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Ecological Theory and Ethnic Differentiation among Human Populations¹

by William S. Abruzzi

ALTHOUGH ENVIRONMENTAL CONSIDERATIONS date to the earliest theoretical publications in anthropology (cf. Mason 1896, 1905; Wissler 1917, 1926; Kroeber 1923, 1939; Forde 1934; Steward 1955), the study of human ecology—applying general ecological concepts and methods explicitly to the analysis of human populations—is a conspicuously recent analytical approach in the field. Only in the past decade have the research findings of animal and plant ecologists been systematically employed by anthropologists adopting an expressly ecological focus. For the most part, ecological theory in anthropology has developed independent of advances in related fields.

Many anthropologists have rejected the extension of general ecological theory and methods to human populations on the grounds that ecology is a biological science, based upon research on populations whose principal adaptive mechanisms are inherited genetically. Human groups, such critics argue, employ culturally acquired adaptive mechanisms whose operation cannot be accounted for by ecological (i.e., biological) principles (Netting 1968:11–12; Bennett 1976). Two distinct bodies of ecological theory and method have, therefore, resulted: one for human populations and one for the rest of the organic world.²

¹ This article is a revised version of a paper presented at the 76th annual meeting of the American Anthropological Association in Houston, Texas, in December 1977. Appreciation is expressed to Brian Foster and Donald Hardesty for their valuable comments upon that earlier draft.

² The treatment of human populations as unique within an ecological context has inadvertently been perpetuated by ecologists as well. Most textbooks in ecology (cf. E. Odum 1971) discuss humans superficially and usually only in terms of the problems created by indus-

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This bifurcation of ecological approaches has been increasingly called into question, and several researchers have suggested methods for applying general ecological concepts and principles to the analysis of human populations (Rappaport 1968; H. Odum 1971; Hardesty 1975, 1980; Little and Morren 1976; Yellen 1977; Abruzzi 1981).

The assumption that ecology is necessarily a biological science is premature. Although ecologists are concerned—as are anthropologists—with the biology of populations, ecological principles are not strictly biological. Indeed, ecological systems have been most effectively modeled as energy-flow systems, determined by thermodynamic principles (Margalef 1968; H. Odum 1971; E. Odum 1971:37–85). In his discussion of ecological succession, for example, Margalef (1968) emphasizes that while the properties of a specific ecological community are a function of the organisms that comprise it, the laws which determine the evolution of ecological communities are inherent in the energetic—not biological—relationships within and between systems subject to natural selection. Because ecological principles are independent of the specific biological composition of a community, they apply to all ecological communities.

Since any system that includes living components constitutes an ecological system (H. Odum 1971:58), human communities are suitable for examination in a formal ecological framework. Human and nonhuman communities are variants of ecological communities and thus have structural similarities that suggest the value of their being analyzed from a unified ecological perspective (see Abruzzi 1981:12–57). Both human and nonhuman communities constitute material systems through which energy flows and by which populations and their resources are mutually regulated (Margalef 1968; Rappaport 1968; H. Odum 1971; E. Odum 1971; Little and Morren 1976; Harris 1980:183–206). Both contain a high degree of diversity, the maintenance of which is fundamentally dependent upon the continuous input of energy from external sources (H. Odum 1971). The fundamental units of human and nonhuman communities alike are variable in size and composition and respond to spatial and temporal variations in the abundance and distribution of resources (Wilson 1968; Kummer 1971; Abruzzi 1979, 1980). Finally, both human and nonhuman communities transform potential energy into social organization, and the processes that generate the division of labor (i.e., resource partitioning) appear to be as important to the organization of human com-

tribal pollution or rapid population growth. Few ecologists have attempted systematically to explain human behavior through the application of general ecological concepts. For a notable exception, see H. Odum (1971).

munities as they are to the evolution of nonhuman systems (Harris 1964, 1977; Blau 1967; Levins 1968; Abruzzi 1981).

Current anthropological research that incorporates the analysis of human populations within the framework of general ecology, employing its concepts and methods explicitly, offers the potential of giving many traditional anthropological concerns a broader theoretical significance. The formation and maintenance of ethnic boundaries within multiethnic communities may be one area of social behavior that could benefit from the explicit application of ecological theory.

Anthropological analyses of ethnic relations have experienced a marked change in orientation during the past two decades. Previously, the concepts of *culture*, *tribe*, and *ethnic group* existed unchallenged as fundamental units in the anthropological classification of human populations. Traditional use of these concepts implied the existence of distinct, integrated social units whose boundaries were clear and unambiguous. The models and explanations offered to account for existing patterns of ethnic differentiation and interaction likewise assumed the discreteness of the units under investigation. The empirical validity of such ethnic units has come under serious review during recent years. Following Leach's (1954) challenge to the traditional conception of ethnic groups, the literature critical of the application of this and related concepts has grown rapidly (Barth 1956, 1964a, b, 1969a; Wallerstein 1960; Moerman 1965; Helm 1968; Vayda and Rappaport 1968; Cohen and Middleton 1970; LeVine and Campbell 1972; Despres 1975). The definition of ethnic units tends to be considered problematic. Indeed, much of the current literature on the subject implies that traditional anthropological use of ethnic unit concepts resulted in naive oversimplifications and derived from the ahistorical approach that characterized most anthropological research (Moerman 1968, Maquet 1971, LeVine and Campbell 1972).

With the variability of ethnic boundaries accepted and demonstrated empirically, a new set of questions has emerged as a central issue in the anthropological analysis of ethnic relations. In the place of typologies of ethnic interactions, anthropologists have concerned themselves with the mechanisms and processes involved in the origin, maintenance, rearrangement, and disappearance of ethnic boundaries among local populations. Traditional approaches based upon a static conception of discrete ethnic groups proved incapable of dealing with the dynamics of these new concerns. Among the more fruitful recent approaches to the question of ethnic boundary formation have been those that have employed an ecological or material focus and that have concentrated upon competition over scarce resources in conjunction with the allocation of labor required for efficient resource exploitation (Barth 1956, 1969a; Harris 1964; Shibutani and Kwan 1965; Cohen 1969; Despres 1969, 1975).

Although several researchers have adopted an expressly ecological framework for analyzing ethnic relations, most have not employed a coherent set of ecological principles to predict the conditions under which distinct ethnic groups are likely to exist within human communities. While the approaches taken have provided a useful, and perhaps necessary, step towards an ecological understanding of ethnic relations, a broader appreciation of ethnic group formation may be gained by employing ecological theory more explicitly. Following a clarification of certain conceptual issues regarding the definition of species and ethnic units, a general model of speciation (resource partitioning) in multispecies communities will be employed to explain the formation of ethnic boundaries within human ecological communities.

THE SPECIES CONCEPT

A major objection to comparing the formation processes of species and ethnic groups derives from the belief that these are not commensurate units: that species are genetic units con-

nected by the ability to exchange hereditary material, while ethnic groups are social units with a much lesser degree of biological integrity or meaning. Although a detailed discussion of the species concept would be inappropriate at this time, a few summary comments are in order.

The view that species are discrete biological units, defined by their ability to exchange genetic material, is not a realistic representation of the species concept as applied in contemporary biological and ecological research. Interfertility is not the primary defining criterion of species status. Within the biological species concept (see Mayr 1963; 1976:479-525), "species are more equivocally defined by their relation to non-conspecific populations ("isolation") than by the relation of conspecific individuals to each other. The decisive criterion is not the fertility of individuals but the reproductive isolation of populations" (Mayr 1963:20). The distinction between sterility and reproductive isolation is illustrated by one simple example (Mayr 1963:90). The mallard, *Anas platyrhynchos*, and the pintail, *Anas acuta*, are among the most common freshwater ducks in the Northern Hemisphere. Together they number as many as 100,000,000 individuals, with breeding ranges that largely overlap. Yet, while these two species display complete interfertility in captivity, they are reproductively isolated in the wild, with the number of hybrids estimated at 1 in 1,000. Hence, "cross-fertility does not prove conspecificity" (Mayr 1963:91; cf. Carson 1975).

The existence of *circular overlap* and *asymmetrical sterility* further demonstrates the absence of necessarily clear genetic boundaries between species populations. Circular overlap occurs when "a chain of intergrading subspecies forms a loop or overlapping circle of which the terminal links have become sympatric without interbreeding, even though they are connected by a complete chain of intergrading or interbreeding populations" (Mayr 1963:507). Numerous cases of circular overlap are known, principally among birds. Asymmetrical sterility is illustrated by the species *pipiens* (Mayr 1963:42). Five strains of this species are known: one in western Europe, one in northern Germany, one in southern Germany, and two in the Mediterranean area. While males of the southern German strain experience normal interfertility with females of the other two European strains, the reciprocal crosses—between females of the southern German strain and males of the remaining European strains—are sterile, with less than 1% interfertility. To complicate matters, American *pipiens* are fully fertile with the northern German strain but more or less sterile with the other four.

Sokal and Crovello (1970) discuss the practical difficulties of defining species boundaries through tests of interfertility. By illustrating the necessity of incorporating phenetic considerations and subjective criteria into testing procedures, they demonstrate the absence of a clear genetic foundation in species classification. Sampling procedures from which tests of interfertility are performed, for example, must be based upon phenetic characteristics. Confusion is added to classification procedures by the existence in many populations of males and females with markedly different phenetic characteristics, and the classification of different sexes of the same population as distinct species has occurred. The existence of sibling species—those that differ very little phenetically but display distinct breeding habits, habitat preferences, and other important distinguishing characteristics (cf. Mayr 1963:33-58; 1976:509-14)—likewise complicates the process of determining precise species boundaries. A study of light flashes among fireflies of the genus *Photuris*, for example, yielded a classification of 18 species in place of the original 2 or 3 (Barber 1951). This reclassification led to the discovery of important additional characteristics associated with the variation in light flashes, including breeding season and habitat preference.

Because interfertility between two populations cannot always be determined by a clear, qualitative decision, subjective

criteria necessarily enter into investigations of interbreeding between such units. Arbitrary levels must be assigned as the deciding criterion of successful interbreeding, with the levels employed varying from one investigator to another (Sokal and Crovello 1970). Penetrance, production of a zygote, birth of a viable offspring, and development of a fully fertile offspring have each been employed by different researchers as criteria of interfertility between species populations. Researchers who agree upon a particular level, moreover, may disagree on the proportion achieved within that level needed to determine successful interbreeding.

Defining species boundaries, then, is by no means clear and obvious, simply a matter of reporting the evident genetic discontinuity in nature. For the most part, fertility is not a criterion of species status among local populations. Where considerations of fertility are employed, complications necessitate subjective decisions by individual investigators which introduce variation into species classification procedures. Practical difficulties in applying a biological or a genetic species concept have produced many species classifications necessarily based upon phenetic characteristics. The reality of this situation severely undermines the notion of the precise genetic basis of species categories. In most cases, species boundaries are neither precise nor genetic. Reproductive isolation between two sympatric populations generally involves a host of isolating mechanisms, most of which have nothing to do with the ability to exchange genetic information (see below). Consequently, the occurrence of well-circumscribed species is the exception rather than the rule (Mayr 1963:90; Sokal and Crovello 1970:148).³

Species status among local populations must be viewed as variable and dependent upon local selective conditions, rather than as qualitatively prescribed by a priori, species-specific characteristics. Among the numerous attributes that can function to separate two sympatric populations reproductively, the very degree of interfertility between two closely distributed species may vary from one local population to another. Population biologists and ecologists have therefore directly concerned themselves with the mechanisms and processes producing changes in species boundaries among local populations and with the relation that speciation and species replacement have to the evolution of encompassing ecological communities (Mayr 1963, 1976; Levins 1968; Margalef 1968; Brookhaven National Laboratory 1969; Whittaker 1975; Cody and Diamond 1976).

DEFINING ETHNIC UNITS

For purposes of cross-cultural research, Naroll (1964) listed six criteria by which a "cultunit" might be defined: language, political organization, territorial contiguity, distribution of traits under investigation, ecological adjustment, and local community structure. Although he recognized that these

³ At the heart of the Darwinian revolution (Mayr 1972) is the notion that species are more or less distinguishable units constantly changing in response to selective pressures imposed upon local populations. Darwin (1958[1859]:67) himself viewed species as subjective categories without clearly definable boundaries: "I look at the term species as one arbitrarily given for the sake of convenience to a set of individuals closely resembling each other, and that it does not essentially differ from the term variety, which is given less distinct and more fluctuating forms." The evolutionary independence of local populations has led several researchers to question the utility of a generalized species concept. Ehrlich and Raven (1969) argue that taxa larger than the local population are not meaningful genetic units (i.e., breeding populations). They attribute retained similarities among separated local populations of the same species to the independent effect of similar selective pressures rather than to gene flow and note that strong selective pressures can act as a powerful evolutionary force even in the face of continuous and counteracting gene flow. Sokal and Crovello (1970:148) concur in this position, stressing that "nothing is to be gained by the additional abstraction to the species level, but much is lost, namely accuracy, for no two localized populations are alike."

characteristics do not necessarily vary concordantly, he defined the cultunit in terms of the first three.⁴ Naroll's proposal generated considerable discussion regarding the method of ethnic unit classification. The issues raised during that discussion clearly illustrate the difficulty of defining ethnic units on the basis of sociocultural criteria and the similarity between this problem and that of species classification.

Problems associated with the use of language in ethnic unit classification are representative of the difficulties of defining ethnic boundaries using sociocultural criteria. The issue of mutual intelligibility of languages corresponds to that of circular overlap and asymmetrical sterility among closely related animal populations. Naroll (1964:285) indicates the problem that linguistic continuums (which occur more often than not) pose for ethnic unit classification: "If, as seems to be the case, Eastern and Western Timbira are mutually unintelligible dialects but are connected by over a dozen geographically intermediate dialects, each of which is readily intelligible to its neighbor, where does Eastern Timbira stop and Western Timbira start? Where is the skin of the culture here?" Equally instructive of the problem of employing linguistic criteria in defining ethnic units is Sorenson's (1967) description of multilingualism within households in the central Northwest Amazon. Individuals marrying into a village, according to Sorenson, retain the use of their native languages, resulting in longhouses with individuals speaking four or more mutually unintelligible languages.

