Lect. 18. Ecology, climate, gene flow, neutral theory

30 March 2017

Announcement: Exam Thursday April 6th, TLS 154, Scantron, bring number 2 pencils, and your people soft number. Lectures 13-18 only.

Last Time …

- Genetic drift
- Effective population size
- Implications of drift for conservation biology
- Bottlenecks
- Founder events
- Gene flow

This Time …

- Interaction of drift (bottlenecks), gene flow, selection (climate, ecology) → population genetic structure
- Genetic drift revisited
- Neutral theory
- How molecules evolve

Good question posed after class last time…

- Although gene flow homogenizes populations, will the resulting large meta-population have less variation?
- Note: we are talking about gene flow in the absence of selection and drift.
- The metapopulation is larger and should not be less variable within (but **among-population variability** is reduced).

Small poplns. + low gene flow + genetic drift = increased differentiation among populations

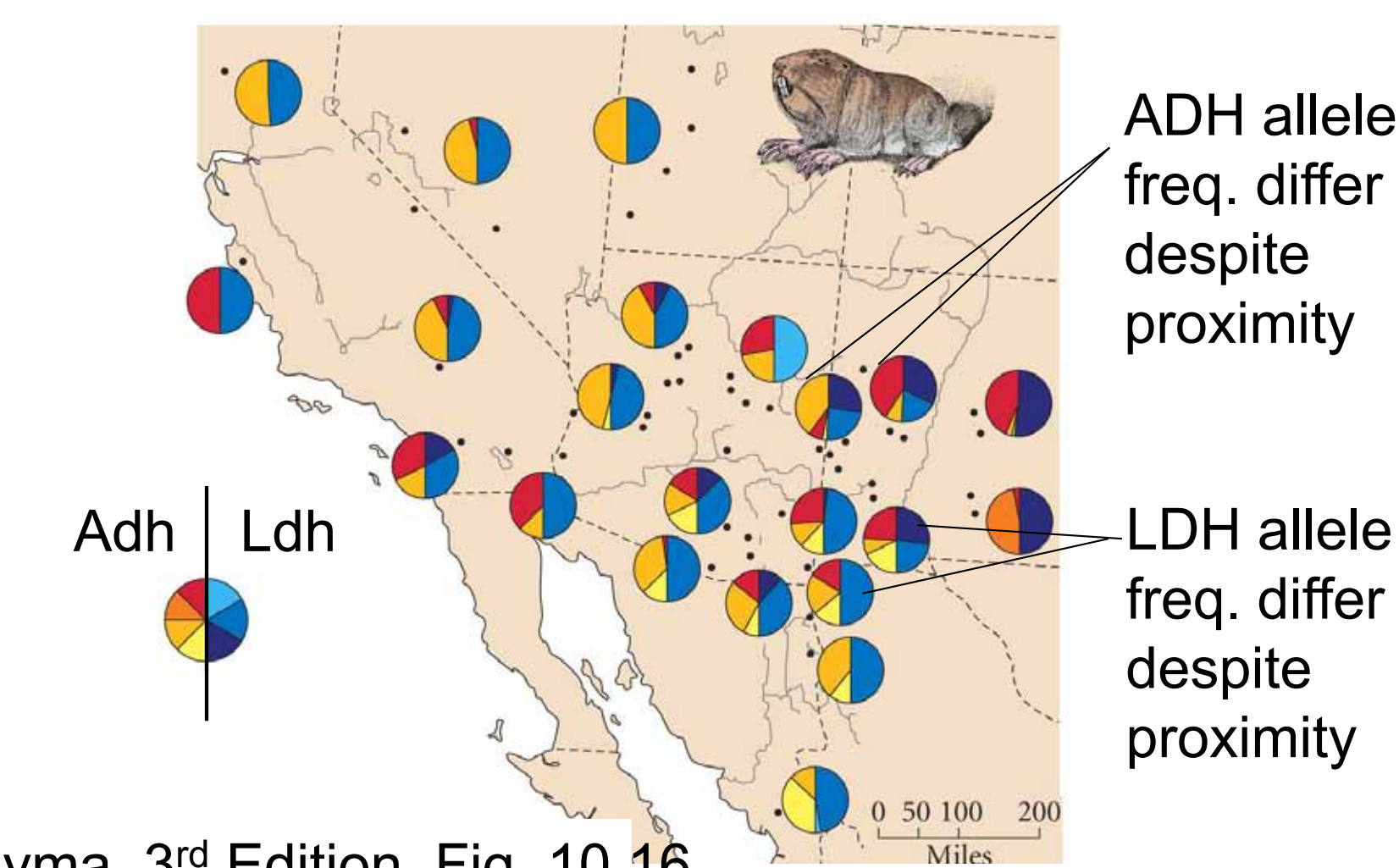
In Natural Populations: Balance BTW Gene flow, Drift, Selection

Balance btw selection, drift and gene flow can maintain variability.

Lake Erie, banded water snake. Selection differs between environments

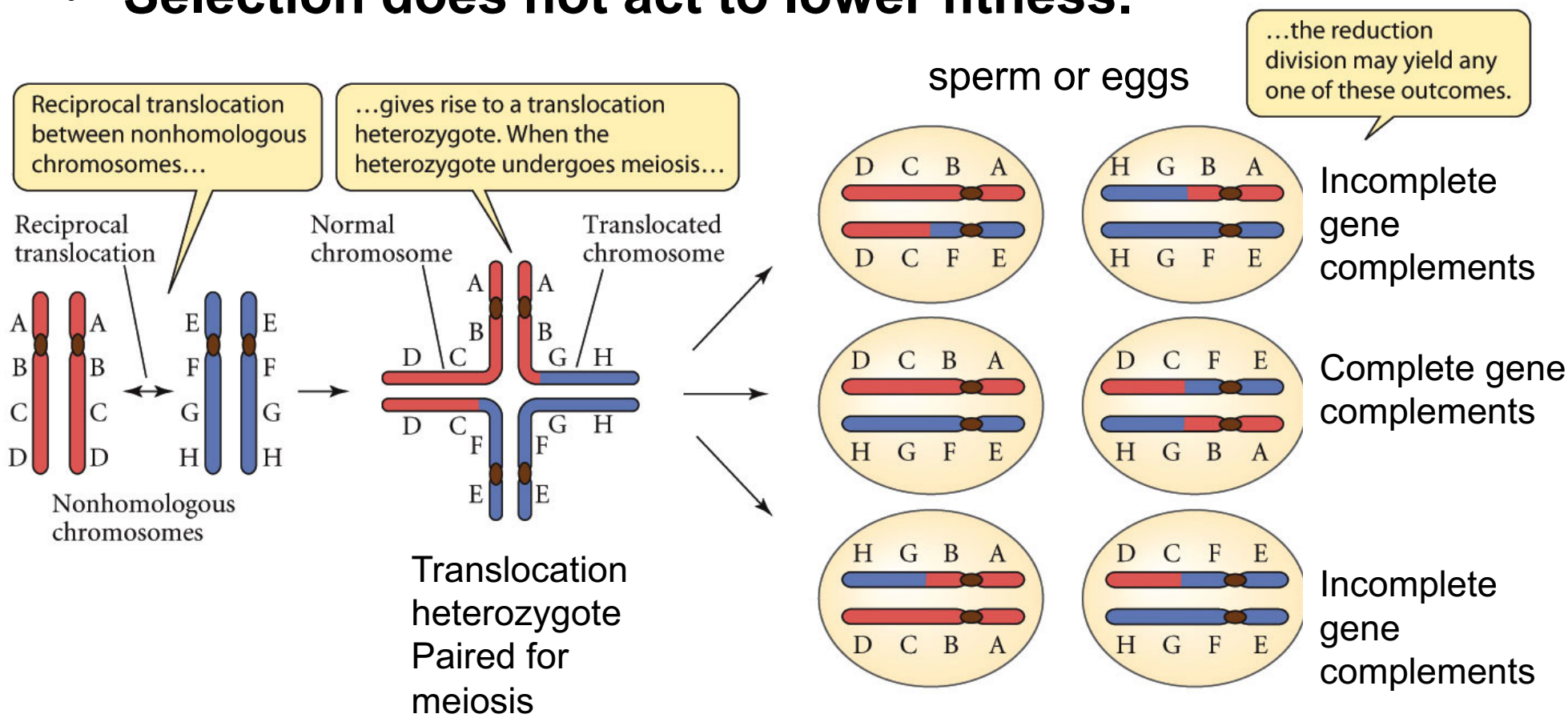
Pocket gopher, *Thonomys bottae*

- High among population genetic differences = low gene flow, small population sizes
- Strong selection unlikely in this case



Futuyma, 3rd Edition, Fig. 10.16

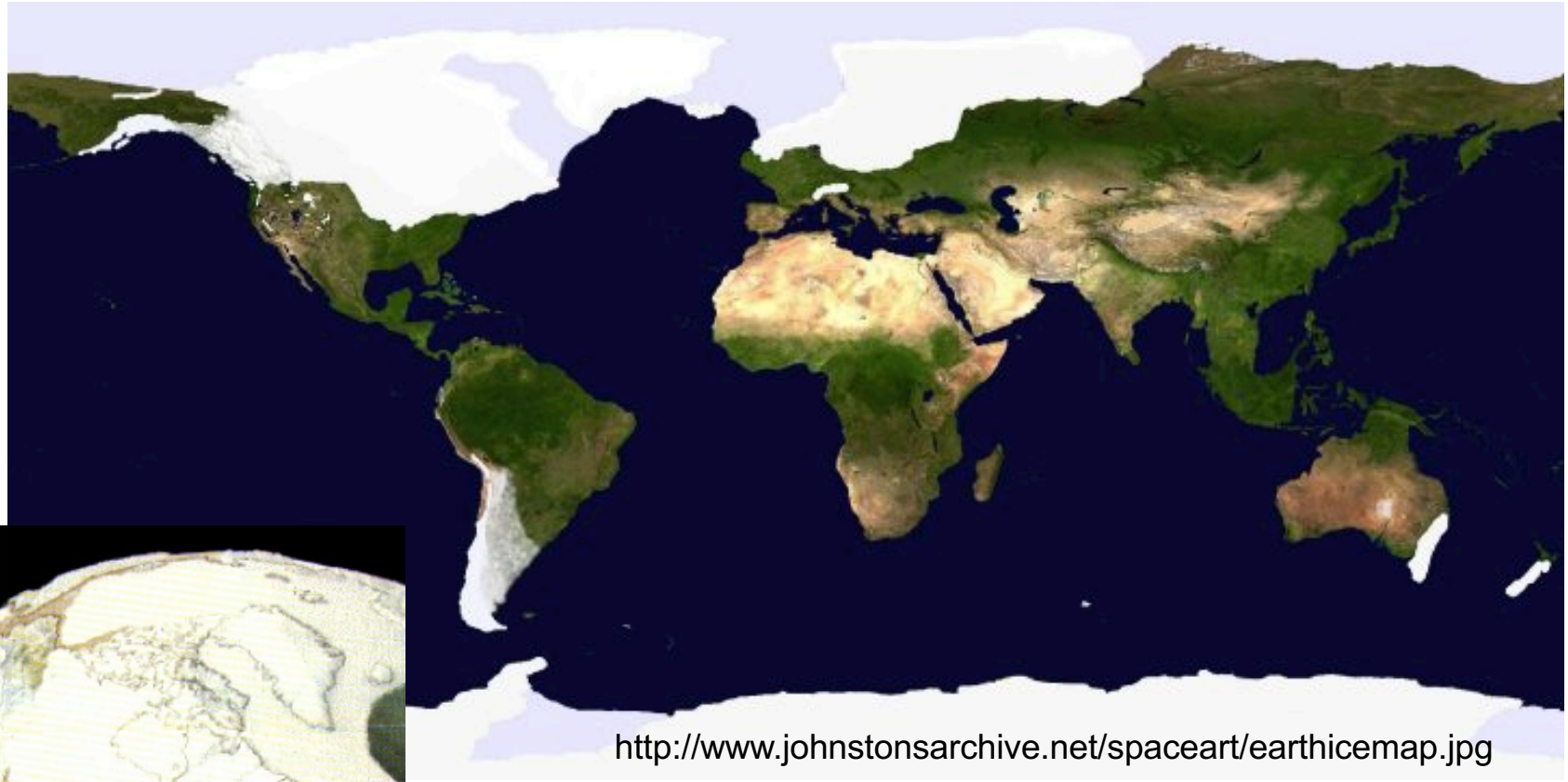
- Pocket Gophers have different chromosomal translocations fixed across species/subspecies.
- Reciprocal translocations lower fitness.
- They can only be fixed by genetic drift.
- **Selection does not act to lower fitness.**



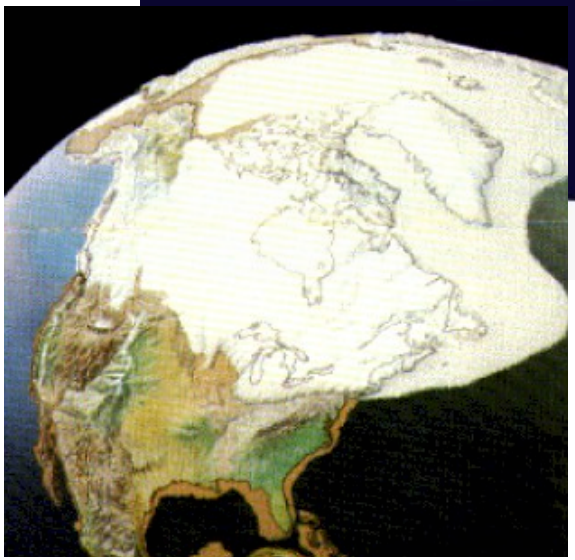
Futuyma 3e, Fig 8.25

The interaction of bottlenecks, drift, gene flow, and selection (climate, ecology)

Last Glacial Maximum



http://www.johnstonsarchive.net/spaceart/earthicemap.jpg



20,000 years before present
Last glacial maximum. Populations forced south into isolated refugia

http://home.earthlink.net/~icedneuron/iceagemap.jpg

The footprint of rapid expansion of populations after the LGM can be seen today in low genetic variability in populations occupying previously glaciated territory.

