Managing ecosystems for resilience and resistance

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Lecture 4 a. Genetic erosion, monitoring and management

In the last lecture we explored the importance of genetic biodiversity for resistance and resilience of ecosystems, in this session we will explore the varying ways in which management of natural resources can lead to a reduction of genetic diversity (genetic erosion), how molecular ecology might be useful for monitoring and how we might better manage genetic diversity.

Genetic erosion
Genetic diversity, and biological diversity in general can be eroded in many ways but one of the single most cited threats to global biodiversity is habitat degradation and fragmentation. Habitat fragmentation leads to a reduction in population size and increase in the isolation if populations, often in a matrix, which is not favourable to either dispersal or colonisation. The genetic consequences of habitat fragmentation include:

1) Loss of genetic diversity directly through sampling effects (genetic bottlenecks).
2) Random genetic drift in small populations.
3) Restricted gene flow and subsequent inbreeding.

In addition the loss of populations, which are genetically distinct or unique, can lead to the rapid loss of intra-specific genetic diversity.

These genetic consequences coupled with ecological consequence of fragmentation, such as allee effects, increased demographic stochasticity and ultimately a reduction in the effective population size of species may drive species into a so-called extinction vortex (Frankham, 2002).
In addition to habitat degradation genetic erosion can also result from mismanagement of natural resource for example by over exploitation of a harvested species, domestication, inappropriate use or management of seed sources or germplasm during habitat rehabilitation.

Use of molecular markers to inform management

Molecular markers can be used to better understand the genetic consequence of fragmentation by investigating the mating systems and dispersal of species in fragmented landscapes. This can enable use to better appreciate the scales over which population are truly isolated, and if the intervening matrix is really a barrier to gene flow. Furthermore, one can confirm the levels of inbreeding within a population. Contemporary gene flow within a landscape may be especially important as it may be very different from historic levels of population differentiation.

Some key applications of molecular tools include.

- Identifying priority populations for conservation, e.g. genetic refugia.
- Understanding the impact of habitat degradation on reproductive ecology
- Estimating the effective population size ($Ne$) (Box 1).
- Monitor management impacts on genetic diversity.
- Law enforcement (forensic genetics).

Management of on farm Agroforestry genetic resource

Agroforestry systems may be especially important as a means of conserving forest biological diversity especially in light of the increasing demand for productive land, and consequently conversion of forest to agricultural land. Often 100’s of forest species are used in these landscapes. Agroforestry systems may be especially important for the conservation and sustainable use of tropical tree species and their genetic diversity. Not only do they increase the size and extent of populations but these “on –farm” trees may provide connectivity between natural forest fragments.

Little is known about the value of agro forestry systems for management and maintenance of genetic resources. Domestication of trees may lead to rapid genetic erosion of species as a consequence of bottlenecks caused by the collection of seeds from a very limited number of maternal parents and the widely varying practices of propagation in agro forest systems. For example this might include taking cuttings for clonal propagation of material. Such management may ultimately lead to inbreeding and reduced fruit production. This is both deleterious for conservation of such species and for farmers who depend on non-related matings for successful fruit production.

The impact of domestication on genetic diversity was investigated in a model species *Inga edulis* (Ice-cream-bean) (Hollingsworth *et al.*, 2005).

*Inga edulis* is a fruit native to South America. It is widely grown, especially by indigenous Amazonians, for shade, food, timber, medicine, and production of the alcoholic beverage *cachiri*. 
Using microsatellite markers genetic diversity was compared between five natural and five planted populations of *I. edulis*. Sampled leaf material from 88 natural (old growth forest, primary forest) and 101 planted trees were analyzed. Allelic diversity was significantly lower in the planted populations (Hollingsworth *et al.* 2005). Mean allelic richness was 39.3 in natural populations compared to only 31.3 in planted stands. This reduction in allelic richness is the result of loss of rare alleles, a sensitive measure of genetic bottlenecks.

While there was an overall decline in genetic diversity in planted populations they still contained 80% of the variation found in the wild populations, indicating that extreme genetic bottlenecks were not a problem in this species during domestication. Extensive pollen flow (from a large number of fathers) to the forest source maternal trees may help to buffer against bottlenecks in this case. However, contrasting results have been observed in other tree species used in agro-forestry e.g (Lengkeek *et al.*, 2005), in 22% of cases tree nursery stocks have been established from only a single maternal tree, indicating extreme genetic bottlenecks in the nursery stock.

