

Fragmentation genetics in tropical ecosystems: from fragmentation genetics to fragmentation genomics

Chris J. Kettle

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Abstract Tropical regions are experiencing unprecedented economic and population growth. This goes hand in hand with increase habitat fragmentation of tropical ecosystems. Understanding the genetic consequences of these spatial and temporal changes across landscapes is critical to conservation of the vast majority of global biodiversity. This virtual issue of Conservation Genetics, presents six empirical and one review paper showcasing fascinating and important findings with regard to how habitat fragmentation impacts on genetic diversity in rare or endangered tropical species. The message from these papers is clear, fragmentation has a number of serious genetic consequences, which can contribute to undermining the viability of species in fragmented landscapes. Conservation genetics provides a powerful tool to inform both conservation and management of species and genetic resources. But, careful consideration is needed to ensure studies apply appropriate sampling designs and genetic analysis to better test hypothesis. Next generation genomics offers great opportunities to provide even more answers and greater resolution of the consequences for adaptive genetic variation, to ensure future tropical landscapes are resilient.

Keywords Fragmentation · Conservation genetics · Genomic · Extinction · Tropical biodiversity

Introduction

Habitat degradation and fragmentation continues across the tropics almost universally unabated despite these regions harbouring the vast majority of global biodiversity. Readers will be well aware of the many genetic implications of habitat fragmentation (Finger et al. 2014), including loss of genetic diversity, restricted gene flow, elevated inbreeding all of which can push species toward extinction. These processes are alarming in themselves. Yet, all species face additional pressures through anthropogenic environmental change, not least climate change and the introduction of novel pests and disease. Sufficient adaptive genetic variation provides the one trump card most species have to respond to these challenges. Genetic diversity is recognised as a major component of biological diversity by the Convention of Biological Diversity, but largely remains a neglected issue in policy and conservation planning. Understanding how fragmentation undermines adaptive genetic variation is thus vital for tropical conservation science and the basis of fragmentation genetics as a field in conservation.

In 2012, as part of the annual meeting of the Society of Tropical Ecology, we held a symposium of scientist from around the world. The two unifying features were that we were conservation geneticists and all worked on tropical ecosystems (Kettle & Finger 2013). I am delighted to introduce one of the many fruitful outputs of our meeting, a virtual special issue of Conservation Genetics “Fragmentation genetics in tropical ecosystems”. This virtual issue includes significant findings on how habitat fragmentation impacts on genetic diversity in rare or endangered tropical species. Fragmentation is a cryptic process. Different organisms experience the environment and the ‘matrix’ between habitat islands very differently. There are also

C. J. Kettle (✉)
Ecosystem Management, Department of Environmental System
Science, ETH Zurich, Zurich, Switzerland
e-mail: chris.kettle@env.ethz.ch



Fig. 1 Agro-forest landscape mosaic, increasingly common across the tropics. This specific example is the landscape of Koorg, Western Ghats, India, a richly bio diverse habitat and home to the tree species *Vateria indica* (Ismail et al. 2014a, b) Photo ©Chris J. Kettle

confounding temporal effects as different generation times, maturation and life history traits mean different species respond very differently to the same landscape mosaics (Döbert et al. 2014). It is thus pertinent that this issue includes studies from such a wide range of organisms. From some of the largest and completely immobile; tropical tree species, standing some 40 m in height (Ismail et al. 2014b); to small yet surprisingly, highly mobile insects (Boff et al. 2014).

All creatures great and small!

Fragmentation genetics offers great promise as a means to inform the management of resilient tropical forest landscapes. Numerous critical factors such as, gene flow through migration and dispersal, mating systems and inbreeding, are notoriously difficult to study using conventional field based observation. Further, many processes have a clear temporal effect which means there may be a lag in the genetic responses to fragmentation. Genetic studies enable the comparison of contemporary and historic gene flow, providing useful insights.

Most tropical regions are experiencing rapid and widespread population growth, with increased economic development and demand for food. For many tropical countries this mirrors forest transition experienced in temperate regions several hundred years ago (Corlett 2013). Establishing resilient tropical landscapes that retain biodiversity, provide ecosystem services and meet growing demands of society is therefore a major challenge (See Fig. 1, for an example landscape).

Trees provide numerous ecosystem services and the structural basis for most terrestrial biodiversity. Understanding how well they can survive and maintain genetic diversity in fragmented agro-forest mosaic landscapes is a high priority. Ismail et al. (2014b) use paternity analysis of wild seedlings in the forest tree *Vateria indica* to explore patterns of genetic diversity and contemporary gene flow by pollen and seed dispersal using 12 nSSR loci by sampling all adult trees in fragments and some 694 progeny from one continuous and several small isolated fragments. Their results indicate that despite considerable fragmentation the current patterns of pollen-mediated gene flow appear to be sufficient to prevent genetic erosion and inbreeding. Nursery trials highlighted that selection favours outbred progeny. Thus, under more extreme fragmentation, this could compromise seedling recruitment as has been shown in other tree species in this landscape (Ismail et al. 2014a).