Northern Hemisphere

Northern purity Southern Richness

Species showing less variability in the northern vs southern parts of range

Allozymes	Taxon name	Location	Reference
P*lethodon cinereus*	Salamander	E. USA	Highton & Webster, 1976
Ovis dalli	Wild sheep	Nearctic	Sage & Wolff, 1986
Pinus contorta	Lodgepole pine	NW America	Cwyner & MacDonald, 1987
mtDNA			
Triturus cristatus	Crested newt	Europe	Wallis & Arntzen, 1989
Neotoma floridana	Eastern wood rat	Boreal N. America	Hayes & Harrison, 1992
Passerella iliacea	Fox sparrow	N & W America	Gill, Mostron & Mack, 1993
Papilio polyxenes	Swallowtail butterfly	N America	Sperling & Harrison, 1994
Ambystoma maculatus	Spotted salamader	Missouri Ozarks	Phillips, 1994
Microtus agrestis	Field Vole	Scandinavia	Jaarola & Tagelstrom, 1995
Sternotherus minor	Musk turtle	SE USA	Walker et al. 1995

Hewitt, G. 1996. Some genetic consequences of ice ages, and their role in divergence and speciation. Biological Journal of the Linnean Society 58, 247-276.

Reasons for northern purity?

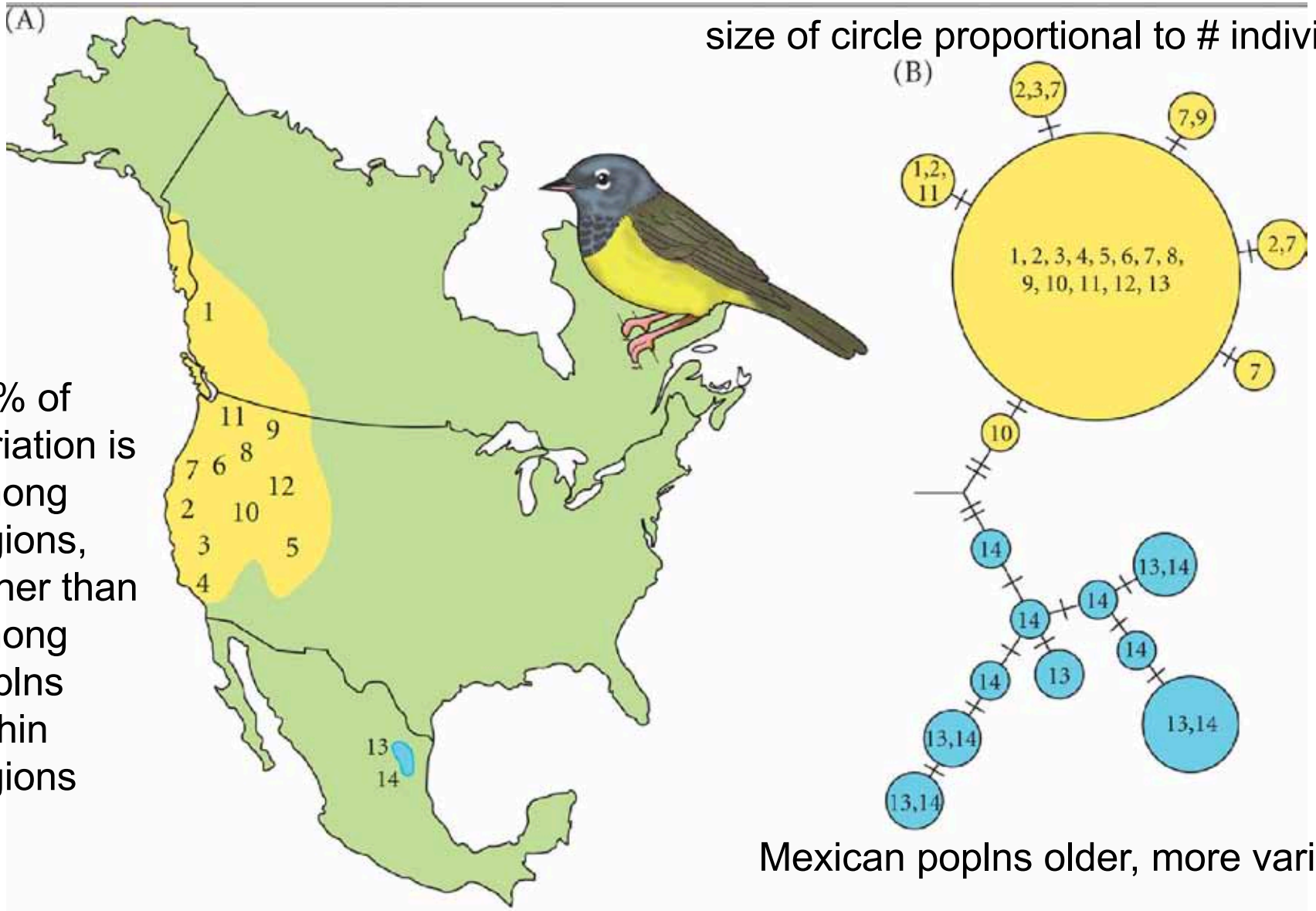
- Rapid spread into unoccupied territory
- Repeated bottlenecks. Long distance colonization
- Lack of time for differentiation

