Hybridization & Conservation

Natural hybridization can create genetic diversity, e.g. plant species of hybrid origin, genetic exchange among micro-organisms.

But genetic hybridization due to human disturbances (particularly introduced species, but also habitat fragmentation modification) can compromise the genetic integrity of existing species to the point of causing extinctions.

New Zealand grey duck (*Anas superciliosa*) hybridizes with ***introduced*** mallards (*Anas platyrynchos*).

- Mallards are common but NZ greys are rare.
- So NZG tend to mate with mallards, simply b/c more readily available.
- So pure NZG are disappearing rapidly.
- The same pattern is true for mallards hybridizing with and **genetically swamping** endemic Hawaiian ducks (*A wyvilliana*) and Australian black ducks (*A rogersi*).

Northern spotted owls (*Strix occidentalis caurina*) declined to low numbers by loss of old growth forest. NSO now rare and logged habitat is being colonized by barred owl (*Strix varia*), which produces fertile hybrids with NSO. If BO become more common than NSO, genetic swamping is a risk. Example shows how ***habitat modification*** can create hybridization problems.

Ethiopian wolf (*Canis simensis*) and domestic dog (*C. familiaris*). *C. simensis* has become rare (< 500 individuals) as afro-alpine ***habitat has become fragmented***. *C. simensis* is similar to both wolf and coyote, origin not resolved (trichotomy in tree), consequently also similar to domestic dog.

(Ohead: Gotelli et al. 1994, Figs, 1,2 [& table 2],

Domestic dogs much more common.
Matings of male dogs and female Ethiopian wolves observed.
Microsatellites show genetic introgression.

(Ohead: Gotelli et al. 1994, Figs 4,5)

Domestic cat (*Felis catus*) swamping European wild cat (*F sylvestris*) and African wild cat (*F Libyca*). LOTS of other examples from carnivores alone.

(Ohead: Wayne & Brown 2001, Table 7.1, p. 150-152 BOLD cases indicate threat of genetic swamping)

Lots of examples from freshwater fish (Allendorf et al 2001)

- introductions common for sport fishing,
- fish hybrids are often fertile.

Overall: hybridization is a geographically and taxonomically widespread problem.

Hybridization: interbreeding of individuals from genetically distinct populations, regardless of the taxonomic status of the populations.

Can result in three general outcomes:

1. Hybrid zone: area of contact between genetically distinct populations where hybridization occurs.

Geographically localized, does not affect genetic integrity of two parent populations.

2. Hybrid swarm: a population of individuals that are all hybrids by varying numbers of generations of backcrossing with parental types, and by mating among hybirds

Less localized, blurs genetic integrity of parental populations.

This blurring of genetic integrity is called ***genetic introgression*** - gene flow between populations that hybridize. The ***proportion of admixture*** is the proportion of alleles that come from each of the parental taxa. Introgression/admixture/gene flow is not necessarily symmetrical - so one of the parent taxa might be genetically swamped by the hybird swarm, while the other is not.

What determines direction of asymmetry in introgression? Hybrid mating behavior, habitat selection, etc… anything that affects which of the parental taxa the F1 is more likely to mate with.

3. Hybrid taxon: independently evolving stable population or group of populations with a unique set of heritable traits, distinct from the two or more parent taxa from which it arose

New genetic boundaries established when hybrid species forms (red wolf debate, more later).

Detection of hybridization.

Allendorf et al argue for use of genetic rather than morphological data.

(1) If a hybrid swarm contains individuals with high percentage of alleles from one parental taxon, then they will be hard to identify w/o genetic data.
(2) Morphology doesn't distinguish ***F1 hybrids*** (each parent was different species) from ***backcross hybrids*** (one hybrid parent and one parental species parent)
(3) Situations with just F1 hybrids can be addressed by eliminating the hybrids. Hybrid swarms with backcrosses will be harder to rectify. Smooth variation in degree of hybridization, rather than a dichotomy between F1 hybrids and nonhybrids.

Hybrid Index is used to assess how far a population has progressed from early hybridization (F1 only) stages to well-established hybrid swarm.