Hymes (1968) severely criticizes the one-language/one-culture notion and maintains that language is too general a concept to be of use in ethnic unit classification. Language can be divided into several distinct variables, including vocabulary, grammar, specialized codes, and phonology, each of which may vary independently and have important implications for social and ethnic distinctions. Mutual intelligibility, he adds, depends upon a complex of factors, many of which are nonlinguistic. Hymes (1968:29) quotes Nadel (1947:13) to illustrate his general point:

We shall meet with groups which, though they are close neighbors and possess an almost identical language and culture, do not regard themselves as one tribe . . . ; and we shall also meet with tribes which claim this unity regardless of internal differentiation. Cultural and linguistic uniformity, then, does not imply, and cultural and linguistic diversity—at least within certain limits—not preclude the recognition of tribal unity.

Similar criticisms apply to other sociocultural criteria that might be used in ethnic unit classification (LeVine and Campbell 1972:84-99). Because sociocultural characteristics vary continuously, they are incapable of delineating discrete, substantive ethnic groups. Furthermore, since individual sociocultural characteristics evolve in response to more or less independent selective pressures and do not necessarily vary collectively, the application of different definitional criteria could easily produce conflicting ethnic classification schemes.

As with efforts to define species boundaries, problems associated with ethnic unit classification arise from the contradiction of imposing a static classification scheme—no matter how necessary—upon inherently variable, evolutionary phenomena. Ethnic units within specific communities, like local species populations, are more or less distinguishable aggregates whose degree of differentiation is a function of prevailing ecological conditions. In a comment similar to that cited earlier for species, LeVine and Campbell (1972:99) emphasize that the occurrence of well-circumscribed ethnic units is not the rule, but the exceptional case requiring explanation. The discreteness of species and ethnic units alike, moreover, appears greater among

⁴ Naroll did not propose the cultunit to represent any substantive unit, but rather offered it simply as "an arbitrary definition whose justification is its convenience in cross-cultural surveys" (p. 291).

the more complex and broadly adapted members of each class, perhaps because of the greater breadth of their respective niches and the evolutionary exclusion of close competitors that this implies.

Socioculturally defined ethnic units are also likely to bear little relation to specific evolutionary processes (Leach 1964). Maquet (1971:7-8) illustrates this point for East Africa:

The kingdoms situated on the western shores of Lake Victoria were using the same techniques to cultivate similar crops; all the Lacustrine groups followed the same basic rules to count descent, to organize marriage; several of them had established about the same specific institutions (feudal ties existed in Ankole, Burundi, Rwanda); some myths and cults were widely spread in the area . . . ; social stratification and political systems were organized along the same patterns. There are thus cultural phenomena that seem to cross societal boundaries; to ignore that aspect of them is to distort the cultural picture of the region.

The numerous problems inherent in the delineation and application of socioculturally defined ethnic units have led several anthropologists to propose the population as an alternate analytical and investigative unit (Vayda and Rappaport 1968, Little and Morren 1976). Unlike a culture, society, ethnic group, tribe, or cultunit, the population contains a specific empirical referent that can be universally applied. The population also represents a more appropriate unit for analyzing evolutionary processes. Since selective forces operate upon local populations, it is upon these adaptive units that the examination of evolutionary processes must concentrate. The incidence and variability of social and behavioral characteristics, including those associated with the maintenance of ethnic boundaries, vary from one local population to the next, and it is only through an explicit spatiotemporal analysis at this level that an understanding of the sources of variation within and between human groups can be achieved. For these reasons, the concept of an *ethnic population* is proposed here as an alternative to that of an ethnic group.

A population in ecology consists of "an assemblage of organisms with a considerable number of characteristics in common, a similar origin, and no barriers that prevent individual members' freely interbreeding with one another when heterosexual organisms are brought together" (Boughey 1973:1). Accordingly, an *ethnic population* may be defined as an assemblage of persons with a considerable number of behavioral characteristics in common,⁵ a shared historical identity,⁶ and a higher incidence of marriage with members of the same population than with members of other populations. As with local species populations, local ethnic populations must be viewed as analytically and functionally distinct from the larger, more abstract categories with which they are associated. Local ethnic populations must also be recognized as variable in their dimensions, with

ethnic boundary configurations being a function of the ecological conditions imposed upon specific multiethnic communities.

Marriage assumes central importance in the definition and analysis of ethnic populations. Continuity and distinction among local ethnic populations is ultimately maintained by the fact that marriage between members of the same population occurs more frequently than marriage between members of different populations. Ethnic endogamy reduces the opportunities for choice in ethnic identification and preserves the differential distribution of distinctive ethnic characteristics within a community. Complete intermarriage among ethnic populations, on the other hand, eliminates local ethnic distinctions, since marriage functions (as does mating among species populations) to transfer a population's distinct adaptive characteristics from one generation to the next. In the case of ethnic populations, the adaptive characteristics transferred through marriage and threatened by interethnic marriages are material and behavioral and include wealth, access to resources, subsistence strategies, child-rearing practices, and participation in specific economic, political, social, and religious activities and organizations (see Davis 1941, Merton 1941, Goody 1976). Intermarriage among interacting ethnic populations has the same diluting effect upon differentiation within human communities that interbreeding among local species populations has within multispecies communities.

The extent of ethnic endogamy indicates the degree of ethnic differentiation within a community. Other criteria included in the definition of an ethnic population serve principally to distinguish this unit from other less enveloping social groups. These secondary criteria suggest that the organization of ethnic populations is more complex and encompassing than that of other social units. They also function as isolating mechanisms by enhancing ethnic identity within a community (see below).

Several advantages derive from the use of the concept of an ethnic population. First, ethnic populations are defined in terms of local empirical criteria rather than through the a priori imposition of external categories and their associated characteristics. This position is in agreement with that taken by Barth (1969b: 13-15). The definition of an ethnic population also recognizes an analytical distinction between this unit and many less integrated social groupings, such as political factions and religious congregations—a distinction that is not clearly made in Barth's definition of an ethnic group. At the same time, since the concept of an ethnic population acknowledges variability in the degree of ethnic status within a community, a framework is provided for examining the evolution of such less integrated social groups into more discrete and encompassing ethnic populations—as, for example, in the case of the Mormons. Since the recognition of local ethnic distinctions is based upon functional rather than purely cultural criteria, several populations considered analytically distinct by some researchers—including cultural, racial, religious, and caste groups—may more parsimoniously be treated as manifestations of equivalent ethnic phenomena, at least as regards their formation, maintenance, and dissolution as distinct social units. Finally, the acceptance of statistically definable ethnic populations (distinguished in terms of the degree of endogamy) standing in more or less distinct economic, political, and social relations to each other enhances our ability to determine the degree to which clear ethnic units exist within specific local communities in a more precise spatiotemporal framework.

Selection for the effective organization of populations within human communities clearly does not rely upon genetic mechanisms, but rather depends upon the transmission of learned behavior patterns. Biological, ecological, and social scientists alike, however, have recognized the broad applicability of natural selection as an explanatory model (Lotka 1922, 1945; Campbell 1965, 1973; Harris 1968, 1979; Margalef 1968; H. Odum 1971; Bohannan 1973; Ruyle 1973; Chagnon and Irons 1979). Campbell (1965:27) maintains that the applicability of

⁵ The common behavioral characteristics of an ethnic population include the criteria listed by Hardesty (1975, 1980) as defining the niche or "total ecological lifestyle" of a "cultural species"—that is, the specific resources exploited and the methods of resource exploitation associated with such units. Resources exploited and the techniques and organization of resource exploitation are important characteristics distinguishing local ethnic populations. However, because manifestly nonecological behaviors may perform important functions in a population's "life-support system" (Little and Morren 1976; cf. Rappaport 1968)—most notably as isolating mechanisms maintaining local ethnic distinctions (see below)—many apparently unimportant yet common behaviors may be of great significance in distinguishing local ethnic populations. As with species populations, the specific characteristics that are important in distinguishing local ethnic populations must be determined empirically in each instance.

⁶ The importance of a historical dimension in ethnic status lies in the depth that it adds to ethnic differentiation. Whether real or putative, assertions of common origin attach a greater temporal, and thus social, significance to an ethnic unit than to any other social group. The claim of historical distinction as a group—that is, a notion of direct descent and continuity from some ancestral population—underlies the primacy of ethnic identification over all other social identities.

a "variation and selective retention" model rests upon the presence of three criteria: "the occurrence of variations," "consistent selection criteria," and a "mechanism for the preservation, duplication or propagation of . . . selected variants." All of these features are inherent to human sociocultural systems.

Neither clear species nor ethnic distinctions can be accepted, then, as given within local communities. Rather, the discreteness of species and ethnic populations alike must be recognized as determined by local ecological conditions and thus variable from one community to another and within the same community through time. Since both species and ethnic boundaries function to regulate competing populations' access to resources, the recognition that in one case the proximate causes (mechanisms) of behavior may be largely inherited while in the other they may be primarily learned should not preclude the possibility that the ultimate causes (selective pressures) in both cases may be the same. Behaviors associated with the maintenance of local species and ethnic boundaries may be viewed within the general framework of "life-support systems" (Little and Morren 1976), that is, in terms of the role they play in advancing the interests (survival) of specific populations within their respective communities.

The significant question becomes under what conditions it is advantageous to have two or more distinct populations in a community and how such distinctions are created and maintained. With this question in mind, a general ecological model of species formation will be presented and its application to the formation of ethnic boundaries suggested.

THE EVOLUTION OF SPECIES BOUNDARIES

Isolating mechanisms are the "most important set of attributes a species has because they are, by definition, the species criteria" (Mayr 1963: 89). Inasmuch as species boundaries are defined by reproductive isolation, an explanation of the origin of species boundaries must account for the existence of isolating mechanisms separating sympatric populations. Since isolating mechanisms function to distinguish contiguous populations and reduce the incidence of interbreeding, it becomes necessary first to determine the conditions that select for two or more reproductively isolated populations within a community⁷ to the exclusion of one uniform population.

Selection theory predicts that in competition the "advantages must go to those organisms whose energy-capturing devices are the most efficient in directing available energy into channels favorable to the preservation of the species" (Lotka 1945: 185). If two populations are complete competitors and one is dominant over the entire niche,⁸ the more efficient competitor will expand and the less efficient competitor will contract until one population is completely eliminated from the arena of competition (Gause 1934, Hardin 1960).⁹ If, on the other hand, two

⁷ The term *community* as used here does not refer to a specified spatial unit, but rather denotes one level of analysis (along with the individual organism, the population, and the ecosystem) in general ecology. A community is defined as all the populations within a given area.

⁸ The ecological *niche* is the multidimensional position occupied by a population in the flow of energy through a community. The niche includes the physical space, functional role (including consumptive and nonconsumptive behaviors), and distribution along environmental gradients associated with a population. The *fundamental niche* corresponds to the position occupied by a population in a given territory in the absence of competition, while the *realized niche* consists of the actual portion of the fundamental niche filled by that same population within a particular community comprised of a specific set of competing populations. See Levins (1968: 39-65) and Vandermeer (1972) for discussions of the niche in ecological theory and Hardesty (1975, 1980) for discussions of the niche concept as it applies to human ecology.

⁹ Miller (1969: 65) distinguishes two strategies of competitive exclusion: exploitation and interference. The former occurs "when

populations vary in their relative competitiveness in different portions of the niche, complete exclusion may not result. Instead, each population may evolve to occupy a restricted portion of its fundamental niche where the competing populations exist sympatrically (Crombie 1947, Brown and Wilson 1956). *Character displacement* indicates that competing populations have evolved to exploit limited and noncompetitive ranges within their fundamental niches in territories where their distributions overlap. As additional species enter the competition, niche differentiation proceeds further and each population must occupy an increasingly reduced portion of its fundamental niche.

Environments differ in the degree to which resources are evenly distributed and may vary from having resources uniformly spaced (i.e., fine-grained) to having them coarsely distributed either spatially, temporally, or both (see Levins 1968: 10-38; Vandermeer 1972: 114-16). Other things being equal, the more profitable it is energetically for an organism to subsist on one resource to the exclusion of another, the greater is the selective advantage of two distinct populations over one uniform one, provided sufficient resources exist to support such specialization. Individual resources may also differ significantly regarding the mechanisms needed for their efficient exploitation and, therefore, in terms of the appropriate morphological and behavioral adaptations required. The greater the difference in the adaptations demanded for the efficient exploitation of two resources, the greater is the selective advantage of two distinct populations, each subsisting on one of the available resources. "Only if the resources are fine-grained and quite similar is a single uniform population theoretically superior" (MacArthur and Connell 1966: 98). The origin of species thus lies in the selective advantage of two distinct populations in place of one uniform population for the efficient exploitation of available resources.

Resource partitioning through interspecific competition may be illustrated by two examples, one experimental and one natural. The experimental example involves two species of flour beetles of the genus *Tribolium*. When individuals of both species are placed in an artificial ecosystem containing only wheat flour, one species consistently eliminates the other (Crombie 1947). Which species survives depends upon the climate imposed upon the ecosystem. One population expands under conditions of high temperature and humidity, while the other dominates under cool, dry conditions, even though members of each population can survive under a variety of temperature and humidity regimes in the absence of competition. If flour is replaced by whole-grain wheat, however, the two populations can coexist indefinitely, with each population exploiting distinct portions of the wheat grain. The example from nature concerns two varieties of nuthatches, *Sitta neumayer* and *S. tephronata*, distributed from east to west across Asia (Boughey 1973: 90-91). While these populations overlap in their ranges of distribution, *S. neumayer* occupies territory to the west of this overlap zone without *S. tephronata*, and *S. tephronata* exists to the east of it with no competition from *S. neumayer*. Where they exist separately, the two populations are quite similar in the range of variation displayed by bill length (a strong influence on resources exploited), coloration, and other important characteristics. Where they overlap and offer competition to each other,

two or more individuals or species have free access to a limiting resource and the outcome of competition is determined by their relative abilities to use the resources efficiently." The effect of interference, on the other hand, is "to prevent the access of a competitor to a required resource." According to Miller (p. 66), exploitation is more characteristic of populations that are strongly influenced by physical factors, while interference is more typical of those that are "biologically accommodated." These latter populations are generally those whose members have larger bodies and longer generations.

however, they have evolved quite distinct and nonoverlapping ranges in the variation of these same characteristics. Differential competitive abilities in different portions of the niche have resulted in each population's exploiting a fraction of its fundamental niche in territories where their distributions overlap. Competition has been eliminated not by complete exclusion of one population from a given territory, but by the elimination of competition in specific portions of the niche through selection for more specialized adaptations.

