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EVOLUTIONARY PROCESSES AND THEORY: THE ECOLOGICAL-GENETICS INTERFACE

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**ABSTRACT**

The evolutionary process is reviewed in terms of the ecological-genetics interface based on genetic diversity in natural populations of plants and animals, using the environmental-genetic correlation methodology at three geographic levels: (1) Local, several species in Israeli microsites; (2) Regional, 21 species across Israel and 2 species in the Near East; and (3) Global, 1111; 184 and 189 species in three studies across the planet. The species analyzed are taxonomically unrelated, and vary in their ecologies, demographies, life histories, and other biological variables. They were mostly tested by horizontal starch gel electrophoresis for allozymic diversity, averaging 25 gene loci, and other genetic polymorphisms. In addition, ten studies involved DNA polymorphisms.

The following results were found at all three geographic levels: (1) The levels of genetic diversity vary nonrandomly and are structured within and among populations, species, and higher taxa; and (2) Genetic diversity is correlated with niche width, and partly predictable, primarily by ecological factors. These results corroborate the adaptive, environmental theory of genetic diversity. They were also verified for several allozyme loci in controlled laboratory experiments in pollution biology. Natural selection in its various forms appears to be a major force maintaining, differentiating and orienting evolutionary change in protein and DNA polymorphisms.

**Keywords:** Ecological-genetics interface, genetic diversity, ecological diversity, adaptations, natural selection.

**INTRODUCTION**

**Ecological-Genetics: Past, Present and Future**

Modern evolutionary theory integrates population genetics and ecology, in the science of ecological-genetics (Ford, 1971). Ecological-genetics deals with a central evolutionary problem, the origin and evolution of adaptations and species based primarily on ecologically oriented genetic polymorphisms. It attempts to evaluate the ecological forces that mould genetic diversity in nature and consequently the evolution of populations and species.

The spectacular developments of molecular biology has allowed the analysis of individual genetic diversity, and hence the study of genetic structure of populations and species (reviewed in Lewontin, 1974; Ewens, 1979; Wills, 1981; Karlin, 1982; Nei, 1987). Thus, ecological-genetics has shifted largely from visual to biochemical polymorphisms, analyzing the ecological variables which maintain genetic polymorphism and their correlation with phenotypic diversity. Yet, the relative importance of the forces in nature interacting at the molecular level in genetic divergence, i.e., population size and structure, mating pattern, mutation, recombination, migration, selection and genetic drift, remain as enigmatic

and controversial as ever. Ironically, the great genetic diversity found in nature (Nevo, 1978, 1988a,b; Nevo et al., 1984) caused more confusion than elucidation of the relative roles of these forces. The problem is central to evolutionary theory: what proportion of genetic diversity in nature is the basis of adaptive evolutionary change (Lewontin, 1974)?

#### **Molecular population genetics**

Genetic diversity within species is central to evolutionary biology and its two major processes, adaptation and speciation. Molecular biology permitted the characterization of genetic diversity among individuals, populations and species (Lewontin, 1974). It did so, first, by using the relationship between genes and proteins. Second, by elucidating, at the DNA level, the structure, expression, function, mechanism, and evolution of genes, intergenic spacers, and multigene families, employing recombinant DNA methodologies (ref. 3-9 in Nevo, 1988b). A comprehensive compilation of genetic maps of viruses, bacteria, plants, animals and humans, was published (O'Brien, 1990). These maps elucidate the extent of clustered, conserved, convergent and divergent linkage relationships of homologous genes across phylogeny (Dutta, 1986). They highlight genome organization and evolution, but do not explore ecological correlates.

#### **Population ecology**

Ecological diversity on both macro- and microgeographical scales is also central to adaptation and speciation. Theoretical and experimental evolutionary ecology has dramatically advanced the theory of niche, ecosystem and biota evolution, as well as energy flow in nature (e.g., Hutchinson, 1965; MacArthur, 1972; Whittaker and Levin, 1975; May, 1978; Ehrlich et al., 1977; Pianka, 1978; Diamond and Case, 1986; Arthur, 1987; Wilson, 1988; Van Valen, 1965, 1974, 1991).

The recognition of the ecological genetics interface and the theoretical and empirical developments of population genetics and ecology, as well as molecular evolution, are evident. Nevertheless, a genuinely synthetic and mature science of evolutionary population biology did not emerge from the individual disciplines of population ecology and genetics despite some insights (e.g., Baker and Stebbins, 1965; Levins, 1968; Sammeta and Levins, 1970; Creed, 1971; Gillespie, 1974; Clarke, 1975; Felsenstein, 1976; Endler, 1977; Brussard, 1978, Roughgarden, 1979; Karlin and Nevo, 1976, 1986; Karlin, 1982; Parsons, 1983; Shorrocks, 1984; Harper, 1977; Hedrick et al., 1986; Nevo 1988c, 1991a,b).