(Ohead: Allendorf et al. Fig 1: unimodal and bimodal hybrid zones - different amounts of introgression/admixture - important b/c this illustrates the VARIABILITY of consequences of hybridization for species' genetic integrity)

Hybrid index - see ohead Allendorf et al fig 1:

- For each individual, obtain multilocus genotype.
- Given the allele frequencies in each parental taxon, calculate the relative probability that the individual's multilocus genotype came from that taxon.
- E.g. if individual has an allele that is found in only 5% of individuals in parent taxon A, but in 50% of individuals in parent taxon B, then it is more likely to belong to taxon B.
- The relative probability of being B in this case is 0.5/(0.5+0.05) = 0.91
- Multiply these relative probabilities across all loci to get a single value for each individual, which will range from 0 (pure A) to 1 (pure B).
- Plot a frequency distribution of the multilocus probabilities:
- Bimodal - most individuals are purely one parent taxon or nearly so - little introgression.
- Unimodal - older hybridization with more complete introgression
- If unimodal, the genetic introgression need not be symmetrical, e.g. trout example in Allendorf et al Fig 1.

Six types of hybridization

(Ohead: Allendorf et al Box 2)

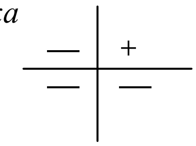
Allendorf et al basically take the 3 outcomes above (hybrid zone, hybrid swarm, hybrid taxon), and break each outcome into two classes based on the cause of hybridization - natural and anthropogenic.

Cause of Hybridization	
Natural	***Anthropogenic***
Hybrid zone (3)	No introgression (4)
Natural introgression (2)	Hybrid swarm, widespread introgression (5)
Hybrid taxon (1)	Hybrid swarm, complete admixture (6)

increasing admixture

Case 1: Taxon of hybrid origin that now has own gene pool with reproductive isolation This is the case when hybridization is a natural evolutionary origin. *Action: Do nothing other than conserve like any other species*.

Case 2: Little genetic divergence between two species that differ in morphology and ecology. Snail example, *Partula tainata* and *P suturalis.* Clark et al argue these are two species with ***molecular leakage***: "the convergence of neutral and mutually advantageous alleles in two species by occasional hybridization". In crosshair analysis this is case 6, so concur. *Action: treat 2 taxa as separate ESUs.*



Case 3. Geographically limited hybrid zone, genetic divergence remains strong elsewhere. Barton & Hewitt (1985) found that hybrids are disfavoured by selection in most hybird zones, but persist in limited area of contact due to constant production. As Mayr and Obrien argue, the two species are still distinct ESUs. *Action: Do nothing about hybrid zone, treat as 2 ESUs.*

Case 4. Anthropogenic hybridization with no introgression. If F1 is sterile, then there is little threat to genetic integrity of the two parent species, as long as both are common. (The parent species are 'good' under the strict Biological Species Concept, with complete reproductive isolation.).

Still may be problems due to wasted reproductive effort, especially if one parental species is common and the other is rare. E.g. Lehman et al. 1991 - where wolves are very rare compared to coyotes (Quebec), wolves often mate with coyotes and local 'wolf' population shows a lot of coyote introgression.

Action: (1) remove F1s. This reduces wasted mating effort - if species are short lived, probably just let them die on their own, AND…
(2) Eliminate cause of hybridization (e.g. remove introduced species, restore habitat that allowed invasion)

Case 5. Anthropogenic hybridization, widespread introgression. Difficult to do anything about the populations that are now hybrid swarms b/c difficult to recognize hybrids w/o genetic data on individual by individual basis.

Action: maintain remaining pure populations, expand them via introduction to areas w/o hybridization threat.

Allendorf et al. "Hybridized populations are of little conservation value, although they could have other values"

E.g westslope cutthroats hybridized to introduced rainbow trout. Cherry Creek rotenone/antimycin project.

Case 6. Anthropogenic hybridization, complete admixture. Hybrid swarm so far progressed that one of the parent stocks is swamped. No pure stocks to conserve, e.g. New Zealand grey ducks swamped by mallards. *Action: Allendorf and some others say conserve the hybrid (it has alleles not found in the 'swamping' parent species), others say call it a loss.*

Considering proposed action, it is critical to determine if hybridization is natural (no action) or anthropogenic (try to eliminate it). If can't distinguish natural/anthropogenic, then must either:

(1) fail to protect natural hybrids (see Obrien & Mayr)
or
(2) protect anthropogenic hybrids, to the detriment of parental taxa (promote genetic swamping).