

# Can Biogeographic Models Be Used to Predict the Persistence of Mussel Populations in Rivers?

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**Abstract.** The relative immobility, long lifespan, filter-feeding habits, and parasitic glochidial stage of freshwater mussels make them especially vulnerable to habitat fragmentation, and many species of mussels are declining or endangered. Biogeographic models can be used to make predictions about the persistence of rare species in a fragmented landscape. A metapopulation is a system of local populations connected through dispersal. Long-term conservation of mussel species requires that viable mussel populations be protected. Determining what constitutes a viable mussel population requires several steps. Existing metapopulation models should be empirically tested using mussel data. These models should then be modified to encompass the unique life history characteristics of mussels and the linear nature of riverine systems.

## Introduction

Twenty-five years ago McArthur and Wilson (1967) introduced the equilibrium theory of island biogeography. This theory states that the number of species present on an island results from a balance between continuous colonization and extinction. In the 1970s island biogeography theory was considered the most important theory for reserve design, and this theory gave rise to continuing arguments about whether to allocate one large or many small reserves, or the SLOSS (single large or several small habitat patches) debate (Hanski and Gilpin 1991). Recently, stream ecologists have applied the island biogeography model to lotic ecosystems as a means of determining recovery rates from disturbances (for review, see Gore and Milner 1990).

At the same time island biogeography theory was developing, another theory was published by Richard Levins (1969, 1970), who was trying to develop a model to control insect pest species over a large region within which local populations fluctuated asynchronously. He coined the term "metapopulation" to describe a system of local populations connected through dispersal, or a "population of populations." Like the theory of island biogeography, the metapopulation concept is closely linked with the processes of population turnover, extinction, and establishment of new populations (Hanski 1989). Metapopulation models are important tools for understanding distribution and abundance of organisms at large spatial scales. Because these models integrate local population

dynamics with immigration and extinction events occurring between population sites, they form a bridge between the traditionally separate domains of population ecology (local abundance) and biogeography (regional occurrence). There are some major differences between metapopulation theory and island biogeography theory. Island biogeography is concerned with many species occupying a set of islands or habitat islands, whereas metapopulation models are concerned with many populations of one species. Island biogeography theory assumes a continuous source of colonists, but in metapopulation theory dispersal is between local populations themselves.

Part of the challenge in understanding the dynamics of species distributions in patchy habitats comes from the different ways in which researchers have defined patches and local populations (Pickett and White 1985). These problems can be simplified by asking questions about the distribution of individuals and species at biologically relevant spatial scales (Lord and Norton 1990). In metapopulation terminology the *local scale* refers to the scale at which individuals move and interact with each other in the course of their routine feeding and breeding activities. The *geographical scale* is the scale of the species' entire geographical range; individuals typically have no possibility of moving to most parts of the range. *Metapopulation scale* is a regional scale at which individuals infrequently move from one place (local population) to another, typically across habitat types

that are not suitable for their feeding and breeding activities, and often with substantial risk of failing to locate another suitable habitat patch in which to settle (Hanski 1991).

Although metapopulation theory is well-developed (Hanski and Gilpin 1991), many empirical questions about how metapopulations function remain to be answered (Harrison 1991). Many species with a formerly continuous spatial distribution are being turned into possible metapopulations by habitat fragmentation (e.g., spotted owl). Metapopulation models can aid in conservation planning by making predictions about species persistence under various patch size and dispersal conditions. Metapopulation structure has important genetical consequences for conservation (Gilpin 1991). The decade-old SLOSS controversy is fundamentally a metapopulation question (Hanski and Gilpin 1991).

The relative immobility, long lifespan, filter-feeding habits, and parasitic glochidial stage of freshwater mussels make them especially vulnerable to habitat disturbance, particularly habitat fragmentation. There have been major declines of mussel populations and species diversity in North America over the past century (see Neves 1993, this volume). One major cause of these declines has been the fragmentation of river drainages through impoundments and channelization, which alter flow and sedimentation patterns. Because of their dependence on appropriate substrate and flow conditions, freshwater mussels are naturally distributed in patches in rivers. Fragmentation acts to increase patchiness and to increase the distance between patches. These effects may have major consequences for the metapopulation structure of mussel species, particularly rare species and those with narrow fish-host requirements. Contact with an appropriate fish host and the location where young mussels are shed from the host is largely due to chance, and only juveniles that reach a favorable habitat survive (Neves and Widlak 1987). Because only larvae can move between patches and juvenile survival is low, potential rates of colonization of empty patches (i.e., local populations) are already low. Conservation of mussel species is critically linked to preserving a viable metapopulation structure for these species. In riverine systems, fragmentation has not only decreased available habitat for mussels but also exponentially increased the difficulty of dispersal between local populations because dams and channelization impede the movement of host fish or alter their normal behavior. As local populations are eliminated and dispersal distances are increased between other populations, demographic and genetic constraints will diminish the ability of local populations to respond to even natural stochastic

events much less human-induced environmental change (Wilcox 1986, Murphy et al. 1990).