Resource partitioning in ecological communities derives from the competitive advantage of specialization. Species whose adaptive strategies are concentrated upon the exploitation of a limited set of resources tend to be more efficient in obtaining those resources than species that exploit a broad range of resources. Because of the competitive advantage of specialization, natural selection produces the greatest number of species possible within a given community, as resource partitioning occurs, up to the limits set by available resources. Inasmuch as the community serves as the principal source of the selective pressures imposed upon its constituent populations, however, the evolution of ecological communities (succession) must be viewed as a mutual-causal process. While speciation and species replacement contribute to the evolution of ecological communities, they also serve as mechanisms for "adapting parts (populations) to evolving systems" (H. Odum 1971:159).

Stability in ecological systems is increased by "maximizing the number of links in the food web of the community" (Leigh 1965:777).¹⁰ Each new niche permits the maintenance of an additional species which, through its contribution to community regulation, functions to lower relative system energy requirements. More species and biomass may be supported through the intensive utilization of the same amount of potential energy (Margalef 1968). Speciation and species replacement thus in-

¹⁰ Considerable controversy has surrounded the discussion of complexity and stability in ecological communities (Brookhaven National Laboratory 1969, Holling 1973, May 1973, Cody and Diamond 1976). While MacArthur (1955; MacArthur and Connell 1966) and others have maintained that more complex ecological communities are inherently more stable than less complex ones, May (1973) and Leigh (1976) have cogently argued for the inherent instability of more complex systems. While arguing for the greater theoretical instability of more complex systems, May (1973:75-76) acknowledges the empirical association between complexity and stability in ecological communities. He suggests, however, that factors other than complexity contribute to the stability of such communities, emphasizing their "more thorough exploitation of the community's total resources."

May (1973) and Leigh (1976) maintain that only a very specific form of species diversity contributes to greater community stability. Multiple, density-dependent links between species populations at various trophic levels must exist if population regulation is to be effective. Complexity enhances stability *only* where species interactions furnish redundancy in community resource flows. Only in those communities where such redundancy exists can one population's response to environmental variation be neutralized by the response of competing populations as well as of populations at different trophic levels. This specific form of complexity appears to be the form that is, in fact, most widespread in multispecies communities.

More complex human ecological communities likewise possess a greater capacity for response to environmental disturbances than less complex ones and are more likely to achieve endogenous regulation of community parameters. As with nonhuman communities, the greater redundancy of resource flows in complex human communities underlies their ability to achieve limited internal regulation. Endogenous regulation in human communities can only derive from a diversity of resource flows whereby a failure in one circuit can be compensated for by productivity in another.

The greater stability of complex human and nonhuman ecological communities alike derives ultimately from the productivity and stability of encompassing ecosystems (cf. Sanders 1968, Abruzzi 1981). The complex regulative functions performed within diverse communities require a continuous and substantial flow of resources for their maintenance. Consequently, while capable of mitigating minor disturbances caused by environmental instability, complex ecological communities are particularly vulnerable to major disruptions in the flow of energy. Substantial dislocations in resource availability undermine the selective advantage of specialization and jeopardize the niche differentiation upon which the regulative capacity of complex communities is based.

crease community efficiency, in part, by increasing community stability. Because stability enhances the efficiency of resource exploitation, ecological communities evolve to the most complex point possible within the energetic limits of encompassing ecosystems, making succession a process inherent in the energetic relations within and between ecological systems subject to natural selection (Margalef 1968:82). The agent of ecological succession, then, is natural selection adapting populations to communities and communities to ecosystems.

The role of isolating mechanisms in community evolution now becomes clear. Since specific resource configurations select for appropriate population configurations, a selective advantage accrues to those mechanisms that maintain the adaptive organization of a community and inhibit the rearrangement of its constituent populations. Community stability in certain instances would be threatened by the production of a hybrid population as a result of the interbreeding of interfertile members of populations with distinct resource adaptations. A decrease in community stability would, in turn, reduce the efficiency of resource exploitation and lead to the extinction of certain populations within the community. Under stable ecological conditions, then, selection would favor any mechanism that reduced the incidence of interbreeding among those distinct populations favored by available resources.

Mayr (1963:92) classifies isolating mechanisms into two categories: premating and postmating. Premating mechanisms, because of their greater efficiency, are highly susceptible to improvement by natural selection. These serve to prevent members of distinct populations from engaging in mating behavior and include seasonal and habitat isolation, ethological isolation, and mechanical isolation. Postmating mechanisms reduce the likelihood of successful reproduction once mating has occurred and include gametic mortality, zygotic mortality, hybrid inviability, and hybrid sterility. Mayr (1963:95) stresses that "ethological barriers to random mating constitute the largest and most important class of isolating mechanisms in animals."

Ethological barriers include those behaviors which foster "species recognition." These may be visual, such as the light flashes of fireflies or the mating dances of birds, or they may be auditory, including the familiar sounds of crickets, birds, and frogs. Chemical stimuli may also be employed in species recognition. Chemical stimuli which operate upon the sense of smell are common among mammals, while those that work upon physical contact are widespread among marine organisms. During mating, each behavior (stimulus) warrants an appropriate response, and this response functions as a reinforcing stimulus for a reciprocal response. A proper sequence of behavioral exchanges between a male and a female results in a successful mating, whereas an inappropriate response in the sequence reduces the likelihood of success. Premating isolating mechanisms, including those not directly associated with mating behavior, enhance the efficiency of intrapopulation mating by reducing the potential for interpopulation crosses.

Complete reproductive isolation between two sympatric populations normally results from the redundancy provided by a variety of isolating mechanisms. An increase in the number of independent isolating mechanisms functions like a series of hurdles and results from the operation of natural selection under stable ecological conditions. The evolution of distinct coloration among sympatric populations of the nuthatches mentioned previously now becomes clear. Where the ranges of these birds overlap and selection has favored discrete adaptations, their distinctive coloration functions as an isolating mechanism enhancing species recognition and reducing the likelihood of interbreeding. Where selection favors the existence of two distinct populations, isolating mechanisms evolve to preserve that distinction and reduce the incidence of behaviors that would result in one hybrid population.

Since selection for species distinctions operates to the degree that an adaptive response is genetically controlled, the greater

the heritability of specific adaptive behaviors, the greater is the likelihood that an adaptive advantage possessed by a population will become part of the behavioral repertoire of future generations. Inasmuch as it is possible to select animals that respond to environmental stimuli with increasingly less conditioning until a strain is produced that responds without previous conditioning (Waddington 1957), stable ecological conditions select for increasing hereditary control of reproductive isolation between potentially interbreeding populations. Such developmental canalization is basic to the evolution of complex biological and ecological systems (Stebbins 1968, Slobodkin 1968, Margalef 1968). The significance of the species boundary, then, derives from the fact that reproductive isolation protects against the dissolution of each population's distinct, integrated, and coadapted gene system (Mayr 1963:423).

Accordingly, a breakdown in the barriers to mating between two sympatric populations results from a change in resource availability to a situation favoring a single population. In such cases, one hybrid population replaces two parental ones. Sometimes the barriers between two populations break down so completely over an extended area that a "hybrid swarm" results (see Mayr 1963:118-25). A hybrid population serves as a bridge between two parental populations and demonstrates again that reproductive isolation may have nothing to do with sterility.

The conditions underlying the formation of species boundaries may be summarized as follows: Where natural selection favors the existence of distinct adaptations, discrete populations are likely to occur to the exclusion of one uniform population. The development of numerous, genetically inherited isolating mechanisms reduces the incidence of interbreeding between sympatric populations and insures that evolutionary gains accrued to local populations are not lost through the sharing, and thus dilution, of adaptive genetic material. The specific configuration of populations within a particular community is a function of the resources available in conjunction with the dominance relationships present. Selection for discrete populations contributes to, and is a product of, the evolution of ecological communities. Furthermore, while community stability selects for the improvement of isolating mechanisms, the advancement of these mechanisms promotes community stability. Succession is, therefore, a mutual-causal process. Conversely, a breakdown in the operation of isolating mechanisms and the consequent emergence of hybrid populations results from a change in the structure of resource availability within a community such that the previous population configuration is no longer selectively advantageous.

THE FORMATION OF ETHNIC POPULATIONS

The implication of selection theory for the formation of ethnic populations seems clear. Where energetic demands for the efficient exploitation of different resources favor distinct adaptive strategies within the same community, selection should produce two or more socially discrete populations to the exclusion of one uniform population. The organization of human communities derives from the labor requirements for effective resource exploitation within the conditions imposed by encompassing ecological systems (Harris 1964). In certain human communities, it may be energetically cheaper for distinct populations to exploit limited and nonoverlapping sets of resources, with each population trading its surplus to neighboring populations concentrated in different niches, than for one undifferentiated population to exploit the total range of available resources.

The most common examples in the anthropological literature of discrete, sympatric ethnic populations occur precisely in those communities in which the populations concerned are associated with specialized resource exploitation. These include contiguous nomadic and sedentary populations (Barth 1956, 1961, 1964a;

Turnbull 1965; Haaland 1969; Dyson-Hudson 1972; Horowitz 1972; Nelson 1973; Peterson 1978), populations concentrated in extensive systems of preindustrial trade (Cohen 1969; Eitzen 1973; Foster 1974, 1976; Fidler 1978), and communities focused upon the exploitation of plantation agriculture (Goldschmidt 1947; Wolf 1959; Geertz 1963; Harris 1964; Shibutani and Kwan 1965:160-61, 183-85; Despres 1969; Grebler et al. 1970).

The distinct requirements imposed for successful exploitation of a herding or hunting (nomadic) niche contrast sharply with those needed to occupy a farming niche. Most significant is the differential demand for mobility. The survival of grazing animals, be they domestic or wild, demands that these animals be mobile in their search for pasture and water. Human populations that exploit these animals must likewise be mobile. Farmers, on the other hand, must remain stationary and tend to their land and crops. Each adaptation demands a distinct repertoire of supportive behaviors. An energetic advantage thus clearly exists, under certain conditions, for distinct populations concentrated in each of these two niches rather than one uniform population exploiting both plant and animal resources.

The demands of extensive trade within preindustrial communities—exchange of information between trading centers regarding the conditions of supply and demand, speed, and large extensions of credit and trust among complete strangers in the absence of protective institutions—are effectively overcome by the concentration of trade in the hands of one distinct population (Cohen 1969:17-22). The concentration of a distinct population on the management of preindustrial trading enterprises also facilitates negative reciprocity (Foster 1974).

Plantation agriculture involves the use of large amounts of land for the purpose of raising labor-intensive cash crops. This strategy of resource exploitation demands the massive employment, during critical periods in the agricultural cycle, of unskilled labor under the direction of a small, highly capitalized and managerially skilled entrepreneurial class and is characterized by the absence of an occupational continuum between these two groups. Since the short-term demand for unskilled labor limits its annual productive value, labor in plantation systems has historically been obtained primarily through slavery, immigration, or the employment of migrant workers (Shibutani and Kwan 1965:162). In each case, the adaptive strategies demanded of laborers and owners have yielded markedly distinct life-support systems.

These three contexts provide, fully developed, the clearest examples in the anthropological literature of the evolution of distinct adaptations among potentially competing human populations. They also furnish the most lucid instances of pronounced ethnic distinctions within human communities. Overt competition, while not absent in these situations, has been reduced through the development of more or less symbiotic relations, imposed in part by the greater power of the dominant population, and through the institution of complex regulations regarding ethnic interactions, particularly intermarriage.

Competitive exclusion operates among human populations. If two populations enter into competition over the exploitation of a given set of resources, the more efficient competitor expands against the less efficient one, and the latter population is eventually excluded from the contested portion of the niche. Competitive exclusion may result in the complete local elimination of one of the competing populations or, if the complexity of the community permits, its restriction to a reduced portion of its fundamental niche. The configuration of the less dominant population's realized niche will depend upon the breadth of the successful competitor's dominance. The less efficient competitor may be reduced in numbers either through actual expulsion from the habitat or through incorporation into the more successful population. The incorporation of members from a less dominant population may comprise a significant component in

the expansion of a successful population (Barth 1964*b*, Dozier 1970, Cohen and Middleton 1970, Newcomer 1972).

Character displacement through niche diversification occurs within human communities, reducing the level of competition between two populations while permitting a continued overlap in their territorial distribution. Inequality exists in such relationships, however. Consistent with comparable energy flows in other ecological communities (Margalef 1968:16), ethnic interactions within human communities are asymmetrical and function to maintain, even increase, the differential organization and control that exist. The distribution of subsistence strategies among the Rwanda in East Africa (Lemarchand 1966) illustrates the occurrence of character displacement through niche diversification as one population expands into the habitat of another. The range of resources directly exploited by Hutu farmers appears to vary with the length of time they have been in contact with Tutsi herders. In central Rwanda, where the penetration of the Tutsi into Hutu territory is the oldest, Hutu participation in independent herding is least and the castelike distinctions that separate the two groups socially are the most elaborate. In northern Rwanda, where contact between these two populations is more recent and less intense, Hutu involvement in herding is much greater and "ethnic coexistence" prevails.

Niche diversification through competitive exclusion may ultimately result in human populations' achieving an equilibrium in which they exchange the products of their differentiated niches. The potential for developing symbiotic relationships is perhaps more characteristic of human competitors than of most other populations. This is most clearly illustrated by the consistent development of interdependence between contiguous nomadic and sedentary populations throughout much of Africa and the Middle East. As with nonhuman populations, however, competition among human populations is potentially variable. While it is likely that certain populations within ecological communities may be in varying degrees of competition with each other, it is unlikely that any community, especially a human one, will have many populations that can be considered truly symbiotic. Nomadic pastoralists and sedentary cultivators exhibit important symbiotic exchanges; yet they present a significant degree of competition with each other, as land is a finite resource required by both. The level of competition between such juxtaposed populations becomes particularly acute during periods of reduced productivity, such as those which accompany a drought. In the same manner, competition for land is by no means absent among the castes of India (Epstein 1962, Berreman 1967), the profit of merchants derives from the price paid by their customers, and the wages of laborers on plantations must come directly from the profits of the entrepreneurs (and vice versa).

