 1.5 million years ago. Similarly, Johanson and White (1979: see Fig. 7) claim evidence for two lineages from 2.5 to 1.0 million years ago, but (p. 326) reject proposals for three lineages (see below). Tobias (1976: 407) also argues for a two-lineage model:

> The lineage of the *A. robustus/boisei* superspecies was apparently sufficiently distinct in behavior and ecological preferences from the line of *Homo* as to have permitted the two lineages to co-exist in Africa for something like 2 m.y. or even more.

Leakey and Walker (1976) argue for at least two separate, coexisting lineages. The abundant hominid fossil discoveries in East Africa in recent years have led to proposals of three, or perhaps four, contemporaneous species of Plio-Pleistocene hominids (Leakey, 1974, 1976: 177–178; Leakey and Isaac 1976: 323; Walker and Leakey, 1978: 66; see also Pilbeam and Gould, 1974).

Multi-lineage hypotheses based on more diverse and better dated fossils have not produced a re-examination of the ecological meaning of competition and the SSH. This is logical only if the CEP and SSH are taken—incorrectly—to be two sides of the same, dispensable formulation. General statements to the effect that the proposed species must have been ecologically divergent have appeared (e.g., Washburn and Ciochon, 1976: 96), but inquiries are needed into the ways in which their niches could have been different and the degrees of difference necessary for stable coexistence in various contexts (Leakey and Walker, 1976: 573–574). The very abundance of the new fossil material has increased the importance of developing an ecological framework for relating fossil and other evidence to various positions. If, as seems likely, the fossil evidence compels the abandonment of a single-species hypothesis,[1] then the issue of competitive exclusion will shift onto debates concerning the presence of two or more lineages, with the CEP wielded or shunned, respectively, by the lumpers and splitters in the new domain of proposals.

The CEP has been discussed by Swedlund (1974), who qualifies but generally supports the SSH. Conversely, Hardesty (1972: 462–463) questions its application to early hominid hunter-gatherers using Mayr's (1963b: 80) observation that generalized species, or those with low population densities, may present exceptions to the most obvious outcomes of competitive exclusion—extinction or strong ecological divergence. For the most part, however, advocates of sympatric multi-species views seem to accept the CEP-SSH relationship developed by Wolpoff (see below), and then argue backwards that the fossil evidence indicates that the CEP is wrong or inapplicable. The depreciating qualifier, "so-called," now appears in some references to the principle (e.g., Isaac and McCown, 1976: 273; Tobias, 1976: 379). It should be apparent that this point of view will have little cogency to paleontologists who insist that the principle is sound, and the more powerful evolutionary logic is applied in the reverse direction.

Wolpoff, the CEP and the SSH

Wolpoff (1968, 1971, 1974, 1976a) has most thoroughly and consistently argued for a single-species hypothesis based on the CEP. A summary of his argument identifies several important issues and indicates why human paleontologists generally associate the CEP with one, restricted, ecological outcome—extinction of all but one hominid species.

Wolpoff (1968: 477) begins by acknowledging a difficulty that shadows this question: "In discriminating fossil species in closely related animals, we are forced to give a morphological answer to a behavioral question...." That stated, the single-species

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[1] Wolpoff in fact now considers the SSH disproved by fossil evidence from East Africa (M.R. Russell, personal communication).

hypothesis is defined and its logic explored: ". . . for ecological reasons stemming from man's primary cultural adaptation, no more than one culture-bearing hominid species could have arisen or have been maintained" (1968: 477).

Wolpoff links hominization to bipedalism and to the defensive and offensive use of tools, as evidenced by reduction of the canines. Interacting cause-and-effect relationships tie this adaptive pattern to culture, which enables the transmission of tool manufacture and use across generations. Whereas individual changes in locomotor patterns, manipulative ability, and tool-use characterize some other primate species, hominids evolved into dependency on the full set of factors, and especially culture:

> Culture plays a dual role as man's primary means of adaptation, as well as the niche to which man has morphologically adapted. In this sense, all hominids occupy the same adaptive niche (Wolpoff, 1968: 479).

Once cultural capabilities characterized a hominid population the potential for use of environmental resources was greatly expanded. According to Wolpoff (1968: 480), this capability makes competitive exclusion of all but one hominid species unavoidable. Since some of the sympatric hominids would not have "the ability to resist competition from other species that utilize the same or similar resources of the environment" (Mayr, 1963b: 66), all but one would perish. Wolpoff recognizes but disallows an alternative outcome—character divergence or displacement:

> Because of the way culture-bearing hominids utilize their environment, subsequent adaptation could not reduce competition. Rather than narrowing the range of utilized environmental resources, such adaptation could only broaden this range, and thus increase the amount of real competition (Wolpoff 1968: 480).

Wolpoff (1968: 480) emphasizes the relationship between competitive exclusion and the evolution of hominids as culture-bearing species. He notes that persons arguing for sympatric species usually imply or state that cultural abilities were characteristic of only one of them. Thus, these authors tacitly accept Wolpoff's hypothesis about the relationship between culture and competitive exclusion, but they preserve multispecies interpretations by allowing only one to be cultural. This remains an attractive option (see Robinson, 1972; Walker and Leakey, 1978). But in Wolpoff's view it creates one dilemma in avoiding another: cultural capacities cannot be invoked in the evolutionary scenario for at least some hominid lines. This puts "an entire theory about hominid evolution . . . at stake" (Wolpoff, 1968: 480).

Wolpoff's is a compelling position. It clearly delimits the range of issues that have to be discussed in reconsidering the SSH, the CEP, and hominid paleoecology:

(1) Does ecological understanding of the CEP justify this kind of application?

(2) Does this application accurately capture the effects of ecological competition? Is such competition inevitable? Are there factors that might prevent it or factors that need to be considered in addition to it?

(3) How similar can resource use be and avoid competitive exclusion?

(4) What kinds of ecological differences allow closely related, sympatric species to mitigate resource competition and co-exist stably?

(5) Does a highly generalized use of environmental resources necessarily follow from the potential to use culture, bipedalism and tools to exploit multiple resources? Specifically, would competition necessarily broaden the range of resource use for competing species with flexible behavioral capacities?