More recently, it has been brought into question whether farms should increase on-farm genetic diversity with seed collected from local forests, to reduce the risk of inbreeding depression. One assumption of this is that the local on farm material is of local origin, if however, these on farm trees are non-local in origin, introduction of local genetic variation, may be counterproductive leading to productive losses, as a result of dilution of the genotypes with favourable traits for farmers, such as large fruits, good flavour, or resistance to pathogens. Dawson (2008) using neutral marker variation, demonstrate that in the case of *Inga edulis*, in fact on farm planted stands are not of local origin. Some tentative indications of the importance of boat transport and movement of seeds between watersheds is shown.

In summary the efficiency of agro-forestry systems to maintain genetic diversity of forest tree species is greatly dependent on the ecology of the target species, education of farmer and their willingness to adopt management practices, such as sampling many mother trees so as to maintain genetic diversity within these systems.

**Monitoring restoration efforts**

Forest restoration or the establishment of new populations requires material for planting, ensuring that the genetic diversity of the planting material used for restoration is maintained in essential for long term sustainability of such populations.

During the collection of seed material for restoration genetic diversity can be lost in the following ways:

- **Sample seed from too few maternal trees**
- **Sample maternal trees over too narrow an area**
- **High variance in fertility (cryptic), this can lead to a few individuals contribute disproportionately to a seed crop**
- **Elevated proportion of inbred seedlings in nursery (cryptic) as a result of the nursery environment being more benign than forest floor.**
In a study of nursery material established for the restoration of the critically endangered tropical conifer *Araucaria nemorosa* Kettle *et al.* (2008) demonstrated that despite adopting best practices in terms of seed collection, cryptic processes led to the loss of genetic diversity and elevated levels of inbreeding in nursery reared seedlings. This resulted from cryptic effects of high variance in seed production where very few mothers contributed the majority of viable seed and inbred individuals not being selected out in the nursery. In the case of *A. nemorosa* sampling of seedlings directly from the forest floor was recommended as a more efficient strategy for sampling genetic diverse nursery material (Kettle *et al.*, 2008).

### Over harvesting and Effective population size

In the late 18 Century the global Cod, Herring and most other “great sea fisheries” were considered as inexhaustible natural resources. We now know this to be far from the case, with many high profile fish stock collapses. Over exploitation of fish stocks through the continual industrialisation and mechanisation of fishing fleets has changed not only the abundance of target species, but also changed the physical and trophic structure of marine ecosystems.

Genetic erosion has been considered of little significance in fisheries because genetic erosion is only predicted to be of concern in very small populations. Even collapsed fish populations’ census population sizes are predicted to be larger enough to buffer against genetic effects. For example the Newfoundland cod fisheries closed at 22000 tons, equivalent to several million fish in the population.

Recently, the extent to which the census and effective population size may differ in fish populations was brought into question (Hauser *et al.*, 2002). Characteristics of marine organisms, such as high fecundity, a strong bias in reproductive success, large variation in year class strength and size dependent fecundity, may reduce the effective population size (*N*<sub>e</sub>, see box 1) by several orders of magnitude, millions of fish may in fact equate to an effective population size of only thousands or even hundreds of individuals (Hauser *et al.*, 2002).

### Box 1 Effective population size

*N*<sub>e</sub> was developed by (Wright, 1931) and defined as "the number of breeding individuals in an idealized population that would show the same amount of dispersion of allele frequencies under random genetic drift or the same amount of inbreeding as the population under consideration".

The effective population size is usually smaller than the absolute census population size (*N*). *N*<sub>e</sub> can be calculated using a number of different approached using data on the reproductive out put of individuals over time, the change in allele frequency and reduction in heterozygosity over time. This is based upon the theoretical expectation that heterozygosity declines at the rate of 1/2 *N*<sub>e</sub> per generation

That is the \[ H_t = H_0 (1-1/2 N_e) \]

Where *H*<sub>0</sub> is the heterozygosity at time zero and *H*<sub>t</sub> is the heterozygosity at time *t*. (see Frankham, 2002, Allendorf and Luikart, 2007) for detailed descriptions
Using a comparative study, the levels of genetic diversity in two populations were quantified using samples of scales taken at time intervals. One population, Tasman bay had not experienced fishing before the start of the scale collection and stocks were at there natural level while the second population has already been extensively exploited. Using microsatellite markers it was possible to reconstruct the rate of loss of genetic diversity.