MacGillivray's Wabler

Cytochrome b mtDNA haplotypes

Older Populations more Variable

size of circle proportional to # individuals

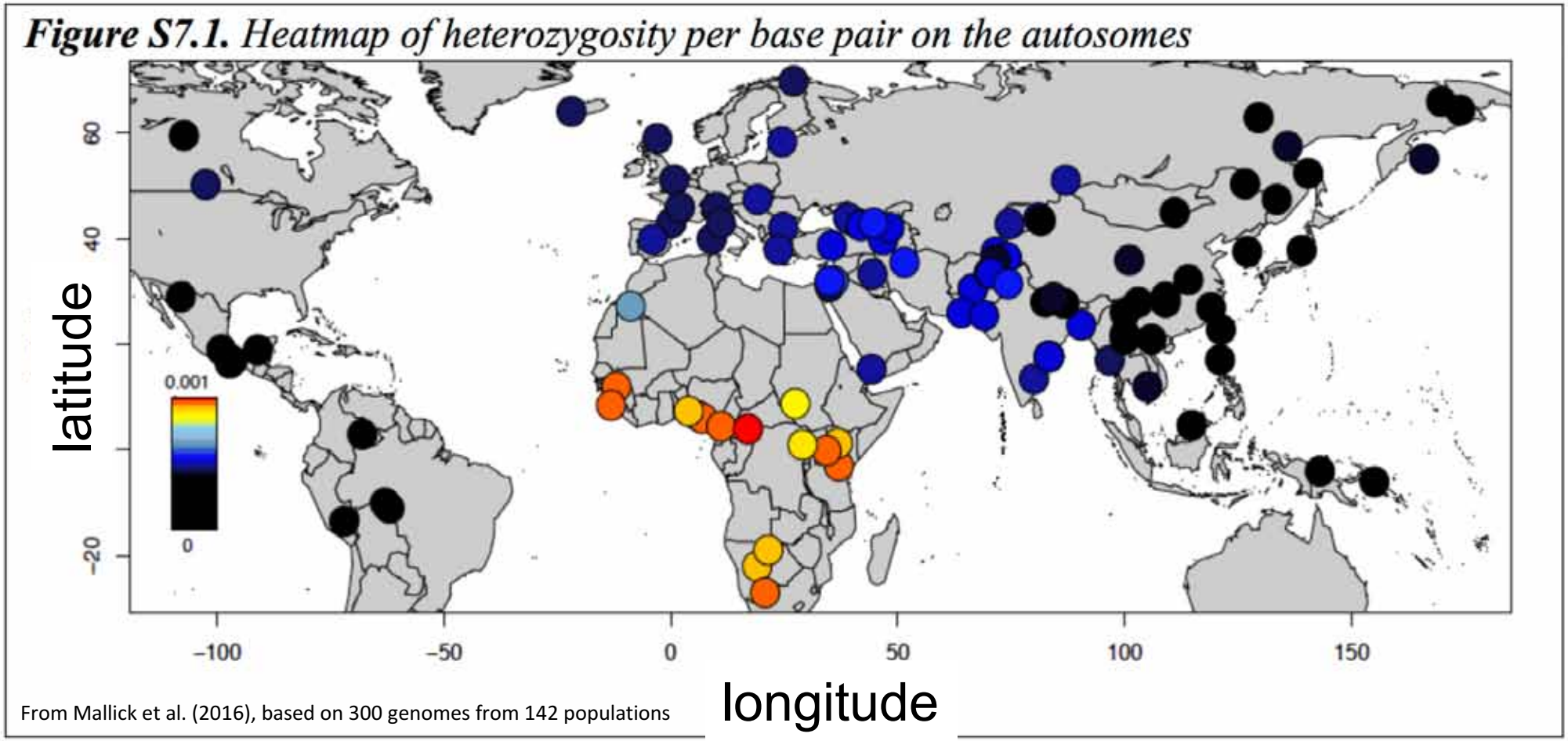


90% of variation is among regions, rather than among poplns within regions

Mexican poplns older, more variable

EVOLUTION 3e, Figure 9.33

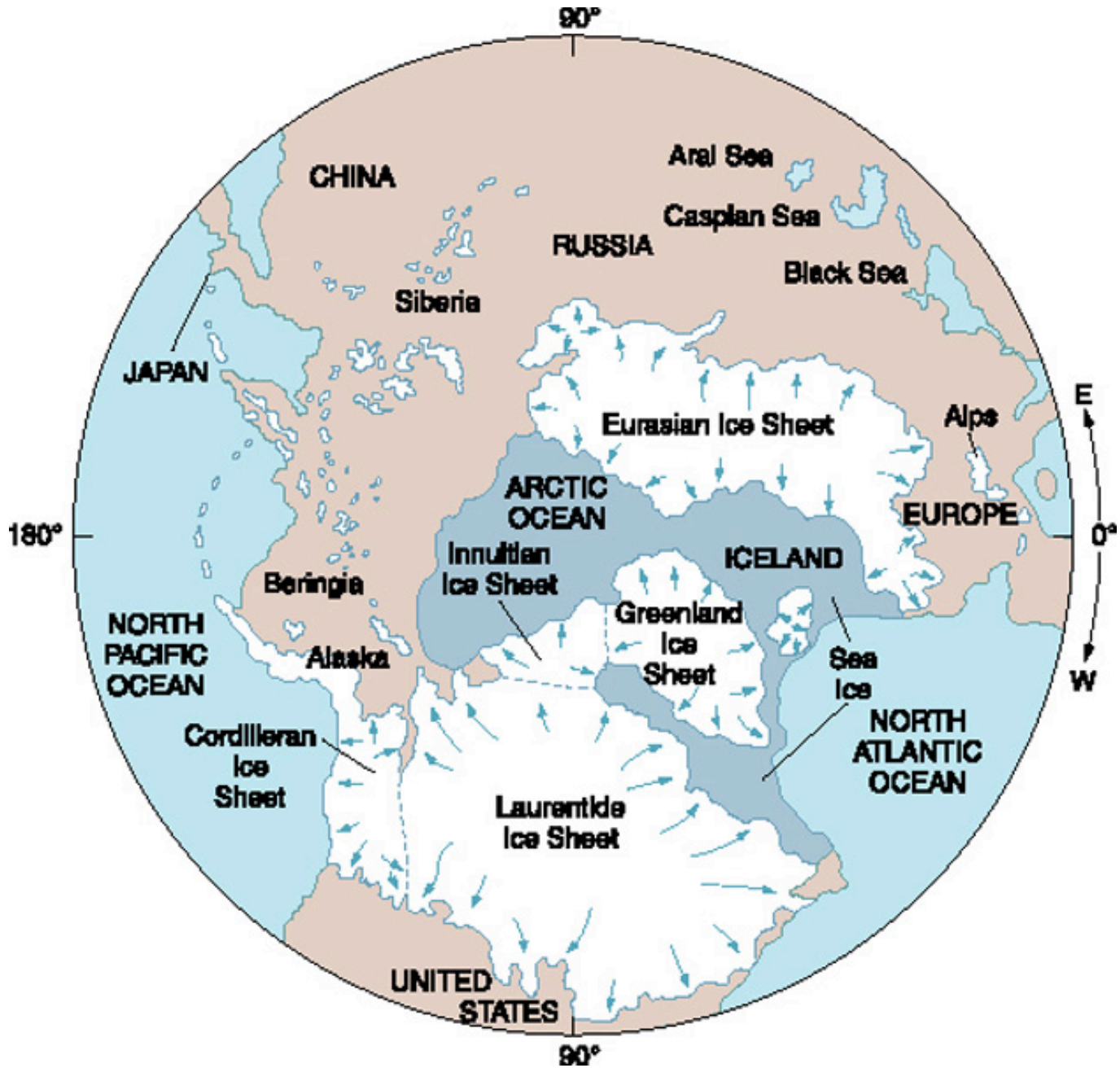
Human genetic variation greatest in Africa; least in most-recently-colonized areas.



Mallick et al. 2016. based on 300 genomes, 142 populations

Southern Hemisphere: purity vs richness pattern seen in reverse

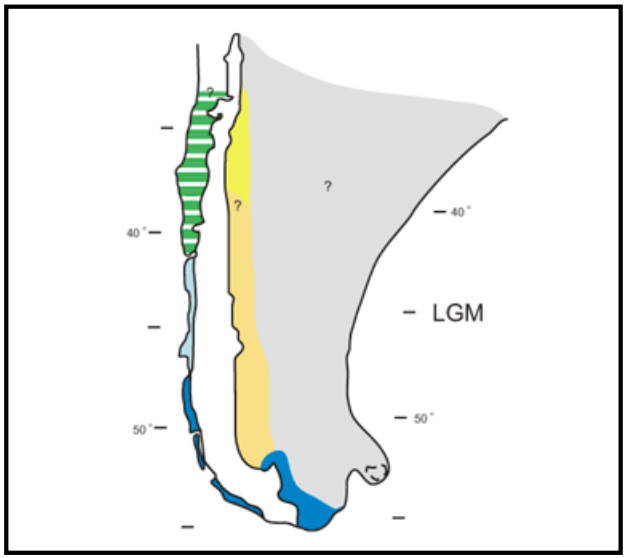
Max. Pleistocene glaciation; Northern Hemisphere



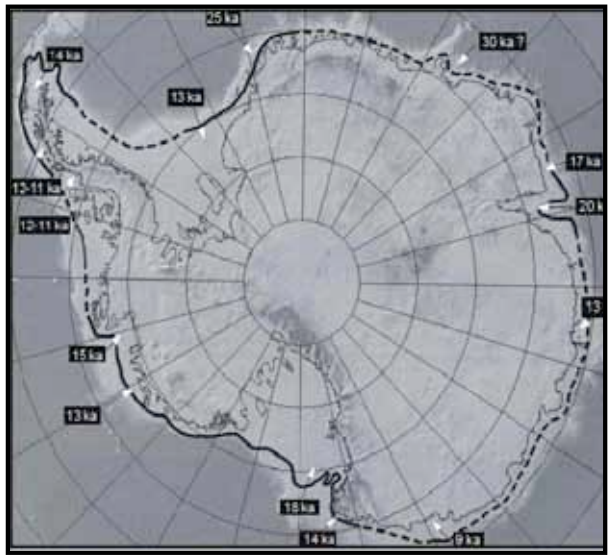
http://higheredbcs.wiley.com/legacy/college/levin/0471697435/chap_tut/images/nw0352-nn.jpg