(6) What operational or ecological mean can be assigned to the statement that culture is the hominid niche? Is this an appropriate analytic load to place on these concepts?

(7) What kinds of evidence are needed to increase understanding of the answers to these questions? Specifically, can ecological or other studies reduce the difficulty of interpreting morphological evidence related to behavioral patterns set in antiquity?

In the aggregate the questions focus on this point: Wolpoff (1976a: 95) claims that "the single species hypothesis, at least as presented by Brace, Mayr, and myself, is based on an ecological contention." Answers to these questions will show that this

contention is not ecologically valid. The present paper deals mainly with questions (1) and (2); the remainder will be considered in a future publication (Winterhalder, in preparation).

THE COMPETITIVE EXCLUSION PRINCIPLE

The mathematical form and assumptions of the principle

The mathematical form of the CEP is given by Volterra and Lotka's modification of the logistic equation for population growth (Ayala, 1969: 1076, 1970b: 130–136). Two species, S_1 and S_2, competing for the same limiting resource, have instantaneous rates of growth given by

$$\frac{\partial N_1}{\partial t} = r_1 N_1 \left(1 - \frac{N_1}{K_1} - \frac{\alpha N_2}{K_1} \right)$$
$$\frac{\partial N_1}{\partial t} = r_2 N_2 \left(1 - \frac{N_2}{K_2} - \frac{\beta N_1}{K_2} \right) \tag{1}$$

Here the subscripts denote the two species; r is the innate rate of increase; N is the number or biomass of the organisms present; K is the carrying capacity, or the maximum equilibrium number (or biomass) of one species in the absence of the other; α and β are the competition coefficients (α expresses the restraining effect of an S_2 individual on the growth of S_1; β, the restraining effect of an individual of S_1 on the growth of population S_2).

These equations assume that population growth for either species is proportional to r and to the number of individuals (N). For the non-trivial case, with r_1 and $r_2 \neq 0$, and N_1 and $N_2 > 0$, the interaction described by the two equations reaches equilibrium when

$$\frac{\partial N_1}{\partial t} = \frac{\partial N_2}{\partial t} = 0$$

In this case coexistence is possible with a stable equilibrium only if

$$\alpha < \frac{K_1}{K_2} \text{ and } \beta < \frac{K_2}{K_1} \tag{2}$$

Alternatively, these conditions can be expressed

$$\frac{\alpha}{K_1} < \frac{1}{K_2} \text{ and } \frac{\beta}{K_2} < \frac{1}{K_1} \tag{3}$$

It is evident from equation (1) that each individual (N_1) added to a population of species (S_1) decreases its own growth rate ($r_1 N_1$) by a constant amount ($1/K_1$), and that each individual of S_1 added to the two-population system decreases the growth rate of S_2 by a constant amount (β/K_2). Parallel relationships hold for S_2. By these definitions the conditions for a stable equilibrium of coexisting species (Eq. 3) can be interpreted to read that an individual of one species must inhibit its own population growth more than it inhibits the population growth of the other species (Ayala, 1969: 1076) (Fig. 1). Coexistence is thus possible when individuals compete to a greater degree with conspecifics for a limiting resource than with congenerics for the same resource. Theoretically this condition is not hard to meet.

The assumptions incorporated into the CEP become clearer when it is put in mathematical form. The following list is based on Ayala (1970b: 131–133), Armstrong and McGhee (1976: 318–319), Darlington (1972), Gilpin and Ayala (1973: 3590), Schoener (1974: 34–35), and Smith (1972):

(a) r is a constant from $N_j = 0$ to $N_j = K_j$ (it is unaffected by population density);

(b) individuals in the populations have identical demographic characteristics (i.e., there is no age structure);

(c) the relationship between population growth and density is linear (equal to $1/K_j$);

(d) there are no time lags, thresholds or stochastic effects in any of the relevant interactions;

(e) the inhibitory effect between species (e.g., α/K_1) is constant for all $N_j = 0$ to $N_j = K_j$ (competition affects are not altered by density);

(f) there is no spatial patterning in the competing species or their environment (e.g., this is a "point" model, one assuming spatial homogeneity of process);

(g) there are no temporal fluctuations in the relevant environmental components or parameters;

(h) the interaction between species is directly affected by only one limiting resource over the full range of the relevant parameters: the species engage in "*single-resource competition*" (Darlington 1972: 3152);

(i) the resource in question is of uniform quality (e.g., size, nutritional value);

(j) the quantity of the resource available to S_1 is strictly a function of the population density of S_2; and,

(k) no evolutionary or behavioral changes occur in either species. This list is probably not exhaustive, nor are all of the assumptions listed fully independent. Still, they indicate what is sacrificed when competition is expressed in the parameters of logistic equations. MacArthur (1972: 255–256) and Wangersky (1978) cogently summarize these and other assumptions of the Lotka-Volterra equations and their derivatives.
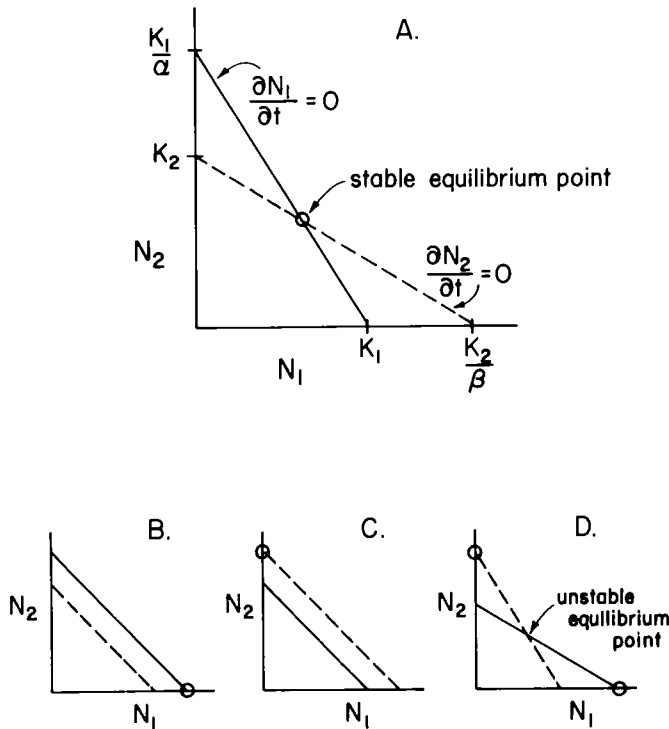

Fig. 1. Two-species competition diagrams, based on logistic equation assumptions. In a two-species system each species will decrease in numbers if its population size is above the zero growth line and increase in numbers if below. The equilibrium outcome(s) for each situation are circled. Case A represents the conditions of carrying capacity (K_1 and K_2) and competition coefficients (α and β), which generate stable coexistence. In B and C one species always eliminates the other. In D there is an unstable equilibrium point; the outcome in this case is extinction of one or the other species, depending on initial conditions. See Pianka (1978: 175–182).

