FRAGMENTS, EXTINCTION AND RECOLONIZATION: THE GENETICS OF METAPOPULATIONS

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ABSTRACT

The idea of a metapopulation - a group of local populations in a patchy habitat - recurs in both ecology and evolutionary biology. Although the metapopulation concept is at least 50-75 years old, it has recently resurged, as natural habitats become fragmented and are lost because of humans' use of resources. However, fragmentation is not the same as habitat loss per se, and patchy habitats do not necessarily make metapopulations. Some populations may behave naturally as metapopulations and are characterized by extinction of some local populations and recolonization of empty patches from the occupied patches. Alternatively, other populations may be forced into a metapopulation dynamic by human-caused habitat fragmentation or other introduced disturbances. The genetic effects of habitat fragmentation or introduced disturbance are subtle and depend on frequency of migration between patches, rates of recolonization of empty patches, and levels of genetic variation before fragmentation began. Other than generally reducing population sizes, the effects of metapopulations on breeding practices or adaptive evolution depend on the amount of genetic variation remaining within local populations, how genetically differentiated from each other local populations become as a result of local extinctions and recolonization, the strength of natural or artificial selection, and whether selection is locally strong enough to result in adaptation to local conditions. We offer limber pine (*Pinus flexilis* James) as an example of a forest tree species that experiences metapopulation dynamics.

INTRODUCTION

While ecosystems may appear to the untrained eye as uniform mantles laid on the earth, the naturalists' view encompasses landscapes teeming with an exceptional variety of life, from tiny microbes to majestically giant trees. Both views have changed, however, as we continue to modify and develop our world. Perceptions of an altered world begin to converge and all are aware of the small fragments remaining from the unbroken vistas that used to be. As a result, our views of the populations inhabiting these fragmented landscapes also change. Rather than thinking of vast populations, we envision groups of survivors isolated in smaller and smaller pieces of suitable habitat. The worldwide loss of habitat and the prospect of declining species means that biologists must come to understand the dynamics of subdivided populations, and the conditions that permit species to persist as collections of smaller groups (Hanski and Simberloff 1997; Simberloff 2001). But further, habitat fragmentation will have long-term effects, altering the genetics of populations and the potential for evolutionary change in the future (Barton and Whitlock 1997).

The purpose of this paper is to describe current approaches to the biology and genetics of subdivided populations. First we will define what is meant by metapopulation, the term most commonly associated with population subdivision. Second, we describe the genetic theory of subdivided populations and examples of population genetic studies. Third, we discuss how these concepts apply to forst species, using Limber pine (*Pinus flexilis* James) as an example.

DEFINING METAPOPULATIONS

Research on the effects of patchy environments on populations has a long and storied history (Addicott *et al.* 1987; Wiens 1976; see Hanski and Gilpin 1997; Hanski 1999). On the one hand, arguments abounded over the role of patchiness in regulating population growth and whether spatial and temporal patchiness affects density-dependence (e.g. Andrewartha and Birch 1954). On the other hand, a tradition of examining genetics and evolution in patchy environments also developed, particularly in examining the relative influences of genetic drift, gene flow, and selection in a series of small populations (Wright 1978; Barton and Whitlock 1997). Similarly, the dynamic theory of island biogeography (MacArthur and Wilson 1967) created a conceptual framework for understanding the effects of patchiness on the composition of multi-species communities. It is from these traditions that the idea of a metapopulation arose (Levins 1969, 1970; den Boer 1968). After a quiescent period, interest in metapopulations recently resurged with the application of population biology to conservation of species in fragmented habitats (Hanski and Simberloff 1997).

A metapopulation comprises a group of local populations in a patchy habitat, linked by limited migration, where the number of occupied habitats is determined by extinction and recolonization of the local populations (Levins 1969, 1970; Hanski and Simberloff 1997; Harrison and Taylor 1997, Hanski 1999; Hastings and Harrison 1994). In this sense, a metapopulation is a "population of populations", with each local population having its own population growth or decline, while the entire constellation undergoes dynamic cycles of habitat patches being occupied, emptied by local extinction, and recolonized by dispersal from occupied patches (Figure 1). Classic metapopulations, as originally envisioned by Levins (1969), are difficult to distinguish from subdivided populations that do not undergo regular extinction and recolonization (Harrison and Taylor 1997; Hastings and Harrison 1994; McCullough 1996). Habitat patchiness itself does not define a metapopulation. If regular movement, either by individual animals or by pollen and seeds of plants, encompasses a number of patches, the amalgam of habitat will likely constitute a single breeding population (type B in Figure 1). At the opposite extreme, if a series of habitat patches are isolated enough to prevent successful dispersal or pollination, each patch comprises a single population (type C in Figure 1). Metapopulation stability and persistence is not possible if each habitat patch is so small that local extinction is likely but recolonization does not occur. Eventually, all local populations are expected to go extinct (Harrison and Taylor 1997; Thrall *et al.* 1998).