To preserve mussel metapopulations we must first recognize them. What constitutes a viable metapopulation structure for mussel species? The first step in answering this question is to empirically test existing metapopulation models using data from mussel populations. The next step is to modify these models to take into account the unique life history characteristics of mussels and the linear nature of riverine systems. The end product should be a model designed to allow identification of mussel metapopulation structure. In this paper I describe some basic, often-tested models that are a good starting point for examining mussel metapopulations. I then discuss the types of data needed to empirically test these models. Finally, I consider how mussels may or may not meet some of the key assumptions of these models.

## Metapopulation Models

The two models described below were selected because they are rudimentary to more complex models. One should have a good understanding of them before examining more complex models. Furthermore, these models have been tested more frequently than other models; therefore, predictions made about mussels can be compared to those made about other organisms in different systems.

### *Levins' Model*

Levins distinguished between the dynamics of single populations and a set of local populations and introduced a variable to describe the latter,  $p(t)$ , which denotes the fraction of habitat patches occupied by the species at time  $t$ . In Levins' (1969) model:  $dp/dt = ip(1-p) - ep$ , in which  $i$  and  $e$  are the probabilities of local immigration and extinction (i.e., in or out of a local population or habitat patch), respectively. If  $p = 1$ , all population sites are occupied, and if  $p = 0$ , regional extinction has occurred. The immigration rate is the number of successfully colonized empty patch sites/time, and the extinction rate is the number of extinctions in occupied sites/time. Levins (1970) also considered a stochastic version of this model in which  $e$  is random rather than constant. Levins' model assumes a quadratic function for the immigration rate and a linear function for the extinction rate. It predicts a unimodal distribution (Figure 1) and no correlation between distribution and abundance (Gotelli 1991). It is unrealistic in that it assumes (1) local populations are either extinct or at their carrying capacity, ignoring local dynamics; (2) movements from an occupied patch are assumed to be equally likely to all

other patches (i.e., the spatial arrangement of patches is ignored); (3) the rate of colonization is assumed to be proportional to  $p$ ; and (4) all local populations have the same, constant extinction probability.

In spite of its limitations, Levins' model is fundamentally important in highlighting a key aspect of metapopulation dynamics: metapopulation persistence requires that, for a given extinction rate, the colonization rate exceeds a threshold value; and that for a given colonization rate the extinction rate is smaller than a threshold value (Hanski 1991). Numerous empirical examples have demonstrated that the extinction rate decreases with increasing area of habitat patches and that the colonization rate decreases with increasing isolation, such as in small mammal populations (Hanski 1986), birds (Dorp and Opdam 1987), frogs in successional ponds (Sjogren 1991), *Daphnia* (Bengtsson 1989, 1991), spiders (Schoener and Spiller 1987), freshwater snails (Bronmark 1985), and aphids (Addicott 1978). For a given average isolation between habitat patches, metapopulation persistence requires that the average patch area is greater than a threshold value; and for a given average area of patches, their average degree of isolation must be smaller than a threshold value (Hanski 1991). The model predicts that a species may be missing from systems of small habitat patches and from systems in which the average degree of isolation is great, even if the patches may offer temporary support to local populations. Carter and Prince (1981) propose that the geographical distribution limit of many plant species may be explained by metapopulation dynamics along a gradient of decreasing habitat patch density.

Numerous variations of Levins' model have been proposed which make the model more realistic by incorporating factors such as changes in colonization ability, habitat patch size and isolation, compensatory effects between colonization and extinction rates, effects of immigration on local dynamics, and heterogeneity between habitat patches. These are thoroughly summarized by Hanski and Gilpin (1991).