As a set, these assumptions are highly restrictive and unrealistic. Most are unlikely to hold for long-lived species, like hominids, with complex behaviors and ecological adaptations. Strictly interpreted, the CEP should be applied only in situations with no habitat heterogeneity in space and time and no variability in demographic or ecological characteristics within a population of organisms, or between species. Further, these equations portray only certain kinds of competitive interactions (Schoener, 1974: 35–36; Stewart and Levin, 1973: 171; Morse, 1974: 818; Pianka, 1976: 115), those in which the magnitude of the competition coefficient is "proportional to the products of the densities of the two interacting species" (Levine, 1976: 903).

This list of qualifications indicates why a simple application of the CEP itself is not an adequate basis for analysis of hominid paleoecology. However, as will be shown below, more useful theory can be obtained by relaxing certain of these assumptions to achieve greater realism. Nearly all such modifications lead away from predictions of the type envisioned in the SSH.

Verbal interpretations and experimental tests of the CEP

In non-mathematical language the CEP has several definitions. These are attractive in part for their apparent simplicity and "lawfulness." One form (Hardin, 1960) postulates a situation in which two species have only one resource, which they share. Because the two are not likely to be identical in their competitive abilities, however small the difference, the less efficient will eventually be eliminated. Hardin takes this to indicate that two species cannot have the same niche (cf. Whittaker and Levin, 1976: 30).

Ayala (1970b: 129) distinguished two formulations of the CEP,

> ... depending on whether the two species are required to be ecologically identical for the principle to apply, or whether competition for at least one limiting resource is taken as sufficient condition for coexistence to be impossible.

The former states that identical species cannot coexist (e.g., Diamond, 1978: 323). This is probably true, but of little interest because even conspecific individuals are not ecologically identical. The latter formulation weakens the condition by replacing identical with similar, leaving a good deal to rest on the ambiguity of the word "similar." A third formulation states that "two species cannot coexist if they share one or more resources essential for the survival of the species" (Ayala, 1970b: 129), sometimes with the stipulation that the resource be limiting. Jaeger's definition (1974: 33) is an example:

> When two species jointly utilize a vital resource that is in short supply, either in abundance or availability to the species, one of the species will eventually eliminate the other from the habitat where their distributions overlap.

This definition comes close to the mathematical form of the CEP, without, of course, expressing all of its qualifications.

Whittaker and Levin (1976: 30) place competitive exclusion into the context of evolutionary ecology:

> the unique identification of niche with species within a particular community ... [is] ... the result of competitive exclusion, the dynamic process of natural selection at the species level. More precisely, when two or more species attempt to fill the same role in the same community, no stable balance can be struck between them.

Two important considerations stand out here. Competitive exclusion is an evolutionary process, not an event (as is often implied in applications of the CEP). And great or complete niche overlap within a community is an unstable condition, not an impossible one. Seen in this way, competitive exclusion is rich in possibilities besides extinction. These authors (1976: 68) offer this definition: "The principle of competitive exclusion states that in a stable community, no two species can be limited by the same factor." Much of the development of competition theory centers on the subtlety and abundance

of the "limiting factors" that can structure relationships among competing species in stable communities.

Biologists diverge widely on their evaluation of the CEP and on the importance they assign it. For Hardin (1960: 1297), its development signaled a "renaissance of understanding." Andrewartha and Birch (1954), and Ayala (1969, 1970b, 1972), however, think the principle either invalid or trivial—a "trite maxim" (Cole, 1960: 348)—depending on how it is stated. Others (e.g., Stewart and Levin, 1973) point to the severe limitations of the CEP itself, but also find it a fruitful theoretical departure point. Hutchinson, for instance (1950, 1961, 1965, 1975), has made it central to a broad and provocative set of theoretical developments (summary in Whittaker and Levin, 1976). These comments divide against and for, depending respectively on whether they focus on the principle itself or on what can be done with it through modification.

Ayala (1969, 1970b) produced experimental evidence, using competing *Drosophila,* which he believed to "invalidate" the CEP. His results and his interpretation have been cited by anthropologists (e.g., Swedlund, 1974: 520; Summers and Neville, 1978) to raise doubts about the CEP. Biologists disagree, however, on their meaning (Gause, 1970; Ayala, 1970a, Stewart and Levin, 1973: 188–190; Darlington, 1972; Gilpin and Justice, 1972; Gilpin and Ayala, 1973; Whittaker and Levin, 1976: 33–34). Ayala showed that stable coexistence of two species competing for a limited food resource in a confined space was possible under circumstances that violated the conditions derived from equation (1). In particular, "mutual inhibition" could be quite strong between the competing species [i.e., $\alpha > K_1/K_2$ and $\beta > K_2/K_1$] that stably coexist (1970a). This contradicts the CEP condition for stable coexistence [equation (2)]. Ayala thus rejects the principle that

> two species cannot coexist in the same territory indefinitely if they compete for a resource available in short supply which is essential to their survival . . . [and the corollary] . . . that if two species coexist more or less stably in the same territory they do not compete for the same essential resource (1969: 1078–1079).