Whether exclusion is achieved (1) through exploitation and/or interference, (2) through the elimination of an unsuccessful competitor by expulsion or incorporation, (3) through niche diversification, with or without the development of symbiotic relations, or (4) through any combination of the above, the effect is the same. One population is eliminated from access to specific resources.

Since different strategies of resource exploitation select for distinct patterns of labor organization, selection within human communities would favor any mechanism that maintained the adaptive organization of a community. Inasmuch as ethnic endogamy maintains local ethnic distinctions, selection would specifically favor those mechanisms that reduced the incidence of intermarriage among ethnic populations in communities where ethnic specialization occurs. Although the specific cluster of isolating mechanisms varies from one human community to another (Barth 1969*b*: 14), under stable ecological conditions the number of independent isolating mechanisms separating two or more local ethnic populations should increase with time. Reproductive isolation underlies the recurring pattern of ethnic

relations associated with expanding pioneer populations (Shitani and Kwan 1965, Schermerhorn 1970). Initial flexible interactions evolve into more rigid, stereotyped exchanges as the number of immigrants increases and the competition over resources intensifies. Anglo-American relations in the American West provide an example of this pattern (see also Peterson 1978).

Isolating mechanisms among human populations are just as varied as those that separate nonhuman populations, and premating mechanisms are likewise the most efficient and the most susceptible to selective improvement. Premating mechanisms that foster "ethnic visibility" are quite common. Such mechanisms limit or stereotype the interactions of local populations and, by heightening the recognition of ethnic identity, reduce the likelihood of interethnic marriage. Premating isolating mechanisms among human populations include residential concentration, occupational specialization, distinct forms of dress and speech, separate public facilities, public rituals, prescribed and proscribed patterns of social interaction, courtship and marriage rules, folklore, and any other factor that exhibits local ethnic distinctions.

Since selection for ethnic differentiation operates upon learned behavior patterns, the more such isolating mechanisms become institutionalized (see Barth 1967) as part of the explicit rules of a community (i.e., part of the law, religious doctrine, or governing ideology), carrying unambiguous community response, the greater is the likelihood that they will be maintained in that community in the following generation. Stable ecological conditions, therefore, select for increasing legitimacy of the social and reproductive isolation of potentially competing ethnic populations.

An increase in the complexity of isolating mechanisms separating ethnic populations reduces the permeability of ethnic boundaries and standardizes social behaviors as they relate to intra- and interethnic relations. As LeVine and Campbell (1972: 159) note, "since the role relations set not only the most frequent opportunities for observation, but also the most frequent opportunities for interaction, the stereotypes are likely to lead to socially adaptive, appropriate behaviors a large portion of the time."

A "self-fulfilling prophecy" with respect to interethnic transactions develops which serves to legitimize the distinctions that exist. Pluralist ideologies, which further legitimize ethnic distinctions, canalize social separation and thus increase the barriers to interethnic marriage. Berreman (1967), discussing caste ideology in India, argues that the emergence of a broad consensus within communities is inimical to the stability of such pluralist systems. Consensus, he stresses, would result in common behavior which threatens the existence of caste boundaries (cf. Bailey 1957). Barth (1969*b*: 18) concurs on the role that indigenous belief in the legitimacy of ethnic distinctions plays within local communities: "So also can all ethnic groups in a poly-ethnic society act to maintain dichotomies and differences. Where social identities are organized and allocated by such principles, there will be a tendency towards canalization and standardization of interactions and the emergence of boundaries which maintain and generate ethnic diversity within larger, encompassing social systems."

Given the conditions imposed upon multiethnic communities, individual maximization is achieved by employing the existing organization to one's own advantage (Bailey 1957, Cohen 1969). The interests of members of the dominant population are served by retaining the boundaries and dichotomies that exist. Members of the subordinate population, who do not possess the power to eliminate existing boundaries, serve their interests by publicly adopting the behavioral correlates of those boundaries during intra- and interethnic transactions.

Where the existence of distinct adaptations within the same community is energetically superior, then, stable ecological conditions should select for an increase in the number *and*

legitimacy of isolating mechanisms separating two or more ethnic populations, leading to a greater concordance between ethnic boundaries and certain behavioral characteristics. The possession of such "common cultural characteristics" within local populations is a part of, not a cause of, the formation of distinct ethnic populations, however (see Shibutani and Kwan 1965, 148; Barth 1969b: 11). Indeed, the extent to which certain behaviors are common to members of an ethnic population suggests the degree to which local populations are discrete and functionally distinct ethnic units.

The formation and maintenance of distinct ethnic populations must be viewed as a function of niche diversification at the community level. The selective advantage of clear ethnic boundaries derives primarily from the demands imposed upon labor. Labor demands, in turn, are a function of the specific pattern and intensity of resource exploitation imposed upon local communities (for example, by population pressure or colonial domination). Where the demands of a specific productive system place a selective premium upon discrete populations, the efficiency of human information processing and group coordination are increased by the existence of clear and unambiguous boundaries separating these populations. Clear ethnic boundaries also function to improve productive efficiency by reducing the likelihood of competition between members of interacting populations within the community.

Since the organization of populations within any ecological community is a function of the availability and distribution of resources, a breakdown in the barriers to marriage between ethnic populations results from a change in the conditions of resource exploitation to a situation favoring a different community organization, perhaps even one uniform population. The emergence, decline, and transformation of socially significant ethnic units have been ubiquitous and may be seen as adaptive responses to changing material demands imposed at the community level (Wallerstein 1960, Harris 1964, Fried 1966, Cohen and Middleton 1970, Newcomer 1972, Young 1972, Noel 1973, Friedman 1973).

In summation, then, it has been suggested that populations in human communities respond to conditions of resource availability in much the same way as populations in nonhuman communities. Through competitive exclusion, human populations will, to the degree that it is selectively advantageous, develop more or less discrete adaptive strategies within the same community. The greater the selective advantage of distinct adaptations within local communities, the greater is the likelihood that socially discrete ethnic populations will be associated with those adaptations. The evolution of numerous, legitimized isolating mechanisms within human communities enhances ethnic distinctions by reducing the incidence of intermarriage between members of interacting ethnic populations. By minimizing the incidence of intermarriage, isolating mechanisms protect the advantageous position of the dominant population. At the same time, clear and stable ethnic boundaries provide security and predictability in ethnic relations for members of the subordinate population, who are unable to alter the organization of the community to their own advantage.

Since the formation of ethnic boundaries among local populations contributes to and is a function of the stability of the larger community, stable ecological conditions result in a mutual-causal amplification of community stability and ethnic distinctions. A breakdown in the operation of isolating mechanisms among local populations results from a change in the organization of resource exploitation within a community and, therefore, in the demand for labor. Significant population distinctions may no longer be selectively advantageous, or some intermediary population (labor source) may be needed.

This article has suggested that the formation of distinct ethnic populations in multiethnic communities results from the same process that leads to species formation in multispecies communities. The similarity of species and ethnic differentia-

tion derives from the fact that both species and ethnic populations are more or less distinguishable, adaptive units in the flow of resources through their respective ecological communities. A greater understanding of both processes may be gained, therefore, by approaching each as a manifestation of the same organizational response of ecological communities to the selective pressures imposed by conditions of resource availability. The suggestion is also that human communities are variants of ecological communities and that the organization and evolution of all ecological communities, regardless of their specific biological composition, can be explained from identical theoretical principles.

Comments

by JUDITH BROWN and THOMAS E. DURBIN

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24 VII 81

The development of a general model of speciation (resource partitioning) in multispecies communities explaining the formation of ethnic boundaries within human ecological communities should include a review of the species concept, the definition of an ethnic unit, the evolution of species boundaries, and the formation of ethnic populations. Abruzzi has addressed himself to these considerations with varying degrees of success.

We agree that the traditional concept of species was too static, that dynamic boundaries surround all species populations, and that, under certain circumstances, various species populations will interbreed. Mechanisms evolve preventing such interbreeding as long as diversity of species is ecologically or thermodynamically advantageous. Focus on this phenomenon is indeed important.

Abruzzi has well reviewed the many definitions of ethnic units, and his proposed definition of the ethnic population can be readily applied to the communities of the Valley of Toluca, Mexico (Durbin 1970, 1974, 1976; Brown and Durbin 1977; Reina 1965). Barrios and entire communities of specialized potters in Metepec, San Pedro Tecamatepec, and Temascalzingo, serape weavers in Coatepec Harinas, rebozo weavers in Tenancingo, basketry makers in Santa Ana Tlapatlán, Toluca, and wooden-utensil carvers in Ixtapan de la Sal and Tonatico can be identified as such ethnic populations. These barrios and communities may be viewed as aggregates whose degree of differentiation is a function of prevailing ecological (economic) conditions. They have occupied clearly differing economic niches since prequest times, niches that are only now being threatened by modernization-industrialization and the accompanying dramatic socioeconomic changes.

In Abruzzi's discussion of the evolution of species boundaries, the first two of Campbell's (1965:27) criteria for the applicability of natural-selection model are well illustrated, but the mechanism is viewed as operating only on the species level while widespread recent theorizing suggests the possibility that such mechanisms operate on the level of the individual and even on the level of the gene. Would such a concept affect the author's proposals? In any case, this third criterion, analogous to genetic transfer of chosen variants, may be fulfilled in the ethnic population example by the institutionalization of values encouraging endogamy.

That species boundaries evolve primarily because of the selective advantage of two distinct populations in place of a uniform one and that resource partitioning in ecological communities derives from the competitive advantage of specialization and presumably contributes to the evolution of ethnic

boundaries are acceptable. However, that when a multispecies population becomes thermodynamically inefficient hybridization or a single-species takeover will result may be more easily observed in the ethnic population; more examples in nonhuman ecological systems would have been more supportive of this point. The general trend of nature is, of course, normally toward producing isolated species (diversification). Certainly, in the Valley of Toluca, industrialization is rendering inefficient the traditional economic and ethnic diversity, encouraging the appearance of a single, more uniform socioeconomic Mexican-national entity.

Abruzzi refers to Margalef (1968:16) in noting that, consistent with comparable energy flows in other ecological communities, ethnic interactions within human communities are asymmetrical and function to maintain, and even to increase, the differential organization and control that exists. This can be observed in the Valley of Toluca, with elite populations rigidly maintaining the status quo and nonelite specialist populations doing so until the issue of dominance by the elite populations may be forced at some future time. The traditionally stable ecological conditions have indeed selected for the social and reproductive isolation of these potentially competing populations, although at present a breakdown in the operation of isolating mechanisms among the local populations has occurred and significant population distinctions are no longer selectively advantageous under new socioeconomic conditions. Viewing ethnic populations not as unchanging, isolated units, but as dynamic, fluctuating entities which respond to ecological change allows for much better understanding of the Tolucan situation.

by RICHARD C. FIDLER

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Abruzzi's basic concept of applying an ecological approach to the analysis of ethnic differentiation and the structure of multiethnic societies is both illuminating and valid. This has been evident since the pioneering work by Barth (1956) on the ecologic relationships of ethnic groups in Swat. Barth's article contains, in its four summarizing "viewpoints" (p. 1088), the foundations of Abruzzi's major premises, that (1) the distribution of ethnic groups is controlled by ecological factors, (2) different ethnic groups can establish stable coresidence in an area if they exploit different ecological niches, (3) if two groups are able to exploit the same niche fully, the more powerful will normally replace the weaker (Abruzzi's "competitive exclusion"), and (4) if different groups exploit the same niches but the weaker can better utilize marginal environments, the groups may coreside (Abruzzi's "character displacement"). My concern regarding Abruzzi's article is, therefore, not his application of ecological theory to ethnic questions, but his tendency to do so too literally.

Ecological theory has contributed greatly to the analysis of many aspects of human societal relationships—urbanism and warfare are two other topics that have recently employed it, and its relationship to social structure was cemented by the classic study by Steward (1955). It has always worked best when taken as an *analogy* for societal behavior rather than as a formal *model*. The problem, and danger, of the latter usage is a renascent form of "ecological determinism." A prime example of this liability is Abruzzi's treatment of the formation of ethnic populations. He states that "where energetic demands for the efficient exploitation of different resources favor distinct adaptive strategies within the same community, selection should produce two or more socially discrete populations to the exclusion of one uniform population." This implies that ethnic diversification is a *requirement* for efficient exploitation of varied resource niches, not merely one of several potential social adaptations. It ignores the evidence in both the scientific

literature and empirical observation that uniform communities can and do exploit two or many, many more differing resource niches. The Fulani of northern Nigeria (Hopen 1958; Stenning 1959, 1965), for example, not only practice settled agriculture and nomadic pastoralism, but have a recognized and frequently utilized transitional continuum between the two polar techniques. Contemporary American society alone is sufficient to belie the literal application of Abruzzi's proposition; the only resolution is to accept the definitions of occupation and ethnicity as synonymous. By marrying a farmer's daughter, have I engaged in interethnic marriage? This statement also assumes that "efficient" exploitation of resources is somehow preordained as the inexorable demand of social systems, when in reality humans, both as populations and as individuals, are notorious for placing other concerns and principles before those of rational energetic efficiency. Idi Amin's expulsion of the Ugandan Asians, Pol Pot's purges, and the American love for the heavy gas-guzzling automobile are but three of the vast variety of examples of this specific quirk.

The above statement, especially when combined with the later one that "the formation and maintenance of distinct ethnic populations must be viewed as a function of niche diversification at the community level," also ignores the historical realities of contemporary multiethnic societies and probably of most such societies throughout human history. Specific traceable events and decisions in the political, economic, and demographic histories of multiethnic societies such as Malaysia, Hawaii, and Nigeria are the causes of their contemporary ethnic pluralism. Ethnic specialization in the exploitation of differing resource niches unquestionably contributes vastly to their ability to maintain stable coresidence today, but it is not what made the Chinese different from the Malays or the Japanese different from the Caucasian *haole* and is only one of the many factors that retards their amalgamation. Given an untouched and untouchable island ecosystem—an ethnic Galapagos—Abruzzi's contentions might hold true; add one boatload of immigrants and the model is swamped by ramifying complexities.

