

25 Islands as Models in Population Genetics

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The concept of the population as a solitary entity has been an important one throughout the history of population genetics. The species is often considered as a single panmictic unit in population genetics theory. Attempts at the application of population genetic theory have often depended upon an assumption that gene frequencies could be determined in a population, and that the forces which act to direct changes in gene frequency can be estimated. In practice, this has proven to be difficult. As a result, because of their physical isolation, islands provide some of the best opportunities for examining the validity of population genetic theories. On an island, the population can be defined and the complexity of forces which affect levels of genetic variability can be simplified.

The island population, as a concept, is obviously the epitome of the finite population. As such, differences between island populations, which must of necessity have a defined upper size, with populations from continental regions, which may be several orders of magnitude larger, allow the testing of some of the predictions of stochastic theory. It is surprising that the island population does not seem to have played an especially important role in the neutralist/selectionist controversy, and the reasons for this are not clear.

When a population goes through a "bottleneck" in size (i.e., spends one or more generations at a small size), it will lose much of the genetic variability that existed prior to the bottleneck. Island populations are more susceptible to bottlenecks than are mainland populations, simply because of their smaller initial population size, which is due to the circumscribed area occupied by the island population.

When considering continental shelf islands, two additional factors may contribute to the genetic differentiation of the island population. If the island population were formed as a relict population when the continental shelf island was formed, genetic drift will be the most

important force changing gene frequencies. On the other hand, if the island population were the result of a migrational introduction, the initial sampling event at the time of founding will be the most important factor shaping the genetic makeup of the population.

The initiation of a population on an island, whether it comes about by migration of a founder(s) or by creation of a relict population through a severance of physical contact with the continent, results in certain forces acting to effect genetic changes. Most of these changes are the result of the sampling of the genetic constitution of the source population that founds the new island population. This sampling, whether it be called founder effect (Mayr 1963) or bottleneck effect (Nei, Maruyama, and Chakraborty 1975), will act to reduce genetic variation, and to redefine the genetic selective interactions that can take place between the remaining variants. Electrophoretic data, summarized below, indicate that these changes do occur. Comparisons of morphological evolution in island populations indicate that they are often marked by distinct morphological changes which are not always attributable to adaptation to the island environment. Many such changes, in fact, seem more appropriately to be attributed to the sampling of genetic variants that will occur (even for quantitative, polygenic traits) when a founder event occurs (Berry 1964; Kilpatrick 1981).

The Concept of Migration for the Island Population

There is an important consideration in the use of islands as observational models for population genetics, i.e., all islands are not created equal. There are at least two major forms of islands: continental shelf islands and oceanic islands (Williamson 1981). There should also be a third grouping of habitats which may form a type of island; these are the habitat islands (Kilpatrick 1981), and may also include caves and lakes (Culver 1982). The primary difference among these forms of islands is the

potential for immigration of genes from a source population on the mainland. Oceanic islands can basically be considered to have little or no immigration, continental shelf populations have a very limited amount of migration, and habitat islands may have an even greater level of migration because of easier movement of individuals over terrestrial habitat compared to aquatic environments. The islands of Lake Erie fall into the group, continental shelf islands.

The concept of islands has formed a framework for some of the earliest model systems used to investigate the effects of gene exchange between populations. Wright's "island model" (1940, 1951) is one of the most extensively investigated theoretical models incorporating both selection and migration. In many ways, it epitomizes the approach taken by population genetics to the consideration of the "island." The species is thought of as being composed of a number of subpopulations, largely isolated from one another, but each subpopulation receiving some migrants each generation. Migration into a subpopulation takes place at random from all remaining populations, so that there is no explicit accounting for distance. The model was one of the first to be capable of defining the magnitude of selective differences and the magnitude of migrational exchange which will lead to the extremes of isolation or panmixis in the species as a whole.

In many respects, migration, although the most important factor in Wright's island model, is actually a rather unimportant factor in the evolution of many island populations. We may actually more appropriately consider the lack of migration to be the overriding parameter. Especially in the case of oceanic islands, migration can be ignored. In such situations, the analysis of natural populations and the application of theory to this analysis become simplified. In the case of continental shelf islands, or habitat islands, lakes, and caves, the measurement of migration becomes more important (and more difficult).