Difficulties arise in evaluating this work because, in practice, the CEP is a tautology built on linked definitions of species and niche. It cannot be disproved by facts (Hardin, 1960: 1292–1294). By definition, two species cannot coexist if they have identical niches, but, by definition, all species have different niches, making a "clean" test impossible. This circularity is one reason that the CEP as such offers poor guidance for taxonomic assessments of fossil materials. Drawing on this difficulty, Gause (1970) has replied that Ayala's results demonstrate only that the two *Drosophila* species had different niches; they can therefore hardly invalidate the CEP. Darlington 1972: 3152–3153) also argues that while resources were limited, they were neither directly nor exclusively limiting to the two species, as is required for the CEP to pertain. Darlington points out that in the mixed species situation, "each [species] becomes part of the other's niche, and the niches are no longer identical." Other biologists question Ayala's "invalidation" by noting that some assumptions of the CEP and logistic equation do not appear to hold in the experiment. Gilpin and Justice (1972) use Ayala's evidence to show that the *Drosophila* birth and death rates were not linearly dependent on population density. This violates assumption (c) above. Gilpin and Ayala (1973; also Whittaker and Levin, 1976: 33–34) note that Ayala's results reflect nonlinear responses [(e) above] of the *Drosophila* populations to density changes.

The CEP cannot be disproved empirically, but one can ask if the requisite assumptions apply. This amounts to questioning its generality (Stewart and Levin, 1973: 188–192). It implies that the importance of competitive exclusion must be debated largely in terms of factors other than the principle itself—mainly evolutionary ecology and demography. Ayala's results demonstrate that strict adherence to the assumptions of the logistic equation must be demonstrated by persons invoking the CEP programmatically. In addition, the experiment shows that two species forced to co-reside in highly artificial laboratory conditions designed to approach the restrictive assumptions of the CEP can still stably coexist (cf. Gause, 1934). They do so because of very subtle

differences in their responses to the ecological circumstances of a competitive environment.

Character displacement

Character displacement (Brown and Wilson, 1956) refers to situations in which differences between closely related species are enhanced in zones of sympatry, compared to areas without overlap or interaction. It is attributed to competitive exclusion ("ecological displacement"; Brown, 1958: 154) and to reinforcement of reproductive isolating mechanisms due to secondary contact. Convergent evolution in the zone of allopatry may also be important in assessing this phenomenon (Brown and Wilson, 1956: 284). Character displacement commonly refers to morphological changes resulting from natural selection (Grant, 1972). It is a process on an evolutionary time scale, as distinct from expansion and contraction of a "realized" niche, a behavioral response on a short-term, ecological time scale.

Brown (1958) suggested that character displacement was important in the origin and subsequent evolution of sympatric hominid species. However, Schaffer (1968) applied a character displacement hypothesis to the assessment of early hominid fossils from South and East Africa with only moderate success.

Grant (1972) has refined the definition of character displacement and reviewed evidence for the phenomenon. He points out difficulties in Brown and Wilson's (1956) treatment and circumvents some of these by asking first what would be the character state in the sympatric zone if character displacement were not a factor. Sympatric displacement can occur due to localized adaptation or continuation of a cline—i.e., for reasons other than competition between related forms (e.g., Grant 1972: Fig. 4). Grant's definition directs attention to theoretical arguments that indicate that in some circumstances convergence should result from congeneric competition within a community (1972: 41–42; Fig. 1; Cody 1973).

Character displacement—divergent and convergent—may have been important in the macro-evolution of hominid lineages, but more precise hypotheses about the expected results of congeneric competition require an examination of niche theory, presented below.

* * *

This section answers the first question: Is Wolpoff's application of the CEP congruent with our ecological understanding of it? In its simple or programmatic form the CEP is too restricted by unrealistic assumptions to be useful for hominid paleoecology, especially as it is invoked in support of the SSH. Verbal interpretations have an appearance of "lawfulness," but obscure the stringency of the conditions under which they would pertain. The CEP cannot be disproved or shown inapplicable by fossil evidence for more than one sympatric hominid. This means that important results will come from examining the reality and importance of the assumptions and the effects of relaxing them. This shifts the discussion to derivatives of the CEP, and into the realm of evolutionary and community ecology. Character displacement hints at the possible, non-extinction results of competitive exclusion, as does Whittaker and Levin's definition of competitive exclusion itself.

With such drawbacks it may seem odd that some ecologists have made the CEP a centerpiece of theory. The problem disappears by examining how ecologists use the CEP. Though ostensibly a principle of extinction and biotic poverty, it is in the exploration of the form, maintenance, and the richness of species diversity in communities that the CEP assumes a powerful heuristic role. It is a peculiarity of hominid paleontology that the principle has become a basis for denying the possibility of such diversity.

Leigh (1968; also Hutchinson, 1975: 497) has commented on this peculiar history of the Lotka-Volterra equations. Derived from the physical sciences, they were originally developed to explain the behavior of simple laboratory communities. The intent, however, was a larger and unrealized one:

The original motivation for studying simple experimental communities was, however, rather different. People hoped thereby to develop and refine the theory to an extent sufficient to permit direct extrapolation to more complex natural communities. This program was a failure, for the curious reason that simple experimental communities are too unstable and erratic to exhibit lawful behavior (Leigh, 1968: 8).

Despite this, the equations have proved to be—in Leigh's phrase—"pregnant with consequences" when modified to explore the evolution of diversity, character displacement, the mechanics of competitive advantage, and the allocation of roles or niches within a community (Leigh, 1968: 6–10). Even Gause, the experimental forebearer of the CEP, maintained a clear distinction between the elementary processes represented in his experiments and the complicated phenomena of nature (e.g., 1934: 2–3, 20).

Darlington (1972: 3153) has summarized the drawbacks of the CEP well:

> The phrase "competitive exclusion" is . . . misleading. It suggests a static situation, a fencing out, rather than a process. It overemphasizes extreme and oversimplified cases without clearly relating them. . . . It has fostered pointless controversy about the possibility of coexistence of competitors, when what is needed is explanation of the fact that they do coexist.

In different ways Jaeger (1974: 34–35), MacArthur (1972: 255), and Margalef (1975: 151–152) all make the same point.

NICHE RELATIONSHIPS AND COEXISTENCE

Competitive exclusion must be understood in the context of the niche. In the state of pure competition described by the CEP assumptions, niche relationships are unstable and communities decompose through extinctions to simple assemblages (Margalef, 1975: 151–152). This hypothetical outcome results largely from the absence of variability allowing organisms to evolve or adopt the specializations that produce the quite subtle and stable niche differences in communities. Starting from a CEP orientation, we can ask what factors besides competition operate to determine niches, and which are important? What effects do they have? The factors considered below— predation, life-cycle and frequency-dependent selection, temporal fluctuations, spatial heterogeneity, niche dimensionality, and density-independent effects—represent modifications of the CEP assumptions in the direction of greater realism.