Perhaps the root of this problem can be found in Abruzzi's treatment of the concepts and definitions of species and ethnic populations, for although he demonstrates that the two are very much alike they are most definitely *not the same*. One demonstrative aspect of this fact that he does not discuss is the difference in their immutability, that is, in the permeability of their self-identifying boundaries. A mallard duck may be able to interbreed with a pintail if it so chooses, but it has no mechanisms under its control to *become* one. The more ethnic boundary distinctions are drawn from phenotypic characteristics (such as skin color) the more this holds true for humans as well. But, as Abruzzi himself states, "selection for the effective organization of populations within human communities clearly does not rely upon genetic mechanisms, but rather depends upon the transmission of learned behavior patterns." What is learned can be unlearned; what is transmitted can be transformed. Since ethnic distinctions rely less upon the existence of differences than on the *perception* of differences, both individuals and populations can actively direct identity changes to suit their current strategic requirements. Perceptual boundaries are ideational—they are boundaries of the mind, and minds can change and be changed. Etruscans become Romans become Italians; in one life span a Palatine German immigrant transmogrifies into an American WASP; but a rose is a rose is a rose.

It is in the usages human populations, as compared with nonhuman species, *make* of their ethnicity that Abruzzi's model breaks down. It is in these enormously variable usages that the excitement of the social sciences is found. Abruzzi's article provides a great contribution to our understanding and analyses of these complex behaviors, but it is only a beginning.

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The author's synecological approach to the explanation of ethnic diversity not only makes sense out of some old anthropological puzzles, but also identifies new analytical units and research strategies. Perhaps equally important is the clear statement of the interface between biology and culture in ecological theory. The use of general ecological principles in human ecology does not demand the assumption that human behavior is genetically inherited; it does demand the assumption that biology and culture have some common underlying principles that can be used to explain their variability in time and space. Perhaps the key principles are energetic, as the author implicitly argues, or economic. Perhaps they are statistical. Abruzzi follows Margalef and Eugene Odum, among others, in positing deterministic, energetic principles to explain the evolution of ecological communities and, as a special case, ethnic diversification. That is one possibility, but, as I am sure he is aware, another school of thought about community development would explain ethnic diversification by statistical principles. Rather than ultimately reducing adaptive problems to the laws of thermodynamics, Simberloff, Raup, Gould, and others ask whether the problems of adaptation are not sufficiently complex in each case to justify treating a species adaptation as a statistically independent event. If so, species or ethnic groups within a community emerge or become extinct randomly. My point is that general ecological theory offers several competing explanations of community diversification and that more attention must be given to sorting out these alternatives as better or worse models of ethnic patterns. Abruzzi might also consider how data on human ethnic diversity can contribute to modifying or rejecting general ecological principles originating in the study of nonhuman species. We can, after all, play a role in the *development* of general ecological theory.

With regard to the "diluting effect" of interethnic marriage, is it not possible that a *new* ethnic group is formed by the offspring of such marriages? If so, interethnic marriage could actually increase ethnic differentiation.

I have some question about the relationship between stability and community diversity. Does diversity promote stability of the community, or does a stable environment promote diversity? The author treats this question in some detail in a footnote without really getting into the implications of variable and stable environments for understanding ethnic patterns.

by PETER HINTON

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In the concept of ethnic population, the idea of ethnicity is linked with the ecological concepts of population and speciation. Thus an ethnic population is defined as "an assemblage of persons with a considerable number of behavioral characteristics in common, a shared historical identity, and a higher incidence of marriage with members of the same population than with members of other populations." Consequently the phenomenon of exogamy/endogamy assumes central importance, so that "the extent of ethnic endogamy indicates the degree of ethnic differentiation within a community." There is a difficulty intrinsic to these propositions which seriously detracts from the value of Abruzzi's concept. This is the fact that it is logically impossible to measure degrees of endogamy until one determines the group boundaries within which the endogamy occurs (after all, the whole of the human species is an endogamous group). This entails the identification of general criteria for group identity. Abruzzi does not help us very

Abruzzi: ECOLOGY AND ETHNIC DIFFERENTIATION

much here: the idea of "an assemblage of persons with a considerable number of behavioral characteristics in common [and] a shared historical identity" is so general as to be of dubious utility.

Abruzzi's reasons for tendering such a general definition are clear enough: he is aware of the pits into which others have fallen in defining and identifying ethnic groups and is anxious to avoid taking a false step himself. In so doing he follows Barth in preferring definition of ethnic groups "in terms of local empirical criteria" to "a priori imposition of external categories and their associated characteristics." He recognizes that Barth makes no clear analytical distinction between ethnic and other (e.g., political, religious) criteria for membership and believes his own concept is better because it "recognizes an analytical distinction between this unit and many less integrated social groupings." But this formulation once again begs the whole question: does ethnicity have any special integrative power, and, if so, what is it derived from? I find it hard to see how one can retain the notion of ethnicity at all in such an argument without recourse to unsatisfactory mystifications like Geertz's assertions about the binding power of "primordial sentiments."

Further, it is my view that, for all its currency, the idea of ethnicity has nothing to add to the perfectly serviceable concept of culture. In fact, by its combination of empty psychologism and obfuscation of important political and economic processes it has retarded our understandings. Recent innovations in anthropological thought have come from quite different directions: among these developments I would number the rekindling of interest in the process of social evolution and the adoption of ecological frameworks. I would like Abruzzi to have considered the epistemological standing of the idea of species with that of ethnicity towards a critical evaluation of both: in fact, at several points he seems on the verge of doing just this. These are by far the most interesting parts of the paper. In the event, his effort is directed fundamentally at breathing life into ethnicity by wedding it with speciation, a step away from potentially fruitful lines of enquiry.

by M. G. HURLICH

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Abruzzi provides a useful exercise in applying ecological theory to a specific issue in anthropology. Several strong points of his paper stand out. First, I agree wholeheartedly that ecological theory and methods are productively applied to human populations in the analysis of a limited (but growing) set of questions, among them whether cultural restrictions on reproductive behavior lead to maximization of reproductive success (Blurton-Jones and Sibly 1978) and whether hunter-gatherer foraging strategies are predictable by consideration of ecological factors (Winterhalder and Smith n.d.). I suspect that questions of group formation, maintenance, and dissolution will also eventually have partial answers supplied by application of ecological theory. Second, Abruzzi's focus on what it is that maintains boundaries between ethnic groups seems well placed. In fact, refinement of the nature of boundaries (Barth 1969b) would be productive, since it is unlikely that ethnic boundaries form only as a consequence of the requirement to maximize energetic efficiency.

Several weaknesses in his paper, unfortunately, also stand out:

1. Competitive exclusion is a theoretical statement that has as only one of its predictions the elimination of the less successful population from a portion of its niche. Unstable equilib-

rium points at which both populations survive are, though rare, theoretically possible outcomes (Winterhalder 1980). Further, because of both genetic and behavioral variations no two populations are *complete* competitors. Finally, the competitive exclusion principle is a tautology in that no data can be mustered to test it. By definition, to the extent that populations overlap they do not compete, and vice versa. Consequently, competitive exclusion cannot without further examination be invoked as an explanation for resource partitioning between ethnic groups, to the extent that such partitioning does in fact occur.

2. Key concepts need to be defined or amplified. What, for example, is meant by selection or selective pressure as applied to the origin of ethnic groups? How are we to measure energetic efficiency (in calories, money, time)? Finally, from whose perspective should energetic efficiency be assessed (for example, that of the owners of plantations, of the slaves who farm them, or of the entire collective population)?

3. Abruzzi equates ethnic groups with species but discusses them as gene pools with barriers minimizing gene flow across their borders. Ethnic groups are like neither species nor gene pools, however, in that they have means other than mating for population recruitment (Barth 1969b). Also, hybrids, or, in Izikowitz's (1969:45) term, "middle groups," can form, leading to new ethnic identities, in ways Abruzzi argues are unlikely for species. Perhaps most commonly, as Izikowitz notes (p. 145), middle groups form "in contact zones between Western societies and the traditional ones."

Underlying these comments is the more basic criticism that to understand the evolution of any aspect of human culture or behavior it is not sufficient to argue by analogy or to assume that evolutionary and ecological theory are applicable. Rather, the utility of theory must be demonstrated. We must also ask if, at this point in its development, it imposes an unfair burden on ecological theory to have it explain the origin of human ethnic groups. If an attempt such as this is less than fully successful, however, we must not be tempted to throw the baby out with the bathwater.

by JOHN C. KENNEDY

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8 VII 81

While I differ with Abruzzi over how far his argument can be applied, I commend him for presenting a consistent (if somewhat dry and mechanical) explanation of the formation and maintenance of ethnic boundaries. Three reservations may be noted.

First, since Abruzzi's brand of ecological theory is more solidly grounded in formal biological/ethological theory than that of earlier ecological anthropologists, old questions about applying biological theory to cultural differentiation arise. Rather than addressing this issue, Abruzzi overdraws his discussion of various biological mechanisms at the expense of their application to a wide variety of ethnographic materials.

Secondly, the absence of any discussion of urban minority groups, Fourth World peoples, and many other types of ethnic populations that are arguably sympatric invites speculation about the applicability of his argument. For example, the ethnic status of Fourth World groups such as the Sami, Amerindians, and Australian Aborigines is changing. The economic threats posed by hydroelectric and mining developments, along with the worldwide human-rights movement, have recently caused these peoples to forge new ethnic minority organizations. Their ethnic identity is no longer purely local, but shared with Sami or Aborigines elsewhere. As Mitchell (1956), Kleivan (1970), and Spicer (1971) have noted, changing identities often require new ethnic symbols. Moreover, unlike the examples of ethnic populations Abruzzi provides, contemporary Fourth

World peoples are not necessarily in competition with their neighbors so much as in indirect competition with the urbanized and industrialized majority within their national borders. These and other factors lead me to believe that the changing boundaries of many ethnic populations are better analyzed in economic, social, and political terms than in those proffered by Abruzzi.

Finally, Abruzzi does not make clear what he means by ethnic boundaries—a shortcoming common to much of the ethnic literature. For me, ethnic boundaries are largely normative in function; they define acceptable behavioural limits for a member of an ethnic group (Kennedy 1981). Boundaries often restrict one's choice of marriage partners, as Abruzzi notes, but they also place many other social constraints on the incumbent of a particular ethnic status.

While noting these shortcomings, I fully endorse Abruzzi's intention, as the issue of the ethnic boundary formation has received too little attention, ecological or otherwise.

by H. B. LEVINE

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Abruzzi has made a case for more use of ecological theory in relation to ethnic-group formation, but there are important limitations to the perspective. He begins his summary cautiously, saying that "populations in human communities respond *in much the same way* as nonhuman populations" (my emphasis), but then he moves on to assert more boldly that "the formation of distinct ethnic populations in multiethnic communities results from the *same process* that leads to species formation" (again, my emphasis). The question is how alike ethnic-group formation and speciation are and how far one can go in using the same theoretical principles to explain both.

Abruzzi is convincing that there are fundamental similarities, and I have no quarrel with his emphasizing labor demands or his pointing out the analogy between adaptation to them and niche diversification. This all works especially well with the discrete ethnic populations he chooses to discuss: contiguous nomadic and sedentary peoples, trading groups in preindustrial communities, and particular forms of plantation agriculture. Reliance on these cases provides a limited perspective, however; situations in which ethnic identification cuts across numerous "niches" in a single society or in which ethnic groups are not localized, not discussed here, constitute quite a chunk of the anthropological literature on ethnicity. At a much more fundamental level, I would emphasize that because ethnic "selection" and "isolating mechanisms" are sociocultural phenomena and their dynamics unfold in sociocultural terms, the similarities and parallels between the configurations of human ethnic identities and nonhuman species do not provide adequate grounds for the assertion that the same processes are at work.

The problems inherent in defining and discussing ethnicity in general in sociocultural terms (mentioned by Abruzzi) only trouble those who assert that discrete ethnic groups definable by a universally applicable constellation of traits should be labelled independently of how the group's (or category's) members and relevant outsiders actually define them. The very failure of a list of sociocultural characteristics to provide a universal definition of "ethnic group" is no problem if we see ethnicity as resulting from flexible sociocultural processes of group and category formation in which varieties of such traits are used by individuals in certain contexts to validate claims to solidarity based on alleged common origin, especially in situations of resource competition. This competition and ethnicity is certainly analogous to a kind of speciation, as Abruzzi makes most clear, but because ethnicity is being accomplished socioculturally the specific mechanisms differ. What people experience, perceive, categorize, and react to is important in a *formative* sense. The experiences and perceptions I am stressing

are fundamentally affected by material circumstance and competition, but, as I have argued and attempted to demonstrate elsewhere (Levine 1976, 1977, n.d.; Levine and Levine 1979), any exclusively materialist approach bypasses the constitutive role of the implicit presuppositions about ethnic identities held by people in their actualization in concrete social situations and is therefore incomplete. These implicit, socioculturally produced suppositions significantly structure and incorporate material realities in dialectical social practices that produce ethnic formations. As a synthetic activity, ethnic-group formation cannot be reduced to the specific ecological aspects of that phenomenon.

The gap between biology and culture mentioned in the opening paragraph of this article still remains. I do acknowledge, however, that the nature of that gap appears to be more subtle and interesting than I had previously supposed.

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I appreciate the author's attempt to explain ethnic differentiation on the basis of ecological theory. It is very interesting to consider the possibility of applying ecological principles to all ecological communities regardless of their biological composition. I have, however, the following objections:

First, I think that Abruzzi overgeneralizes; what is most needed in ethnic studies is still a middle-range theory able to account for particular cases.

Second, the problem of territoriality should be taken into account; the distinction between an ethnic group with an exclusive territory and an ethnic group without one is fundamental to the understanding of ethnic groups and very important from an ecological point of view.

