This Week's Citation Classic

Nevo E. Genetic variation in natural populations: patterns and theory *Theor. Pop. Biol.* 13:121-77, 1978.

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Genetic diversity in nature is central to the evolutionary process. Genetic diversity levels vary nonrandomly among populations, species, and higher taxa and are predictable by ecological factors. The evidence is inconsistent with the neutral theory of molecular evolution. Natural selection in diverse forms appears to be a major force of evolutionary change at both the genotypic and phenotypic levels. [The SCI® indicates that this paper has been cited in more than 575 publications, making it the most-cited paper published in this journal.]

Genetic Diversity Revisited

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Genetic diversity is the basis of the evolutionary process by natural selection and the cornerstone of the fruitful bridge between Darwinism and Mendelism. The discovery of isozymes and their application in population genetics unraveled abundant genetic polymorphisms in natural populations of microorganisms, plants, animals, and humans. Ironically, however, this extensive genetic variation proved theoretically intractable. How much of it is adaptive and contributes to the fitness of organisms? Already during the late 1960s it was explained dichotomically, as either neutral or selective, though obstinate to theory.

Personally, I was first fascinated by phenotypic diversity in nature; later, I became interested in relating genotypic with phenotypic diversity and their interactive relation with the environment. In 1969 I started to look into the genetic diversity of cricket frogs in North America, but realized that only an extensive exploration and critical testing might reveal the mystery of genetic diversity. I also realized that using local, regional, and global approaches

across phylogeny and ecology might highlight the issue better than a narrow research program. Unraveling the genetic basis of the evolutionary process was uneasy empirically as well as theoretically.

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We started in small Israel, with its climatic gradient of increasing aridity stress both south and east, as our ecological theater.³ For me, the interdisciplinary link proved illuminating. Macrogeographic regional studies in Israel³ and the Near East were linked with microgeographic studies involving varied microclimates, soils, and topographies in Israel. Critical controlled laboratory and natural tests, using thermal and chemical pollution on varied marine organisms, proved highly illuminating.⁴ Finally, we approached the phase of integrating all these results with other regions across the planet varying in ecology, demography, and life history.⁵

The 1978 paper was the first synthesis trying to substantiate the environmental theory of genetic variation in natural populations. Natural selection in some form proved to be the major determinant of genetic population structure and differentiation. I suggested that precise and varied critical experiments must be designed to test possible alternative hypotheses, to establish direct cause-effect relationships between ecological and genetic profiles, and to assess the contribution of single and multilocus structures to fitness.

We pursued this research program and substantiated our 1978 synthesis at local, regional, and global scales. We integrated the evidence of 1,111 species across the globe and 38 species from Israel,3 including unrelated plants and animals, 21 of which shared ecological gradients of increasing aridity; we also added several microsite studies of wild cereals, landsnails, and barnacles in Israel. The parallel genetic patterns obtained across all geographical scales in nature⁶ were once again inconsistent with the neutral theory of molecular evolution. Natural selection in its various forms appears to maintain genetic polymorphism and orient molecular evolution at both the protein and DNA level, as was also supported theoretically.7

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