Niche, habitat and ecotope

The niche concept has a history of definitions. Whittaker et al. (1973) differentiate three components: *Niche* refers to the functional role of an organism within a community; *habitat* to the position of an organism's range over a group of communities or over gradients of environmental factors that are partially external to communities. *Ecotope* combines elements of both niche and habitat, describing an organism's response to the set of biotic and environmental variables that affect it.

The distinction between fundamental and realized niche is not apparent in the use of the CEP and SSH in hominid paleontology. Wolpoff's argument, for instance, implicitly refers to fundamental niches. Experimental study has shown, however, that few organisms actually occupy a large or representative portion of their fundamental niche. Colwell and Fuentes (1975) summarize these "competition release" studies and note three kinds of overlap in the fundamental niches of normally coexisting species.

Hutchinson (1950) has distinguished between the fundamental and realized niche of an organism. If the set of environmental factors affecting an organism is organized with each factor as an axis of a multi-dimensional space, then the points in the space where it is viable define a hypervolume representing its fundamental niche. A species' fundamental niche completely defines its aut-ecological qualities (Hutchinson, 1950: 416). Although the image is locational, the relationships envisioned are ecological and functional (Whittaker et al., 1973: 323). The realized niche, in contrast, is the portion of the fundamental niche actually taken up by the organism. Competition and other factors usually exclude a species from some aspects of its fundamental (or potential) niche. By redefining the axes, the hyperspace concept can also be applied to habitat or ecotope (Whittaker et al., 1973: 328).

In Hutchinsons' formal system,

> ... all points in each fundamental niche imply equal probability of persistence of the species, all points outside each niche, zero probability of survival ... (1950: 417).

In fact, the niche hypervolume is not of uniform quality to the organism, a point Hutchinson recognized (p. 417). Whittaker et al. (1973: also Ayala, 1970b: 122) use this observation to modify the hyperspace model in a way critical to this discussion. A species' population response to the conditions represented along an axis of its niche space is of primary concern. A measure of the population response could be density, fitness, or competitive ability. For each axis there is an optimum point for a particular population, and the value of the measure falls off as the margins of the fundamental niche are approached. "The species in its hypervolume forms not a sharply bounded distribution but a population cloud" (Whittaker et al., 1973: 329). The density of the cloud is a direct measure of the population response. This view highlights the gradual transition between, successively, the realized niche, the fundamental niche and the surrounding space; the relative success of organisms in different portions of the hypervolume; and the diffuse nature of the margins of its niche distribution.

The population response cloud of related species can overlap considerably along niche axes so long as some aspect of their optimal positions is separated (Colwell and Fuentes, 1975: 294):

> Species evolve toward scattering of their population centers in the habitat hyperspace— toward difference in habitat. ... The population clouds of species normally, however, overlap broadly if their centers are close together ... (Whittaker et al., 1973: 330).

Further, the response cloud is not static. Population changes, for instance, may cause it to fluctuate over the hypervolume: at low densities organisms occur in the optimal portion; as densities increase some migrate into suboptimal areas, increasingly attractive as density-dependent effects accumulate in the core of the hyperspace (Vandermeer, 1972).

The population cloud concept has special significance if the population measure is fitness. Ayala (1970b: 123) notes that "the probability of survival and reproduction is not the same for all individuals at all points of the hypervolume, nor is it the same for all individuals at any point." For competing species, overlap likely occurs in suboptimal zones and results in increased selection for divergence while preserving a refuge for each. This approach to the niche concept makes a simple but basic point: if variability of environment and population fitness is allowed, competition between similar hominid species will probably not result in abrupt qualitative changes like extinction. It will, however, quantitatively heighten selection pressure for some degree of divergence between the centers of the species' niche spaces.

The distinction between fundamental and realized niche is not apparent in the use of the CEP and SSH in hominid paleontology. Wolpoff's argument, for instance, implicitly refers to fundamental niches. Experimental study has shown, however, that few organisms actually occupy a large or representative portion of their fundamental niche. Colwell and Fuentes (1975) summarize these "competition release" studies and note three kinds of overlap in the fundamental niches of normally coexisting species.

In *niche inclusion* the fundamental niche of one species is included within that of the other. The generalist's tactic in this case is to focus use on non-overlapping niche regions; the specialist relies on highly efficient exploitation of a narrow portion of the generalist's niche, or on interference competition, to maintain itself (Colwell and Fuentes, 1975: 228; also Hutchinson, 1950: 480–481). Vertebrate examples are rare, perhaps because few studies have been completed (cf. Jaeger, 1974), but Stewart and Levin (1973: 183–186) and Schoener (1974: 36) discuss models which give the conditions for a stable equilibrium in this situation. *Coextensive fundamental niches* are well documented in a number of species (Colwell and Fuentes, 1975: 293–294). Separation of realized niches and coexistence in this case requires only that each species be a superior competitor in different portions of their shared fundamental niche. In the third category are cases of *reciprocal niche overlap,* with each species

having a niche region exclusive of the competitor, which "cannot persist [there] even without interspecific competition" (Colwell and Fuentes, 1975: 292; also Hutchinson, 1950: 480–481). Whatever the outcome of competition in the overlap region, each species has a sanctuary that guarantees its persistence.

The general result of Colwell and Fuente's review is the demonstration that species in communities routinely exhibit only a part of their ecological potential.

Determinants of coexistence besides competition

Competition can limit congenerics to stable coexistence in realized niches, even though their fundamental niches may overlap partially, fully or inclusively. But factors besides competition affect the realized niche of a species, and therefore the likelihood of coexistence with congenerics. In an extensive review, Connell (1975: 461) has challenged the prevailing idea "that competition is the sole or even the principal mechanism determining the area in which one finds a species, as opposed to the potential area within which it can live." The non-competition mechanisms cited by Connell and others (Whittaker and Levin, 1976: 69–75; Colwell and Fuentes, 1975: 285) are outlined in the paragraphs that follow.

