1

Ecological genetics

". . . the methods of genetics, diligently applied, obviously give one the power to replace loose speculation and guesswork by irrefutable inductions, and so to lay down a foundation upon which the evolutionist and taxonomist can build with safety."

Trow (1912)

Summary

1 Ecological genetic investigations have traditionally emphasized the integration of field ecology and laboratory genetics. Recent conceptual (e.g., phylogenetic analysis) and methodological (e.g., DNA markers) developments have revitalized interest in ecological genetics.

2 A contemporary vision of ecological genetics is presented as the investigation of the origin and maintenance of genetic variation within and between populations (in the broadest sense), which ultimately leads to speciation.

3 The outcomes of ecological genetic investigations have both pure and applied applications, for example, in the evolutionary consequences of habitat fragmentation, the construction of conservation policies for species reintroduction and for risk assessment of the release of genetically modified organisms.

4 New developments that allow high-throughput analysis of specific genomic loci, combined with the development of environmental genomic approaches to assessing adaptive variation, improved bioinformatics tools for data storage and access, and advanced statistical theory for enhanced data interpretation will provide exciting approaches to ecological genetics in the future.

1.1 What is ecological genetics?

The term ecological genetics was first used in print by Ford (1964) in his landmark book *Ecological Genetics*, although it had been used some years earlier when the Ecological Genetics Group held their first meeting in Aberystwyth in 1956. Ford considered that ecological genetics dealt with the "adjustments and adaptations of wild populations to their natural environment," whilst it was the genius of Darwin and Wallace that brought together ecological ("struggle for existence") and genetic (variation) concepts.

However, interest in genetic variation and its relationship to the environment was not new in the 1960s (Cain and Provine 1992), and had previously been a central element of Turesson's (1922, 1925, 1930) seminal work. Turesson grew populations of plants from different Swedish habitats in a common garden, and was one of the first to grasp the concept that habitat-correlated genetic variation was widespread among plant species. Extensions of this work by Clausen, Keck, and Hiesey (1940, 1948), investigated plant populations from an altitudinal gradient in central California. By growing plants in common gardens at different altitudes, they were able to analyze variation (i.e., local adaptation) that would otherwise have been masked by the use of a single common garden. This was the theme later taken up by gene ecologists (Briggs and Walters

1997). In animals, the link between ecological and genetic variation was thoroughly investigated in the banded snail, *Cepaea nemoralis* (Cain and Sheppard 1950, 1954). Each of the above case studies emphasize the two essential and inseparable aspects of Ford's view of ecological genetics, the combination of ecological fieldwork and laboratory genetics. It was through these types of studies that major syntheses of ecological genetics and evolutionary biology have been made (e.g., Dobzhansky 1970, Grant 1963, 1981, Stebbins 1950).

In the fourth edition of *Ecological Genetics*, Ford (1975, p. 11) stated that "if ecological genetics is to be successfully developed, we need new thinking, new methods, new material." Over the last 25 years, new thinking, new methods and new material have indeed become available and are being successfully used to develop ecological genetics (Berry, Crawford, and Hewitt 1992, Real 1994), much of which has now been encompassed by the phrase "molecular ecology". The renewed interest in the field can be measured in part by the increased incidence of meetings tackling ecological genetic issues and the success of a journal dedicated to the area, only initiated a decade or so ago.

The conceptual developments that have had substantial impacts on the development of ecological genetics have been in areas as diverse as the development of rigorous methods for phylogenetic analysis (Avise 2000), the development of procedures for the detailed analysis of gene flow (Bossart and Prowell 1998) and the development of metapopulation theory (Hanski 1999). The greatest impact of new methods has been the development of protein and DNA markers for the analysis of genetic variation (Baker 2000). Such laboratory advances have meant that vastly greater numbers of increasingly more variable loci can be identified and used; this shows no sign of slowing. In addition, there have been methodological advances in the statistical analysis of quantitative characters (Lynch and Walsh 1998). Furthermore, low-cost computing power and the concomitant development of analysis software, much of which is web-accessible, have opened up the possibilities of the complex analysis of vast amounts of empirical data. These developments mean that detailed genetic analyses are no longer restricted to an elite group of organisms (e.g., mice, *Drosophila*, maize); now ecological genetic procedures and analysis should, at least in theory, be open to any organism.

Classical ecological genetics was principally concerned with documenting and measuring the magnitude of selection in natural systems. Such investigations tended to focus on single populations, in which population size was not an essential feature, and on aspects of the phenotype under simple gene control. In contrast, the contemporary approach emphasizes the importance of population size and structure, the interaction among populations through migration and dispersal (i.e., gene flow), the interaction between local selection and genetic drift, and an expansion of the phenotype to include quantitative and qualitative features (Real 1994).