Classic metapopulations should also be distinguished from source-sink metapopulations or mainland-island metapopulations (type D, E in Figure 1). In these, one or a few populations are either large enough or have sufficient population growth that they never become extinct. Sinks or islands, however, never experience high enough population growth to ensure long-term viability and thus depend upon recolonization from the mainland or from other sources (Hanski and Simberloff 1997; Harrison and Taylor 1997). The critical difference between these models and classic metapopulations is that persistence of the whole is not affected by what happens to islands or sinks (Hanski and Simberloff 1997).

Thus, the long-term persistence of metapopulations seem precarious, depending on a balance between extinction and recolonization of local populations (Hanski 1999; McCullough 1996). Hanski *et al.* (1995) outlined four conditions needed for metapopulation persistence: 1) population structure, which is implied by patchy and fragmented habitats, 2) having no single population large enough to ensure long-term survival, 3) having no habitat patch so isolated that recolonization is impossible, and 4) asynchronous dynamics of local populations, so that simultaneous extinction of *all* local populations is unlikely. Before conservationists took up metapopulation biology as a model for studying newly fragmented species, relatively few examples of natural metapopulations, based on long-term sampling, existed. Two exceptions were the American pika *(Ochotona princeps)* (Moilanan *et al.* 1998) and the Glanville fritillary *(Melitaea cinxia)* (Hanski 1999). Examples now abound (see Hanski and Gilpin 1997; Antonovics *et al.* 1994; Hanski 1999; Webster and

Johnson 2000), although in many cases these are newly-minted and it remains to be seen if they will persist.

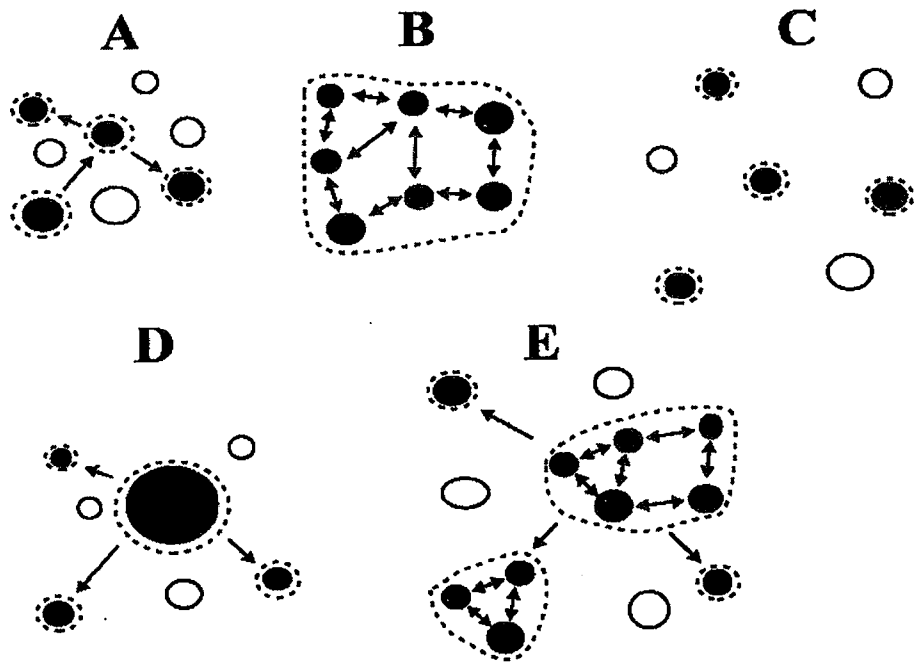

Figure 1. Types of structured populations. Filled circles represent occupied habitat patches; empty circles are vacant habitat patches; dotted lines show extent of local populations; arrows show dispersal. A. Classic metapopulation. B. Patchy environment with a single local population occupying all patches. C. patchy environment with no dispersal among habitat patches (non-equilibrium). D. Source-sink or mainland-island structure. E. Patchy habitat combining aspects of all other types. Redrawn after Harrison and Taylor (1997).