Max. Pleistocene glaciation; Southern Hemisphere

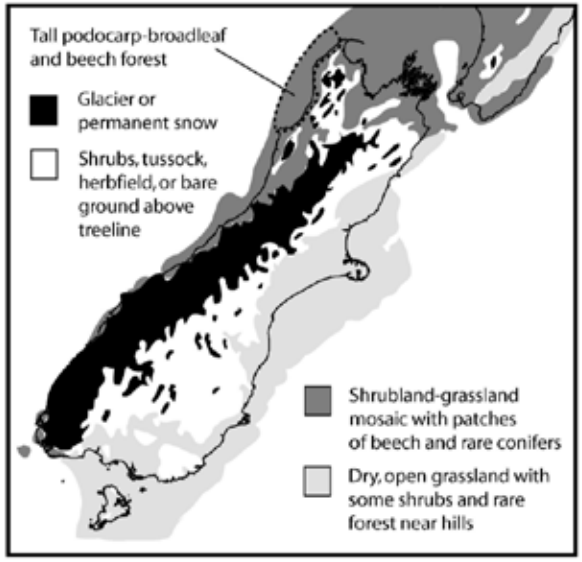
Patagonia, Andes



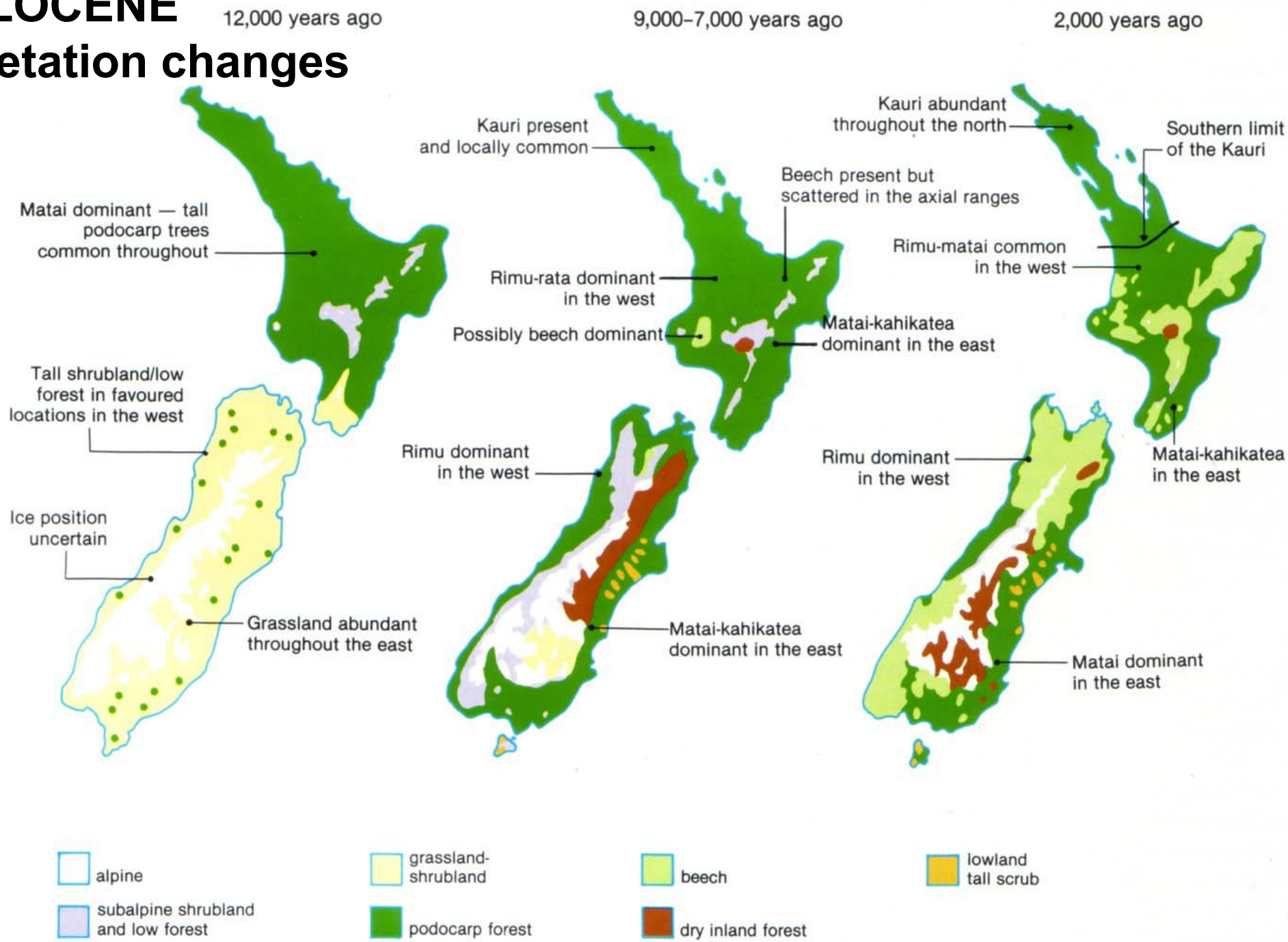
Antarctic



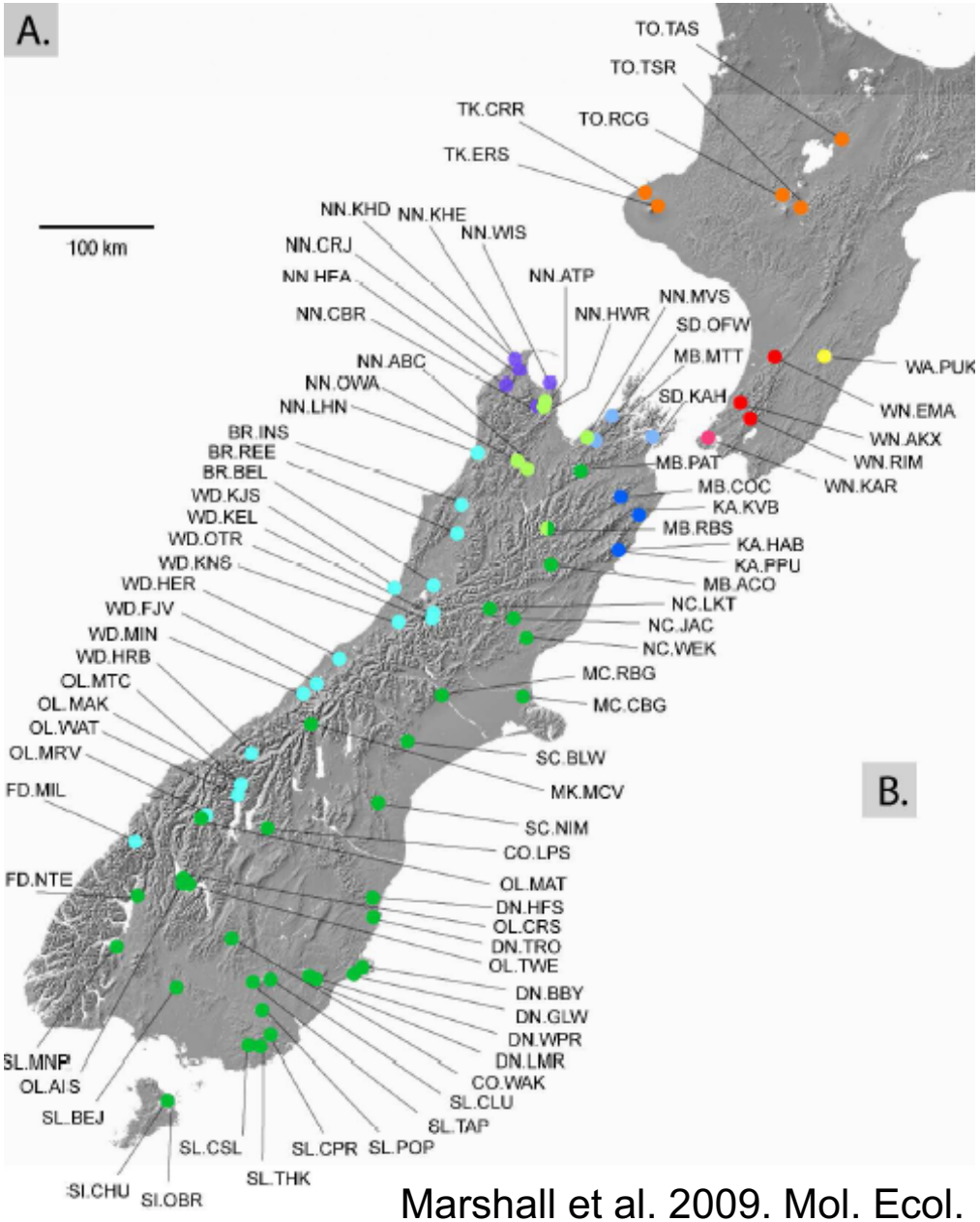
NZ, Southern Alps



HOLOCENE vegetation changes



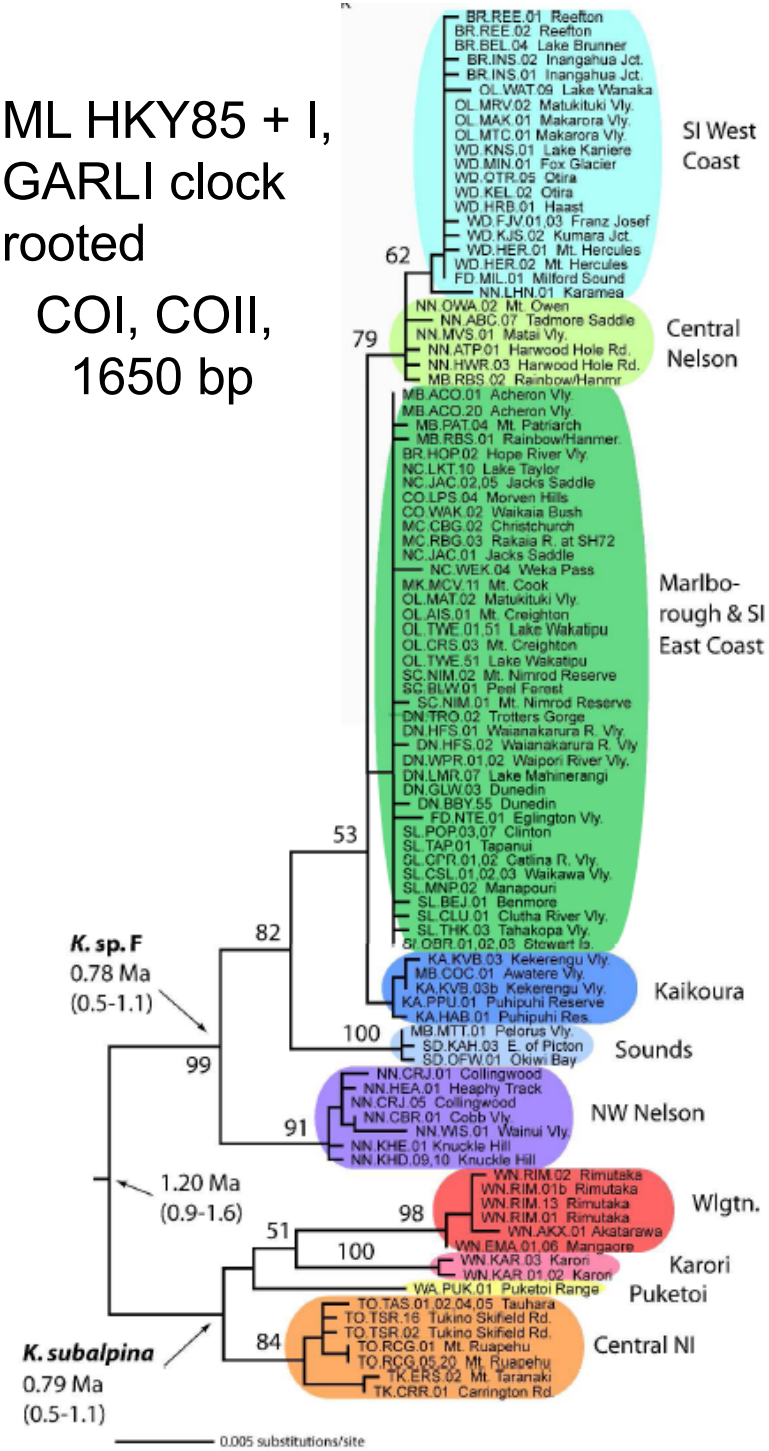
Northern Richness, Southern Purity



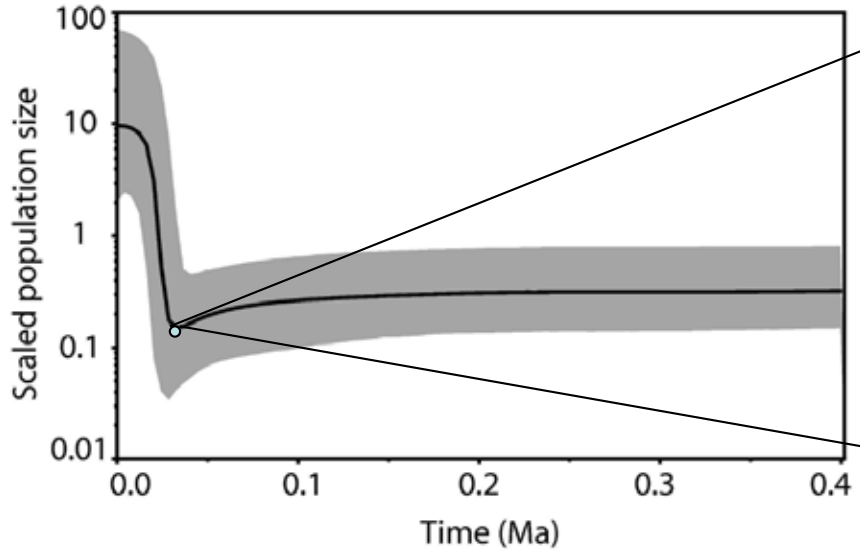
Marshall et al. 2009. Mol. Ecol.

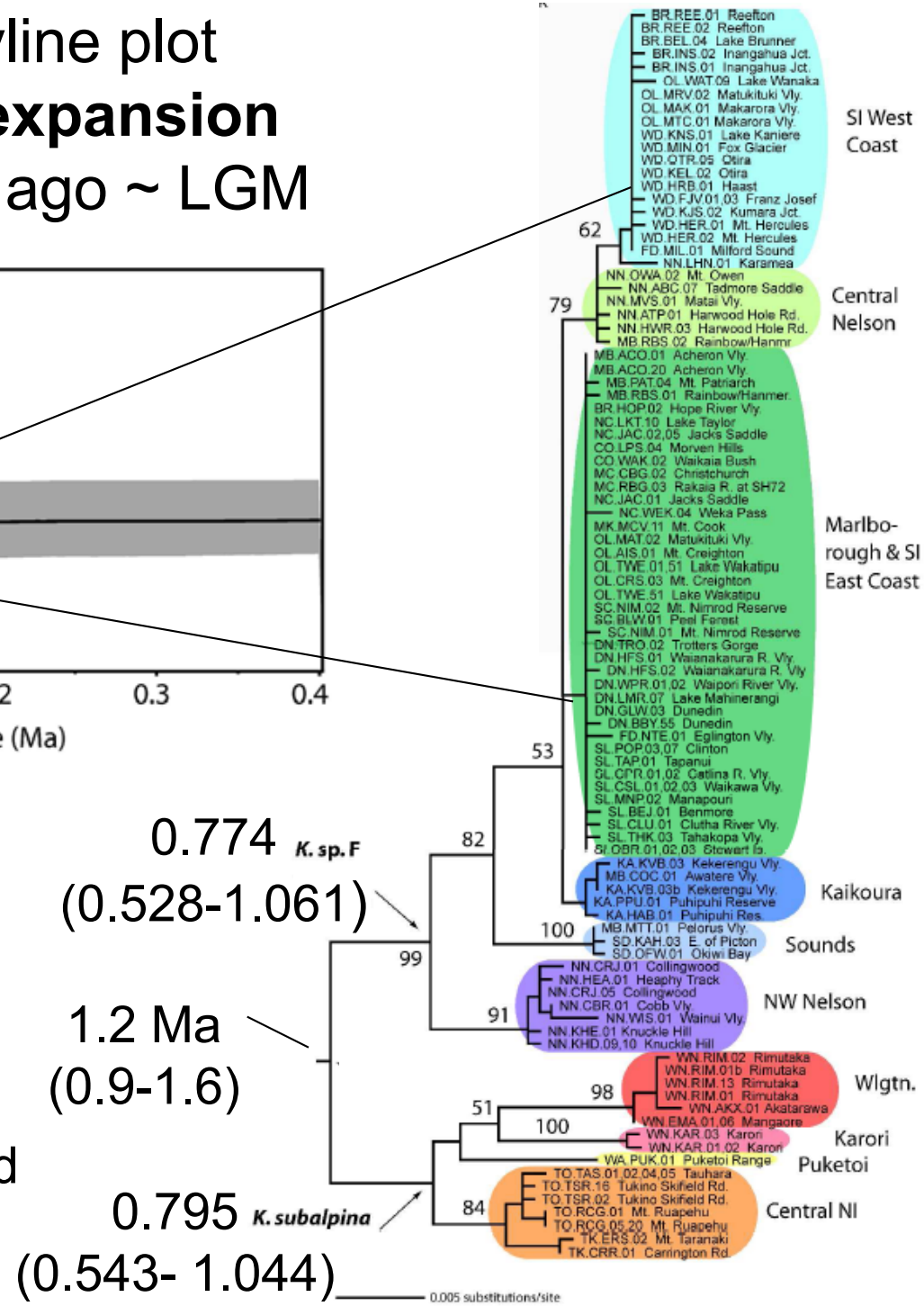
ML HKY85 + I, GARLI clock rooted

COI, COII, 1650 bp



Bayesian skyline plot
Population expansion
20-25,000 yr ago ~ LGM





ML HKY85 + I, GARLI clock rooted

COI, COII, 1650 bp

Definition: Population genetic structure

Structured populations exhibit geographic groups that differ genetically from each other often in an explainable pattern.

Populations with no structure=
no among-population variation or variation that is randomly distributed across geography.

The ecology of an organism affects its response to climate change

Response can be inferred from population genetic structure

¡ Clicking cicadas, 4 endemic spp.

