

# Evolutionary Significant Units (ESUs) & Management Units (MUs)



# Evolutionary Significant (ESUs) Management Units (MUs)

## Lecture Outline

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- **Diversity is Diverse and Complex**
- **Defining Management Units Within Species**
- **Evolutionary Significant Units (ESUs)**
- **Genetic Distinctiveness & ESU's definition**
- **Genetical & Ecological Exchangeability**
- **Measuring & Managing Genetic Diversity**
  - Genetic Variability within Populations
  - Identification of evolutionary distinct populations
  - Defining evolutionary conservation value of populations or areas
- **Molecular Ecology**
- **Summary**

## Diversity is Diverse and Complex!

Difficulties of defining a species can be very informative because it forces us to address organismal behaviour in an evolutionary and ecological context



## Diversity is Diverse and Complex!

### Conservation genetics is about more than endangered species

- it includes understanding the **relationships and diversity** which represent biodiversity
- need not (directly) be an applied science, but **can address issues relating to understanding diversity**
- **may assist planning viable conservation strategies** more than conserving directly



## Diversity is Diverse and Complex!

Should we be conserving species?

**Species only** is a very **simplistic** approach in the real world

- is diversity only the number of species present?
- are all species equally relevant for biodiversity?
- must biodiversity be determined entirely by our species definition?



If not, then what else do we need to know?

## Diversity is Diverse and Complex!

### What questions are really of interest?

- what (genetic) diversity is present within our taxon of interest?
- what diversity is present within a region?
- what does this tell us about the important processes for creating and maintaining diversity?
- can we predict the consequences of a particular diversity level?
- if so, what is the appropriate response?
- what/where should we be saving?
- can we have objective criteria for prioritization?
- is *human activity* reducing diversity or is it a natural process?
- is *genetic pollution* a risk of human movements and introductions?

## Defining Management Units Within Species

**More difficult and controversial than defining species**

Species clearly require management as separate units, but

- some **populations** within species may
  - be on **the path to speciation** and
  - show **significant adaptive differentiation** to particular ecological niches or
  - **significant genetic differentiation**
- ✓ justifying their **management as separate evolutionary lineages** for conservation purposes

## Defining Management Units Within Species

### Evolutionary Significant Units (ESUs)

**genetically differentiated populations that have a high priority for separate management and conservation**

closely related (sometime synonymous) to

- subspecies
- distinct population segments (DPS - Endangered Species Act)

many authors suggest that ESUs, subspecies and DPS all merit separate management and have a **high priority for conservation**

the fundamental idea is that **conservation should aim to preserve**

- **evolutionary processes**
- **adaptive potential**
- **not just current species**

without regard to losing significant variation within species



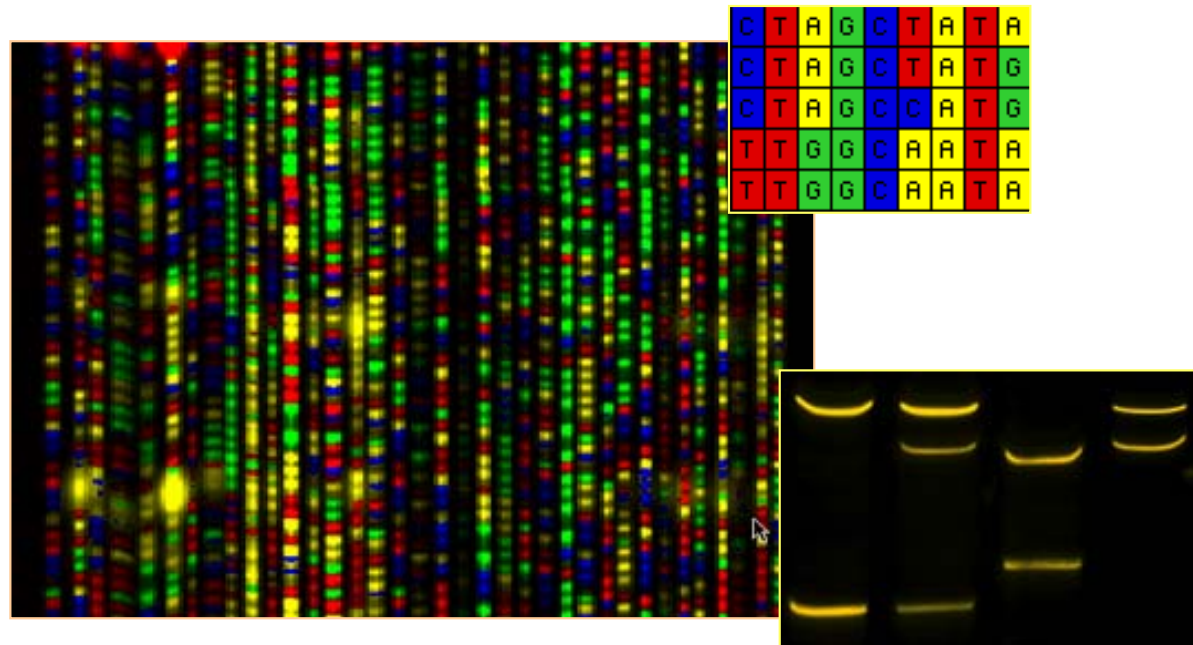
## Defining Management Units Within Species