Fish are a vital source of protein for many rural communities across the tropics. Although the dysgenetic impacts of fishing on fish populations are well known, fragmentation is not traditionally viewed as a problem for fish populations where water bodies are usually large and well connected. Effective population sizes are predicted to be large. However, Aldea-Guevara et al. (2013) demonstrate that populations of *Colossoma macropomum*, an important fish species throughout the Amazon basin may be naturally more fragmented than we expect. Using 13 nSSR loci they show that even in this highly migratory fish species with limited genetic structure, anthropogenic habitat alteration may impact on patterns of genetic connectivity. The need for specific and different habitat types, at different life stages may be one reason for the need to ensure connectivity. These negative effects of anthropogenic fragmentation to aquatic systems need to be considered, as hydrological systems are increasingly modified.

The world-wide decline in bees has attracted considerable media attention, not least for the important role that bees play in the pollination of economically important crops. Bees are also vital to sustaining the genetic diversity in numerous fragmented insect pollinated plant populations through pollen dispersal. Bees are strong fliers and are thought to be highly mobile, yet their sensitivity to the habitat matrix can vary greatly among species. Boff et al. (2014) take advantage of an island study system off the north coast of Brazil, to explore isolation and its impact on genetic diversity, connectivity and inbreeding in the orchid bee, *Euglossa cordata*. Haplodiploid insects are predicted to exhibit an increase in the frequency of inviable sterile diploid males as a result of reduced genetic diversity at the sex determining locus. This could have major impacts for the conservation of bee populations in fragmented landscapes. Using genotypes of 1,245 males at 5 highly

polymorphic nSSR loci, sampled from the mainland and islands—where population size and isolation vary, but the matrix is constant (the ocean) they found no significant difference in the proportion of diploid males, despite evidence of genetic isolation at neutral loci. Gene flow by migration and balancing selection are likely factors maintaining the low frequency of diploid sterile males in these fragmented populations.

In addition to agricultural expansion, urban development is increasing across the tropics and consequently fragmenting many unique habitats. For example, the sandy coastal plains around Rio de Janeiro in Brazil are among some of the most densely populated regions in the world but harbour unique species. Ariani et al. (2013) examine how fragmentation of this *restinga* habitat is impacting on the genetics of the endemic sand lizard *Liolaemus lutzae*. Using mitochondrial DNA sequence data and seven nSSR loci, they reveal three distinct populations, high levels of inbreeding and low genetic variation. Using these genetic data they have been able to inform captive breeding programmes where collecting individuals from populations most under threat, whilst ensuring reintroductions of outbred and genetically diverse individuals into other genetically depauperate sites.

Conservation genetic studies are often criticised because adaptive variation may not be correlated with neutral marker variation. As a novel way to address this problem Habel et al. (2014) explore variation in bioacoustics traits and combine this with analysis of 15 nSSR loci in a study of two species of the African white-eye *Zosterops poliogaster* and *Z. abyssinicus*. These two species are distinct in their habitat preferences. *Z. poliogaster* occurring in high elevation isolated forest patches where populations are naturally fragmented. *Z. abyssinicus* in lowland savannah, where populations are naturally connected. This comparative study over the same spatial scales revealed strong differentiation across the montane forest species for both the neutral markers and the bio-acoustic traits. In contrast the lowland species show no significant differentiation. The low levels of genetic diversity and high differentiation among populations of the montane white-eye highlight the conservation challenges of conserving distinct populations over multiple small and isolated sites.

Bats are important dispersal agents for pollen and seeds in many tropical agro-forest landscapes. Bats are highly mobile and can fly substantial distances to forage for food or to return to roosting trees. Being highly mobile is often posited as a reason that species are not influenced by habitat fragmentation. Ripperger et al. (2013) test this idea by genotyping samples from populations of *Dermanura watsoni* a frugivorous bat inhabiting forest fragments in agro-forest landscapes of northeastern Costa Rica. Surprisingly, they observe significant genetic differentiation

over scales of only 20 km using mitochondrial D-loop sequence data. Both the quality of the matrix and the size of the forest patch explained patterns of genetic variation. Interestingly, they found that habitat parameters measured 30 years previous to the sampling, better explained the current patterns of differentiation, indicated a significant lag in the response time. This not only suggests that highly mobile species can be very sensitive to fragmentation genetics, but that we may not be able to detect the genetic consequences of current fragmentation, as generational length of the target organism may lead to significant lag effects.

Finally, this virtual issue ends with a useful review of the literature on fragmentation in non-aquatic tropical animal species over the last 10 years. Radespiel and Bruford (2014) highlight the need to “disentangle ‘natural’ fragmentation processes from very recent anthropogenic effects” and the pit falls with generating false signals of population change. They survey these recent studies, emphasising that much more care needs to be taken in sampling design and analytical approaches in the future.

Looking forward

Next generation sequencing (NGS) technologies are increasingly feasible to apply to non-model organisms. The development of species-specific markers is no-longer a costly and time consuming exercise. Screening larger numbers of individuals at many more loci and with high levels of resolution is increasingly economically feasible. What is more exciting is that we are starting to now move away from analysing simple genome wide neutral marker variation, to actually dissecting the regions of the genome linked to adaptive traits. Using interdisciplinary approaches combining experimental and evolutionary ecology with molecular genomic and spatially explicit modelling, heralds a new era in ‘Fragmentation genomics’. The papers in this virtual issue highlight the importance of addressing the genetic consequences of fragmentation in tropical ecosystems. Failure to act upon these effects has grave consequences for biodiversity. Fortunately, technological advances mean we are in a position to better and more quickly contribute sound science to ensure the resilience of fragmented tropical ecosystems.

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