

SPECIES DIVERSITY GRADIENTS:  
SYNTHESIS OF THE ROLES OF PREDATION,  
COMPETITION, AND TEMPORAL HETEROGENEITY

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A major goal of many ecologists working toward the development of a broad theory of community organization is to understand the causes of patterns of species diversity (Hutchinson 1959). Factors potentially affecting species diversity have been reviewed several times (e.g., Pianka 1966, 1967, 1974a; Ricklefs 1973) and include (1) time, (2) spatial heterogeneity, (3) competition, (4) predation, (5) climatic stability, and (6) productivity, plus several combinations of these (e.g., Pianka 1974a). Various attempts have been made to synthesize several of these hypotheses into a broad theory accounting for certain sets of observations or experiments. Among these are the predation hypothesis (Paine 1966, 1971), the stability-time hypothesis (Sanders 1968, 1969), and, most recently, a synthesis offered by MacArthur (1972). These syntheses focus mainly on theories (3)–(6) above but differ in their emphasis on the relative importance of each factor. This difference in emphasis revolves around the seemingly contradictory roles of competition and predation in the determination of community structure. Below we suggest that these roles are in fact complementary in their effects, the relative importance of each depending on the trophic level being considered and the overall trophic complexity in a community. We present data from the New England rocky intertidal zone supporting our contention and view this synthesis against patterns of environmental behavior and structural complexity. Our synthesis is not particularly new or novel. Hairston et al.'s classic paper (1960) makes essentially the same point, though it is concerned with regulation of populations and whole trophic levels and not species diversity. However, a realization of the fundamental lesson of their paper seems peculiarly absent from the controversy considered here.

Species diversity is here the number of species present in a community. Following MacArthur (1965), we distinguish between within-habitat comparisons (e.g., comparisons within rocky intertidal, grassland, or forest habitats) and between-habitat comparisons (e.g., comparisons between grasslands and forests, or rocky intertidal and kelp communities). In our view, terms such as lizard, bird, or plant "communities" are misleading and lead to confusion. We refer to such associations as "guilds," assemblages of species utilizing a specific type of resource (Root 1967). We reserve the term "community" for collections of interacting organisms of all trophic positions occurring in a given habitat.