### What defines an ESU?

**Original ESU's definitions** (Ryder, 1986; Waples, 1991) had two components

- **reproductive isolation** (and consequently, genetic distinctness)
- **ecological distinctness** (unique adaptations)

**Recent definitions emphasize more genetic distinctiveness**



## Genetic Distinctiveness & ESU's definition

### Rationale

Although genetics has assumed an important role in conservation biology

- genetic surveys of managed species are far from routine
- there is a perception that genetic analyses are of more significance to long-term than short-term needs
- genetic analysis has lower priority than demographic analysis

### Moritz

- theory and practice are so far apart because the relevance of genetic analyses to practical issues in wildlife management have not been adequately explained and demonstrated
- genetic markers (mtDNA and microsatellites) should be used to define management units within species

## Genetic Distinctiveness & ESU's definition

### Moritz's definition

ESU's should show

- **significant divergence** and **reciprocal monophyly** for mtDNA
- **significant divergence of allele frequencies at nuclear loci**

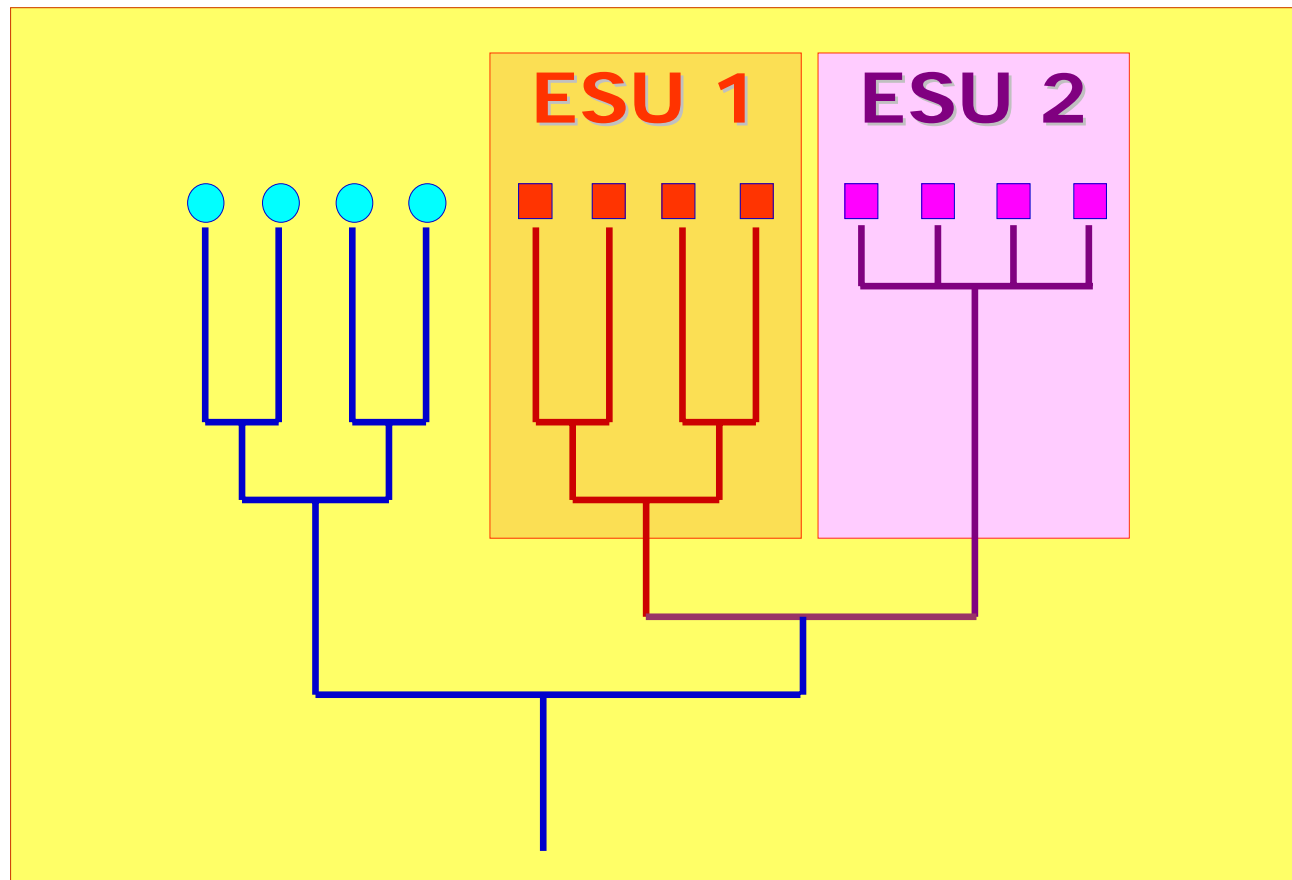
Moritz's ESU's definition implies

- both **historical** and **recent restriction of gene flow**
  - ✓ it makes criteria for genetic distinctiveness more concrete
- evidence for **long term divergence**, continuing in the present
  - ✓ divergence in mtDNA reflects long term restriction of gene flow
  - ✓ **congruence of slow and fast markers** (microsatellites) is **evidence for historical isolation that persists today**

## Genetic Distinctiveness & ESU's definition

### Reciprocal Monophyly

each **ESU** is a **monophyletic group** (ancestral population and all descendant populations) that does not include any portion of the other



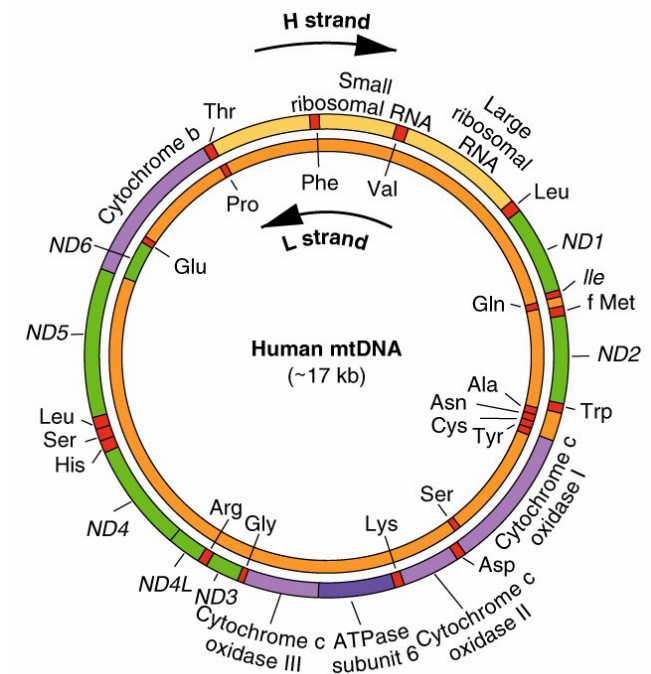
## Genetic Distinctiveness & ESU's definition

mtDNA is a powerful tool in evolutionary biology

- rapid rate of base substitutions
- effectively haploid
- maternal inheritance
  - ✓ reduces  $N_e$
  - ✓ increases sensitivity to genetic drift
- ease of isolation and manipulation

mtDNA can produce **results of considerable practical importance**, but

- the conservation goals must be clearly defined first and the analyses designed to fit the goals