Finally, it should be pointed out that both patchy habitats and metapopulation dynamics may be transient. For instance, if empty habitats arise as a consequence of disturbance like fire, or if habitats become fragmented because of human resource use, the resulting patchy habitat may be conducive to metapopulation dynamics. However, natural regeneration through succession of species and ecological communities can be expected if the disturbance ceases. Thus, understanding whether a metapopulation is stable or whether habitat patches comprise a series of isolated population fragments awaiting species-wide extinction depends on larger-scale regional dynamics and the changing landscape where the metapopulations are embedded (Wiens 1997). For instance, the disappearance of an early-successional plant species from a group of clearings in a forest does not necessarily constitute extinction of a metapopulation.

METAPOPULATION DYNAMICS

Metapopulations exist in a series of discontinuous habitats, linked by limited migration, where the proportion of occupied habitats is determined by extinction and recolonization of local populations (Levins 1969, 1970). The dynamics of a metapopulation can be written as a change in habitat patch occupancy as follows:

$$\frac{dP}{dt} = mP(1-P) - eP$$

This simple model balances the loss of local populations by extinction (*eP*) and the gain of local populations by recolonization of empty habitat patches (*mP*), which occur in frequency *1- P*.

This model, however, assumes the same migration rate and extinction rate affects all habitat patches and more realistic spatially explicit models have been developed (Hanski 1999). A highly successful model for analyzing metapopulation persistence is the incidence function model adopted by Hanski (1999) and colleagues at the University of Helsinki, Finland. Incidence refers to the probability of occupancy of each habitat patch at any given time and is influenced by the size of the patch and its isolation from other patches. The isolation of habitat patches depends on the size of surrounding patches, the distance from a habitat patch to surrounding patches, the relationship between patch distance, and the probability of migration, and whether surrounding patches are occupied. The model has been tested for two metapopulations, the American pika (Moilanan *et al.* 1998) and the Glanville fritillary (Hanski 1999). Both of these case studies entailed long-term population sampling, and in both the incidence model correctly predicted the turnover rate of local populations.

Finally, long-term persistence of metapopulations will be affected by the causes of extinctions of local populations (Hanski 1999). If extinctions occur randomly (stochastically), their causes can be classified into two broad categories: extinctions from demographic stochasticity and extinctions because of environmental stochasticity (Simberloff 1988). Demographic stochasticity increases probability of extinction because of slow population growth and the loss of small local populations. For example, a local population could become extinct if offspring of one sex only are produced for several generations. Environmental stochasticity, on the other hand, leads to extinction because of local disasters of one kind or another, which originate from outside the local populations and equally affect both large and small local populations. Good examples of environmental stochastiticty are extensive forest fires or introduction of a highly virulent and highly infectious disease into a local population, quickly killing all individuals and causing a local extinction. In general, longer persistence of metapopulations is expected if extinctions result from demographic than from environmental stochasticity. Demographic stochasticity disproportionately affects small local populations, so that the overall rate of extinction from demographic stochasticity can be reduced by the "rescue effect" of migrating colonists from larger subpopulations (Hanski, 1999). Environmental stochasticity affects both large and small local populations, and makes long term persistence of the metapopulation more difficult.

GENETICS OF METAPOPULATIONS

Three population genetics consequences, which overlap broadly, will arise when extinction and recolonization become a feature of subdivided populations. These are: 1) the effective size of the metapopulation, 2) the amount of genetic differentiation between local populations, and 3) the potential for evolutionary change in a metapopulation. Successfully predicting how fragmentation and local extinction will change large randomly mating populations depends on whether immigration into local populations continues after initial colonization, whether migrants are randomly drawn from the local populations, and the relative sizes of each of the local populations. Further, predicting the effects of fragmentation on genetics and demography of a species depends on prior history of the spatial structure of a population before the fragmentation begins. For instance, a species that already experienced a history of inbreeding may not be dramatically affected by fragmentation

and isolation because of habitat loss (Hedrick and Kalinowski 2000; Lande and Schemske 1985; Lande 1988; Thrall *et al.* 1998). We discuss each of the three genetic consequences in turn.