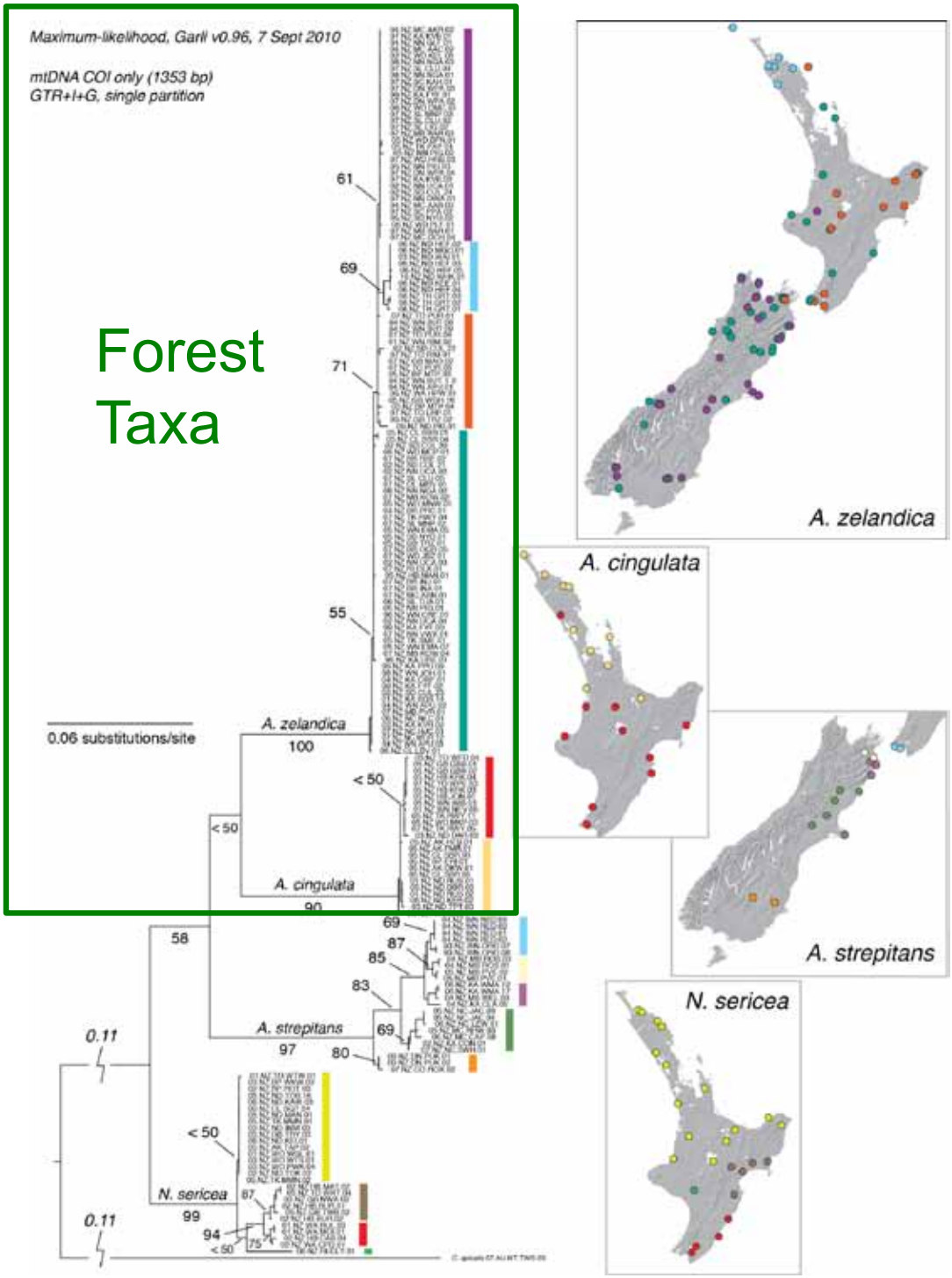
Amphipsalta

Population genetic structure question: Will dry-land scrub taxa respond differently to glaciation than forest taxa?

Notopsalta

Amphipsalta, Notopsalta

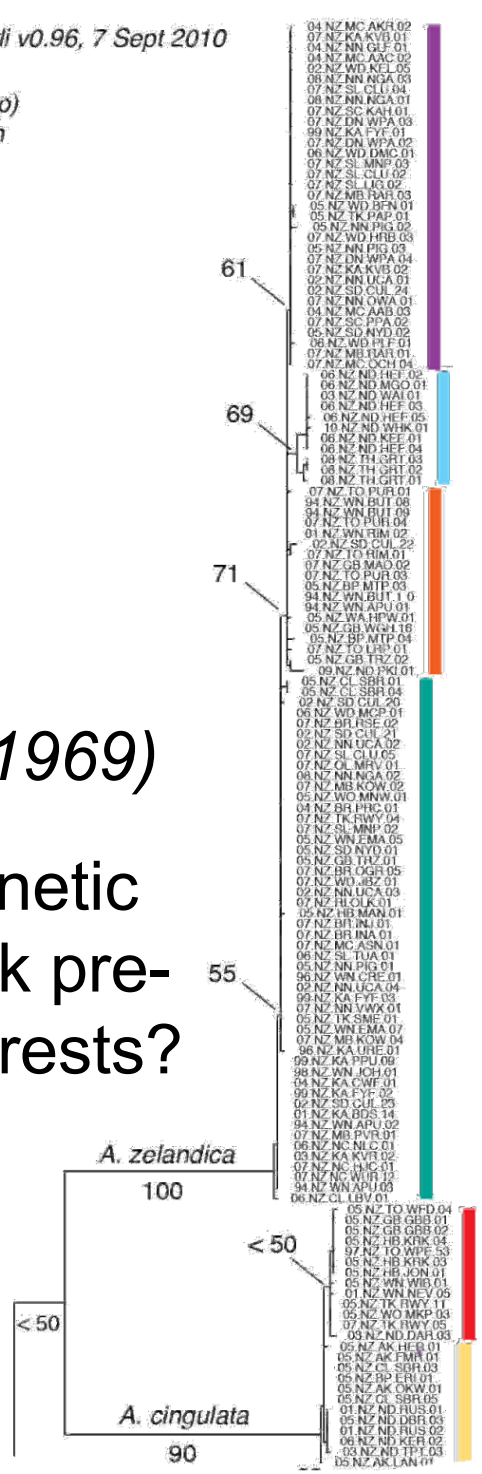
Old species (6-10 Ma), no major radiation

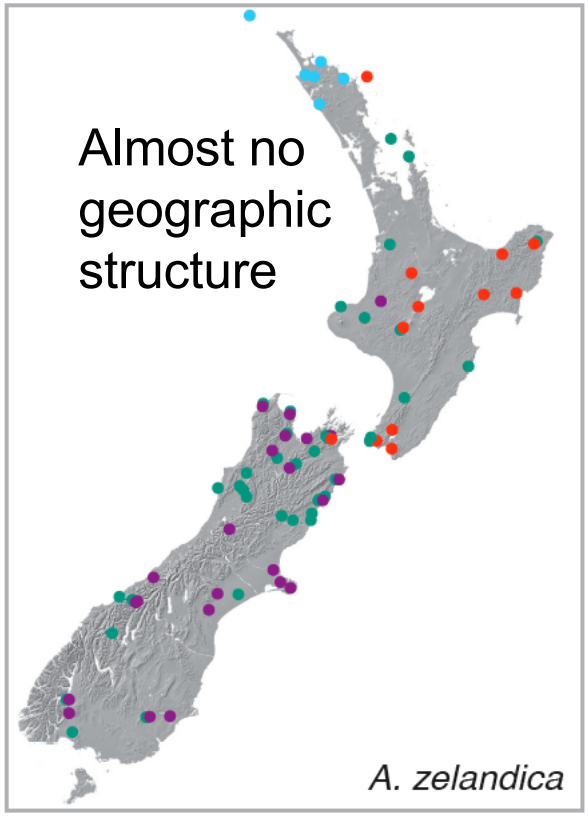


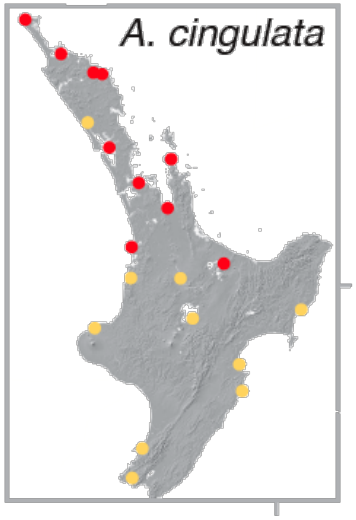
Amphipsalta zelandica
Amphipsalta cingulata (1969)

Forest lineages, little genetic differentiation, bottleneck pre-LGM due to retreat of forests?

Large species more mobile?







Amphipsalta, Notopsalta

What do we predict for dry-land taxa?