From 1950 when fishing and collection of fish scales started, the Tasman bay populations declined by 75% in spawning stock. Using the temporal change in both allele frequency and heterozygosity effective population size was estimated for both populations.

![Graph](image)

**Fig. 3.** Allele frequencies of locus GA28 in Tasman Bay, showing random genetic drift and loss of alleles. The frequency of the most common allele (170) is indicated above the arrow.

Loss of rare alleles in the Tasman bay populations is illustrated in the above figure at a single locus (GA28).

Despite an estimated census population size of three million fish effective population size estimated from the observed decline in genetic diversity in this population was in the range of 180 individuals (Hauser et al., 2002). These results indicate that even fish stock with a census population of several million many be in danger of genetic erosion in the long term. Maintaining effective population sizes an order of magnitude above those recorded in this study should be ensured in order to maintain vital adaptive variation in these fish stocks.

Take home messages from this is even in the most numerous and fecund species genetic erosion can still have an impact on adaptive variation within a population, and setting guidelines for sustainable harvesting levels should take this into account.
Managing crop genetic diversity

Perhaps the greatest challenge faced by global agricultural community is how to develop and improve the productivity of agricultural ecosystems to alleviate poverty and ensure food security in a sustainable fashion. Plant genetic diversity is essential in this endeavour. However, the realities of managing crop genetic diversity are more complicated and practical guidelines are required.

In rural agricultural landscapes many plant species make up biodiversity these can be divided into the following categories.

a) Species which are deliberately cropped or tended or harvested for food, fibre, fuel, fodder, timber, medicine, decoration etc
b) Wild species that occur in natural communities and benefit agricultural systems, through protection, shade and ground water regulation
c) Wild relatives of domesticated species which can interbreed with and enrich the gene pool of their crop cousins.

Maintaining crop genetic resources requires the maintenance of genetically diverse seed origins of crops and to this end government policy is often developed to encourage certified seed sources. Despite this government policy the majority of rural farming communities use traditional seed sources not formal certified seed. For example in the following countries and crops are certified.

- Nepal < 3% of rice
- Burkina Faso < 5% Sorghum
- Mexico < 25% Maize
- Morocco < 13% Durum wheat

Developing indicators for monitoring and managing genetic diversity In Situ (on farms is a first step in helping to conserve this important genetic biodiversity. Table 1, below summaries some of the key indicators proposed which can be used to sustain genetic diversity of crop genetic diversity and wild relatives in-situ.

Table 1. Indicators proposed for monitoring and managing crop genetic diversity.

<table>
<thead>
<tr>
<th>Indicator</th>
<th>Validity</th>
<th>Lowest applicable level</th>
<th>Transferability to higher levels</th>
</tr>
</thead>
<tbody>
<tr>
<td>Domestic plants and harvested wild species</td>
<td>Diploma?</td>
<td>Field</td>
<td>++</td>
</tr>
<tr>
<td>Number frequency and area of distinct landraces</td>
<td>Taxonomy?</td>
<td>Field</td>
<td>++</td>
</tr>
<tr>
<td>Environmental amplitude of area devoted to crop</td>
<td>Does genetic diversity related to abiotic and biotic environmental diversity, what scale?</td>
<td>Region</td>
<td>++</td>
</tr>
<tr>
<td>Durability and evolution of farmer management selection</td>
<td>Do diverse criteria and uses lead to genetic diversity</td>
<td>Farm</td>
<td>+</td>
</tr>
<tr>
<td>Security of traditional knowledge</td>
<td>At what level are the relationships</td>
<td></td>
<td>-</td>
</tr>
</tbody>
</table>
Wild species and crop relatives

| Species covers a wide area and heterogeneous environment range | Relative geographic locations, management | Natural resources administrative district | + |
| Population number and sizes | How does census size relate to durability, minimum viable population | Metapopulation (valley) | ++ |
| Gene diversity, population divergence, and distribution | Relationship between GV and strategy | Population | ++ |