Habitat fragmentation can influence effective population size (N_e), which measures a population in terms of how many individuals contribute to breeding and the amount of genetic variability that would be maintained by random mating in a population of size N_e (Barton and Whitlock 1997). In almost all cases, the effective population size is smaller than the actual numbers of individuals in the population. Effective population size is reduced by any factor that reduces the number of genotypes represented in the population. Typically, these include unequal reproductive success by males and females (i.e. harem breeding), differences in family size (some families are over represented), or recent population bottlenecks. Many formulations of effective population have been developed, differing mainly by whether effective size is reduced by prior population bottlenecks and inbreeding, ongoing reproduction and genetic drift, or the overall loss of heterozygosity in populations (Crow and Denniston 1988; Pannell and Charlesworth 2000; Whitlock and Barton 1997). For our purposes, the reduction in effective population size because of genetic drift, called the variance effective size, provides an intuitive relationship between effective size (N_e) and census number (N):

$$Ne = \frac{4N}{Vk + 2}$$

Because V_k, the variance in reproductive success, is in the denominator, any increase in variance decreases N_e. Variance can be between sexes, between families, or in the case of metapopulations, between local populations. Considering that metapopulations are characterized by local extinction and recolonization, processes that inevitably generate variance in reproductive success among local populations, metapopulations will *always* have smaller effective size than unfragmented populations with the same number of individuals (Barton and Whitlock 1997; Chesser *et al.* 1993; Hedrick and Gilpin 1997; Whitlock and Barton 1997).

Another feature of metapopulations is the genetic subdivision between local populations, which comes almost by definition. Dispersal and gene flow among local populations counter local genetic differences arising from genetic drift or natural selection. Metapopulations are defined in terms of independent dynamics of local populations – with high dispersal and gene flow local populations will not behave independently. It is conceivable, however, that a series of local populations will become genetically differentiated from each other, while at the same time losing genetic variability within each local population. The question arises, then, how much more genetic subdivision will be found in metapopulations compared to fragmented populations that do not undergo episodes of extinction and recolonization? The answer depends upon the number of individuals that colonize and the source of the dispersers (Barton and Whitlock 1997; McCauley 1993; Wade and McCauley 1988). First, genetic variation among local populations will be increased when the number of colonizers is fewer than the number of subsequent dispersers. If initial colonists comprise a small fraction of the total immigration into a local population, the initial colonizers will represent a small fraction of the available genotypes from the occupied habitat patches. The result is genetic bottlenecks and founder effects in local populations. This is described by the formula:

$$k < \frac{2Nm}{1 - \varphi} + 0.5$$

Here, k is the number of colonizers, N is the average size of the source populations, m is the migration rate after initial colonization, and φ is the probability that colonizers carry genes that originate from the same source population. One prediction of this model is that recently colonized populations should be more genetically distinct than older populations, which has been seen in a number of genetic studies of metapopulations of both plants and animals (Giles and Goudet 1997; Hanski 1999; McCauley 1993; Roach *et al.* 2001).

This formula also shows the second important issue, which is the composition of the pool of migrants that move between populations. If migrants have a high positive genetic correlation, φ, they are more related to each other than average, which creates founder effects among colonists and migrants and increases genetic differentiation among local populations. If φ is zero, migrants are drawn at random from local populations and migration will tend to genetically homogenize local populations.

Finally, how will the evolutionary potential of a metapopulation change? This issue is particularly difficult to study, despite rigorous genetic theory and data that describe genetics of small populations (Falconer and Mackay 1996; Lynch and Walsh 1998). First, it is difficult to predict how genetic variation, measured by neutral molecular markers, will relate to fitness-related traits like reproductive success, seed size, pollen production, or dispersal (c.f. Lynch 1996). Fitness-related traits are ultimately of greatest importance to conservation and breeding efforts and will influence extinctions of local populations (Frankham1996; Hedrick and Kalinowski 2000). Second, the effects of inbreeding on fitness are quirky. Isolated local populations are expected to become more inbred than those connected to others by dispersal, but whether inbreeding has a negative effect depends upon an element of chance. For instance, the severity of inbreeding depression in a population will be a function of genetic load (the overall number of deleterious mutations in a population), which in turn varies according to the history of past inbreeding (Hedrick and Kalinowski 2000; Lacy and Ballou 1998; Lande and Schemske 1985; Lynch and Walsh 1998; Templeton 1987). Third, the severity of inbreeding depends on environmental variability as well; a highly inbred population in a salubrious environment could prosper (Hedrick and Kalinowski 2000).

