

NEWS AND COMMENTARY

Gene movement in tropical tree populations

Tropical breeding systems: one and done?

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Gene movement between individuals within populations and gene flow between populations can have major impacts on the distribution of genetic variation across landscapes. Gene flow introduces novel genetic variation into populations and reduces genetic differentiation among populations. However, during the first few decades following the Neo-Darwinian synthesis, gene flow proved to be difficult to measure accurately. It was not until molecular genetic markers became available that parentage analyses made possible accurate descriptions of contemporary gene movement patterns (for example, Ellstrand and Marshall, 1985). Over the past 30 years many plant species have been the subject of parentage analyses, including a number of tropical tree species. The lower densities that characterize most of the tropical trees allow more accurate estimates of gene movement patterns owing to less pollen parent ambiguity. Studies measuring the levels and distances of gene flow within fragmented tropical landscapes have been particularly popular. Generally, reported gene flow rates are high (>50%), and insect-vectored pollen is often transported up to several kilometers (Hamrick, 2010).

Ottewell *et al.*, 2012, describe pollen movement patterns within a population of the canopy palm, *Oenocarpus bataua*, located in an undisturbed wet forest in northwestern Ecuador. The thoroughness of this paper's data analyses separates this study from many of its predecessors. Not only did their results demonstrate extensive gene movement within and into the study site, but they expanded their analyses to estimate the mean effective pollen pool size and the pollen dispersal kernel. Further, measures of local

tree density, the location of known flowering individuals and the genetic relatedness of adult trees were used to interpret the results. This comprehensive approach expands our knowledge and understanding of gene movement within natural populations of tropical trees, especially the ecologically important palms. However, this and similar studies are limited as most of the studies of gene movement are conducted during a single reproductive event and within a single landscape (Hamrick, 2010). This limits the generalization of their results to other reproductive events or landscapes, as well as our ability to ask certain important questions. The first question, of course, is just how variable, temporally or spatially, are the parameters and patterns that result from a well-designed and executed parentage analysis? In other words, are estimates of gene movement based on a single reproductive event and location representative of multi-year patterns and values? How do mating patterns vary from landscape to landscape (representing different habitat types, population densities, pollinator availability, etc.) and year to year (varying levels of flowering, varying climatic factors, loss or gain of reproductive individuals, etc.)?

The value of long-term studies, to our understanding of evolutionary processes, is illustrated by studies that have monitored natural selection in populations of a variety of organisms over time (for example, Darwin's finches (Grant and Grant, 1989) and cultivated barley (Clegg *et al.*, 1972)). Many of these papers have become classics and are routinely cited in textbooks. Also, many long-term studies, although not established to address questions of contemporary concern, because of their comprehensive nature, provide important insights into questions of world-wide concern, such as climate change (for example, the yellow-bellied marmot, *Marmota flaviventris* (Armitage *et al.*,

1976; Ozgul *et al.*, 2010) and cultivated barley, *Hordeum vulgare* (Clegg *et al.*, 1972; Allard, 1988)).

There are several reasons why most parentage analyses of tropical trees lack spatial breadth and temporal depth. To properly execute a parentage analysis over a single reproductive event at one study site requires considerable time and resources. Trees must be located, which can be challenging in dense tropical forests with difficult terrain, mapped and sampled for genetic analysis. A 130-ha area may not seem very large, but searching and accurately mapping such sites may take months to accomplish. It is also essential to identify every reproductive adult tree because pollen coming from the missed adult trees will be erroneously classified as immigration events. Tissue collection from a 30-m high-canopy individual tree is also a challenge unless bark tissue can be used. Seed collections may also present problems if seed shadows from different individuals overlap (Sezen *et al.*, 2009). Establishing replicate study sites across varying habitat types multiplies the time and resources needed, even if suitable sites can be identified. Replicating the study across multiple years further increases costs and fails to satisfy our appetite for rapid publication. Besides, the question always arises, how much is enough? The answer is usually, 'It depends...' Not to mention that the maintenance of collecting and exporting permits is a matter of constant worry and headache.

There are, however, compelling reasons to move towards multi-site and multi-year studies. It is thus critical to better understand the long-term effects of habitat disturbance on the ability of species to maintain natural levels of genetic variation. Population genetic theory predicts that fragmentation of once continuous populations should lead to long-term decrease in genetic diversity and increased inbreeding. Both these

consequences should reduce the species' ability to respond to directional environmental changes. If, however, natural levels of gene flow are maintained or even increased (Hamrick, 2010) in disturbed landscapes, the genetic effects of habitat fragmentation may be mitigated. Accurate estimates of effective population sizes, rates of gene flow and levels of inbreeding obtained for natural and disturbed sites, and across several reproductive events are necessary for dependable predictions.

A more comprehensive understanding of gene movement within highly disturbed landscapes can also be used to identify individuals that are critical to the maintenance of genetic connectivity within landscapes, as well as individuals that attract the most pollen donors and produce the most genetically diverse progeny. This information is essential for the development of landscape management plans, designed to maintain individuals that are essential to the conservation of the breeding structure within landscapes. An understanding of gene movement can also be used to design sampling

schemes that ensure the use of genetically diverse propagules for habitat restoration efforts. Clearly, it would not be advisable to commit limited resources to develop management plans based on results from a single site and reproductive event.

CONFLICT OF INTEREST

The author declares no conflict of interest.

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