The occurrence of unique alleles in continental shelf islands (Kilpatrick 1981) suggests an interplay between a low, but continuing, immigration of continental alleles, a low input of new alleles by mutation, and a specific set of selection pressures unique to the island population. This same interplay may not occur in oceanic islands where there does not seem to be that same number of unique alleles found in populations that can be compared to conspecific continental populations. Since mu-

tation rates should be similar in the two cases, the reason for this difference in the occurrence of unique alleles is unclear (Kilpatrick 1981). The marked occurrence of endemic island species on oceanic islands, however, points up the ability of populations to adapt to such habitats, and, of course, to adapt by acquiring unique alleles compared to the source population.

Levels of Genetic Variability in Island Populations

One of the most direct ways of measuring genetic variability existing within natural populations has been the use of protein electrophoresis. This methodology has now been applied to over 1,000 species of plants and animals (see reviews in Fuerst, Chakraborty, and Nei 1977 and Nevo, Beiles, and Ben-Schlomo 1984). Although there is some question concerning the exact percentage of the extant genetic variation which electrophoresis detects, the large amount of data collected from a diverse group of organisms makes it the method of choice for comparing island populations with continental populations.

Some comments are necessary in order to place the data in a context that can explain alterations in genetic variability that may be due to an island habitat. In general, the measure of genetic variability most widely used is the average heterozygosity (also referred to as gene diversity). This is a measure of the expected proportion of heterozygous individuals in a population exhibiting Hardy-Weinberg genotypic proportions and the observed allele frequencies in the sample. The contribution of an allele to the measured level of heterozygosity is greatest for alleles with an intermediate frequency (for instance between 0.2 and 0.8 allele frequency in the population). Such alleles have been found to occur relatively rarely in natural populations (Chakraborty et al. 1980). Most loci have a common allele (frequency greater than 0.8) and one or more rarer alleles; in fact, the majority of loci in a large proportion of natural populations have a predominant allele which has a frequency greater than 0.95. Such loci contribute in a relatively small way to total heterozygosity.

Similarity of Genetic Variability in Newly Established Populations because of Gene Frequency Distribution

When a population goes through the sampling which occurs at the time of a bottleneck, the pattern of allelic

loss will not be the same at all loci. The majority of loci, which contain a predominant allele and some rare alleles, will tend to become homozygous, with the loss of the rare alleles. This will have a minor effect on reducing genic heterozygosity. Those loci which contained two alleles with intermediate frequency will tend to retain both alleles, and they will tend to remain intermediate in frequency. This will result in relatively small losses of genic heterozygosity overall, unless the bottleneck is unusually severe. Theoretical studies of the genetic effects of bottlenecks were first performed by Nei, Maruyama, and Chakraborty (1975), and subsequently expanded by Maruyama and Fuerst (1984). We shall consider first the overall loss of genetic variability, and then consider how the allele frequency distribution has shaped the pattern of loss in some island populations.

Loss of Average Genetic Variability

A number of populations inhabiting islands have been studied using protein electrophoresis. Some of the data have been summarized in the reviews of Kilpatrick (1981), Culver (1982), and Nevo et al. (1984). Island populations as a group do not necessarily have lower levels of genetic variability. This seems to be particularly true of species which are strictly island dwelling, especially if they are island endemics. Many of these species seem to have levels of genetic variability equal to or greater than many continental species in related taxa (see, for example, the studies of the *Anolis* lizards summarized in Gorman and Kim 1976).

When conspecific populations inhabiting island and continental habitats are compared, the situation is seen to reflect some of our expectations concerning island populations. The island populations, especially in mammals, exhibit lower levels of genetic variability. Kilpatrick (1981) reports that in twelve comparisons, levels of heterozygosity were between 4.6% and 90% reduced in island populations. Among eight comparisons which involved close congeneric pairs, seven comparisons showed reduced variation in island population, with an average reduction of heterozygosity of 77%.