## Genetical & Ecological Exchangeability

### Critics to the ESU concept

- **evolutionary significant units are essentially equivalent to, and should be abandoned in favour of, phylogenetic species**  
(Cracraft, 1997)
- **genetically defined ESUs ignore adaptive differences**  
(Crandall et al., 2000)
  - **unlikely detected within species with high gene flow**  
even though populations may have adaptive differences and warrant separate management
  - populations **with low gene flow** that have been differentiated by genetic drift may be designated as separate ESUs  
even though they may not be adaptively distinct

## Genetical & Ecological Exchangeability

### Critics to the ESU concept (Crandall et al., 2000)

The reciprocal monophyly criterion may be overly strict

- **guarantees that historical restriction of gene flow** occurred
  - **ecologically important genetic differences** may have accumulated without this pattern
  - conversely, **long accumulation of neutral genetic differences** may result in **little ecological divergence**

If the goal is **to maintain adaptive potential**, need to

- consider these possibilities
- restore focus on adaptations, not just neutral genetic variation

## Genetical & Ecological Exchangeability

### **Cross-hair Analysis** (Crandall et al., 2000)

Populations can be classified according to whether they show recent or historical ecological or genetic exchangeability

**Cross-hair analysis** attempts to delineate whether there is

- there is **adaptive differentiation**
- there is **gene flow**
  - **historical**
  - **due to recent admixture**

**Cross-hair analysis** leads to

- **more adequate management recommendations**



# Genetical & Ecological Exchangeability

**Cross-hair Analysis** (Crandall et al., 2000)

Populations are given + or - classifications

Time Frame			
Recent		+ / -	+ / -
Historical		+ / -	+ / -
		Genetic	Ecological
		$H_0$ Exchangeability	

**+ reject  $H_0$  of exchangeability**, evidence exists for divergence

**- accept  $H_0$  of exchangeability**, failure to detect divergence

# Genetical & Ecological Exchangeability

## Cross-hair Analysis (Crandall et al., 2000)

### Genetic Exchangeability

- concerned with the **limits of spread of new genetic variation through gene flow**
  - rejected (+)** when there is evidence of **restricted gene flow**
  - accepted (-)** when there is evidence of **ample gene flow**
- evidence for gene flow is ideally **based on multiple nuclear loci** but also on mtDNA or cpDNA

Time Frame		
Recent	+ / -	+ / -
Historical	+ / -	+ / -
	Genetic	Ecological
	$H_0$ Exchangeability	

# Genetical & Ecological Exchangeability

## Cross-hair Analysis (Crandall et al., 2000)

### Ecological Exchangeability

- based on the factors that define the
  - fundamental **niche**
  - the **spread of new genetic variants through genetic drift or natural selection**

Time Frame		
Recent	+ / -	+ / -
Historical	+ / -	+ / -
	Genetic	Ecological
	$H_0$ Exchangeability	

# Genetical & Ecological Exchangeability

## Cross-hair Analysis (Crandall et al., 2000)

### Ecological Exchangeability

**rejected (+)** when there is evidence for population differentiation due to **genetic drift or natural selection**

features interpreted as reflecting **adaptive differentiation**

- **life history traits**
- **morphology**
- **habitat**
- **QTL traits under selection**

Time Frame		
Recent	+ / -	+
Historical	+ / -	+
	Genetic	Ecological
	$H_0$ Exchangeability	

# Genetical & Ecological Exchangeability

**Cross-hair Analysis** (Crandall et al., 2000)

Recent and historical time frames distinguish

- natural evolutionary processes of limited gene flow  
 **$H_0$  rejected (+)** in the **historical-genetic** category

