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The resilience of forest fragmentation genetics – no longer a paradox – we were just looking in the wrong place

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Editorial Text

Over the last decade, several studies and reviews have documented the apparent resilience of widespread tree species to the population genetic consequences of habitat fragmentation and disturbance (e.g. Lowe 2005; Lowe et al 2005; Kramer et al 2008; Bacles and Jump 2010). Classically, under conservation genetic principles, decreases in population size and density of trees, caused by habitat fragmentation and disturbance activities such as logging, are expected to reduce genetic diversity, increase genetic differentiation and potentially increase inbreeding (Lowe et al 2004). Yet a large number of forest tree species are able to ameliorate these population genetic pressures through a variety of mechanisms. The first is through extensive gene flow via pollen and/or seed (in many cases over 10s of km; e.g. White et al 2002; Bacles et al 2005), which can maintain connectivity even in highly fragmented and degraded landscapes where trees persist at very low densities in matrices of varied land use (e.g. Breed et al 2011; Lander et al 2011). The second is due to the long-lived nature of trees and the existence of overlapping generations on single sites that serves to retard the loss of genetic diversity (e.g. Lowe et al 2005; Petit and Hampe 2006; Bacles and Jump 2010; Davies et al 2010). Thirdly, flexible mating systems in some species can circumvent self-incompatibility to allow selfed progeny to form (Ward et al 2005), particularly when faced with an Allee effect (lack of compatible mates within a landscape).

In the decade since a previous focal issue of *Heredity* on this topic (Lowe 2005), research to examine the resilience of forest trees to the genetic impacts of fragmentation have included assessments of gene flow dynamics (e.g. Bacles et al 2006; Hardesty et al 2006; Ottewell et al 2009), spatial genetic structure and cohort formation in natural populations (e.g. Cavers et al 2005; Hardesty et al 2005; Kremer 2005), comparisons of genetic diversity in pre-disturbance adult populations versus post-disturbance seedling populations (Kettle et al. 2007), and analysis of the mating system and fitness

consequences of low mate availability (e.g. Breed et al 2012a & b).

As perhaps could have been predicted, the last 10 years of study have shown that forest trees are not completely resilient to the population genetic consequences of forest fragmentation. Rather impacts vary by species and context, and are more nuanced than simple losses of genetic diversity and increased differentiation among populations. For example, some of the key consequences of forest fragmentation have now been identified as increased inbreeding depression in progeny sired in a fragmented landscape (e.g. Breed et al 2012b) and genetic diversity and fitness loss due to low numbers of mating partners and low pollen diversity (e.g. Breed et al 2012a; Breed et al 2014).

In this latest focal issue of *Heredity* we introduce five important studies of neotropical trees and Eucalypts (Breed et al 2015a & b; Davies et al 2015; Rymer 2015; Vinson et al 2015) that further advance our understanding of forest fragmentation genetics, and are described below. Overall, from these and other recent studies, our understanding of forest fragmentation genetics has developed in three key areas. First, it can be argued that in focusing on adult populations to understand the population genetic and fitness consequences of forest fragmentation, we have been looking in the wrong place. Instead, we need to focus attention on the progeny sired in impacted landscapes and their relative success in regenerating in a range of conditions. Second, we now understand that variation in mating and breeding systems is an important factor determining the type and magnitude of response. Third, the specific landscape context (e.g. scale and land-use type) and nature of impact (e.g. fragmentation vs. logging) are also important variables influencing response. A continued focus on these three areas is likely to be scientifically fruitful and deliver real progress on management strategies for trees in impacted landscapes. In particular, a more quantitative approach to linking changes in

pollination to mating systems to fitness is likely to yield important insights on the mechanisms driving the changes we observe (e.g. Vanbergen et al 2013). We look forward to reviewing new hypotheses, developments and latest research in this area in 10 years time!

Overview of the focal issue studies

The first study (Breed et al 2015a) takes as its context the global problem of changing pollinator availability and dynamics in fragmented landscapes. With many tree species being animal-pollinated (at least in tropical systems), the genetic diversity and fitness of progeny of woody plants sired in fragmented landscapes are expected to decline due to shifts in plant-mating patterns (for example, reduced outcrossing rate and/or pollen diversity due to habitat fragmentation and/or changes in pollinator community composition and behaviour, Vanbergen et al 2013). This hypothesis is tested by Breed et al (2015a) in a case study of three ecologically divergent *Eucalyptus* tree species, and from a meta-analysis of the literature. For the two eucalypts pollinated by small insects, increased selfing and decreased pollen diversity was correlated with increased fragmentation, but no such relationship was evident for the eucalypt species pollinated by a mobile bird. In a meta-analysis of forest tree studies across all ecosystems, habitat fragmentation was observed to be generally correlated with decreased pollen diversity and increased selfing rates in progeny, but more mobile pollinators (e.g. birds) tend to dampen these mating-pattern shifts. Thus habitat fragmentation was found to generally have a negative impact on the diversity and inbreeding levels in progeny, but this impact was greater in tree species with less mobile pollinators.