However, into this brave new world, Ford's (1975) argument, that the choice of material for ecological genetic investigations is of the utmost importance, is still valid, albeit with modifications in the light of nearly 30 years of additional research and development. Thus, it is necessary to have a clear, testable hypothesis. In addition, the ideal study taxon should: (i) have a known ecology; (ii) be easy to collect; (iii) have a short life-span so that numerous generations can be investigated; (iv) have genetic variation that is easily recognized and interpreted and is capable of statistical analysis; (v) be at a high enough density that it can easily be found; and (vi) be easily maintained in the laboratory or greenhouse. However, it is rarely possible to fulfill all of these criteria. Ford (1975, p. 9) indicated that the choice of material seems "rather an art than a science", and stated that "the more rewarding decisions are generally reached by a thorough . . . grasp of the essentials of the problem to be solved, estimated in the light of much knowledge and experience".

Lifetimes of research are often required for robust investigations of ecological genetics, and require a combination of detailed fieldwork and the application of genetic (now usually molecular) techniques. However, importantly ecological genetics requires experimentation, as emphasized by Ford (1964). Documentation of variation needs to be combined with the generation of hypotheses that can be empirically tested. We have interpreted contemporary ecological genetics as the investigation of the origin and maintenance of genetic variation within and between populations, which ultimately leads to adaptation and speciation. Ecological genetics provides the means by which mechanisms of speciation can be understood and the patterns of genetic variation in nature investigated.

1.2 Why study ecological genetics?

The picture of modern ecological genetics that emerges is one of relevance to the interaction of large-scale geographic patterns of demography with genetic dynamics among small, partially isolated, and potentially locally adapted populations. Framed in such a context, ecological genetics is of both great pure and applied scientific interest. Adaptive radiation, the evolution of ecological diversity within a rapidly multiplying phylogenetic lineage, is one major research area where the combination of ecological and genetic analysis has been particular valuable (e.g., Schluter 2000).

The debate over the introduction of alien species and release of genetically modified (GM) organisms and their potential impacts on the environment and closely related species is an area where a combination of fieldwork and experimental work, within an ecological genetic framework, is likely to produce exciting pure and applied science. One of the major environmental concerns over GM crops relates to transgene movement into wild relatives, where the pattern of hybridization will affect the scale and rapidity of any ecological change, plus the feasibility of any necessary containment. In the UK, one of the species of most concern is the widely cultivated oilseed rape (*Brassica napus*), since it has numerous wild relatives (e.g., *Brassica rapa*) that are either native or naturalized. Using remote sensing, Wilkinson et al. (2000) identified possible sites of sympatry between *B. napus* and *B. rapa* across 15,000 km^2 of south-east England. In 1998, two sympatric populations were found over the entire survey area, and in 1999, every newly recruited plant in these populations was tested for hybridity using a combination of flow cytometry and nuclear DNA markers. Despite the size of this investigation, only one hybrid was observed among 505 plants screened in the *B. rapa* populations. Thus, it is possible to investigate the interaction between populations of domesticated and wild organisms.

As human impacts on habitat landscape increase, and habitats are fragmented, the interactions between wild and domesticated populations become more complex. Similarly, wild populations that were once large and connected by gene flow may become fragmented, and the population size diminished (Frankham, Ballou, and Briscoe 2002). Under such conditions, migration becomes critical for the reestablishment of local populations, so that gene flow may counter some of the detrimental effects of inbreeding depression. Similarly, changes in habitat management may have significant influences on the genetics of rare species. For example, in the UK, the Red Squirrel (*Scirius vulgaris*) is a nationally rare species, although it is locally common in the fragmented coniferous woodlands of northern England and the Scottish Borders. Using a combination of detailed analysis of habitat fragmentation and analysis of microsatellite variation in museum specimens of *S. vulgaris*, Hale et al. (2001) were able to show that the creation of a large coniferous plantation (since the 1960s) was enough to produce miscegenation of *S. vulgaris* populations up to 100 km apart. Thus, the genetic consequences of habitat change may occur hundreds of kilometers away from the site of change.

Any ecological genetics program that focuses on demographic and genetic variation across large-scale geographic variation has obvious implications for conservation. Populations that are small and locally adapted may also suffer from increased gene flow through the disruption of locally adapted genotypes. However, any migrants into these populations may not have equal effects on local population growth and fitness. Thus, knowledge of the genetic diversity that exists among migrants is essential when constructing conservation policies for species reintroduction or augmenting declining populations (Frankham, Ballou, and Briscoe 2002). For example, conservation organizations are increasingly interested in ensuring that only local seed is planted within specific areas. This, of course, raises the issue of what is meant by local: the same population, the same county, the same country or even the same continent.

Conservation biology and GM risk assessment are not the only areas where the results from ecological genetic investigations are a valuable applied tool. The long-term sustainability of ecological systems depends on the ability of organisms to adapt and respond to changes in their biotic and abiotic environment. The methods for studying adaptive evolution in contemporary populations provided by ecological genetics are equally important in assessing the ability of organisms to respond to both local and global environmental perturbations. Furthermore, it is now possible to investigate the genetic and ecological outcomes of major environmental changes, for example, the effects of the last glaciation on the recolonization of Europe by plant and animal species (e.g., Hewitt 2000, Taberlet et al. 1998). The accurate reconstruction of historical species' range shifts and correlation with past climate change offer great potential for improving predictions of floral and faunal adaptive response and gene flow under future rapid climate change scenarios.