Time Frame		
Recent	+ / -	+ / -
Historical	<b>+</b>	+ / -
	Genetic	Ecological
<b><math>H_0</math> Exchangeability</b>		

# Genetical & Ecological Exchangeability

## Cross-hair Analysis (Crandall et al., 2000)

Recent and historical time frames distinguish

- natural evolutionary processes of limited gene flow  
 $H_0$  rejected (+) in the historical-genetic category

form

- recent population isolation  
+ in the recent-genetic category

Time Frame		
Recent	+	+ / -
Historical	+ / -	+ / -
	Genetic	Ecological
	$H_0$ Exchangeability	

# Genetical & Ecological Exchangeability

**Cross-hair Analysis** (Crandall et al., 2000)

Recent and historical time frames distinguish also

- secondary contact  
 $H_0$  accepted (-) in the recent-genetic category

Time Frame		
Recent	-	+ / -
Historical	+ / -	+ / -
	Genetic	Ecological
	$H_0$ Exchangeability	

# Genetical & Ecological Exchangeability

## Cross-hair Analysis (Crandall et al., 2000)

Recent and historical time frames distinguish also

- secondary contact

$H_0$  accepted (-) in the recent-genetic category

form

- long term-gene flow

$H_0$  accepted (-) in the historical-genetic category

Time Frame		
Recent	+ / -	+ / -
Historical	-	+ / -
	Genetic	Ecological
$H_0$ Exchangeability		



## Genetical & Ecological Exchangeability

### Cross-hair Analysis (Crandall et al., 2000)

- **16 categories of divergence** between two populations
- **recommended management actions** are given for **8 categories**
  - strong emphasis on top right quadrant

Time Frame		
Recent	+ / -	+ / -
Historical	+ / -	+ / -
	Genetic	Ecological
	$H_0$ Exchangeability	

# Genetical & Ecological Exchangeability

## Cross-hair Analysis (Crandall et al., 2000)

	Genetic	Ecological
Recent	+	+
Historical	+	+

separate species

+	+
-	+

treat as separate species

+	+
+	-

# Genetical & Ecological Exchangeability

## Cross-hair Analysis (Crandall et al., 2000)

	Genetic	Ecological
Recent	-	+
Historical	+	+

### treat as distinct populations

- recent admixture
- loss of genetic distinctiveness

	Genetic	Ecological
Recent	+	-
Historical	+	+

### treat as single population

- if natural convergence on ecological exchangeability

### treat as distinct population

- if anthropogenic convergence

# Genetical & Ecological Exchangeability

## Assignment examples – Black Rhinoceros

O’Ryan et al. (1994) used mtDNA to argue for two subspecies with separate management

### Cross-hair Analysis

- insufficient grounds to reject either genetic or ecological exchangeability
  - populations show gene flow
  - habitats are similar

	Genetic	Ecological
Recent	-	-
Historical	-	-



The species should be managed as a single population

## Genetical & Ecological Exchangeability

### Assignment examples – African Elephant

Georgiadis et al. (1994) found a **reciprocal monophyletic relationship among mtDNA**

- authors argued that the genetic diversity was simply **isolation by distance due to drift** across their geographic range
- habitat of different populations is sufficiently similar to **accept ecological exchangeability**

	Genetic	Ecological
Recent	+	-
Historical	-	-

*Loxodonta africana*



The species should be **managed as a single population**

## Genetical & Ecological Exchangeability

### Assignment examples – Cryan's Buckmoth

Legge et al. (1996)

- **adequate gene flow**
  - no evidence to reject **genetic exchangeability** based on either mtDNA or allozymes
- **evidence to reject recent** but not historical **ecological exchangeability** between populations
  - adaptive significance of the ecological differentiation

	Genetic	Ecological
Recent	-	+
Historical	-	-



*Hemileuca sp.*

The species should be **managed as distinct populations** although gene flow consistent with current population structure is allowable

## Genetical & Ecological Exchangeability

### Assignment examples – Puritan Tiger Beetle

- **mtDNA** show **low gene** flow and **significant differentiation**
  - evidence to reject **genetic exchangeability**
- not **ecological exchangeable** based on habitat parameters

