

COMMENTARY

Genetic estimation of dispersal in metapopulation viability analysis

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For geographically closed populations, it has long been known that the dynamics of rare populations are affected by demographic stochasticity, and that a short string of 'bad luck' (of the random variable demographic outcomes in a finite population) can easily drive rare populations to extinction. The commonly taught approximation for calculating this extinction risk, $P(\text{extinction}) = (\frac{d}{b})^{N_0}$ (where d, b and N_0 are the respective death rate, birth rate, and initial abundance), clearly shows how sensitive population fate can be to initial abundance (Gotelli, 2008). However, when populations are geographically connected to others, immigration can 'rescue' rare populations from becoming extinct, and the connectivity of multiple populations created by dispersal greatly bolsters the persistence probability of the overall population. As dispersal amongst fragmented habitats increases a population becomes panmictic; overall abundance is enhanced through connectivity and the impact of demographic stochasticity on extinction risk decreases. Conversely, if dispersal is completely impeded by the loss of connectivity among habitat patches, the dynamics in each local population will be more greatly affected by local abundance, birth and death (Clobert et al., 2001). Between the realms of zero and panmictic dispersal resides the concept of a metapopulation (Levins, 1969, 1970).

Theoretical studies have demonstrated the positive nonlinear relationship between metapopulation viability and the rate of dispersal among the component sub-populations (Hanski, 1999). Thus, it is not surprising that Greenwald (2010) found metapopulation viability in ambystomatid salamanders to be affected by methodological approaches to estimating dispersal that produce disparate results. The genetically based approach to estimating contemporary (as opposed to historical) rates of dispersal in a metapopulation viability framework will nevertheless be of use to many. The unique viability issues that a rare or declining population faces often requires development of original population models that match the available data and knowledge. For

future users of Greenwald's approach, I suggest using a programming language to develop a population model that matches the situation (Caswell, 2001; Bolker, 2008). Use of canned software packages can produce biased predictions when the user is forced to make complex modeling assumptions about levels of density dependence, environmental stochasticity, probability density functions describing stochastic processes, mutation rates and more (Morris & Doak, 2002). Moreover, it is not universally true that population viability is insensitive to initial abundance (Greenwald, 2010). Because of demographic stochasticity, Allee effects, inbreeding depression and other factors, a small population's risk of extinction can be highly sensitive to abundance (e.g. see the simple equation above). Thus, careful attention should be paid to both the actual and genetically effective levels of abundance that viability projections are initiated at.

Nevertheless, the assumptions made in Greenwald's (2010) models should not take away from the novel use of genetically based estimates of dispersal in a metapopulation viability analysis. In the past, many have used dispersaldistance functions to parameterize dispersal in population models. Underlying these functions is the biological assumption that a landscape is homogeneous; a single probability density function describes an individual's random chance of moving a given distance, regardless of where it is coming from, where it is going to, and the habitat it must cross to get there (i.e. akin to the dispersion of gas molecules in a room). Dispersal-distance functions might adequately describe wind dispersal of seeds, movement of invertebrate larvae in oceans and other passive forms of dispersal. However, a single homogeneous function cannot capture the complex processes involved in the movement of a vagile animal from one location to another across a heterogeneous landscape that is reap with both costs and benefits to dispersal and philopatry.

Greenwald's (2010) use of genetic-assignment tests for estimating contemporary dispersal in and out of specific locales (Berry, Tocher, & Sarre, 2004; Paetkau et al., 2004) offers a realistic alternative for incorporating dispersal into spatial population models, especially for animals that make active dispersal decisions. For each patch of suitable habitat (e.g. breeding ponds for ambystomatid salamanders) within a region, biologists can assay a range of loci for a sample of individuals and determine the most common genetic makeup for each sub-population (or geographic locale). The genetic make-up for each individual can then be compared to the sub-population mean to determine the likelihood that the individual was born in the local sub-population relative to the likelihood that the individual is an immigrant that was born elsewhere. The more this process is repeated across suitable habitats within a region, the greater the chances that an immigrant's origin can be assigned; thus providing information about the emigration, transfer and immigration phases of dispersal rates between specific locales in a heterogeneous landscape.

A further appeal of the genetic-assignment test for estimating contemporary dispersal is that all organisms have DNA. Given that appropriate tests can be developed for an organism's mode of reproduction (sexual, asexual, etc.) and level of chromosome ploidy, the genetic-assignment approach could serve as a universal way of estimating heterogeneous dispersal amongst locales within a metapopulation. We must nevertheless remember that assignment based on analysis of a small set of gene loci could lead to high rates of misclassification and biased estimates of dispersal. In the future, it would be useful to compare estimates of dispersal attained from genetic-assignments tests to those attained from a rigorous multi-location (i.e. multi-state) capturemark-recapture analysis (Lebreton & Pradel, 2002). Such comparisons could help identify sources of bias in dispersal estimated from genetic-assignment tests. If sources of bias were consistent, then they could be accounted for with advancement of the statistical models.

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