Competition, Predation, and the Structure of the Ambystoma-Rana Sylvatica Community

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COMPETITION, PREDATION, AND THE STRUCTURE OF THE *AMBYSTOMA–RANA SYLVATICA* COMMUNITY[1]

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Abstract. Populations of six species of amphibians were manipulated in field enclosures to study the biological tractability of current concepts of the organization of natural communities. Experimental communities with a known composition of mature eggs were introduced into screen enclosures in a pond to assay the importance of competition and predation to the ecology of amphibian larvae in temporary ponds. The competitive ability of each population was measured by its survivorship, mean length of its larval period, and mean weight at metamorphosis. Three simultaneous experiments (requiring 70 enclosures and 137 populations) were replicated in a randomized complete-block design for variance analysis.

The assumptions of the classical Lotka-Volterra model of competition were tested by raising *Ambystoma laterale, Ambystoma tremblayi,* and *Ambystoma maculatum* in all combinations of three initial densities (0, 32, and 64). All three measures of competitive ability were affected by competition with other species. Higher-order interactions decreased the variance of the outcomes of the experiments as species were added to the communities. The statistical effects of these higher-order interactions between the densities of competing species often exceeded the simple effects of competition. The increase in community stability with the addition of species to the community is not predicted by the classical models of community ecology.

The second experiment tested the effects of adjacent trophic levels on the structure of the three-species community. Eggs of *Ambystoma tigrinum,* a predator, and *Rana sylvatica,* an alternate prey of *Ambystoma tigrinum,* were added singly and together into systems with 16 eggs of species in the Maculatum species-group. *Ambystoma tigrinum* was a predator if it acquired an initial size advantage by preying on *Rana sylvatica* tadpoles; otherwise it was principally a competitor. *Rana sylvatica* adversely affected the Maculatum group by competing with invertebrate prey for periphyton and photoplankton. The three species in the Maculatum group had nearly the same response to the addition of both *A. tigrinum* and *R. sylvatica.*

Ambystoma texanum, which occurs sporadically in southern Michigan at the northern limit of its range but not on the study area, was introduced as a test for community saturation. *Ambystoma texanum* was successfully raised alone. When mixed with the Maculatum group, *Ambystoma texanum* had a low survivorship, a small body size, and a long larval period. The native species were affected equally by the introduction of *Ambystoma texanum,* demonstrating the complexity of the food web and the ecological pliability of salamander larvae.

The uncertainty of the temporary pond environment precludes extreme ecological specialization among these species of salamanders. Coexistence is a consequence of the relative advantages of the species in different years and the long adult life spans. The complexity of the food web and "predator switching" are probably important elements of the density-dependent interactions that contribute to the stability of communities within seasons.

The concept of the community has its historical roots in the thought of the seventeenth-century naturalists who recognized that species of plants and animals occurred in natural assemblages. The implications of this observation were slowly realized by natural historians. By the middle of this century, ecologists were discussing a theory of the community. Allee et al. (1949:436) defined the community as "a natural assemblage of organisms which, together with its habitat, has reached a survival level such that it is relatively independent of adjacent assemblages of equal rank; to this extent, given radiant energy, it is self-sustaining." Dice (1952) added that the community is the highest level at which life can be organized. Hence, it is in the context of the community that evolution occurs.

Recently ecologists have departed from the functional definition of the community to a rather arbitrary concept that defines the community as the group of organisms being studied. Ecologists now study "grassland bird communities" (Cody 1968), "Drosophila communities" (Levins 1968), and "diatom communities" (Patrick 1968). The concept of the "community matrix" (Levins 1968, Vandermeer 1970) originally was restricted to groups of species that compete with one another.

My thesis is that these natural groupings of species are organized by interspecific interactions that can be discovered and evaluated by experimentally dissecting the community into smaller components. There is a large corpus of laboratory studies, beginning with those of Chapman (1928) and Gause (1934), that involved simple ecological communities with few interacting species. These simple communities are described satisfactorily by elementary

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