	Genetic	Ecological
Recent	+	+
Historical	+	-



*Cicindela puritana*

- **strong adaptive differentiation**
- recommendation to **manage** the two populations **as separate units for conservation purposes**

## Conservation Goals

It is important to distinguish between

### 1. Gene Conservation

- the use of genetic information to measure and manage genetic diversity for its own sake

### 2. Molecular Ecology

- genetic analyses as a complement to ecological studies of demography
  - more straight forward
  - of more use to wildlife managers faced with short-term management priorities



## Measuring & Managing Genetic Diversity

Managing genetic diversity is **more relevant to**

- ✓ **long-term planning**
- ✓ **policy**

than to

- ✗ short-term management of threatened populations
  - ✓ few noticeable exceptions (e.g. **translocations** )





## Measuring & Managing Genetic Diversity

mtDNA has been used in this context to

- **measure genetic variation within populations**, especially ones thought to have declined recently
- identify evolutionary divergent sets of populations, including the **resolution of ESUs**
- **assess conservation value of populations or areas from an evolutionary or phylogenetic perspective**

# Measuring & Managing Genetic Diversity

## Genetic Variability within Populations

### Aim of quantifying mtDNA variation within populations

- test for the **loss of genomic variability**, generally as a consequence of reduction in population size
  - ✓ conservation significance if the loss of variation translates to reduced individual fitness

### This is a **weak application of mtDNA**

- ✗ **lack** of any theoretical or empirical evidence for a strong **correlation between mtDNA diversity and diversity in the nuclear genome**
- ✗ low mtDNA diversity is correlated with low nuclear gene diversity in some cases but not others

# Measuring & Managing Genetic Diversity

## Genetic Variability within Populations

- low mtDNA diversity has been reported in rapidly expanding species
  - northern elephant seals
  - parthenogenetic gekos



*Mirounga angustirostris*

- moderate to high mtDNA diversity has been observed in declining species subjected to intense harvesting or in species otherwise suggested to be inbred
  - coconut crabs
  - humpback whales



*Megaptera novaeangliae*



*Birgus latro*

## Measuring & Managing Genetic Diversity

mtDNA has been used to

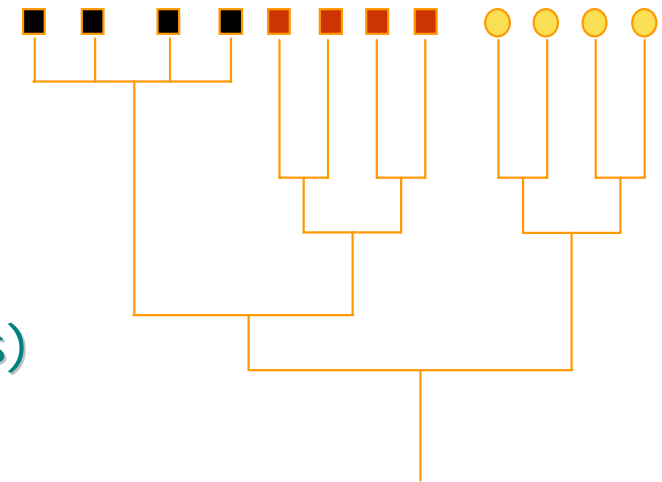
- ✓ measure genetic variation within populations, especially ones thought to have declined recently
- identify evolutionary divergent sets of populations, including the **resolution of ESUs**
- assess conservation value of populations or areas from an evolutionary or phylogenetic perspective

# Measuring & Managing Genetic Diversity

## Identification of evolutionary distinct populations

## Identification of taxa with independent evolutionary histories

- prerequisite for managing biodiversity
- groupings variously referred to as
  - species
  - subspecies
  - evolutionary significant units (ESUs)