New developments in DNA extraction technology have been incorporated in ecological genetic approaches. It is no longer necessary to collect whole organisms; all that is required is a small amount of suitable material. Furthermore, the use of preserved materials means that it is possible to add a temporal dimension (tens, even thousands of years) to investigate genetic diversity and structure. Also, hundreds of samples may be readily analyzed for large genomic segments. Thousands of markers are available, which are variable at many different levels. However, the next major development will be through environmental genomics initiatives, where the expression patterns of genetic variants in different environments can be investigated. Genetics is here to stay as an essential component of ecology, while ecology will become increasingly important for the interpretation of data emerging from genomics research programs.

REFERENCES

Avise, J.C. 2000. Phylogeography. *The History and Formation of Species*. Cambridge, MA: Harvard University Press.

Baker, A.J. 2000. *Molecular Methods in Ecology*. Oxford: Blackwell Science.

Berry, R.J., Crawford, T.J., and Hewitt, G.M. 1992. *Genes in Ecology*. Oxford: Blackwell Science.

Bossart, J.L. and Prowell, D.P. 1998. Genetic estimates of population structure and gene flow: limitations, lessons and new directions. *Trends in Ecology and Evolution*, **13**: 202–6.

Briggs, D. and Walters, S.M. 1997. *Plant Variation and Evolution*. Cambridge: Cambridge University Press.

Cain, A.J. and Sheppard, P.M. 1950. Selection in the polymorphic land snail *Cepaea nemoralis* (L.). *Heredity*, **4**: 275–94.

Cain, A.J. and Sheppard, P.M. 1954. Natural selection in *Cepaea*. *Genetics*, **39**: 89–116.

Cain, A.J. and Provine, W.B. 1992. Genes and ecology in history. In R.J. Berry, T.J. Crawford, and G.M. Hewitt, eds. *Genes in Ecology*. Oxford: Blackwell Science, pp. 3–28.

Clausen, J., Keck, D.D., and Hiesey, W.M. 1940. Experimental studies in the nature of species, I. The effect of varied environments on western North American plants. *Publications of the Carnegie Institution*, 520.

Clausen, J., Keck, D.D., and Hiesey, W.M. 1948. Experimental studies in the nature of species, III. Environmental responses of climatic races of *Achillea*. *Publications of the Carnegie Institution*, 581.

Dobzhansky, T.G. 1970. *Genetics of the Evolutionary Process*. New York: Columbia University Press.

Ford, E.B. 1964. *Ecological Genetics*. London: Methuen.

Ford, E.B. 1975. *Ecological Genetics*. London: Chapman and Hall.

Frankham, R., Ballou, J.D., and Briscoe, D.A. 2002. *Introduction to Conservation Genetics*. Cambridge: Cambridge University Press.

Grant, V. 1963. *The Origin of Adaptations*. New York: Columbia University Press.

Grant, V. 1981. *Plant Speciation*. New York: Columbia University Press.

Hale, M.L., Lurz, P.W.W., Shirley, M.D.F., Rushton, S., Fuller, R.M., and Wolff, K. 2001. Impact of landscape management on the genetic structure of red squirrel populations. *Science*, **293**: 2246–8.

Hanski, I. 1999. *Metapopulation Ecology*. Oxford: Oxford University Press.

Hewitt, G. 2000. The genetic legacy of the Quaternary ice ages. *Nature(London)*, **405**: 907–13.

Lynch, M. and Walsh, B. 1998. *Genetics and Analysis of Quantitative Traits*. Sunderland, MA: Sinauer.

Real, L.A. 1994. *Ecological Genetics*. Princeton, NJ: Princeton University Press.

Schluter, D. 2000. *The Ecology of Adaptive Radiation*. Oxford: Oxford University Press.

Stebbins, G.L. 1950. *Variation and Evolution in Plants*. New York: Columbia University Press.

Taberlet, P., Fumagalli, L., Wust-Saucy, A.-C., and Cosson, J.-F. 1998. Comparative phylogeography and post-glacial colonization routes in Europe. *Molecular Ecology*, **7**: 453–64.

Turesson, G. 1922. The genotypical reponse of the plant species to the habitat. *Hereditas*, **3**: 211–350.

Turesson, G. 1925. The plant species in relation to habitat and climate. *Hereditas*, **6**: 147–236.

Turesson, G. 1930. The selective effect of climate upon plant species. *Hereditas*, **14**: 99–152.

Wilkinson, M.J., Davenport, I.J., Charters, Y.M., Jones, A.E., Allainguillaume, J., Butler, H.T., Mason, D.C., and Raybould, A.F. 2000. A direct regional scale estimate of transgene movement from genetically modified oilseed rape to its wild progenitors. *Molecular Ecology*, **9**: 983–91.