Similar results can be seen for other terrestrial vertebrate taxa (for one example in lizards, see Gorman et al. 1975). It is not clear whether a pattern exists for birds, since relatively few comparisons involving island and continental species have been made, and because levels of genetic variability seem to be slightly lower in birds than in terrestrial mammals (Nevo et al. 1984). For

fishes, species inhabiting isolated lakes, such as the rift valley lakes of Africa and the Sea of Galilee, seem to have low levels of genetic variability (Kornfield et al. 1979, Eschelle and Kornfield 1984). Comparisons involving isolated and nonisolated populations of fishes have not been reported, however.

It is even less clear whether there is a relationship between island habitat and genetic variability (measured by electrophoresis) for invertebrates. Among insects, *Drosophila* populations inhabiting islands seem to exhibit the same spectrum of variability as seen in continental populations (Yang, Wheeler, and Bock 1972; Ayala 1975). Other species show declines of genetic variability in island populations, for example, the spittlebug *Philaenus spumarius* (Saura, Halkka, and Lokki 1973) and the Mediterranean fruit fly, *Ceratitidis capitata* (Huetel et al. 1980).

Nevo et al. (1984) produce a single table comparing levels of genetic variability in island and continental populations of the same species (their table 5). It is difficult to determine exactly which species they have included in the table, since there seem to be potentially more pairs of comparisons than they have included in the table. An examination of the data presented shows slight decreases in the mean of average heterozygosity and percentage of polymorphic loci, when that mean is calculated over the various species included in the analysis. The study is not as carefully done as that of Kilpatrick (1981), and the authors have concluded that the decreases are not significant (based on consideration of the standard deviations of heterozygosity over the species).

The Effect of the Allele Frequency Distribution on Genetic Loss

In addition to the reduction of heterozygosity in island populations, the distribution of this heterozygosity over different loci is altered. One aspect of this alteration is the increase in the percentage of essentially monomorphic loci in populations on islands. In mammals, Kilpatrick (1981) showed that there was a significant increase in monomorphic loci for both continental shelf and oceanic island populations compared to conspecific mainland populations.

The pattern of this loss is important as well. In the only electrophoretic study so far published on Lake Erie populations, Browne (1977) showed that there was only a slight decrease in average heterozygosity in island