Ecology still focuses primarily on biodiversity and ecosystems (i.e., the number and coexistence of organisms and species) and the factors determining their patterns, yet, it largely ignores genetic diversity within and between species. Only a few ecologists provide data which is directly relevant to empirical and theoretical population genetics. Likewise, population geneticists are still preoccupied with the neutral or selective nature of molecular polymorphisms. They rarely incorporate much relevant abiotic and biotic factors from the real world, or introduce ecological parameters into their models and interpretation of observed patterns. One of the obvious bridges between ecology and genetics, is the origin and evolution of sex (e.g., Michod and Levin, 1988), and recombination (Korol et al., 1990).

#### **The problems and methodologies of ecological-genetics interface**

A major problem in the integration of population ecology and genetics is that the conceptual and empirical frameworks of genetics and ecology are



not easily matched, partly due to their largely still unknown complexities. For example, what is the ecological significance of genetic population pattern? Or, how can the high order complexities of ecology and genetics, mult niche and multilocus diversities, respectively, be meaningfully associated? Likewise, to what extent are allele frequency configurations and genome organization affected by deterministic, ecological and population parameters as against random factors such as founder effects, initial conditions, bottle-necking, sampling and random drift fluctuations? How can these complex problems be tackled?

Out of several methodologies investigating the ecological-genetics interface (see Nevo, 1988a) we focused in our studies of protein (Markert, 1975) and DNA diversities on the methodology of genetic-ecological correlations. These (see Nevo et al., 1984, Nevo, 1988a) inferentially demonstrate the adaptive significance of genetic polymorphisms. If conducted on many loci, populations and unrelated species involving varied and contrasting ecologies, demographies, and life histories, then any emerging pattern, if repetitive and consistent over many taxa in space or time, must be robust (Nevo, 1983a). Furthermore, the emerging patterns may roughly indicate the relative contributions of each of the biotic subdivisions, i.e., ecological, demographic, and life history, to adaptive evolution. This is true for allozymic diversity (Nevo et al., 1984, 1990; Nevo and Beiles, 1991) but also holds for DNA diversity (Nevo, 1991a). A major hypothesis tested in most of our studies was the niche width variation hypothesis (Van Valen, 1965). In its genetic variant, i.e. the niche-width, genetic variation hypothesis (Nevo, 1978, 1988a) it predicts positive correlation between heterozygosity and the spatial or temporal ecological niche width.

In our global analyses of animals and plants (Nevo et al., 1984), we also correlated heterozygosity or genetic polymorphisms with the following parameters: ecological (life zone, geographic range, habitat type and range, climatic region); demographic (species size and population structure, gene flow and sociality); and life history (longevity, generation length, fecundity, origin, mating system and reproduction mode). The neutral theory of molecular evolution (Kimura, 1983) never questioned specific examples of adaptive evolution at the molecular level. Neutralists believe that adaptive evolution occurs through positive Darwinian selection, but only in a small proportion of genes, while most molecular evolutionary change and polymorphisms are propelled by mutation input and random genetic drift output (Kimura, 1983; Nei, 1987).

#### Ecological-Genetics research program at the Institute of Evolution

Here I will briefly overview the ecological-genetics research program conducted extensively and intensively at the Institute of Evolution, University of Haifa, Israel, since 1977 (Nevo, 1990). During the last 15 years we studied genetic polymorphism in plants and animals in an attempt to highlight the ecological-genetics interface. The basic idea underlying all these studies was to highlight the genetic structure and divergence of individuals, populations and species, living under interacting abiotic and biotic environmental stresses. Our ultimate goal was to evaluate the relative importance of the evolutionary forces in nature causing genetic change of protein and DNA diversities at the micro- and macrogeographical levels (Nevo, 1988a,b,c).

We employed the extraordinary physical and biotic ecological diversity of Israel, across a relatively small area, as our natural laboratory (Nevo,

1986b, 1988c). Our ecological-genetics studies in animals and plants were based on the aridity stress and climatic unpredictability, doubly tested in Israel across southward (200 km) and eastward (70 km) aridity gradients (Nevo, 1992b). We also tested thermal (Nevo et al., 1977), and chemical stresses, including inorganic metals (Hg, Cd, Pb, Zn, Cu) and organic (crude oil, detergents) pollutants. The pollution biology studies involved both a-posteriori (e.g., Nevo et al., 1977); but, more importantly, a-priori critical tests under controlled laboratory conditions (Nevo et al., 1983a; Nevo, 1986a). Consequently, we analyzed, either in nature or in the laboratory, specific environmental stresses causing evolutionary genetic changes in population genetic structure and differentiation.