As in general models of evolution, adaptive evolution in metapopulations depends on the amount of genetic variation in the population as a whole. However, metapopulation dynamics mean that genetic variation within each local population is a balance between migration, genetic drift, and selection in each local population (Barton and Whitlock 1997; Lynch 1996). The problem arises because, like genetic drift, the strength of selection on a trait is a function of effective population size. Therefore, selection will be able to change allele frequencies in local populations only if $N_e s > N_e m$, where N_e is effective population size, s is the strength of selection, and m is the migration rate. Although natural selection in large populations can be a strong force, in small populations where N_e is small, drift will predominate unless selection is very strong. In other words, small local population size means that most genetic variation will be selectively neutral. This has two consequences for metapopulations. On the one hand, it will be more difficult for favorable alleles to increase in frequency. On the other hand, deleterious alleles will have an almost equal chance of becoming common in small populations, which will decrease overall productivity of the metapopulation and may increase the likelihood of extinction of local populations (Lynch 1996). Finally, when migration becomes severely restricted so that $N_e s > N_e m$ and habitat patches have different environmental circumstances, local adaptations may evolve (Barton and Whitlock 1997).

A FOREST METAPOPULATION: LIMBER PINE

Limber pine represents a case of a species whose distribution has changed from continuous to patchy and currently displays metapopulation dynamics (Webster and Johnson 2000). At the last glacial maximum, 14 000 years ago, limber pine was widespread throughout the eastern side of the Rocky Mountains in Colorado and Wyoming, but currently is characterized by a patchy distribution, restricted to high stress habitats on a broad elevational gradient, from low hills in the short grass prairie (1 630 m) in the east to treeline (3 400 m) in the mountains (Schoettle and Rochelle 2000; Wells and Stewart 1987). Patches of limber pine can persist for decades, but occasionally go extinct from stochastic events like wildfires. Climax limber pine populations

appear to persist because local extinctions caused by wildfires are rare. Seeds seldom survive longer than 2 years in soil and being wingless, they cannot disperse by wind on their own. Nonetheless, burned sites are rapidly recolonized by seeds dispersed by birds, mainly Clark's nutcracker (Webster and Johnson 2000). While limber pine forms climax stands, in some environments it is also an early successional species. Therefore, disturbances in other forest types open habitat for limber pine, which gradually become smaller as succession proceeds. Consequently, limber pine populations are patchy and constantly undergo episodes of extinction and recolonization.

Despite this wide range and patchy distribution, limber pine shows little genetic or morphological differentiation related to elevational changes (Latta and Mitton 1997; Schoettle and Rochelle 2000; Schuster *et al.* 1989; Schuster and Mitton 1991, 2000). Genetic studies indicate, that within local populations, pollen is dispersed evenly among trees (Schuster and Mitton 2000) but that seed dispersal by birds results in local clusters of related individuals (Schuster and Mitton 1991). Differences in pollen phenology along elevational gradients could limit gene flow via pollen between local populations (Schuster *et al.* 1989), but low between-population differentiation suggests gene flow by stepping-stone pollination across intermediate populations. Dispersal of seeds, which can be carried up to 22 km from the parent tree by birds (Lanner and Vander Wall 1980), would result in gene flow across the elevational gradient. Genetic analysis of isolated populations on the short grass prairie in north-central Colorado demonstrated occasional long distance pollen flow and levels of genetic diversity similar to those in larger mountain populations (Schuster and Mitton 2000). The only large genetic differences in limber pine are on a regional geographic scale that may reflect isolation in Pleistocene refugia on the Great Plains east of the Rocky Mountains and in the Great Basin west of the Rocky Mountains (Lata and Mitton 1997; Mitton *et al.* 2000).

Limber pine represents an interesting counter-example. Despite living in metapopulations on a broad elevational gradient, limber pine shows remarkably low morphological and physiological variation (Schoettle and Rochelle 2000). Other species with long distance dispersal of seed by birds show similar genetic patterns (Bruederle *et al.* 1998). This is in contrast to wind-pollinated species that also depend on wind for their primary mechanism of seed dispersal. These species show not only local genetic differentiation, but also differentiation within local populations (e.g. Rehfeldt 1997). The capacity in limber pine for either physiological plasticity or broad physiological tolerances may be adaptive for a species that occupies an altitudinal gradient, but that has high levels of gene flow. In this case, the metapopulation structure of limber pine may have resulted in evolution for generalized physiology, where colonization of isolated habitat patches requires the ability to withstand a variety of environmental conditions. In terms of adaptation in metapopulations, limber pine represents a case of large effective population size because of gene flow, combined with strong selection for plasticity or tolerance because of colonization of new habitat patches. Limber pine may be a case where turnover of local populations, combined with high dispersal and gene flow, results in evolution of a generalist lifestyle capable of tolerating a wide variety of environmental circumstances.

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