Third, the distinction between generalists and particularists is also very important ecologically, but the author does not pay much attention to it. In many cases the key to understanding ethnic differentiation is based on this distinction.

Fourth, I do not believe that the distinctive criterion of the ethnic group is ethnic endogamy, not because endogamy is unimportant but because it is important in any process of social differentiation, not only in ethnicity.

Apart from these objections, I find the paper interesting and insightful, although a good part of it follows from what has been said by Barth and Despres.

by MICHAEL MOERMAN

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Abruzzi's paper forcibly reminds us that man's existence must conform to biological constraints, closely and cogently applies ecological theories of speciation to ethnicity, and produces a reasonably clear hypothesis for testing: "The greater the selective advantage* of distinct adaptations* within local communities*, the greater is the likelihood that socially discrete* ethnic populations* will be associated with* those adaptations." The asterisked terms will require careful definition. Selective advantage and distinctive adaptation are hard to define noncircularly. The notion of community (e.g., Mainland Southeast Asia? Irrawaddy drainage area?) will need appropriate delimitation, and so will the degree of "association" and the scale of "adaptation." (Are the Karen, for example, to be associated with wet- or dry-rice farming when the Pho Karen largely do one and the Sgaw largely the other?) It is likely to be around the terms "socially discrete ethnic populations," however, that clarity and cogency will be most difficult and even problematic. It will perhaps always be possible for an investigator to stipulate what *he* means by an ethnic population. Perhaps he would require that its members claim com-

mon origins, language, pottery, way of life, etc. Insofar as ethnicity is, as here, biologically modelled, inbreeding might be a major criterion, however much it might have to be whittled at to cover populations like the Chinese of Indonesia. For some kinds of research (maybe in archeology), the issue of whether and how the investigator's notions of ethnicity and his demarcations of populations relate to those of the people he studies may not matter. But in that ethnic labels are words in naturally spoken languages, they exist in a world of meanings. How do they matter at all if they don't matter to the people who use them and about whom they are used? A flock of empirical issues is flushed out. Does this population have a notion that corresponds to ethnicity as I, the investigator, have defined it? Does it recognize my criteria for it? How does it operationalize these criteria? Since the criteria are meaningful, operationalization is probably different in different situations. Does one of its members say to or about another, "We speak in the same way," sometimes referring to native dialect but sometimes to same generation, in one way in courting and another in trading? Of most ethnographic cogency and universality, when does it matter? The proper use of any categorization label, such as an ethnic name, depends more on locally recognized rules of relevance than on local rules of accuracy.

The empirical issues are not just fieldworker's delights. They go directly to Abruzzi's theory, for it must be discovered in particular instances whether the adaptive differentiations he points to are *ethnic* and, if so, by whose criteria. Herders may always live differently from farmers, but are the differences (among Arabs, Tibetans, and Mormons, for example) *ethnic*, and by which lights?

Abruzzi has imported a critically relevant area of biological theory and data to an area of major anthropological concern. The functional equivalence of speciation to ethnic group formation is an intriguing speculation. It is clearly premature, however, to say, with him, that "the implication of selection theory for the formation of ethnic populations seems clear."

by F. L. PELT

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Abruzzi makes a valuable contribution to the analysis of human populations in terms of general principles of biological ecology. I have some doubt, however, about the clarity and consistency of his terminology. The term "population" in ecology stands for "a collective group of organisms of the same species occupying a particular space." In accordance with this, a "human population" is generally understood to stand for *all* members of the human species in a community. At some places in this paper the author uses the term in this way, but his "ethnic population" represents an ethnic group within the population, for which in my opinion "ethnic subpopulation" would be more appropriate and also more in accordance with terms like "subculture."

Studies like this would benefit from taking into account the recent advances in evolutionary thought that have developed in ethology; concepts such as "evolutionarily stable strategy," "kin selection," and "meme" might be very useful indeed (see Dawkins 1976).

by ERIC BARRY ROSS

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Abruzzi presents a cogent argument for the potential of ecological theory to help us understand the process of ethnic

group formation. Nevertheless, so thoroughgoing an ecological perspective perhaps inevitably disregards the important and often paramount role of political economy, thus occasioning some naive interpretations. For example, though it may be true that a system of plantation agriculture employing slaves or migrant workers will eventuate in pronounced ethnic distinctions between owner-managers and the laboring population, it is rather simplistic and, indeed, obfuscatory to describe the emergent ethnic relations as "symbiotic" (even if "asymmetrical") and thereby discount the exploitative character of the underlying economic relations.

I would suggest that Abruzzi's model is not likely to be of equal cogency in all multiethnic situations, particularly where historical questions of political economy are crucial for understanding the ongoing construction of the environment in which the processes of ethnicity unfold. For example, the ethnic division between Protestants and Catholics in Northern Ireland does not seem to me to be satisfactorily accounted for by a purely ecological discussion of niche diversification. Ethnic segregation in Ulster may in a sense reduce resource competition between members of the two ethnic populations (though not in any symbiotic way), but it has evolved—at least since the mid-19th century—as a strategy of Ulster Unionists (allied with English Conservatives) to reduce unity (and indeed maintain a constant tension) between Protestant and Catholic members of the working class and to mitigate the potential for competition between the Protestant masses and the Protestant bourgeoisie. As Farrell (1980:16–17) writes, "The Ulster Unionists kept up their organization, cemented the Orange [ultra-Protestant] link and secured the allegiance of the Protestant workers by a systematic policy of discrimination against Catholics which left the Protestants with a virtual monopoly of the well-paid skilled trades" and simultaneously "prevented any effective labour or trade union movement from developing in Belfast." Occupational differentiation thus became a marked characteristic of ethnicity in Northern Ireland (with Irish Catholics generally relegated to the lower-paid, less skilled jobs), but such "niche diversification at the community level" was a function of active discrimination—i.e., forcing of ethnic boundaries—in employment (and in education and housing) by the regnant political and economic group in order to segment a working class whose unity would threaten their own class interests (cf. Bew, Gibson, and Patterson 1979).

This process is even more clearly encapsulated in the example of the cotton-manufacturing and coal-mining town of Oldham in Lancashire, England. There, as elsewhere in the county in the 1840s, Anglo-Irish working-class solidarity and the involvement of many Irish in English trade unionism (often in leadership roles) led the Tory establishment to encourage anti-Irish sentiment, most notably in the promotion of Protestant (or Orange) Associations. The owners of the Oldham collieries provided financial backing for such groups; by the early 1860s the Orange Order dominated the labor force in the collieries, and by the early 1870s most Oldham miners were voting Tory (Foster 1974:219, 234). As hostility toward the Irish grew among English workers, there was an intensification of ethnic identity and residential separation among the Irish population, with a corresponding decline in their class-oriented activity. As Foster observes (p. 245), "While in the 1840's the Oldham Irish had defied the priesthood in order to join trade unions and support the Chartists, the 1850's saw a definite increase in Church control. Church-controlled friendly societies and Catholic young men's associations made their appearance to parallel those among the English." It is worth adding that in nearby Liverpool the Tory political machine, in its efforts to subvert the issues upon which working-class unity might be developed, elaborated ethnic and sectarian divisions to such an unparalleled degree by the end of the 19th century that it was said of Conservative Boss Salvidge that he "roused the working-class electorate of Liverpool to heights of passionate feeling . . . not

with any demands regarding housing, or wages, or conditions of labour, but with the correct procedure for the conduct of divine service in the Church of England" (Salvidge 1934:29).

These examples are offered to suggest how, in ignoring the political economic structuring of a given environment, Abruzzi's model must miss the extent to which the process of ethnic group formation, beyond its ecological character, is often a function of more fundamental class relations. In missing the class dimension of capitalist society there is the danger of reducing the exploitative character of capitalism—often manifested in but distorted by its ethnic forms—to innocuous functionalist terms.

by T. S. VASULU

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In trying to explain ethnic differentiation in terms of ecological principles, Abruzzi, in this creditable paper, splendidly brings out the similarities between the definitions of "species" and "ethnic group" and the validity of these two definitions for identifying species or ethnic boundaries and proposes the concept of "ethnic population" as an alternative to "ethnic group." I accept that the concept of ethnic population is advantageous, defined as it is in a more "precise spatiotemporal ecological framework," but I am not sure of its universal applicability to the analysis of factual data.

The four criteria for an ethnic population do not altogether exclude ambiguity. For example, the problem of precise identification of ethnic differentiation arises in cases in which populations of *different* "historical identity" have "behavioral characteristics in common." It is also not hard to find populations that, while "endogamous" and sharing a "historical identity," exhibit *varied* "behavioral characteristics." Furthermore, like the linguistic criteria in the definition of "ethnic group," the "behavioral characteristics" in "ethnic population" are complex, overgeneral, and dependent on a number of variable factors the identification of which for distinct ethnic boundaries is not a simple task.

It seems to me that the distinction between "ethnic population" and "local ethnic population" is not made clear. The Yānādis, for example, are one of India's largest tribal populations, unevenly distributed primarily in southern Andhra Pradesh. Two divisions exist, Manchi Yānādis and Chāllā Yānādis. Among Manchi Yānādis, three local breeding populations can be identified: insular Yānādis, representing a fast-disappearing hunting-gathering stage; semi-isolated colony Yānādis, who in addition to being hunters are agriculturists; and urban Yānādis, who practice neither hunting nor agriculture. The Chāllā Yānādis form a separate small endogamous group, with few behavioural characteristics in common with the others but a shared historical identity. Again, the Kodavas and the Amma Kodavas are contiguous populations of Coorg district, Karnataka. They share a historical identity and a number of behavioural characteristics but form separate endogamous units, the Amma Kodavas being the smaller, Brahminical, and vegetarian. A fruitful explanation of ethnic differentiation in these two populations can doubtless benefit from the application of ecological principles, but the difficulty is defining the "ethnic populations." By which criterion are the Yānādis to be defined as an ethnic population—historical identity or endogamy? Do they constitute two endogamous ethnic populations or local ethnic populations of common historical identity? Similarly, can Amma Kodavas and Kodavas be considered as local ethnic populations or ethnic populations, and on what criteria? I would suggest that the definition of "ethnic population" better fits an ecological framework for the formation of ethnic boundaries than the identification of ethnic populations in a general anthropological context.

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Attempts to traverse the gulf between biological and social theory can be unusually valuable in anthropology. They are also unusually vulnerable. The first quality requires that they be encouraged, despite risk; the latter demands that they be evaluated by high standards, explicitly stated.

What should we expect from Abruzzi's paper, or others that attempt to interpret what is generally regarded as a socio-cultural phenomenon with biological theory and concepts developed for different circumstances and questions? I suggest these guidelines:

1. Is the mode of interdisciplinary argument clearly set out, logically compelling, and consistently followed?

2. Are the disciplines accurately represented in appropriate detail and breadth? Are relevant subtleties and uncertainties conveyed fully? (This requires that the author be conversant with contemporary scholarship in two fields.)

3. Does the combination advance understanding, leading to insights not otherwise obtainable? Nothing is gained and simplicity is lost if such work only generates another way of saying what was already known about a subject. In effect, is knowledge advanced or decorated?

4. Does the combination of ideas produce operational models or hypotheses matched to fresh acquisition or evaluation of data? Recent advances in evolutionary ecology and behavioral biology offer untold opportunities for armchair speculation in biospeak about old anthropological issues. Yet, if the scientific legitimacy conferred by evolutionary biology is to be carried into the social sciences along with its terminology and concepts, then its scientific *procedures* must also be transferred and used. This can take the form of hypothesis testing (Smith 1978) or assessment by strong inference (Platt 1964).

These are difficult guidelines, and partial success is often laudable in biocultural analysis. However, in each respect the present paper has significant shortcomings.

1. The mode of interdisciplinary argument is to conflate terminology and concepts from the biological and social sciences and then claim that they are subject to the same type of analysis because both are ecosystem processes. Human communities composed of ethnic groups are taken to be analytically the same as natural communities composed of species (or populations), mainly because collections of persons called ethnic groups are difficult to define and bound, as are collections of organisms called species. This apparently makes them analytically commensurate, as it would also a collection of buildings representing a species of architectural style, but the difficulty of defining and bounding a set of units with variable and multiple traits does not make them the same for specific analytical purposes. The important question "What would 'commensurate' mean in this context?" is not examined.

Similarly, "ethnic group" becomes "ethnic population" because the word "population" has a material referent and a place in ecological theory. It is the word "ethnic" that is troublesome, however, and it is retained as the modifier. Thus, the definition of ethnic population contains phrases like "considerable number of behavioral characteristics in common" and "a shared historical identity," which reintroduce Naroll's problematic criteria. The criterion actually used is intragroup marriage, a manifestly social process which gains little by association with the word "population."

2. The use here of biological and ecological theory presents major difficulties (I leave the social theory of ethnic groups to others). Basic conceptual errors lead, when combined, to biological sections rife with non sequiturs in the guise of reliable generalities. Three examples will make the point:

Natural selection has run amuck. Biologists agree that natural selection operates predominantly at the level of individuals and

almost never at the level of species, communities, or ecosystems. Consistent application of this principle underwrites advances in evolutionary and behavioral ecology in the last decade (Williams 1966; Orians 1971, 1975; Wilson 1973); anthropologists adapting biological theory for human studies (e.g., Durham 1976, Richerson 1977) are equally adamant about the importance of this observation. Yet, at critical junctures throughout the present paper are phrases like "selective forces operate on local populations," "selection for the effective organization of populations," and "natural selection adapting populations to communities and communities to ecosystems." This error is related to another, the claim that biological systems such as natural communities evolve by processes which have as goals community-level efficiency, effectiveness, or stability. This may sometimes be true in human communities (Boehm 1978), but there is no basis in evolutionary biology for such generalizations.

The second error is the confusion of speciation theory with ecosystem theory. The article intends to provide a "general model of speciation (resource partitioning) in multispecies communities." Actually, speciation theory (e.g., Bush 1975, Stanley 1979) is not presented, nor is it equivalent to resource partitioning as is suggested parenthetically and throughout the paper. Ecosystem concepts like resource partitioning or character displacement assume populations already acting as species (that is, reproductively isolated); they deal with the coevolution of species in communities and not with speciation as such. The concepts Abruzzi is using and the analysis he intends by their application do not match. Ecosystem theory and speciation theory are currently different and mostly incompatible bodies of ideas. A similar mistake is the parenthetical equation of "the evolution of ecological communities" with succession.