Linking in situ to ex situ activities

| Ex situ backup for vulnerable species, In-situ priorities for recalcitrant species | Scale of sampling, replenishment, and use strategies. | Individual collection | ++ |
| Cooperative links between ex-situ institutions and farming communities | Information and seed exchange protocols, benefit-sharing and technology transfer. | National programs |

Understanding farmer’s choices is a route to understanding how diversity is maintained in rural systems. “Uses are selective forces” multiple uses are equivalent to diversifying selection, thus fosters adaptive variation. New “one stop shop” varieties lead to a decline is the use of multiple varieties and thus facilitates genetic erosion. Furthermore, the maintenance of genetic diversity on farms is more likely if mechanisms are in place to stop the erosion of traditional knowledge.

Wild relatives are often the weeds in farmer’s fields. However, crops and relatives often share beneficial insects and microbes as well as pests, and disease, these wild relatives may also serve as a source of new genes, thus the maintenance of genetic diversity of wild relatives in agricultural landscapes is highly desirable.

Key refs:


Managing ecosystems for resilience and resistance

**Lecture RES4b. Genetic diversity resistance and resilience, why is genetics important?**

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This lecture will introduce the concept of genetic diversity and its importance for conferring resistance and resilience to ecosystems.

It is becoming increasingly apparent that, in order to sustain ecosystems in a desirable state to provide the services and resources which we depend upon for our well being, we must manage them in such a way that we do not erode natural resilience. Genetic diversity forms the fundamental building blocks of life and its maintenance is essential for organisms to be able to adapt and respond to the challenges of natural and novel environments. Whether it is the evolution of a new virulent strain of a pathogen, adaptation to anthropogenic climate change or the accidental introduction of an alien pest or disease, organism and ecosystem resilience to such processes is dependent upon sufficient genetic diversity. The erosion of genetic diversity is not easily discernible, and our understanding of how genetic diversity relates to higher levels of biodiversity is only beginning to be brought into question. Scientific understanding of these relationships can provide insights in to how best to manage the resistance and resilience of ecosystems. This lecture will explore the importance of genetic diversity. The following lecture will examine how scientific understanding may help us understand and predict genetic erosion how we might manage resources to avoid this.

**Genetic diversity**

The Convention on biodiversity (CBD), describes biodiversity as “the variability among living organisms from all sources including, *inter alia*, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part: this includes diversity within species, between species and ecosystems.”

However, genetic biodiversity is currently seriously neglected by the CBD see (Laikre et al. 2010).

Genetic biodiversity, can be separated into two categories, inter-specific genetic diversity, that is the diversity between species and intra (within) specific diversity. Inter-specific genetic diversity is the phylogenetic distinctiveness between species, for example two species within the same genus are less distinct than two species from separate families. Intra-specific diversity, the level of genetic diversity within a species and populations can be further subdivided in to the following three subcategories:

- a) Adaptive genetic diversity
- b) Deleterious genetic diversity (Lohmueller et al., 2008)
- c) Neutral genetic diversity

**Genetic diversity and resistance:**

Perhaps the best example of adaptive genetic diversity conferring resistance is that of resistance to disease. This is well founded in agricultural science, and indeed there are many cases of sudden and unpredicted collapse of systems, which at least in part are arguably due to low genetic diversity. One dramatic example is the Irish potato famine.
The Great Famine was a calamitous period of starvation, disease and mass emigration between 1845 and 1852 during which the population of Ireland was reduced by 20 to 25 percent. Approximately one million of the population died and a million more emigrated from Ireland’s shores. The principle cause of this famine was the introduction of the potato blight pathogen Phytophthora infestans.

Between 1979-1980 a rust attack on Cuba’s sugarcane by the rust fungus Puccinia melanocephala decimated crops. One cultivar covered over 40% of the sugar cane crop area.