#### Hanski's Core-Satellite Hypothesis

Hanski (1982) formulated an alternative model:  $dp/dt = ip(1-p) - ep(1-p)$ . Hanski's model incorporates the idea that emigrants from surrounding population sites may reduce the probability of local extinction (Brown and Kodric-Brown 1977). This is called the "rescue effect." Hanski's model assumes a quadratic function for both immigration and extinction rates. It predicts a bimodal frequency distribution (Figure 1) and a positive correlation between distribution and abundance; that is, regionally common species have higher average abundances within a community than regionally rare species (Bock and Ricklefs 1983, Gotelli 1991). The predicted bimodal distribution pattern can be explained by the core-satellite hypothesis in which species tend to occur at all similar sites within a region (core species), or they tend toward extinction (satellite species). This model predicts that species will fluctuate randomly between core and satellite modes, and the most rapid dynamics are shown by those species with intermediate regional distributions (e.g., occupy 50% of the sites) (Collins and Glenn 1991). Brown (1984) argued that bimodality in regional distribution is an artifact of sampling at small spatial scales, and a number of alternative models to the core-satellite model also predict this outcome (Gaston and Lawton 1989). The essential assumptions of the core-satellite hypothesis are (1) that all the species considered can establish and maintain populations at each of the sites studied (sites are similar); (2) that the probability of extinction at a site is negatively correlated with the number of sites occupied; (3) that colonization and extinction rates vary randomly and independently between species and over time; (4) that the number of emigrants from a local population increase with the size of the population; (5) that interspecific influences on the parameters of the model, including those for extinction and colonization, are density- and frequency-independent; and (6) that the movement of species from one site to any other is possible and equally likely. Hanski (1982) suggested three ways in which the core-satellite hypothesis could be tested. The first is to seek evidence for bimodality in the frequency of site occupancy by the species. The second is to use long-term population data to document the occurrence of core-satellite switching. The final test is to use detailed knowledge of colonization and extinction rates to measure directly these parameters of the model.

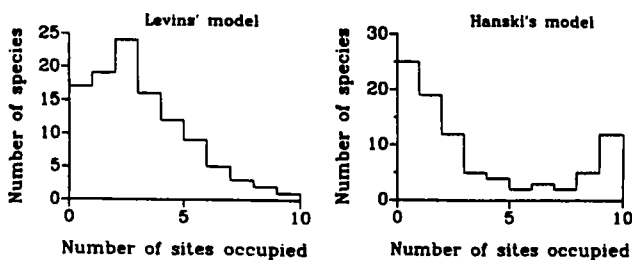


Figure 1. Schematic representation of the predictions of the models of Levins (1969) and Hanski (1982) (from Collins and Glenn 1991).

## Data Needed for Empirical Tests

The best way to test the predictions of the models is to directly calculate colonization and extinction rates of individual mussel species from local populations over a period of time equivalent to several mussel generations. This can be done by comparing the presence/absence of individual species at those sites over time. In rivers that have been carefully monitored over time, this type of historical data is available. Extinction ( $e$ ) and immigration ( $i$ ) rates can be plotted against the number of occupied sites ( $p$ ), and this distribution statistically compared to the distributions predicted by the models. If the data have a Levins-type metapopulation structure, the calculated extinction rates will be linearly and positively related to the number of occupied patches, and the immigration rate will be low when  $p$  is both large (immigration low due to few unoccupied sites) and high (because there are few sites from which a colonist can originate) (Gotelli 1991) (Figure 2). If the data fit Hanski's model, the extinction rate should be a quadratic function (Figure 2): when  $p$  is small, the extinction rate increases as more sites are occupied, but when  $p$  is large, the extinction rate decreases as a result of the immigration from surrounding populations (Gotelli 1991). Regression can be used to determine the relationship between immigration and extinction versus species richness for each site (Collins and Glenn 1991).

Unfortunately, for many rivers historical data is either unavailable or incomplete. An alternative, but less rigorous, method of examining the model predictions is to use multispecies (community) data to compare recent empirical patterns of distribution and abundance to patterns predicted by the models. The distribution of a community of "ecologically similar" species at one instance in time is assumed to be representative of changes in the distribution of individual species over time. Because of the difficulty of obtaining colonization and extinction rates

for many types of organisms, most examinations of these models have used this multispecies "snapshot in time" approach (Gotelli and Simberloff 1987, Collins and Glenn 1990). This is not a direct test of the models because consistency of a pattern with the predictions of a model does not prove that the mechanisms inherent in the model actually produced the observed pattern. However, this method will allow identification of mussel distribution patterns that are a precursor to establishing appropriate assumptions for a metapopulation model developed specifically for mussels. In cases in which a historical data set exists and the model can be tested rigorously, these results should be compared to results obtained using the multispecies approach.