## mtDNA phylogenies can

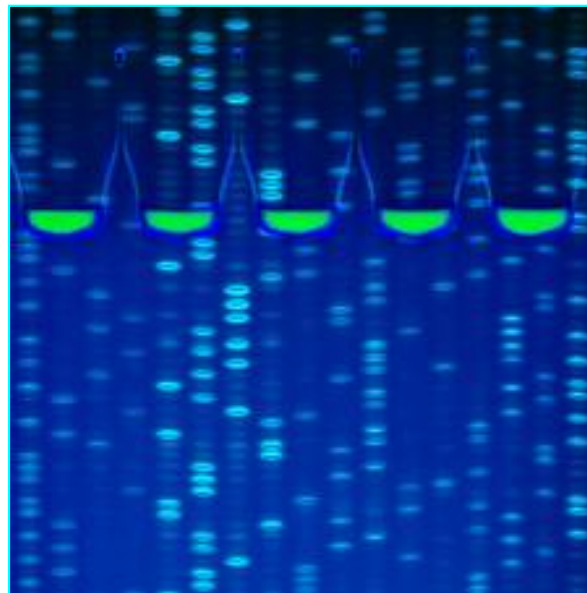
- provide unique insights into population history
- suggest hypotheses about the boundaries of genetically divergent groups (i.e., cryptic species)

## Measuring & Managing Genetic Diversity

### Identification of evolutionary distinct populations

- **mtDNA phylogenies must be used in conjunction with nuclear markers** because given the
  - **lower effective number of genes**
  - **greater dispersal by males** than females

**mtDNA can diverge while nuclear genes do not**





# Measuring & Managing Genetic Diversity

## Recognition of ESUs

Criteria for defining an ESU remains to be established

Suggested thresholds range from

- any population that contributes substantially to the overall genetic diversity of the species and is reproductively isolated

to

- populations showing phylogenetic distinctiveness of alleles across multiple loci

The question that plagues the approach is

**How much difference is enough?**

# Measuring & Managing Genetic Diversity

## Recognition of ESUs

### How much difference is enough?

- no theoretical or empirical justification for setting an amount of sequence divergence beyond which a set of populations is recognized as an ESU

Although

- comparisons to divergences within an among related species may provide an empirical yardstick



# Measuring & Managing Genetic Diversity

## Recognition of ESUs

### Qualitative criterion

avoiding the quantitative question of *how much is enough?*

- to consider the **geographic distribution of alleles** in relationship to their **phylogeny**
  - ✓ gene flow must be restricted for a long period to create phylogeographic structuring of alleles
  - ✓ ESUs should show complete monophyly of mtDNA alleles

However

- ✗ this criterion may be **too stringent**
  - ✗ **well characterized species with paraphyletic mtDNA lineages** have been documented

## Measuring & Managing Genetic Diversity

### Recognition of ESUs

### Again...

➤ it is important to seek **corroborating evidence from nuclear loci**

However, **alleles of nuclear genes** are expected

- to **take substantially longer to show phylogenetic sorting** between populations or species
  - ✓ larger effective population size
  - ✓ slower neutral mutation rate

## Measuring & Managing Genetic Diversity

mtDNA has been used to

- ✓ **measure genetic variation within populations**, especially ones thought to have declined recently
- ✓ **identify evolutionary divergent sets of populations**, including the **resolution of ESUs**
- **assess conservation value of populations or areas from an evolutionary or phylogenetic perspective**

## Measuring & Managing Genetic Diversity

Defining evolutionary conservation value of populations or areas

Extension of the use of mtDNA variation to recognize ESUs

- phylogenetic uniqueness should be considered in **prioritizing species for management**
- **define conservation value** taking account of evolutionary distance
  - ✓ particularly well suited to molecular data

## Measuring & Managing Genetic Diversity

Defining evolutionary conservation value of populations or areas

Then, moving from **species** to **community genetics**

- define **geographic regions** within which **multiple species have genetically unique populations** or **ESUs**
- testing for **congruence of phylogeographic patterns among species** to define geographic regions within which a **substantial proportion of species have had evolutionary histories separate** from their respective conspecifics
- **regions with a high proportion of ESUs** should be accorded **high conservation priority**
  - even if they do not have an array of endemic species as recognized by conventional methods

## Measuring & Managing Genetic Diversity

Defining evolutionary conservation value of populations or areas

'Value' skirts some basic **philosophical and ethical issues...**

- ...what do we mean by the **S** in ESU?
- ...can we justify **ranking species** according to a measure of molecular divergence?
- we can only measure evolutionary significance or value in terms of past history
- we cannot predict which, if any, of these units will diversify to produce future biodiversity
- we must be very clear about the nature of the advice we are providing when we discuss conservation priorities from a molecular evolutionary perspective...