Predation.

Predation can reduce the effects of competition sufficiently that prey species can coexist with coextensive or inclusive niches, and with otherwise strong tendencies towards competitive exclusion (Colwell and Fuentes, 1975: 301; Hutchinson, 1975: 494). In terms of CEP assumptions, this introduces a limiting factor (the predator) besides a common resource; in terms of niche, it means that one or both species are prevented from saturating their fundamental niche. Evidence for the importance of predation comes mainly from invertebrates and plants (Connell, 1975: 464–474; Paine, 1966). Predation may be less effective in limiting competition among the larger terrestrial vertebrates (Connell, 1975: 468, 476), but little evidence has been gathered to test this.

Predation is thought to have been an instrumental selection pressure in early hominid evolution (Wolpoff 1971: 604–605). It could have reduced congeneric competition, contributing to stable coexistence of multiple species.

Differential selection of life cycle stages.

Distinct limiting factors at different stages in the life-cycles of two species can balance competitive interactions, if competitive abilities between the species reverse at the different stages (Ayala, 1970b: 146–148). Conditions for this appear to be restrictive, and the resulting equilibrium unstable. Unfortunately, Lotka-Volterra models incorporating age structure are usually mathematically intractable (Wangersky, 1978: 194). Even so, this kind of effect is problematic for hominids: infant and childhood dependence, parental care and social cohesion (McKinley, 1971; Mann, 1972) probably moderated differential exposure of life stages to ecological conditions.

Frequency-dependent competition and selection.

Selection can promote stability in competitive systems in ways other than simple character displacement (Ayala, 1970b: 151–152). As one of a pair of competing species gains numerical dominance it is subject to greater degrees of intraspecific competition and selection effects:

> ... *intraspecific* inhibition by crowding ... increases as the population increases, so that when the species is rare each of its members competes interspecifically better than when it is common (inverse density-dependent competition) (Hutchinson, 1975: 496).

The rarer species not only competes better but also adapts in directions determined primarily by interspecific competition and may eventually become dominant. The resulting oscillation in competitive ability impedes the course of competitive exclusion and may eventually lead to a more stable, congeneric coexistence. Frequency-dependent selection also means that character displacement will occur more commonly in the rarer species (Ayala, 1970b: 154).

Ayala (1970b: 148–150; 1972: 357) gives the conditions in which frequency-dependent effects can create a stable equilibrium between competing species. He also (1972, 1973) gives laboratory evidence for the effectiveness of this mechanism and describes how it can operate in nature. Most important for the hominid case, niche or habitat heterogeneity can produce frequency-dependent fitness differences for competing species even if their fundamental niches are coextensive (Ayala, 1972: 354).

Little is known about frequency-dependent effects in nature; expressed over niche or habitat heterogeneity they could have been of considerable importance to early hominids.

Temporal fluctuations.

Fluctuations in environment, caused by seasonality, vegetation succession, climate changes, or other factors, can reverse the relative advantages of competing species (Hutchinson, 1950, 1961: 138, 1975: 495; Whittaker and Levin, 1976: 74–75). If competitive differences are not large, environmental instability may indefinitely forestall the course of competitive exclusion. The outcome depends on the frequency of fluctuation relative to parameters of the competitive process (Whittaker and Levin, 1976: 71), but between extremes, "it is reasonable to suppose that there will exist numerous cases in which the direction of competition is never constant enough to allow elimination of one competitor" (Hutchinson, 1950: 420).

Studies of the histories of natural ecosystems, diverse theories available for analyzing hominid and contemporary human adaptations, and field studies of human and primate ecology all converge to suggest that temporal environmental variability is of large importance in hominid adaptation and evolution (Winterhalder, 1980). Despite this, temporal properties and their ecological effects on the time scales longer than a season and shorter than long-term change (e.g., the putative Plio-Pleistocene dessication of subtropical Africa; see Butzer 1978a) have received very little study by anthropologists.

Spatial heterogeneity.

The effects of temporal fluctuations on congeneric and interspecific interactions have been extensively analyzed. Attention to the role of spatial heterogeneity is more recent (Levin, 1974: 207). Comparative study of the results of temporal fluctuation and spatial heterogeneity indicate that the former often introduces instabilities into species interactions while the latter, in contrast, generally produces stability (Smith, 1972; Roff, 1974a; May, 1974: 34–44; Orians, 1975). In part the early emphasis on unstable, or exclusive, outcomes of competition is a result of this uneven history.

Random effects, such as priority of arrival in a location, characteristic of dispersing or fugitive species, can create heterogeneity in otherwise homogeneous environments. They can also augment the preexisting environmental heterogeneity. In these circumstances, local population fluctuations, extinctions and recolonization, and the divergent histories of local patches following the initial development of heterogeneity, can create stably coexisting systems of species that would not occur sympatrically if these processes were absent (Hutchinson, 1950: 419–420; May, 1974: 40–42). "Opportunities for movement and habitat diversification provided by the spatial aspect of environment make possible in a variety of ways coexistence of species which could not otherwise survive together" (Levin, 1974: 22).

The analysis of congeneric competition and resource use in spatially heterogeneous ("patchy") environments is based on optimal foraging theory (see Schoener, 1971, 1974 and Pyke et al., 1977, for summaries). As an example, MacArthur and Levins (1964; also Lawlor and Maynard Smith, 1976) describe two outcomes of natural selection for character displacement with respect to resource use in a patchy environment. First, coexisting species can share the use of a set of resources if they have specialized on different proportional mixtures of that set. Each species is found in those areas that match its most effective use (MacArthur and Levins, 1964: 1207). Theoretically, as many species can coexist as there are stable proportional divisions of habitat. The number decreases as the relevant parameters become less stable (e.g., if productivity

is strongly seasonal) (see Paine 1966: 72). Levin (1970: 416) notes that a proportional combination of biological factors can itself constitute a limiting factor for a species. Second, the congenerics can be separated by their specialized use of a few of the available resources, and perhaps by concomitant morphological specialization, but not necessarily by habitat differentiation. MacArthur and Levins (1964) use "fitness sets" (Levins, 1968) and foraging strategy models (MacArthur and Pianka, 1966) to identify the circumstances in which each of these patterns is expected. Patchy habitats are ubiquitous (Wiens, 1976: Levin and Paine, 1974), and the ecological activities of organisms themselves can create heterogeneity in an otherwise effectively homogeneous environment (Levin, 1974; Charnov et al., 1976).