forest

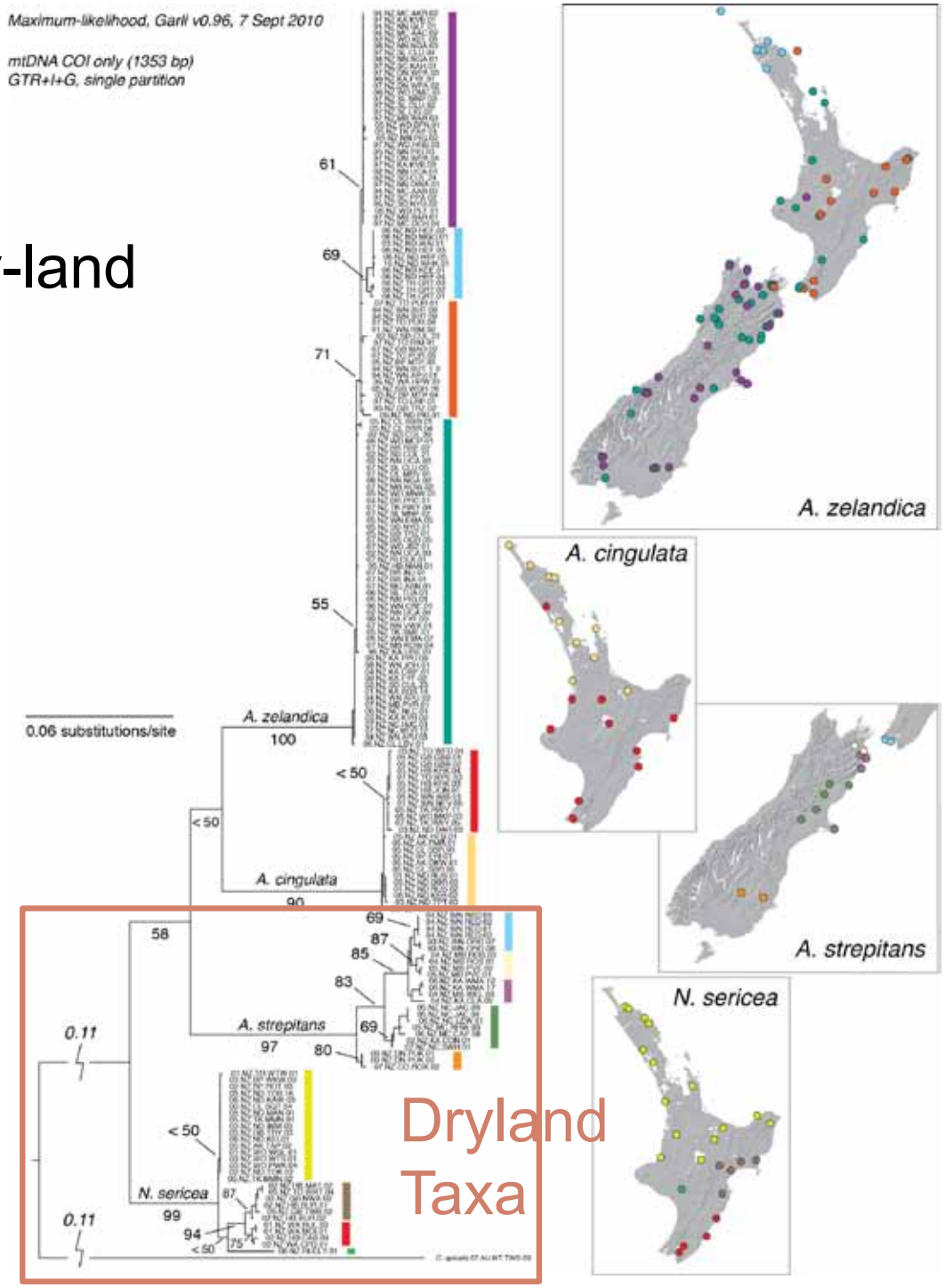
A. zelandica

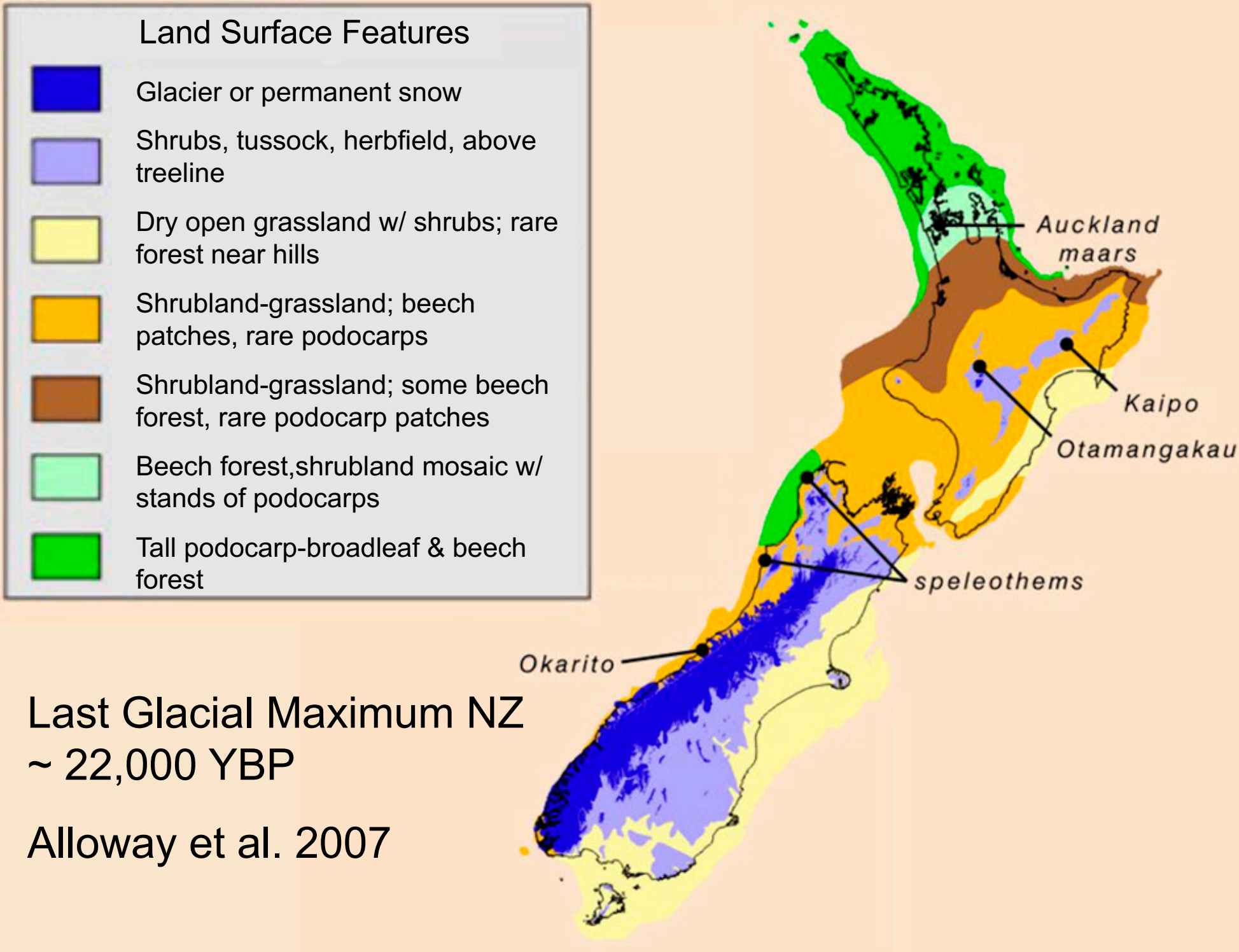
A. cingulata

dry land

A. strepitans

N. sericea



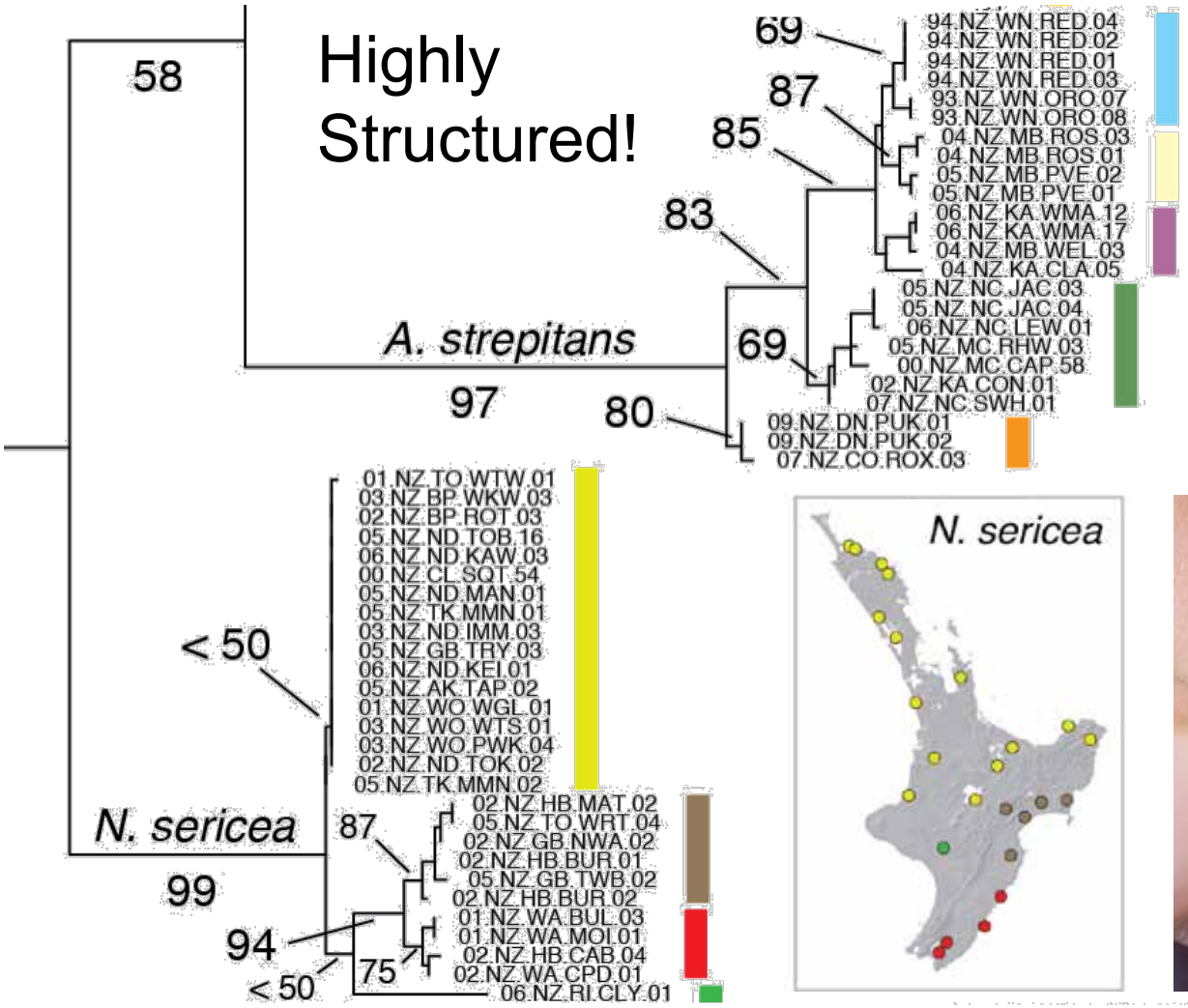


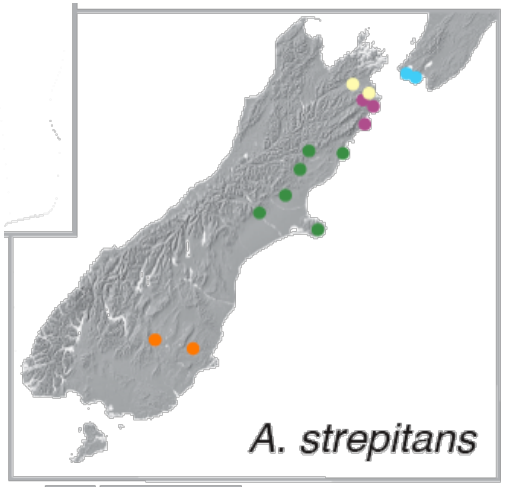
Last Glacial Maximum NZ
~ 22,000 YBP

Alloway et al. 2007

Amphipsalta strepitans, Notopsalta sericea

Dry rock & clay bank species; more geographic structure; survived multiple glacial advances





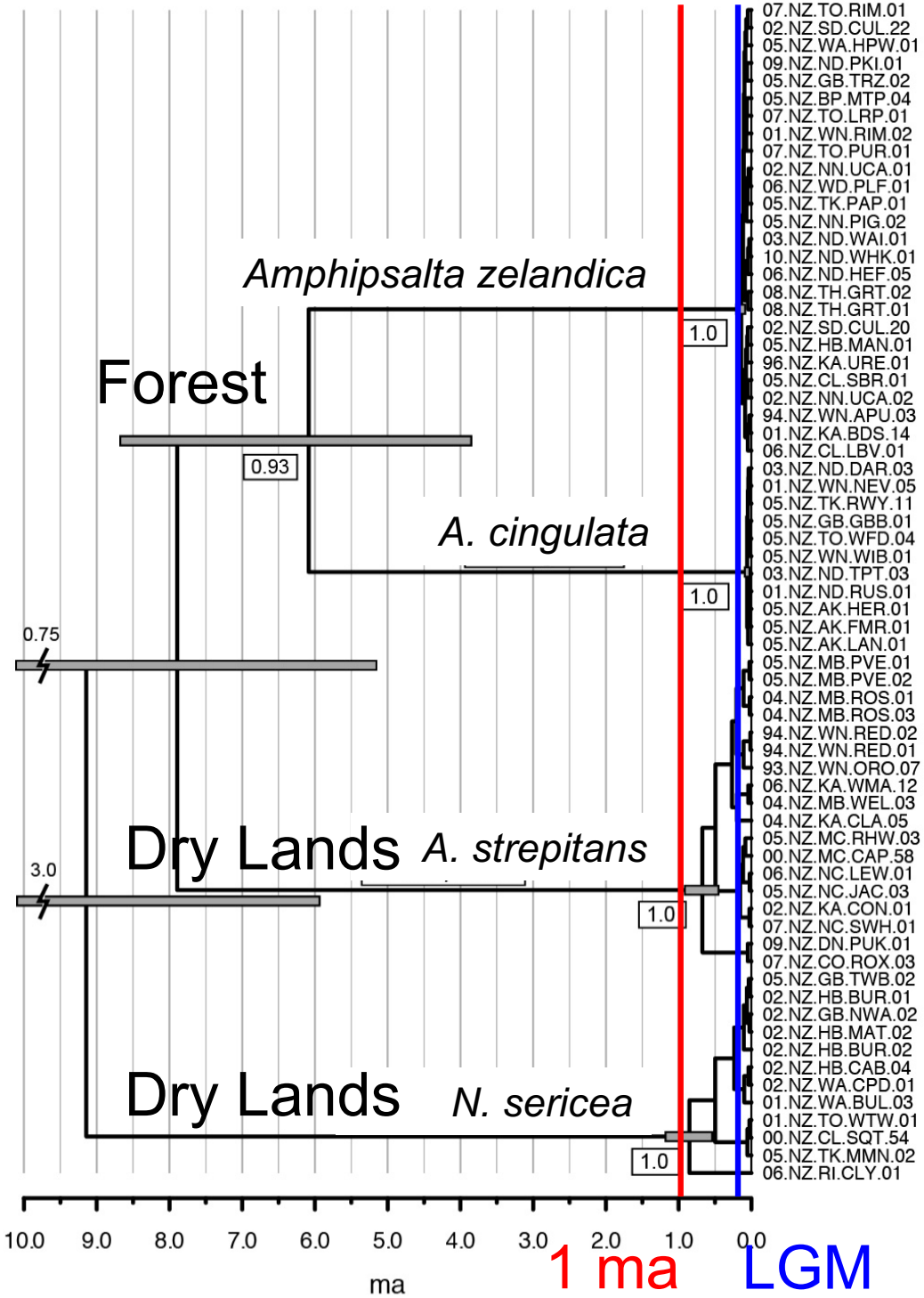
Clear Structure

Relative timing of *Amphipsalta* and *Notopsalta* w/in species diversification.

Molecular clock estimates of clade origination times.

Conclusions: Ecological factors interact with climate and genetic factors to produce patterns of genetic variation we see today.

Long branches suggest past extinctions (or less likely lack of clade formation in the past).



Probability of fixation

- In diploid species, individuals carry 2 alleles at every locus. (2 x N = total alleles in population)

  A new allele arising by mutation represents 1 out of 2N in a population

Frequency new mutant allele = p_t = 1/(2N)

- Given that the initial frequency of a new mutation = 1/(2N)
- And remembering that probability of allele fixation by drift depends on initial frequency
- The probability of fixation under neutrality (no selection) is determined by the population size alone.
- In small populations, both advantageous & mildly deleterious mutations can be fixed by chance (drift)

Remember from Lecture 3. The Decades Since the Synthesis…

- 1953- Watson, Crick and Franklin. Structure of DNA. Followed by deeper understanding of nature of mutation and inheritance.
- 1960's- Debate on the relative amount of variation in natural populations (came to a close at end of 60's).
- 1970's- Debate on the relative importance of selection versus drift. Lewontin vs. Kimura
- 1970's, 80's, 90's, and 2000's- Great improvements in methods of constructing evolutionary trees using computers (great advances in computing speed).

Neutral theory

- Lewontin & Hubby (1966) worried that selection favoring heterozygotes could not maintain variation in natural populations due to genetic load.
- Kimura (1968) argued that because proteins seemed to evolve at <u>steady rates</u>, substitution rate of nucleotides must be driven by random processes (drift) rather than selection.