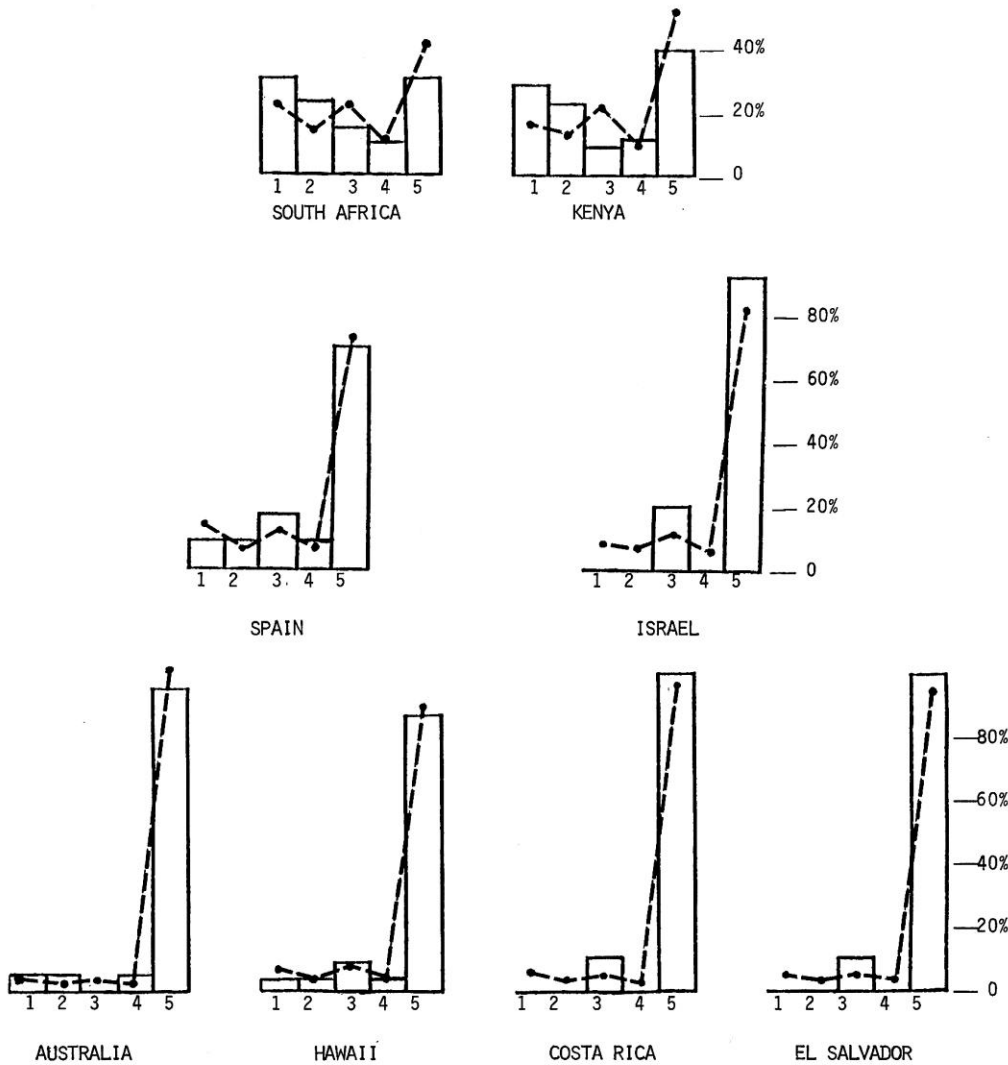


Fig. 25.1. Allele frequency distributions for populations at different stages of colonization of the Mediterranean fruit fly (*Ceratitis capitata*). Populations at the top represent source population in Africa. Populations in the middle are the first stage of colonization into the Mediterranean basin. Populations at the bottom represent the secondary colonizations. Note loss of intermediate and low-frequency alleles, and increase of monomorphic alleles. Population heterozygosity declines only moderately, from about 0.07 for the top, to 0.05 in the middle, to 0.035 for the bottom populations. Data originally collected by Huettel et al. 1980.

populations of *Peromyscus leucopus* (0.071 for islands versus 0.080 for mainland). There was a decrease in the number of polymorphic loci in all three island populations, and only a single rare allele from the mainland populations was found in the island populations. The surviving polymorphic alleles in the island populations had all appeared at intermediate frequencies in the mainland, and consequently could easily be sampled in founding the island populations.

A similar effect is seen in a more detailed study of repeated, serial colonizations carried out by the Mediterranean fruit fly (Huettel et al. 1980). Two different levels

of colonization can be followed, first from source African population to the Mediterranean basin, followed by subsequent colonizations to various other populations such as Australia and Hawaii. The data given in figure 1 illustrates that the pattern of genetic loss following different colonizations preserved the same intermediate frequency alleles in all populations, with the loss of almost all rare alleles. This pattern of allelic loss resulted in island populations which are serially founded appearing similar to one another for their electrophoretic genotypes, an observation which has been noted by Kilpatrick for some mammalian populations.

Other Concepts of Islands

Besides the traditional island (land surrounded by water), it is important to emphasize that other genetic islands occur. These are found in cave populations (summarized by Culver 1982), and in isolated freshwater lakes (such as the East African rift valley lakes), mountain-top habitats, and to a small degree in some isolated refugial habitats which were formed by the retreat of glacial events in the northern hemisphere.

Culver has noted that the pattern of genetic loss for electrophoretic variation in cave populations is not as consistent as for true island populations. This may be because of the possibility of greater levels of genetic migration for such populations, or because of difference in the selective pressures which occur in caves.

The island model of population genetics has recently taken on even greater importance because of the analogy which can be made between an island and the managed habitat of many endangered species. The species may be in a managed reproduction environment, such as a zoo, in which migration is between different islands (zoos) with rare input from a source population. Alternatively, the habitat may be fragmented into small isolated or partially isolated units, with limited size, and limited potential for genetic interchange (Harris 1984).

Models of Speciation/Founder Effect

The island model has formed an important framework for the recent production of models of speciation. The work of Carson and his coworkers on the Hawaiian *Drosophila* has led to the suggestion that founder effects may lead directly to a particular pattern of genetic change directly responsible for speciation (Carson and Templeton 1984). The generality of this model of island speciation has not, however, been completely accepted (Barton and Charlesworth 1984). Discussion of such models is beyond the scope of this summary.

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