#### The evidence

The evolutionary significance of genetic diversity in natural populations of plants and animals was studied and reviewed here, using the environmental-genetic correlation methodology at three geographic levels: (1) Local: two species of wild cereals (barley and wheat) growing in microhabitats differing in microclimate, soil types and/or topography (Nevo et al., 1981, 1983b, 1986a, 1988a,b, 1991), landsnails, on opposing slopes (Nevo et al., 1982) and barnacles varying in temperature regimes in Israel (Nevo et al., 1977). (2) Regional: 38 species in Israel (Nevo, 1983a), 21 ranging from the Mediterranean region to the Negev Desert across a gradient of increasing aridity southwards (Nevo and Beiles, 1988). Wild emmer wheat and wild barley were studied in the Near East Fertile Crescent (Nevo, 1992a, Nevo et al., 1986; Nevo and Beiles, 1989a); and (3) Global: 1111 species of animals and plants (Nevo et al., 1984); 189 amphibian species (Nevo and Beiles, 1991); and 184 subterranean mammals (Nevo et al., 1990), all 3 ranging worldwide.

The species involved in these local, regional and global analyses are largely taxonomically unrelated. They vary in their ecologies, demographies, life histories and other biological variables. They were mostly tested for allozymic diversity by horizontal starch gel electrophoresis at 25 gene loci, on average (range 14-50 loci). In addition, nine genetic systems were studied in subterranean mole rats in Israel, at both the nuclear and mitochondrial DNA diversities (mostly reviewed in Nevo, 1991a), and ribosomal DNA was tested in wild emmer wheat. Likewise, the correlation was explored between DNA diversity and ecology as well as with protein diversity.

#### Patterns and theory

The following patterns were found at all three geographic levels across phylogeny: (1) The levels of genetic diversity vary nonrandomly and are structured among populations, species, and higher taxa. (2) Genetic diversity is partly correlated with, and predictable, primarily by ecological factors. Globally, genetic diversity is high in (i) species or populations within species that live in broader environmental spectra; (ii) large species with patchy population structure and limited migration, as well as in solitary or social species; and (iii) species with small body size, annuals or long-lived perennials, older in time, with smaller diploid chromosome numbers, primarily outcrossing; and plant species reproducing sexually and pollinated by wind. Species with the above characteristics harbour generally more genetic diversity than their opposite counterparts (Nevo et al., 1984).

Globally, genetic diversity is partly correlated and predictable by 3-4 variable combinations of ecological, demographic and life history



variables, largely in this order (Nevo et al., 1984). Ecological factors account for the highest proportion of the 20% explained genetic diversity (heterozygosity) of all species as compared with demographic and life history factors (90%, 39% and 3.5% of the explained variation, respectively). Within particular higher taxa the explained portion of genetic diversity increases considerably (mean 44%, and maximum of 74% in molluscs). However, significant small intercorrelations ( $r$  = mostly 0.1-0.3) occur both within and between the subdivided biotic variables. Therefore, additional critical tests at the population microgeographical level, complemented by biological, biochemical and physiological experimentation, may verify the inferences of causal relationships between biotic factors and genetic diversity. Regionally in Israel, 21 species of plants and animals display genetic parallelism (Nevo and Beiles, 1988). Their heterozygosity increases towards the desert, positively correlated with climatic unpredictability (Nevo and Beiles, 1988, 1989). Finally, plant genetic resources for crop improvement can be predicted by isozyme markers and ecology (Nevo, 1987).

## CONCLUSIONS

The patterns and correlates of genetic diversity at the protein and DNA levels, revealed over many unrelated species subdivided into different abiotic and biotic regimes, strongly implicate selection in the genetic divergence of species (Nevo, 1978, 1983a,b, 1988a,b; Nevo et al., 1984). Natural selection in several forms, but most likely through the mechanisms of spatiotemporally varying abiotic and biotic environments and epistasis, at the various life cycle stages of organisms, appears to be an important evolutionary force leading to a change at the molecular level in many species. Other evolutionary forces and factors including mutation, migration and genetic drift, certainly interact with natural selection, either directly or indirectly, and thereby contribute differentially, according to circumstance, to population genetic differentiation at the molecular level.

The role and relative importance of each evolutionary force and its interactive patterns, and the establishment of direct cause-effect relationships between biotic and genetic factors, is a future challenge at both the protein and DNA levels. The ability to approach generalization depends on many more carefully designed field observations on many populations and species, coupled with critical field and laboratory testing of many loci, singly and in combination, to assess the contribution of protein and DNA polymorphisms to adaptation.

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