Nature 267: 275-276, May 1977. doi: 10.1038/267275a0

Preponderance of synonymous changes as evidence for the neutral theory of molecular evolution

Motoo Kimura

National Institute of Genetics, Mishima, 411, Japan

ACCORDING to the neutral mutation–random drift hypothesis of molecular evolution and polymorphism[1,2], most mutant substitutions detected through comparative studies of homologous proteins (and the nucleotide sequences) are the results of random fixation of selectively neutral or nearly neutral mutations. This is in sharp contrast to the orthodox neo-Darwinian view that practically all mutant substitutions occurring within species in the course of evolution are caused by positive Darwinian selection[3–5]. This paper shows that by comparative studies of messenger RNA (mRNA) sequences reliable estimates can be obtained of the evolutionary rates (in terms of mutant substitutions) at the third positions of the codon, and that the estimates conform remarkably well with the framework of the neutral theory.

References

1. Kimura, M. *Nature* **217**, 624–626 (1968).
2. Kimura, M. *Genet. Res. Camb.* **11**, 247–269 (1968).
3. Fisher, R. A. *The Genetical Theory of Natural Selection* (Clarendon, Oxford, 1930).
4. Fisher, R. A. *Proc. R. Soc.* **B121**, 58–62 (1936).
5. Mayr, E. *Animal Species and Evolution* (Harvard University Press, Cambridge, Massachusetts, 1965).

Neutral theory

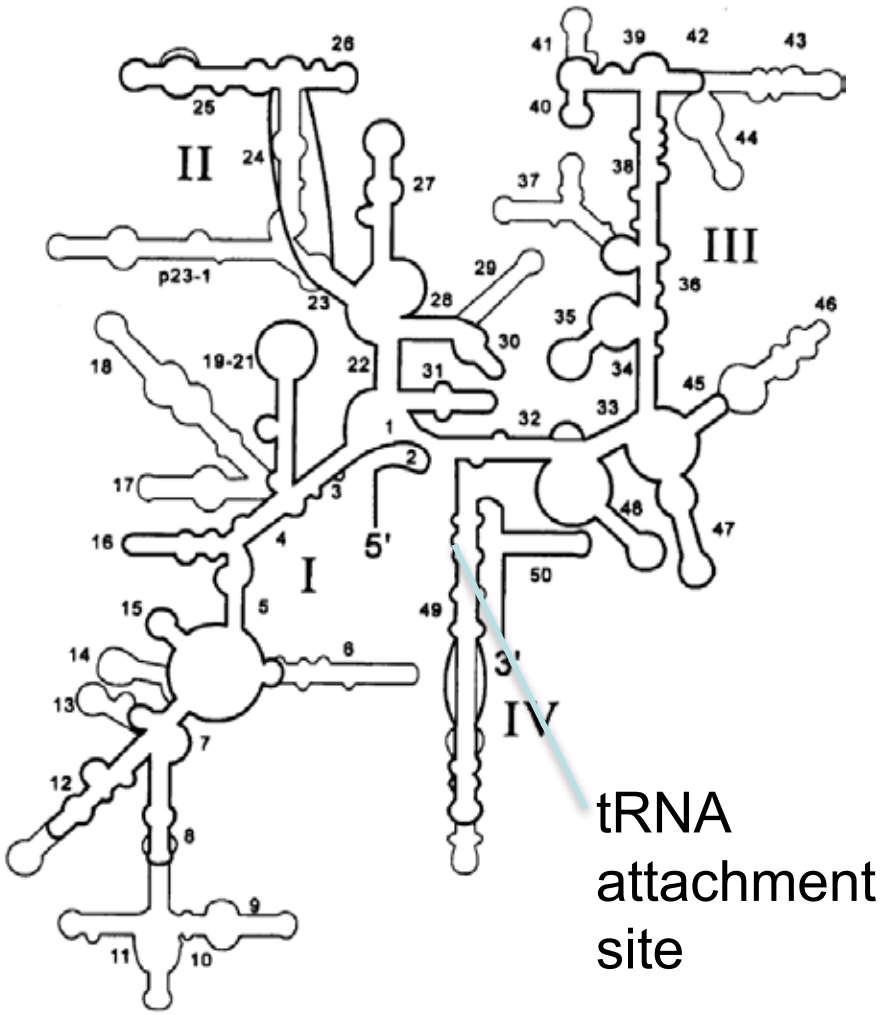
- Does not argue that “morphological, physiological and behavioral features of organisms evolved by random drift.”
- Adaptive features certainly evolve by natural selection, but…
- They constitute the minority of DNA sequence changes.
- Most substitutions do not change amino acids and many of the ones that do, do not affect the function of the protein.

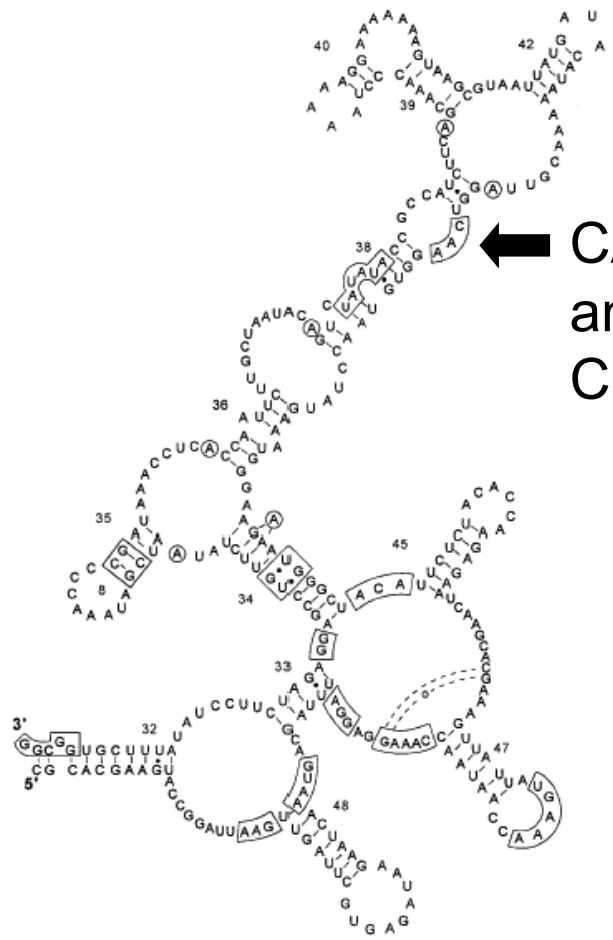
How molecules evolve

- Natural selection at the molecular level preserves sites that are important in structure and function.
- Most substitutions take place at sites that are selectively “neutral”, i.e., a substitution will have no effect on structure and function.

Conservative Characters; Mosaic Evolution

e.g., rRNA secondary structure highly conserved. Primary sequence conserved to various degrees.



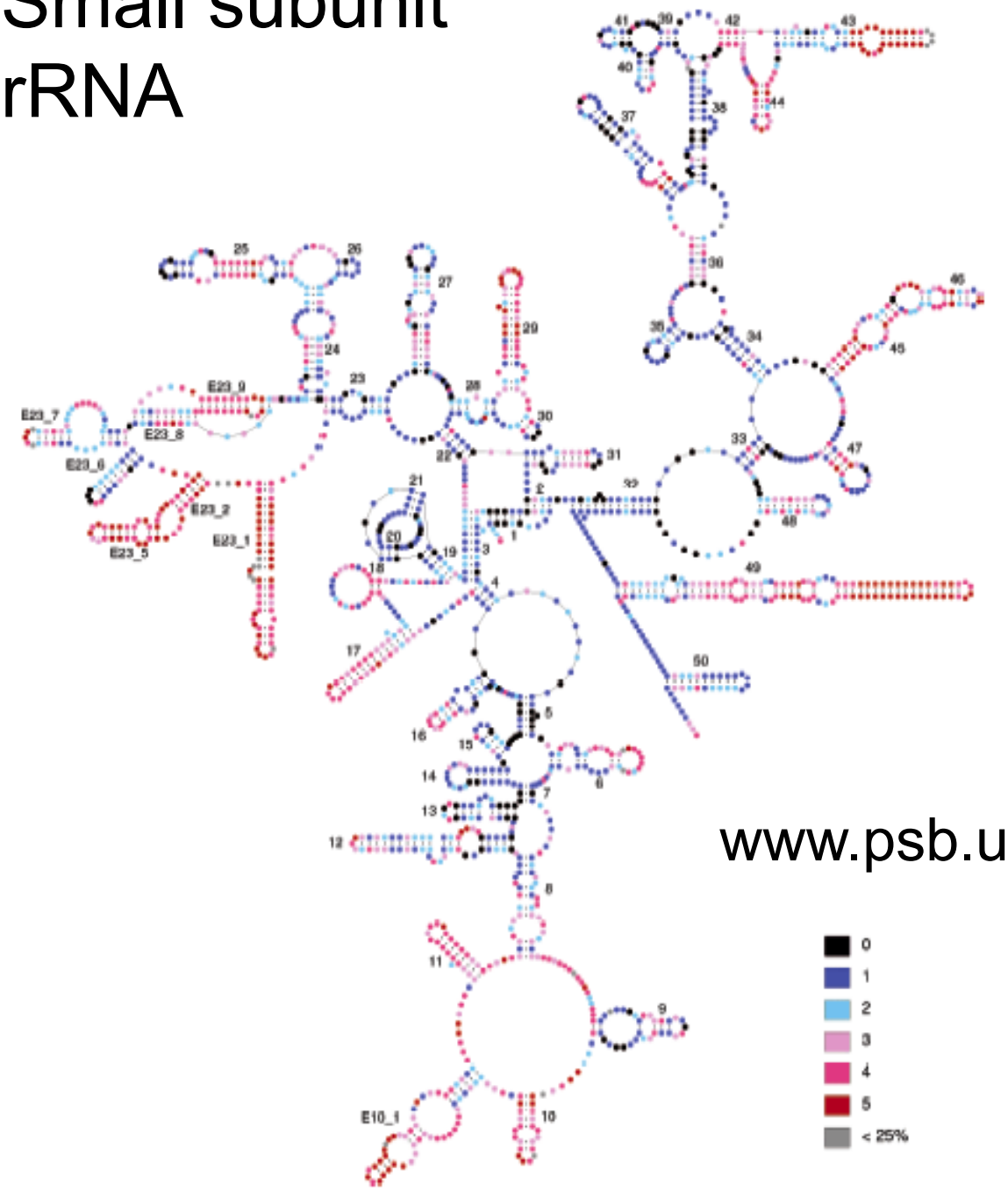


CAA in most animals, CGA in fish!

E. coli compared to mitochondria

Hickson et al. 1996. MBE

Small subunit rRNA



Substitution probabilities vary along a molecule in relation to structural and functional constraints

Red = most variable
Blue = least
Invariable = black

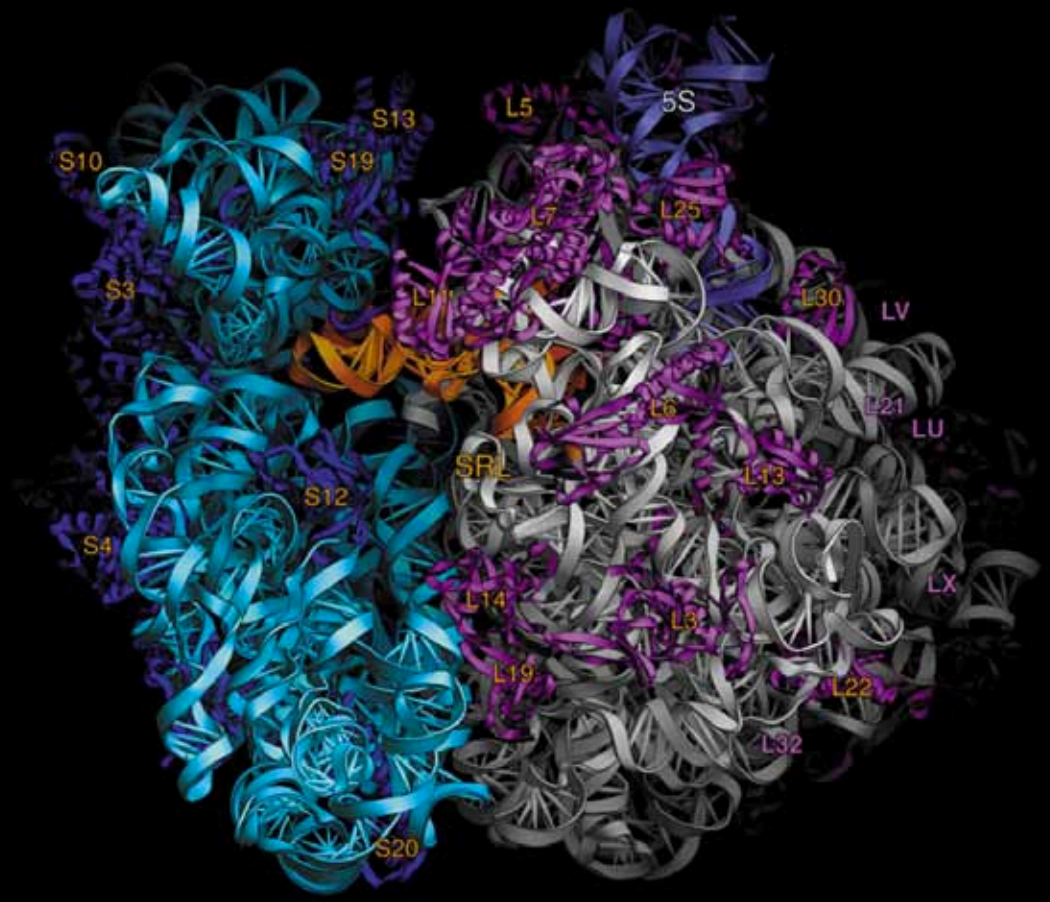
www.psb.ugent.be/rRNA/varmaps

500 eukaryotes mapped onto yeast structure, Yves Van de Peer

Simon et al. 2006. Annual Review of Ecology, Evolution & Systematics

Ribosome tertiary structure plus ribosomal proteins (dark blue & purple)