In 1970 the United States maize crop was hit by a new strain of the Southern corn blight (Cochliobolus carbonum). This epidemic was estimated to destroy over one billion dollars worth of corn in the 1970’s and the impact of this pathogen could be directly tracked on the US stock market. This illustrates the direct impacts that genetic diversity can have on ecological and social systems. Indeed scientists at the time stated:

“Never again should a major cultivated species be molded into such uniformity that it is so universally vulnerable to attack by a pathogen, an insect, or environmental stress. Diversity must be maintained in both the genetic and cytoplasmic constitution of all important crop species.” (Ullstrup 1972).

Disease epidemics have also lead to major changes in more natural ecological systems, for example the introduction in the early 1900’s of Chestnut blight (Cryphonectria parasitica) wiped out chestnut in an area of forest some two million hectares (an area half the size of Switzerland), an estimated 4 billion American chestnut trees, making the species virtually extinct in the US. Similarly, the European elm has been devastated by Dutch Elm disease caused by an ascomycete microfungi Ophiostoma ulmi, killing some 25 million trees in the UK alone. Maintaining the genetic diversity within species will help to reduce the risk of such devastating epidemics.

Despite these lessons, industrial agricultural practices continue with monoculture crop systems with low genetic diversity. Intensive cultivation of a few high yielding varieties and long term application of excessive amounts of chemical inputs severely deteriorates the resilience of many ecological systems and leave them vulnerable epidemics.

Maintaining genetic diversity in cropping systems may be a sustainable solution. The rice producing ecosystems of Asia are now being enhanced by intercropping with multiple cultivars of rice, which both increase yields and reduce the need for chemical inputs (Zhu et al. 2000), and reduce the negative impact of pesticides. Using more genetically diverse rice varieties helps to controls rice blast. In fields where traditional varieties were inter-planted with resistant modern hybrid rice genotypes, rice blast was 94% less severe in susceptible varieties and yields were 89% higher than monoculture farms. Fields with mixtures support more diverse pathogen populations with no single strain dominating, in contrast in monoculture fields one or a few strains dominated, increasing the risk of epidemic outbreak. Using mixed varieties could also slow adaptation of pathogens to resistance genes, as the selection pressure in diverse fields is less.

**Biological Insurance**
Genetic diversity can also provide resilience to unpredicted disturbance in more complex ways. For example in 2002 the Central Yucatan state (Mexico) was hit by a
hurricane which flattened maize crops at the peak of the ripening period, for long cycle landraces. These landraces accounted for about 80% of the total subsistence maize harvest in Yucatan. Although the harvest losses were immense, about 75% of maize farmers were able to salvage at least a small part of seed of their xnuuk-nal varieties. These were plants which were physiologically more advanced when the hurricane hit. This intra-specific genetic diversity not only provided some buffer against the disaster both for crop resilience and livelihoods, but placed an enormous selection sweep, shifting the mean ripening forward in Yucatan maize populations.

Resistance to disturbance:
Identifying the importance of genetic diversity in “natural” systems is more challenging. Recently, insights have come from experimental populations of plant species where the genetic diversity of plots has been manipulated to investigate its ecological consequence.

In an experimental study of a single species dominated coastal system (Hughes & Stachowicz 2004) demonstrated that more genetically diverse plots of Eel grass Zostera marina recover from disturbance (grazing by migrating geese) more quickly than plots with lower genetic diversity. Interestingly at the final sample date there was no significant difference in the shoot density between plots. This implies that while genetic diversity increases the resistance to disturbance (by grazing) it does not impact on the overall resilience.

Genetic diversity and resilience: (ability to recover in the face of disturbance)

There is a growing body of knowledge from community genomics which indicates that intra-specific genetic diversity may also have immediate importance for ecosystems, especially for population resilience to disturbance, productivity, interspecific competition and community structure.

Although much of the evidence comes from experimental manipulations of genetic diversity in artificial communities, there is evidence from natural populations of the links between genetic diversity and ecosystem function. Most documented ecological effects of genetic diversity involve productivity or fitness. The earliest evidence comes from experimental algae populations were Bell et al. (1991) demonstrated that mixed populations were more productive than monoculture populations. The simplest explanation for this is that of sampling or selection effects (Box 1). However other studies using experimental populations of Z. marina have shown negative selection effects where the most productive genotype in a monoculture are less common in mixtures (Reusch et al. 2005). In such cases niche partitioning (Box 1) is conferred as the cause of increased productivity under increased genetic diversity.