## Assumptions and Modifications

The models discussed previously assume that the data being tested meet specific assumptions. Hanski's model assumes a positive relationship between distribution of species and their local abundance, and Levins' model does not. I have examined 16 data sets on the distribution of mussel species within rivers across North America and found distribution and abundance were highly correlated (Vaughn et al., unpublished data), meeting the assumptions of Hanski's model but not Levins'.

Both Levins' and Hanski's models assume that movements from an occupied patch are equally likely to all other patches. Riverine mussels probably do not meet this assumption because colonization can only proceed in one of two linear directions (upstream or downstream), such that patches near an occupied patch are more likely to be colonized. However, this assumption is probably invalid in most systems, linear or nonlinear, because patches closer to an occupied patch are usually more likely to be colonized. Rivers are more in accord with Hanski's view of an environment that changes stochastically over ecological time than with Levins' model in which habitat patches exist as permanent structural entities. Hanski's model assumes that sites are ecologically similar or that all species can establish populations at all sites. This assumption is valid for most mussel species. The distribution of mussels is strongly influenced by gradient and substrate composition (Salmon and Green 1989, Way et al. 1989).

Levins' and Hanski's models assume continuous rates of colonization, but I would expect colonization in mussels to be episodic rather than continuous. Most mussel communities are distinctly age-structured, revealing successful versus unsuccessful recruitment years (McMahon 1991). The probability of extinction of mussel populations is negatively correlated with the number of sites occupied.

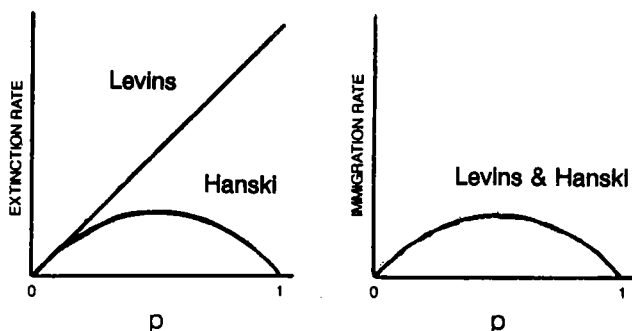


Figure 2. Predicted extinction and immigration rates in Levins' and Hanski's models (modified from Gotelli 1991).

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Indirect evidence for this assumption comes from data on the overall decline of mussel species across North America. In all cases it is the rarest species that are becoming extinct (see Neves 1993, Master 1993 [this volume]). Hanski's model assumes that interspecific influences on parameters of the model, including extinction and colonization, are independent of density and frequency. Mussel communities represent a guild of ecologically similar, sedentary filter-feeders. Very little is known about the role of competition in structuring these communities (Bronmark and Malmqvist 1982, Kat 1982, Bauer et al. 1991). Because mussels disperse between patches as parasitic larvae attached to a fish host, fish densities are predicted to be closely linked to colonization rates. In this volume, Watters (1993) reported that mussel diversity was highly correlated with fish diversity in a number of rivers, and there is some belief that extinctions of some mussel species are linked to the disappearance of their fish host.

Distribution patterns of most organisms vary with the spatial scale examined, and mussels are no exception (Vaughn et al., unpublished data). Metapopulation models can only be used to make meaningful predictions if applied at an appropriate scale of resolution. Levins' and Hanski's models are regional models. The appropriate scale for these models is the scale at which dispersal is possible but infrequent between local populations (Hanski 1991). The size of the region must be scaled to the dispersal distances of the organism in question. For freshwater mussels, these distances are presumed to be ultimately dependent on the dispersal distances of the host fish.

## Summary

The life history characteristics of freshwater mussels make them especially vulnerable to habitat fragmentation, and many mussel species are endangered or in decline. As local populations are eliminated and dispersal distances are increased between other populations, demographic and genetic constraints will diminish the ability of local populations to respond to even natural environmental disturbance, much less human-induced changes. A metapopulation is a system of local populations connected through dispersal. Long-term conservation of mussel species requires that viable mussel metapopulations be protected. Determining what constitutes a viable mussel metapopulation requires several steps. Existing metapopulation models should be empirically tested using mussel data. These models should then be modified to encompass the unique life history characteristics of mussels and the linear nature of riverine systems.

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