Small subunit turquoise



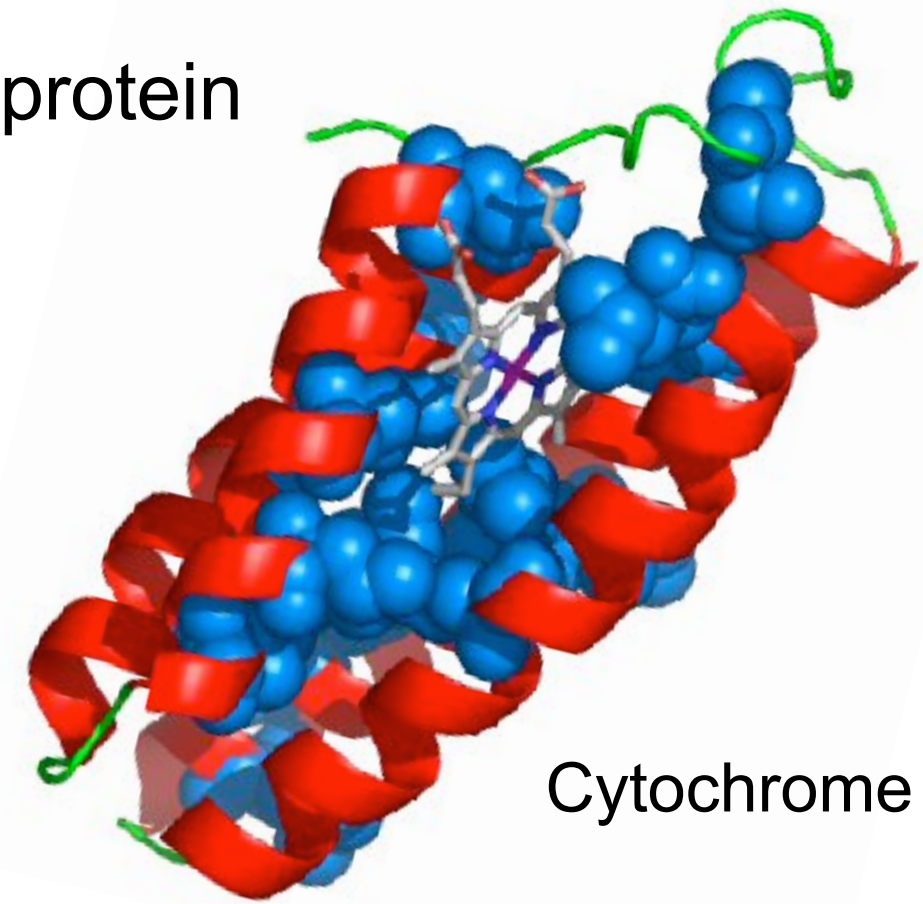
Large subunit gray

http://rna.ucsc.edu/rnacenter/ribosome_images.html

Primary structure = DNA sequence

Secondary structure = AA sequence

Tertiary structure = folded protein



Cytochrome b

http://chemistry.umeche.maine.edu/CHY431/Proteins9.html

Protein coding genes- DNA sequence changes more common at “silent” (synonymous) 3rd positions vs “replacement” (nonsynonymous) 2nd positions

				50										60							
	T	G	L	F	L	A	M	H	Y	S	P	D	A	S	T	A	F	S	S	I	A
HUMAN	ACA	GGA	CTA	TTC	CTA	GCC	ATG	CAC	TAC	TCA	CCA	GAC	GCC	TCA	ACC	GCC	TTT	TCA	TCA	ATC	GCC
R1	T..	..C	...	..T	...	..T	..A	..T	..T	A..	...	...	A..	CTC	..G	..A	...	...	...	G.T	A..
R2	T..	..C	...	..T	...	..T	..A	..T	..T	A..	...	...	A..	CTC	..G	..A	...	...	...	G.T	A..
R3	T..	..C	...	...	..G	..T	..A	..T	...	A..	...	...	A..	ATC	..G	..A	...	...	...	G.T	A..
R4	T..	..C	...	..T	...	...	..A	...	...	A..	...	..T	A..	CTC	..A	..A	..C	...	...	G.T	...
R5	T.T	..C	...	...	...	...	..A	...	..T	A..	T..	..T	AG.	..T	.A.	AG.	...	...	...	G.A	A..
B1	...	..C	...	C..	T..	...	GCA	..T	..T	A..	G.T	..T	A.T	..C	CTA	...	..C	G.T	..C	G.A	...
B2	...	..C	...	C..	...	...	GCA	...	...	A..	G.T	..T	A.T	..C	CTA	...	..C	G.T	..C	G.A	A..
B3	...	..C	..G	C..	...	..T	GCA	...	...	A..	G.T	...	A..	..C	CTA	...	...	G.C	..C	G.A	...
B4	...	..C	...	...	...	...	GCA	..T	...	A..	G.C	...	A..	..C	CT.	...	..C	AAC	..C	G..	...
B5	...	..C	...	C.A	...	...	...	...	...	A..	G.C	...	A..	..C	CTA	...	..C	A.C	...	G.A	...
F1	...	..C	..T	...	..T	..A	..A	...	...	A.T	T.C	..T	AT.	G..	..A	...	...	...	..C	G..	...
F2	...	..C	..T	...	..T	..A	..A	...	...	A.T	T.C	..T	AT.	G..	..A	...	...	...	..C	G..	...
F3	...	..C	..T	...	..T	..A	..A	...	...	A.T	T.C	..T	AT.	G..	..A	...	...	...	..C	G.T	...
F4	...	..C	A..	...	..T	..A	..A	..T	...	A.T	T.T	...	AT.	G..	..A	...	...	...	..C	G.T	...
F5	...	..C	..T	...	...	...	..A	...	..T	A.C	T.C	...	AT.	G.C	...	...	...	..C	..C	G..	...

Substitutions influenced by triplet code of the amino acids

Rodent, Bird, Fish

Kocher et al. 1989. PNAS 86:6196

More complicated than that……

Four-codon family

Six-codon family

Two-codon family

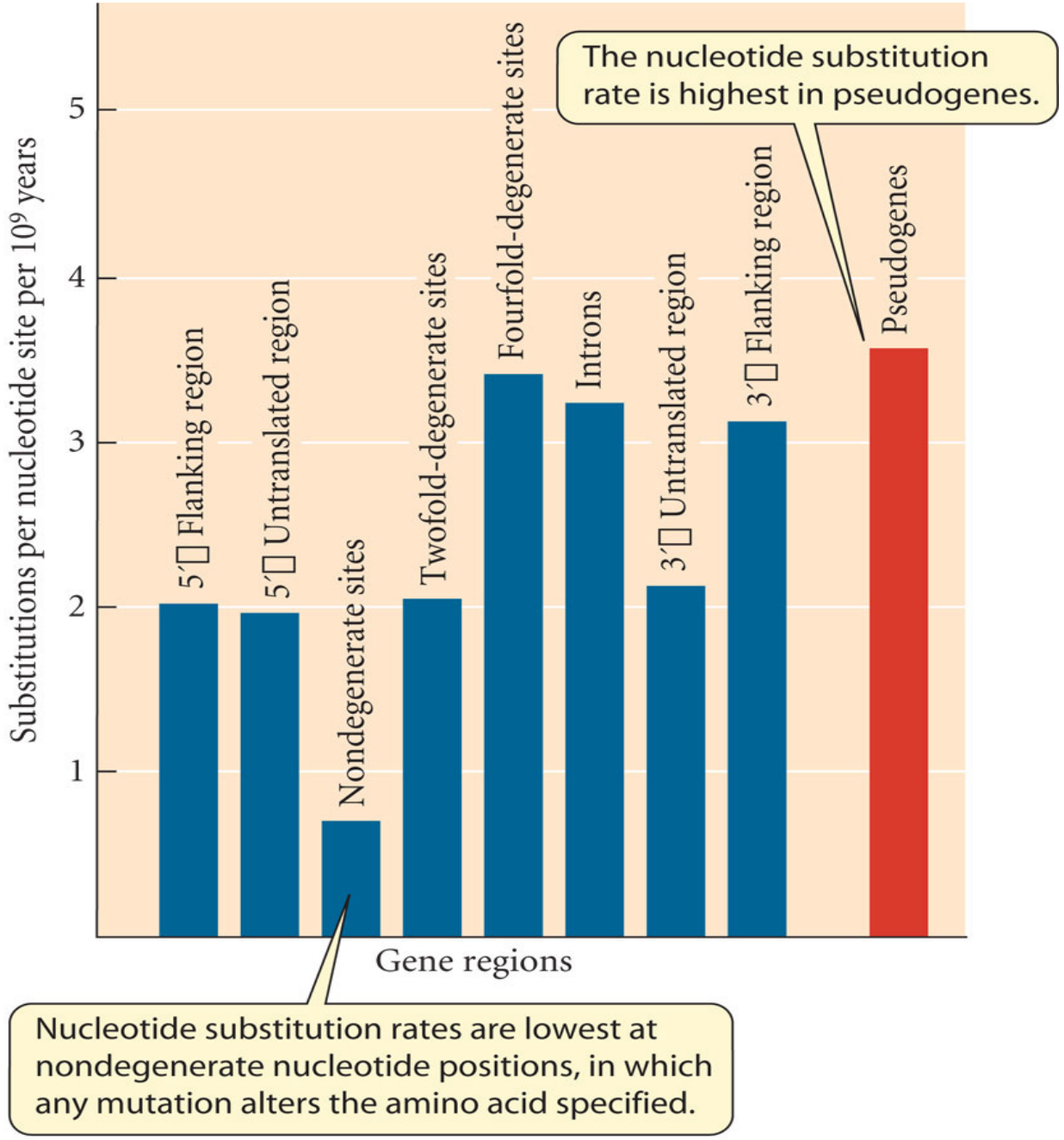
	AGA									UUA	
	AGG									UUG	
GCA	CGA						GGA			CUA	
GCC	CGC						GGC		AUA	CUC	
GCG	CGG	GAC	AAC	UGC	GAA	CAA	GGG	CAC	AUC	CUG	AAA
GCU	CGU	GAU	AAU	UGU	GAG	CAG	GGU	CAU	AUU	CUU	AAG
Ala	Arg	Asp	Asn	Cys	Glu	Gln	Gly	His	Ile	Leu	Lys

Three-codon family

One codon

			AGC								
			AGU								
			UCA	ACA			UA				
		CCC	UCC	ACC			GUC	UAA			
	UUC	CCG	UCG	ACG		UAC	GUG	UAG			
AUG	UUU	CCU	UCU	ACU	UGG	UAU	GUU	UGA			
Met	Phe	Pro	Ser	Thr	Trp	Tyr	Val	Stop			

Note: changing the second position always changes the AA, except in Serine where it can be C or G iff the third position is C or U.



***EVOLUTION 3e*, Figure 10.14**

The end