Winterhalder and Smith (in press) provide evidence for the efficacy of optimal foraging models in the analysis of hunter-gatherer behavior, both ethnographic and prehistoric. This lends confidence to the use of models like that developed by MacArthur and Levins (1974; see above), which have implications for hominid paleoecology. Early hominids might have been dietary specialists, in which case the habitat use of congenerics could have overlapped considerably. However, congeneric species might have been patch specialists and within-habitat generalists (omnivores) and also have existed sympatrically. In this latter circumstance dental anatomy alone would not be sensitive to the ecological divergence allowing coexistence. Diverse kinds of prehistoric evidence (Butzer, 1977; Isaac, 1976a, b) and comparative studies of foraging and niche differentiation will be necessary to examine these or other possibilities. The critical role of spatial heterogeneity in ecological adaptation and competitive interactions highlights the importance of Butzer's (1977: 573) contention that paleoecological analysis must be focused at the local or micro-habitat level.

Niche Dimensionality

In its programatic form the CEP applies only if a single resource is directly limiting for the two competing species. For a variety of reasons, competition expressed on a single dimension is unlikely (Darlington, 1972). If the condition of a single resource— homogeneous in space, time and quality—is relaxed, this general result can be obtained, in so far as the number of species of a certain niche breadth that can coexist in a given environmental range increases with the dimensionality of their niches (MacArthur and Levins, 1967). Relaxing the basic CEP assumption places a special burden on the definition of a resource. For instance, it has already been shown that proportionately different use of a resource set can constitute separate resources for congenerics which have specialized to this type of foraging strategy.

More specific results have been derived from competition models. MacArthur and Levins (1964; see Levins, 1968: 55–65; Stewart and Levin, 1973: 191) suggest that as many species can coexist in a community as there are distinct resources, but no more than that. Levin (1970: 418; Whittaker and Levin, 1976: 31–33) has generalized this result:

> No stable equilibrium can be obtained in an ecological community in which some r components are limited by less than r limiting factors. In particular, no stable equilibrium is possible if some r species are limited by less than r factors.

Levin puts this in terms of limiting factors rather than resources for three reasons. (1) "Distinct" resources is sometimes taken to mean that a refuge for each species in any part of the niche or habitat hypervolume is sufficient for stable coexistence. This may not be the case; some niche dimensions are more equal than others:

> . . . certain dimensions of the hypervolumes [are] of paramount importance. Which dimensions those are is determined by which factors are limiting those species, be those factors resources, predators, or others. Two species cannot coexist unless their limiting factors differ and are independent; this is the only criterion one need examine at a given time and place (Levin, 1970: 415).

(2) Resources are only one possible limiting factor. And (3) distinct resources may not in themselves be sufficient to act as limiting factors, contrary to the MacArthur and Levins (1964) criterion. For instance, if two species feed on distinct but superabundant resources, but both are limited by a single (non-switching, see Whittaker and Levin, 1976: 33) predator, then there can be competitive exclusion (Levin, 1970: 420). Despite the fact that two resources are involved, there is only one limiting factor, the predator.

Stewart and Levin (1973), using somewhat different assumptions, demonstrate that two species can stably coexist on two resources in each of the possible ways for exploiting them: (1) if each uses one resource exclusively, (2) if each uses both resources, and (3) if one species uses one and the other both of the resources. These represent distinct, coextensive and included fundamental niches, respectively (see Armstrong and McGhee, 1976).

Although more realistic than the CEP itself, these models have shortcomings. They usually modify one or at most a few of the CEP assumptions, and their specific results must be considered tentative. The general conclusion, however, is clear: consideration of more than one niche dimension, resource or limiting factor usually uncovers possibilities for stable coexistence of more than one competing species within a community. As suggested earlier, a major difficulty lies in deciding what can be taken as a resource or limiting factor with respect to these models (Whittaker and Levin, 1976: 73). For instance, niche differences in resource or habitat use are fairly obvious, but those that can result from different techniques for locating the same resources in the same habitat (Diamond, 1978: 324) may be less so.

Density-independent effects.

This group of factors influencing the realized niche of a species overlaps somewhat with those cited under temporal fluctuations and spatial heterogeneity, but for the reasons suggested below, it merits separate treatment.

Since Darwin, competition has had a predominant role in explaining the evolution of populations and communities of co-adapted species. Despite this, competition is difficult to observe directly, and indirect procedures for verifying its occurrence and actions are sometimes ambiguous (e.g., Connell, 1975: 462–463; Hutchinson, 1950: 418–419; Pianka, 1976: 124; Schoener, 1974: 28; Wiens, 1977: 591; cf. Diamond, 1978). A long-standing debate in biology (summary in Keith, 1974) thus centers on the relative importances of density-dependent (including competition) and density-independent factors in controlling population and reproductive success, and thereby in structuring evolution. The competition orientation that prevails in contemporary theoretical biology could constitute a bias that should be considered in analysis of topics such as competitive exclusion and sympatric coexistence of hominids. Hence the attention given here to density-independent factors.

Wiens (1977) has made a compelling case that environmental variability must be considered a major factor influencing realized niche relationships. Through ten years of study of bird communities in temperate grasslands Wiens documented significant temporal and spatial variability in competition parameters, and fluctuating niche overlap of what should have been competing, niche-differentiated species. These results strained interpretations of community relationships built purely on competition theory (1977: 590). Wiens notes that competition theory depends on environmental constancy and includes the assumptions that (1) direct, continuous and uni-directional selection operates, (2) the populations are in equilibrium with resources, (3) factors besides competition have insignificant effects on resource use, and (4) history or environmental constraints do not prevent organisms from behaving in the (optimal) ways predicted. The parameters and variables of competition theory models are assumed to behave in ways that may belie their action in nature. The theory may be correct but simply not apply to actual situations.