The second study asks whether some forest contexts are more sensitive than others to population genetic impacts (Davies et al 2015). During the colonization of open landscapes, seed-source bottlenecks can cause a severe reduction in genetic diversity

and is particularly an issue for secondary forest colonizing trees (Davies et al 2010). Under these conditions, pollinator behaviour is expected to be impacted by the great variation in tree density between old growth (low density) and secondary forest (high density). These assumptions are tested for the long-lived, self-compatible pioneer tree, *Vochysia ferruginea*, at old growth and secondary forest sites in Costa Rica (Davies et al 2015). Progeny from both old growth and secondary forest contexts were predominantly outcrossed and experienced low levels of biparental inbreeding, indicating that the mating patterns of *V. ferruginea* are relatively robust to density differences between old growth and secondary forest stands. In addition, pollen-mediated gene flow potentially maintained genetic diversity of open-pollinated progeny arrays in stands of secondary forest adults. These results highlight the importance of conserving primary forest remnants within fragmented landscapes, as they appear directly to promote maintenance of genetic diversity during forest regeneration.

The third study examines the issue of habitat fragmentation disrupting ecosystem processes such as plant-pollinator mutualisms (Breed et al 2012a; Ottewell et al 2009). When such processes are disrupted, mating patterns in remnant tree populations are expected to shift towards increased inbreeding and reduced pollen diversity, with negative fitness consequences for future generations (Breed et al 2012b). However, assessments of mating patterns and the fitness of open-pollinated progeny have rarely been combined in a single study (although see Fuchs et al 2003). Breed et al (2015b) collected open-pollinated seeds of *Eucalyptus incrassata* trees from contrasting stand densities (intact woodland vs. isolated pasture trees) and assessed genetic diversity of pollen, pollen flow and mating patterns, as well as early stage progeny viability. Tree species population density had no impact on mating patterns, adult and progeny genetic diversity, or progeny growth, but was associated with increased mean pollen dispersal. There was evidence for inbreeding depression, apparent as stress-related fungal

infection, but this was not associated with density. *Eucalyptus incrassata* appears to be resistant to the negative mating and fitness changes expected within fragmented landscapes, due probably to strong outcrossing and regular long-distance pollen flow.

The fourth study examines the suitability of remnant trees as seed sources in agricultural landscapes and their potential role in facilitating pollen flow between fragments, both of which have been provoked much previous discussion (e.g. Lowe et al 2005; Breed et al 2011; Lander et al 2011; Breed et al 2012b). Rymer et al (2015) contrast the mating patterns of bat-pollinated *Pachira quinata* trees in continuous forest vs. isolated trees in pasture systems. Although pasture trees experienced some of the longest distance mating events, overall they had higher inbreeding rates and fewer sires than those in continuous forests. A leaky self-incompatibility system was observed, with self pollen having reduced germination on stigmas and slower growth rate through the style, though some trees were incapable of selfing. Self pollination resulted in lower seed set, germination and seedling growth compared with outcrossed progeny. Thus while remnant trees in agricultural landscapes were involved in broader mating patterns, they showed increased but highly variable levels of inbreeding, which resulted in net reduction in progeny fitness.

The fifth study (Vinson et al 2015) used modeling and empirical data from a large-scale experiment to assess the long-term impact of selective logging on two Amazonian rainforest trees with contrasting life histories. *Dipteryx odorata* is a slow growing climax tree, which occurs at very low densities, whereas *Jacaranda copaia* is a fast growing pioneer tree that occurs at high densities. In long term (300 yr) simulations, current Brazilian forest management regulations were sufficient to maintain populations of *J. copaia* but led to a dramatic decline in *D. odorata* populations unless the minimum cutting diameter was increased from 50 to 100 cm over 30-year logging cycles. By

contrast, genetic parameters were only slightly affected by selective logging in these simulations, with minor reductions in the numbers of alleles and genotypes. In the short term, the loss of alleles from observed and simulated populations of *J. copaia* corresponded, whereas real populations of *D. odorata* lost greater diversity than simulated systems. Crucially, forest fragmentation may increase the scale of long-term genetic impacts of selective logging in *D. odorata* through reduced gene flow and effective population size. The different impacts and periods of recovery for each species supported the idea that ecological and genetic information at species, ecological guild or reproductive group levels are essential to help derive sustainable management scenarios for tropical forests, and argue against a 'one size fits all' policy.

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