Problems with the equation of complexity with stability and efficiency are understated in the important footnote on this topic. As a biological generality of any usefulness this idea was buried in 1975: May (1975:164) says that the view that complexity begets stability is "naive"; Orians (1975:139) states that "the popularity of the notions that succession generates diversity and that diversity enhances stability predates empirical or theoretical justification"; and Margalef, who is especially important because his 1968 book is cited by Abruzzi for support of this idea, says (1975:151), "It now seems that most of the discussions on relationships between stability and diversity lead nowhere."

I should note that faulty ecology does not necessarily mean that the derived sociocultural observations are equally suspect; it only means that they do not follow or gain support from biology.

3. A goal of the paper, to give "traditional anthropological concerns a broader theoretical significance" by recasting them in ecological terminology, is similar to Guideline 3. I wonder, though, if anything appears here that was not said by Adam Smith from a material perspective innocent of modern biology.

4. Abruzzi notes that most anthropologists using an ecological framework for ethnic studies have not "employed a coherent set of ecological principles to predict the conditions under which distinct ethnic groups are likely to exist within human communities." This is a fair charge, with, in general, more targets than most of us would like to admit. Still, the predictions given here are not shown to be unique to the ecological approach, nor are they tested. Although an implied goal is to make examination of ethnic differentiation more operational, I am uncertain if this is or can be achieved using ecological ideas. A brief example, the association of Hasidim Jews in New York City with the diamond trade, will suffice: given the prediction "Where the existence of distinct adaptations within the same community is energetically superior, then,

stable ecological conditions should select for an increase in the number *and* legitimacy of isolating mechanisms separating two or more ethnic populations," can "distinct adaptations" be defined in this setting so that they are not tautological with recognition of ethnic groups? Is diamond trading a distinct adaptation from clerking at a department store jewelry counter? What is the "same community" of a diamond trader? Is it the neighborhood, the city, or an international market in precious stones? What does "energetically superior" mean to a diamond trader dealing in money and rocks? Has the U.S. economy been in "stable ecological conditions" for the last century? The operational difficulties associated with such questions suggest that testing of such a hypothesis may be impossible.

Reply

by WILLIAM S. ABRUZZI

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Several commentators have questioned my ecological approach to the analysis of ethnic relations. Fidler, Kennedy, Levine, and Ross either state or imply that by focusing upon ecological considerations I have ignored economic, political, social, and historical factors of central importance. In addition, Fidler criticizes my "tendency" to apply ecological theory "too literally," while Kennedy expresses concern that my explicit use of ecological theory will raise old questions about the application of "biological theory" to sociocultural phenomena. I suspect that these commentators and I differ sharply on the nature of ecological analysis as applied to human communities.

Ecological analysis in anthropology may be divided into two general approaches: *cultural ecology* and *human* (or *systems*) *ecology* (see Anderson 1973). A related distinction exists in general ecology between *autecology* and *synecology*. Autecology is concerned largely with the adaptation of a single organism or population to its environment, while synecology focuses upon a group of organisms or populations interacting as a unit (E. Odum 1971:6). Cultural ecology tends to be autecological (Netting 1968, Bennett 1969), while systems ecology inclines to be synecological (Abruzzi 1981). In cultural ecology, the term "ecological" refers primarily to the natural environment and to the limited set of productive problems that it poses. From this perspective, ecological factors represent a restricted set of considerations in social analysis, and too great an emphasis on them prompts the charge of "ecological determinism" such as that directed at me by Fidler. From the perspective of systems ecology, on the other hand, an ecosystem is considered "as the material path followed by energy" (Margalef 1968:14), and *all* living systems become potential ecological systems subject to analysis by the same general principles.

The principles of systems ecology are energetic, however, not biological. The advantage of an energetics approach to the analysis of ecological communities, as I have said elsewhere (Abruzzi 1981:12), "lies in the simplicity that this approach offers for modeling complex systems and in the potential that it provides for incorporating distinct ecological communities within a unified theoretical perspective" (cf. H. Odum 1971, Little and Morren 1976). Human social behavior is not "reduced" to biology or ecology by the application of energetics models to human communities. Rather, human and nonhuman communities are perceived as variants of ecological communities and explainable from more general theoretical principles. The approach is not reductionist, but *systemic*; local empirical variables are interpreted through the language of more general systems. Economic, political, social, and historical factors are not ignored; they are redefined in terms of general ecological principles. By redefining certain social concepts (e.g., competi-

tion, exploitation, production, and symbiosis) in terms of more general ecological principles, and conversely by operationalizing and testing these general principles in relation to empirical variables within local human communities, our understanding of both ecological theory and the evolution of human communities is advanced.

Fidler claims that ecological theory is more useful when employed as an analogy and considers my explanation weakened by my attempt to apply it as a formal model. I submit that it is *only* through the literal (i.e., formal) application of ecological theory that general ecological principles can be successfully extended to the explanation of human social behavior. In the absence of formal analysis we are left only with metaphors, which can provide little if any predictive explanation of social system behavior. The error in applying metaphors derives from the tendency to concentrate upon "superficial similarities of phenomena which correspond neither in their causal factors nor in their relevant laws" (von Bertalanffy 1968:84). The organismic analogy is a conspicuous example of a metaphor inappropriately applied to human communities (Nisbet 1969). By contrast, the successful exchange of models between ecology and economics (Day and Grove 1975, Rapport and Turner 1977) stems from an appreciation of homologies wherein "the efficient factors are different, but the respective laws are formally identical" (von Bertalanffy 1968:84). While the models exchanged have focused upon *processes*, which are quite similar, recourse to biological and ecological analogies in anthropology has too often compared *structures*, which in fact bear no resemblance to one another. I do not claim that species and ethnic populations are the same, but suggest that the *processes* leading to the formation and maintenance of distinct populations within human and nonhuman communities derive from the same theoretical principles. In order to account for the behavior of phenomena in one context by the use of concepts and principles developed in another—and, by extension, to determine objectively the utility of employing a specific model—it is imperative that such models be applied formally so as not to perpetuate metaphors. In other words, anthropologists need to be *more*, not less, literal in their use of ecological models.

Another issue raised by several reviewers concerns the implications for my model of contemporary evolutionary theories which explain group adaptations through individual or kin selection. Brown and Durbin as well as Pelt inquire whether current developments in evolutionary theory warrant changes in my general propositions. Winterhalder takes a more partisan position; charging that I have let natural selection "run amuck" in my application of the concept to various levels in the organization of living systems, he claims that "biologists agree that natural selection operates predominantly at the level of individuals and almost never at the level of species, communities, or ecosystems." A brief consideration of the issue may clarify its implications for ethnic differentiation.

Although "classical" evolutionary theory involves natural selection operating through individuals (Dobzhansky 1970), the concept of group selection has long persisted within biological evolutionary thought. Darwin (1958 [1859]:270-71) embraced it, most notably to account for the existence of sterile castes among insects, and the concept featured prominently in some early genetic models (Wright 1945). Serious general models of group selection continue to be proposed (Wynne-Edwards 1962, Levins 1970, Boorman and Levitt 1973, Levin and Kilmer 1974, Gilpin 1975, Wilson 1975, 1980). In addition, Darlington (1971) employs group selection to account for the convergence between empirical patterns of regional dispersal and local turnover of carabid beetles in New Guinea and those of species movements worldwide, and group selection has frequently been proposed to explain widespread extinctions and replacements of species and genera in the fossil record (see Stebbins and Ayala 1981). Wilson (1980:

126-30) argues that traditional models of individual selection are insensitive to the indirect effects of (i.e., a community's reaction to) an organism's behavior upon individual fitness. Such models, he claims, are not as capable as are models of group selection of predicting a variety of adaptive relationships among species, including most significantly the evolution of "dependent specialization."

Several critics of group selection have accepted its possibility under certain conditions. Smith (1964:1145) states that in order for group selection to occur species must be "divided into a large number of local populations within which there is free interbreeding, but between which there is little gene flow." These are precisely the conditions defined in many models of group selection (e.g., Wilson 1980) and claimed to represent the normal population structure among animal species (Wynne-Edwards 1964). Group selection has even been accepted by many, including some of its critics, as providing a better explanation than individual selection for the emergence of certain prominent adaptations, notably sexual reproduction (Williams 1971:12-13; Leigh 1977). Although the concept has strong opponents among contemporary biologists (see Williams 1971), it would be incorrect to dismiss it as a theoretical aberration rejected by reputable scientists.

Too great an emphasis has been placed upon the opposition between group and individual selection, however. Several researchers have suggested that this emphasis is misplaced (Leigh 1977, Alexander and Borgia 1978, Wilson 1980). Although group selection may be viewed as promoting adaptations that further the fitness of the population at the expense of individual advantage, group and individual selection are not necessarily in opposition. Group survival may be necessary for individual survival, such as for reproduction or for the maintenance of social systems that enhance individual fitness. In these instances, selective advantages accruing to the group are advantageous to the individual as well, and adaptation is complementary. Wilson (1980:9) suggests that current preoccupation with the opposition between group and individual selection stems largely from the emphasis placed upon self-sacrificial traits. He proposes (p. 10) that selection be viewed in terms of levels of organization: "Selfish genes organize themselves into selfish individuals, which organize themselves into selfish populations, which organize themselves into selfish multi-species communities." Leigh (1977:4542) suggests that those species are favored in evolution "whose genetic systems or social organization favor the evolution of mechanisms reconciling individual with group advantage." The integration of selection among the different levels of organization of living systems and its implications for both evolutionary theory and our conceptualization of the levels themselves is perhaps most clearly expressed by Alexander and Borgia (1978:455, emphasis added):

Group selection is commonly regarded as a problem involving the relative potencies of selection at the two levels of the individual and the social group or population. . . . Life, however, is organized not in a two-ranked hierarchy but in a many-ranked one. Thus, genes function in groups called chromosomes, and chromosomes in groups called genomes, and these merge into hierarchies of individuals, demes, populations, species, communities, and ecosystems. Interactions among subunits within a genome may parallel the interactions of individuals or coalitions within social groups. By comparing the operation of selection at different levels in the hierarchy, we may better understand how differential reproduction has produced the current structures and organization of living systems. Traditional arguments concerned with group selection have focused on interactions among individuals to produce group effects. Under what we call an expanded view of group selection, interactions among entities at all levels in the hierarchy of living systems may be considered in terms of their contribution to patterns of reproduction. Long-continued potent selection at any level in the hierarchy of life is likely to enhance the integrity of entities at that level and reduce the likelihood of conflicts of interest with units at lower levels. This

effect of selection may be responsible for many of the commonplace concepts of biology: gene, chromosome, individual, and family; and in some sense it lies behind the identification of cohesive functional elements such as tissues and organs, various appendages, reflexes, and reflex groups, and of individuality in behavioral acts.

Living systems exist within a hierarchy of organized relationships, and while considerable independence prevails in the behavior of individual units within that hierarchy (be they genes, organisms, populations, or communities), the emergent properties of more inclusive systems select for greater coherence in the activity of subordinate units (see Stebbins 1968, Slobodkin 1968, E. Odum 1969). Consequently, although a system is most efficiently viewed as "not a thing, but a list of variables" (Ashby 1956:40), Alexander and Borgia note that persistent and coherent selective pressures at various organizational levels have yielded more or less discrete units in the hierarchy of living systems. While they acknowledge that the individual organism is apparently the most clearly definable unit among living systems, they also suggest that this unique distinguishability derives in part from the fact that we, the definers, are individual organisms ourselves.

Human organisms, populations, and communities are subsets of living systems and likewise exist within a hierarchy of organized relationships. Certain prominent adaptive units (including kin groups, ethnic populations, villages, urban centers, and states) have appeared independently in the evolution of complex human communities. Notwithstanding the individuality and variability of specific units in the hierarchy of human communities and of the importance of divergent selective pressures, increasingly complex human social systems have similarly evolved through the differential reproduction of subordinate units whose interests and activities were consistent with the survival of higher-level organization. While conflicts of interest certainly persist, the survival of lower-order units becomes inextricably bound to the success of emergent systemic relations. It is in this manner that selection operates in hierarchical living systems—human and nonhuman—to adapt genes to individuals, individuals to populations, populations to communities, and communities to encompassing ecosystems.

A third general issue raised by reviewers concerns current research on the relationship between diversity and stability in ecological systems and its significance for ethnic differentiation. Hardesty questions whether diversity causes stability or vice versa and asks what the implications are of variable versus stable environments for understanding ethnic patterns. Winterhalder dismisses any generalization regarding diversity and stability in living systems as deficient and without theoretical foundation. I have discussed this issue in considerable detail elsewhere (Abruzzi 1981) and will present here only some summary comments taken from that larger discussion.

MacArthur (1955) originally proposed that more complex ecological communities are inherently more stable than less complex communities because of the regulative control that diverse food webs exert over fluctuations in the size of individual populations. Prior to MacArthur's article, species populations within ecological communities had been largely viewed as independent units and species interactions accorded little systemic importance (cf. Andrewartha and Birch 1954). MacArthur's thesis soon achieved near-universal acceptance among ecologists (cf. Elton 1958, Margalef 1968, Brookhaven National Laboratory 1969), prompting May (1973:37) to remark: "The hypothesis that increased food web complexity causes increased stability has, on occasion, been accorded the status of a mathematical theorem" (see also Leigh 1976:65). Several researchers challenged this notion (see Sanders 1968, May 1973, Cody and Diamond 1976). After examining several model ecosystems, May (1973) concluded that no mathematical basis exists for

proposing that greater diversity leads to greater stability in ecological communities. Acknowledging that "in the real world, increased complexity is usually associated with greater stability," May suggested (pp. 75-76) that "if there is a generalization, it could be that stability permits complexity." Sanders's (1968) research among benthic ecosystems clearly supports May's conclusion. Viewed as generalizations about the nature of ecological systems, the two positions are clearly in conflict. Viewed instead as indications of distinct sets of conditions influencing community evolution, the research underlying these two positions illustrates the complex role that selection plays in the evolution of hierarchical living systems.