It is useful to recall that the Lotka-Volterra equations and the CEP are based on point models which assume homogeneity in time and space for the parameters they incorporate. As in these models, if one could freeze the momentary assymetries of relationships in natural communities and then require that the included species

pursue their livelihoods with the resulting handicaps made permanent, many would presumably disappear. Fluctuation and spatial variety, however, prevent this. Competition events in the real world are dispersed in space and separated in time. They can be buffetted by shifts of species relative to the spatial mosaic or by temporal perturbations of various kinds through variable ranges that continuously change competitive balances. Imbalances established in one location may be reversed in another; a competitive advantage to one species for one or many more generations may be reversed before the time span required for competitive exclusion to run its course. Thus, authors besides Wiens are devoting more attention to "the importance of priority and other stochastic effects in the development and structure of natural communities. . . ." (Colwell and Fuentes, 1975: 303; also Jaeger, 1974: 37; Connell, 1975: 474–483, 1978; Hutchinson 1975: 494–495).

The importance of density-independent factors to early hominids is difficult to assess. Little is known about the properties of the effective hominid environment (Butzer, 1978b; Winterhalder, 1980) or the rates and magnitudes of environmental perturbations, and scales of spatial mosaics that would affect competitive interactions in the ways postulated here.

A specific observation of Wiens (1977: 590) and Abrams (1975: 370) should be mentioned. Both found a great deal of overlap in food utilization among bird species with quite different food-gathering morphologies. The birds respond opportunistically and converge on available prey, with the result that they overlap ecologically to a greater degree than would be predicted from morphology. A similar situation could have characterized early hominids (Butzer, 1977: 578). If this is so, it complicates interpretation of associations between fossil morphology and the evidence of prehistoric diet available archeologically. These difficulties again highlight the importance of indirect and comparative study using primates, social carnivores, and hunter-gatherers with a framework that can relate inferences from these sources to the more direct data of paleontology and archeology.

* * *

The materials presented here answer the second set of questions raised by anthropological uses of the CEP: Is competitive exclusion inevitable, or are there factors that might prevent it? What additional factors should be considered when applying competition ideas to interrelationships of early hominids? The discussion has revealed that competitive interactions limit the functional and locational position of a species in a community to a portion of what would be its ecological potential in their absence. Competition thus contributes—often in a stabilizing manner—to the structuring and adjustment of the realized niches that make up a community. It is expressed—and diffused—over niche, habitat and ecotope relationships. In an evolutionary sense these terms are best visualized as a population's response (e.g., fitness) measured over a space with axes representing separate aspects of the environment. Variability of this fitness distribution over each species' niche or habitat space provides substantial opportunity for the evolution of character displacement. Competition may induce extinction, but it is more likely to have a generating role in the evolution and maintenance of intra-community diversity.

Experimental studies show that congenerics that coexist in stable, realized niches can have fundamental niches that are inclusive, coextensive, or partially overlapping. Thus, while competition excludes species from a portion of their fundamental niche, extinction is not inexorable, even for species with completely overlapping autecological qualities.

In natural situations competition is only one influence affecting realized niches. Several other factors are potentially of large significance to the question of hominid coexistence. Predation or other factors (a harsh physical environment, parasitism) limiting population size may preclude competitive exclusion. Frequency-dependent selection may reverse the competitive abilities of two species to favor the rarer one, producing fluctuating, and eventually the evolution of stable, coexistence. Temporal

fluctuations and spatial heterogeneity both generate multiple opportunities for re-versals of competitive advantage, and for the evolution of character displacement on niche or habitat dimensions. When niche dimensionality is taken into account, competition theory indicates that there can be as many coexisting species in a community as there are independent niche dimensions acting as limiting factors. Finally, density-independent factors may be quite significant.

The theory used to examine these factors generally begins with some form of the CEP and varies assumptions in the direction of greater realism. The list of variations given here is not exhaustive. Other factors such as time lags (Wangersky, 1978: 206–210) could also be examined. These modifications usually illuminate the condi-tions that allow or promote the coexistence of related and competing species in enduring communities.

CONCLUSION

There is a superficial ambivalence to the argument developed here. On the one hand, the CEP is a model of a biologically inconceivable situation. This argues against its programmatic use and could be a reason for ignoring it altogether, as some physical anthropologists have chosen to do. On the other hand, the CEP is the starting point for analyzing potential or real interactions among early hominid species. There is only minimal contradiction in this. In a classic paper titled "The Paradox of Plankton," Hutchinson (1961: 143; also 1975: 492–497) argued that the CEP was useful to biologists precisely because it

> can be used to examine a situation where its main conclusions seem to be empirically false. Just because the theory is analytically true and in a certain sense tautological, we can trust it in the work of trying to find out what has happened to cause its empirical falsification.

The discussion given here demonstrates that competitive exclusion creates and sustains diversity instead of precluding it.

A difficulty with the CEP, besides its restrictive assumptions, is its designation of a process with a term that suggests only one, and perhaps the least likely, result of that process—competitive exclusion connotes competitive extinction (Darlington, 1972: 3152). Darlington's own term, competitive repulsion, is perhaps more appropriate. "Emphasis should be on pressures and processes rather than avoidance and bounda-ries" (Darlington, 1972: 3155). This definition is congruent with the population measure ("cloud") model of the niche. It accurately suggests that character or niche displacement is more likely than extinction.

> Coexistence of species competing for a vital resource is conspicuous everywhere around us . . . [because organisms] . . . divide *themselves and their environment* into fractions by complex processes of co-evolution (Darlington, 1972: 3153).

Wolpoff (1971, 1976a) is correct in stating that questions of the sympatric coexistence of early hominids are basically ones of ecology and behavior. But contentions derived directly from the CEP are not the apposite ecological context for evaluating these questions. Models that extend competitive exclusion concepts and that allow for factors besides competition, demonstrate multiple possibilities that anthropologists must investigate when considering hominid coexistence. They also direct attention to diverse sources of pertinent data. Variations on the Lotka-Volterra equations are most powerful when used to examine the form of possible solutions to interspecific relation-ships (Wangersky, 1978: 189). These solutions are the relevant basis for developing alternative concepts to the SSH (Leakey and Walker, 1976: 573–574; Isaac, 1976a: 33; Butzer, 1977).

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