**Box 1.** Mechanisms for increased productivity in association with genetic diversity

A) Sampling or selection effect where a single genotype dominates and drives the increased performance, as is the case with the algae example (commonly observed in crop systems).

B) Facilitation or niche complementarity, where the sum of the genotypes are able to exploit more efficiently the overall resource base.
Increase in primary productivity has been demonstrated in experimental populations of the plant species, *Solidago altissima* (Canadian goldenrod) (Crutsinger et al. 2006). In this study above ground net primary productivity (ANPP), increased with genotype diversity and was 36% greater in plots containing 12 genotypes than plots with a single genotype. This is explained by increased niche complementarity.

Increase productivity has also been demonstrated in insect communities for example complementarity in the form of genetic task specialization is the likely explanation for positive effects in honey bee colonies (stability) high diversity colonies maintain more uniform temperatures than low-diversity colonies in the face of temperature stresses, workers vary genetically in there threshold to temperature at which they begin fanning. More diverse honey bee colonies also exhibit increased productivity and colony longevity. However, the benefits of genetic diversity are not continually increased, for example in bee colonies as relatedness decreases this may eventually disrupt the colony dynamics. Decreased genetic diversity can also have its advantage for example in ant colonies, low allelic richness allows the formation of larger more competitive colonies (Tsutsui et al. 2003).

**Community level effects:** does increase genetic diversity lead to increased species richness?

Within the same trophic level:

Increased genetic diversity within a species can have a positive effect on coexistence of competing plant species, as demonstrated in a study of Black mustard (*Brassica nigra*) (Lankau and Strauss, 2007). Here they demonstrate that genetic variation in the levels of sinigrin (an allelopathic compound) provide a mutual feedback to maintain species diversity as well as genetic diversity. In communities dominated by *B. nigra* the fitness advantage of producing high levels of sinigrin are lower, so genotypes for low sinigrin production are favoured, thus allowing competitive species to invade. As the density of *B. nigra* declines then the fitness benefits of high sinigrin production increase, thus preventing the domination by or other species, if sinigrin levels are uniformly low.

In the tree species *Populus tremula*, variation in genotypes significantly influenced the bark epiphyte community composition, as much as environmental variation. This is one of the first empirical demonstrations of genetic diversity in foundation tree species impacting on associated biodiversity. (Davies et al. 2014)

**Multiple trophic levels:**

Using experimental populations of *S. altissima* studies have demonstrated in addition to increase ANPP, the species diversity of arthropods recorded in the most genetically diverse plots is 27% greater in single genotype plots (Crutsinger et al., 2006). Not only does the herbivore species richness increase, but also the diversity of predatory arthropod species. This relationship might be explained by two mutually exclusive hypothesis the “more individuals hypothesis” predicts a co-relation between arthropod diversity and ANPP, or the “resource specialization hypothesis” because genotypes vary in susceptibility to particular herbivores. Interestingly in this study the effect of genotypic diversity on arthropod diversity is not simply a function of increased ANPP, but it arises as a direct effect of resources available to herbivores. This demonstrates that genetic diversity can be regarded as important as species richness in some plant communities.
Ecosystem level effects

Genetic diversity in dominant plant species can also influence ecosystem level processes such as nutrient and energy fluxes. Using common garden grown trees and model systems of hybrid zones in Cotton wood trees (Schweitzer et al., 2004) demonstrated that genetic diversity of leaf litter can have major positive effects on the rate of decomposition and nutrient flux that are comparable to the effects of species diversity. Here niche complementarity and non-additive impacts on the decomposer community explain the increase rate of decay. Similar findings have been demonstrated in clonal tree species (Aspen, P. tremuloides) forests (Madritch et al., 2006).

What about interspecific genetic diversity?

A new focus of scientists has been concerned not only with the diversity of species within a system but also their distinctiveness. The idea being that functional and ecological similarity are shaped by common ancestry, so species which are evolutionarily more distinct might contribute more to production than close relatives, by increasing niche breadth. Recently, experimental work in grass land experiments has demonstrated that biomass is greatest in communities which show the greatest phylogenetic diversity (Cadotte et al., 2008), that is species which are the most evolutionarily distinct. This poses interesting philosophical questions as to how resources for species conservation might be used.


Suggested reading/references.