Resource partitioning among constituent populations is central to the evolution of complex ecological communities, and an explanation of community evolution rests upon an understanding of the conditions that facilitate this process. All living systems depend upon abundant supplies of potential energy, and ecological communities evolve to the extent that this energy can be converted into productivity. Relatively little potential energy is so transformed, however. The maintenance costs of organisms directly affect net productivity at each trophic level and thus determine the biomass and the level of diversity supportable in a community. Any factor that reduces the cost of community maintenance and increases the amount of energy converted to productivity acts as an *energy subsidy* and enhances community diversity. Conversely, anything that increases maintenance cost is an *energy drain* and reduces community diversity (see E. Odum 1971:43-53). While all phenomena that affect productivity and energy flow in ecological systems may be viewed within an energy-subsidy/energy-drain framework, environmental productivity and *stability*, habitat size and diversity, and exploitation appear to be the most important of these factors affecting the evolution of complex ecological communities (see Sanders 1968, E. Odum 1971, Whittaker 1975). An increase in any of these variables except exploitation generally enhances community diversity.

Limited regulation does occur within ecological communities, however, and the various regulating mechanisms may be divided into *power circuits* and *control circuits* (H. Odum 1971:94). Power circuits are those major channels of energy flow that largely determine a community's organizational structure (e.g., oak trees that process 50% of a forest community's energy budget). Control circuits provide only minor energy flows themselves but are capable of regulating energy flow in the larger power circuits (e.g., when the gathering and planting activities of squirrels affect the future size of an oak population). Control circuits are particularly important for their work-gate functions, whereby one energy flow is enhanced by the multiplicative effect of supplementary energy inputs (H. Odum 1971:44-45). Increasing stability in ecological communities results in large part from a greater redundancy of work-gate functions and from the potential that this offers for circumventing variable energy flows in power circuits. Increases in both the number and the variety of regulating mechanisms—power and control circuits—enhance a community's ability to offset the destabilizing effects of minor environmental variation. Of the interactions that regulate populations within ecological communities, competition and predation are the most apparent (Paine 1966, Whittaker and Woodwell 1972). Competition largely regulates populations within the same trophic level, while predation regulates populations at different trophic levels. Thus, while species diversity at lower trophic levels enhances diversity at higher trophic levels (largely through energy flow in power circuits), species diversity at higher trophic levels also regulates diversity at lower trophic levels (through energy flow in control circuits).

I have already indicated (n. 10) that important constraints exist upon the regulative capacity of complex ecological communities. First of all, community regulation is enhanced not by

a simple increase in species numbers, but *only* by the existence of multiple, density-dependent links between species populations at various trophic levels (see MacArthur 1955, Boughay 1973, May 1973, Leigh 1976). Overspecialization (as when one population has only one predator and one prey) reduces community stability by permitting fluctuations in the size of one population to ramify throughout the food chain (a food web would not exist under these conditions). It was on this basis that May (1973) undermined the widely accepted "complexity begets stability" thesis. Time is another important constraint upon the regulative capacity of ecological communities, as time is required to evolve the complex regulative mechanisms associated with diverse communities. Developmental canalization can only take place under the stimulus of a stable and predictable environment. The control exerted by predators upon the size and diversity of prey populations, for example, is ultimately dependent upon the reliability of those prey populations as resources throughout the year. Thus, the limited community stability that results from the regulative effect of community diversity ultimately derives from the productivity and stability of the encompassing ecosystem. This is true for human ecological communities as well (Abruzzi 1981).

The important issue, therefore, is not whether complexity begets stability or stability promotes complexity, but the development of a synthetic evolutionary model that accommodates the empirical research underlying both of these apparently contradictory positions. In the process, we need to distinguish between model and natural ecosystems and between field, laboratory, and mathematical research (Bradley 1974, Rogers and Hubbard 1974). The properties of model ecosystems depend upon the assumptions built into them. Many ecological models, for example, treat communities as spatially homogeneous (cf. May 1973), even though spatial heterogeneity is characteristic of most natural communities. Rogers and Hubbard (1974) examine a prominent insect parasite-host model as a paradigm of a much wider range of mathematical models. Inspecting the assumptions of the model in the light of field and laboratory research, they find that "features of natural insect parasites differ from those assumed in the model in ways that tend to decrease the instability of interactions" (p. 100). Furthermore, subsets of general models may contain unique properties which are distinct from those attributed to such models and thus display behavior that departs from predictions derived from them. Living systems constitute a unique subset of general systems. Consequently, as Rogers and Hubbard point out (p. 110), "although in general the complex models are less stable than simple ones, the natural situation is not a 'general' case. It is, rather, mathematically atypical" (see also May 1973:76-77).

Inasmuch as environmental stability enhances the productive advantage of resource partitioning within ecological communities and is required for the evolution and operation of control circuits regulating population interactions, ethnic differentiation within human communities should proceed most clearly where stable ecological conditions prevail. Consequently, each of the propositions I have offered regarding ethnic differentiation includes the qualification "under stable ecological conditions." Stable ecological relations also underlie my three contextual examples of ethnic differentiation resulting from resource partitioning among sympatric human populations. Where variable ecological conditions necessitate regular movement between exploitative strategies, on the other hand, rigid ethnic boundaries may present an impediment to that mobility. The West African savanna is a broad semiarid region distinguished by more or less clear ethnic differentiation and interdependence between nomadic pastoral and settled agricultural populations (Stenning 1958, Haaland 1969). Within many particular communities, however, unstable environmental conditions have produced a movement between nomadic and sedentary strategies that has blurred the clarity of the boundaries

between local ethnic populations. In northern Nigeria, for example, the Fulani may be divided into nomadic and sedentary populations, with the latter more closely approaching the agricultural subsistence strategy of nearby Hausa. While some settled Fulani resume a nomadic pastoral existence with each annual return of the dry season, for others the pastoral adaptation is only a circumstantial expedient (see van Raay 1970). Dedication to Fulani identity appears to be associated with commitment to a pastoral adaptation. Those settled Fulani that are more involved in farming, according to van Raay (p. 151), generally speak Habe (the Hausa language) rather than Fulde (the Fulani language), are more likely to eschew participation in traditional Fulani ceremonies, and are less opposed to intermarriage with non-Fulani. Where unstable ecological conditions have selected for movement between contrasting adaptive strategies, a sizeable intermediate population of ambiguous ethnic status—van Raay (1970:151) indicates that nomadic Fulani consider the settled Fulani to have “become Habe” (Hausa)—has apparently emerged which facilitates this mobility.

Some reviewers have questioned the applicability of my model to ethnic relations in urban-industrial communities. Fidler claims that it applies at best to “untouched and untouchable island ecosystems.” Kennedy doubts the ability of my general argument to account for contemporary minorities, while Brown and Durbin suggest that industrialization, at least in Mexico, undermines traditional ethnic loyalties and fosters a uniform national identity. It is clear from the ethnographic literature that ethnicity is at least as important a component of urban social systems as it is of rural communities, whether in industrial countries or in developing nations of the Third World, and that new ethnic identities have consistently emerged within urban-industrial contexts that have had little, if any, previous rural basis (Wallerstein 1960, Cohen 1978, Gugler 1975, Horowitz 1977, Ottenberg 1976). The importance of ethnicity in urban and national arenas has likewise been linked to resource competition (Hannerz 1974, van den Berghe 1976) and to regional economic inequalities (Hechter 1976), and many researchers have noted the presence of an ethnic division of labor in contemporary urban communities (Cohen 1969, Davis 1974, Foster 1974, Hechter 1976, Ottenberg 1976, Keyes 1976). Keyes (1976:209) even remarks that “almost every complex society, whether it be a modern industrial society, a colonial society, or a Third World society, has been shown to have some ethnic division of labor.”

Selection theory as applied to ethnic differentiation predicts that discrete ethnic populations should occur in conjunction with distinct strategies of resource exploitation. Such “distinct strategies” must not be confused with simple occupational categories when discussing urban-industrial communities, however. They are more comprehensive adaptations, as implied by the related concept of life-support systems. In addition, from the perspective of systems ecology, both the natural environment and superordinate political economies form part of the encompassing ecological (material) system affecting an individual community’s productive organization. Rather than demonstrating the futility of applying my ecological argument to urban-industrial communities, as claimed by Fidler, contemporary ethnic relations in the United States appear to illustrate my general propositions.

Expansion of the American economy after World War II placed a premium on individual spatial, occupational, and social mobility that undermined the importance of ethnic identity to individuals successfully participating in the mainstream of this economic growth. Consequently, in spite of the so-called new ethnicity (Novak 1974), traditional ethnic distinctions have declined in importance among second- and third-generation descendants of immigrants, and ethnic endogamy has decreased accordingly (Mindell and Habenstein 1976). Despite extensive

assimilation, several ethnic populations have retained visibility within local and regional communities in the United States, among them Blacks, Hispanics, and Jews. These groups display certain common characteristics: (1) high local (and to a lesser extent regional) residential concentration, (2) prominent ethnically distinct social institutions, and (3) relatively high rates of ethnic endogamy. Each also exhibits a clearly skewed participation in local and regional economies (Dinnerstein and Reimers 1977, Grebler et al. 1970, Broom and Glenn 1969), and ethnic boundaries have been important in their exclusion from mainstream economic institutions. Blacks and Hispanics have been a source primarily of cheap unskilled labor, and it is perhaps significant in this regard that they display a largely inverse distribution in their relative proportions of the total populations of American cities, at least in the Southwest (see Grebler et al. 1970:116). In both cases, obstacles to economic and social mobility that result from rigid ethnic boundaries have facilitated exploitation. Hechter (1976) argues that the universal presence of disadvantaged minorities within prosperous industrial countries indicates the fundamental importance of such ethnic division of labor to the growth of industrial economies. Possessing better resources in the form of skills and organization, Jews have fared better economically than any other population excluded from the mainstream economy. Their success, however, has depended to an important degree upon concentration in specific industries and in occupations and professions emphasizing self-employment, including wholesale and retail sales, medicine, law, and accounting (Dinnerstein and Reimers 1977:126–29). Such specialization minimized direct competition with non-Jews and provided the basis for a network of affiliations that facilitated individual economic advancement. Other examples of high ethnic visibility in local and regional American communities based upon the interrelated features of residential segregation, distinct social institutions, and exclusion from mainstream economic institutions can be given (Wadell and Watson 1971, Nee and Nee 1973).

Many other issues have been raised to which time, unfortunately, will not permit an adequate response. I would, however, like to close with a few general comments. It should be clear from the preceding discussion that I do not espouse a “functionalist” position regarding the relationship between ethnic differentiation and community evolution, as implied by Ross, but recognize the operation of selection at various organizational levels within human communities. The existence of competition between two or more ethnic populations (or any populations, for that matter) does not preclude the simultaneous presence of competition between individuals or groups within these same populations. The apparent ease with which political and economic elites in Britain have been able to exploit the Catholic-Protestant issue, for example, would seem to underscore the fundamental importance of ethnicity to the conflict in Northern Ireland (see Boal, Murray, and Poole 1976), and instances of elite exploitation of ethnic conflicts have been described elsewhere (Cohen 1969, Thompson 1979). On a related matter, the term *symbiosis* in ecology is devoid of the normatively positive valuation attributed to it by Ross. Symbiosis denotes simply interdependence and includes (within the context of multispecies communities) a variety of “lasting, close associations between organisms of different species” (Whittaker 1975:37). Three broad types of symbiotic relations—mutualism, commensalism, and parasitism—are generally distinguished, only the first of which is defined as mutually beneficial. Accordingly, I emphasized that the degree of symbiosis between ethnic populations must be viewed as variable and that such interdependence does not preclude exploitation.

The formation of ethnic boundaries has been a recurring feature of the evolution of complex human communities. Of the

numerous social forces through which individuals have expressed their common interest, ethnicity has been perhaps the most pervasive. Changing social contexts have produced the rearrangement of ethnic boundaries and even the emergence of wholly new ethnic populations. As Hinton notes, the recurrence and persistence of ethnic populations within complex human communities does not derive from the purported vitality of "primordial sentiments." Rather, ethnic populations appear to possess a clear selective advantage over other social units under certain productive conditions. Where competition within human communities selects for disparate populations engaged in distinct strategies of resource exploitation, concurrent selection exists for a mechanism that both facilitates and perpetuates social differentiation. Ethnicity provides such a mechanism (Cohen 1974, Hannerz 1974). Ethnic boundaries, more than those of competing social units, provide a clarity of definition that enhances social differentiation. At the same time, the encapsulation of individuals within relations structured by ethnic boundaries provides a means (endogamy) for the reproduction of social differences. Such visibility and differential reproduction, I have suggested, are prominent features that ethnic populations in human communities share with species in multispecies communities.

One goal of anthropology as a social science is to advance scientific explanation as it relates to human behavior. Modeling is an important feature of that process. While all models are necessarily oversimplifications, simplicity is often required in order to isolate more salient properties of the phenomena we wish to explain. Subsequent corrections and complications of a model increase its ability to explain more precisely under a variety of circumstances. We need to develop formal models of ethnic relations, therefore, that isolate the *conditions* which inhibit or enhance ethnic differentiation. The model presented above offers such conditions. It does not purport to explain all the features associated with ethnic relations, but only proposes several basic conditions underlying ethnic differentiation within a variety of complex human communities. An important contribution of the model lies in its suggestion of a formal similarity between group-formation processes of human and non-human ecological communities. A significant feature of the model is that it permits the incorporation of additional conditions that affect ethnic differentiation, including the distinctions suggested by Martinez Veiga between generalists and specialists and between those possessing and not possessing an exclusive territory. A crucial issue in the application of any general model is the operationalization of key concepts, and this has been a notable problem in the study of ethnic relations. Operationalization of variables can only be adequately performed and evaluated in the context of specific empirical research, however. Because of variations in the content of individual communities and problems of data availability, unique operational solutions often have to be developed for specific ethnographic situations. I will not elaborate on this issue here, therefore, but will deal with the problem more extensively in subsequent research.

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