## Molecular Ecology

General area of application that uses **genetics as a tool for ecologists**

- **to define the appropriate geographic scale for monitoring and managing**
- **to provide a means for identifying the origin of individuals in migratory species**
- **to test for dramatic changes in population size and connectedness**

In general these applications are

- conceptually simpler
- much more **relevant to short-term management issues**

than are those related to gene conservation

# Molecular Ecology

## Defining Management Units or stocks

Simple but powerful and practical application of genetics

- a great deal of effort is spent on **monitoring populations as part of the species recovery process**
- too often, little consideration is given to the **appropriate geographic scale for monitoring or management**
- an exception is with **fisheries**, where it has long been recognized that **species typically consist of**
  - **multiple stocks** that respond independently to harvesting and management
  - **populations that exchange so few migrants as to be genetically distinct will also be demographically independent**

## Molecular Ecology

### Defining Management Units or stocks

In contrast to ESUs

- **MUs** are defined by **significant divergence in allele frequencies** regardless of the phylogeny of the alleles
  - ✓ allele frequencies will respond to population isolation more rapidly than phylogenetic patterns

**mtDNA** is especially useful for detecting **boundaries between MUs**

- **differences between populations will be more readily detected with mtDNA** than with nuclear genes
  - ✓ important when sample sizes are limited as is often the case with threatened species
- mtDNA it is usually **more prone to genetic drift** than nuclear loci
  - ✓ a greater proportion of the variation is distributed between populations

# Molecular Ecology

## Identification & Use of Genetic Tags

Useful application of genetics for short-term management is to provide a source of naturally occurring

- **genetic tags**
  - ✓ **genetic variants that individually or in combination diagnose different MUs**
    - indelible
    - present in all members of a population at all ages
    - can be **used to determine the source(s) of animals** in
      - harvest
      - international commerce
      - areas subjected to impacts or management

# Molecular Ecology

## Identification & Use of Genetic Tags

- particularly useful for **migratory species** where
  - ✓ impacts in one area (e.g., feeding ground) can affect one or more distant MUs
- most effective where the variation within areas is low relative to that between areas
- **maximum likelihood methods** can be used to estimate the **contribution of various MUs to a sample** of individuals taken from a particular
  - feeding ground
  - migratory route
  - commercial harvest

# Molecular Ecology

## Migration and changes in population size

Wildlife managers often face the problem of assessing the degree to which populations are

- connected by migration
- changing in size

**Patterns of genetic variation** provide

- indirect estimates of these parameters
  - rapid development of **methods** for using information on allele distributions and relationships **to infer**
    - ✓ long-term **migration rates**
    - ✓ **trends in  $N_e$**
- significant insights into the **long-term** behavior of populations
  - unclear relevance in conservation studies (short-term management) where populations are often fluctuating in size and/or connectedness

# Evolutionary Significant (ESUs) Management Units (MUs)

## Summary

According to the Evolutionary Significant Units (ESUs) concept

- genetically differentiated populations have a high priority for separate management and conservation
- ESU's should show
  - significant divergence and reciprocal monophyly for mtDNA alleles
  - significant divergence of allele frequencies at nuclear loci

For the ecological and genetic exchangeability concept

- populations within a species may justify management as separate units if they show adaptive genetic differentiation
- delineation of such population requires information on their recent or historical ecological or genetic exchangeability

# Evolutionary Significant (ESUs) Management Units (MUs)

## Summary

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mtDNA has been used to

- measure genetic variation within populations
- identify evolutionary divergent sets of populations
- assess conservation value of populations or areas from an evolutionary or phylogenetic perspective