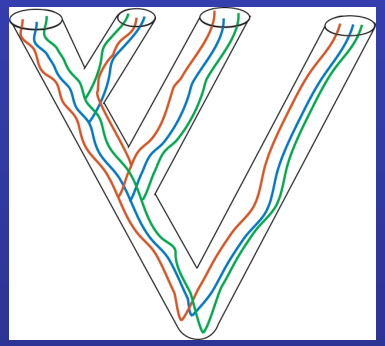
Multilocus phylogeography of Australian birds: navigating the forest of gene trees



Scott V. Edwards
Department of Organismic and
Evolutionary Biology
Harvard University

Overview:
Phylogeography of Australian birds

- *Context*
  - The phylogeographic setting
  - The Carpentarian barrier

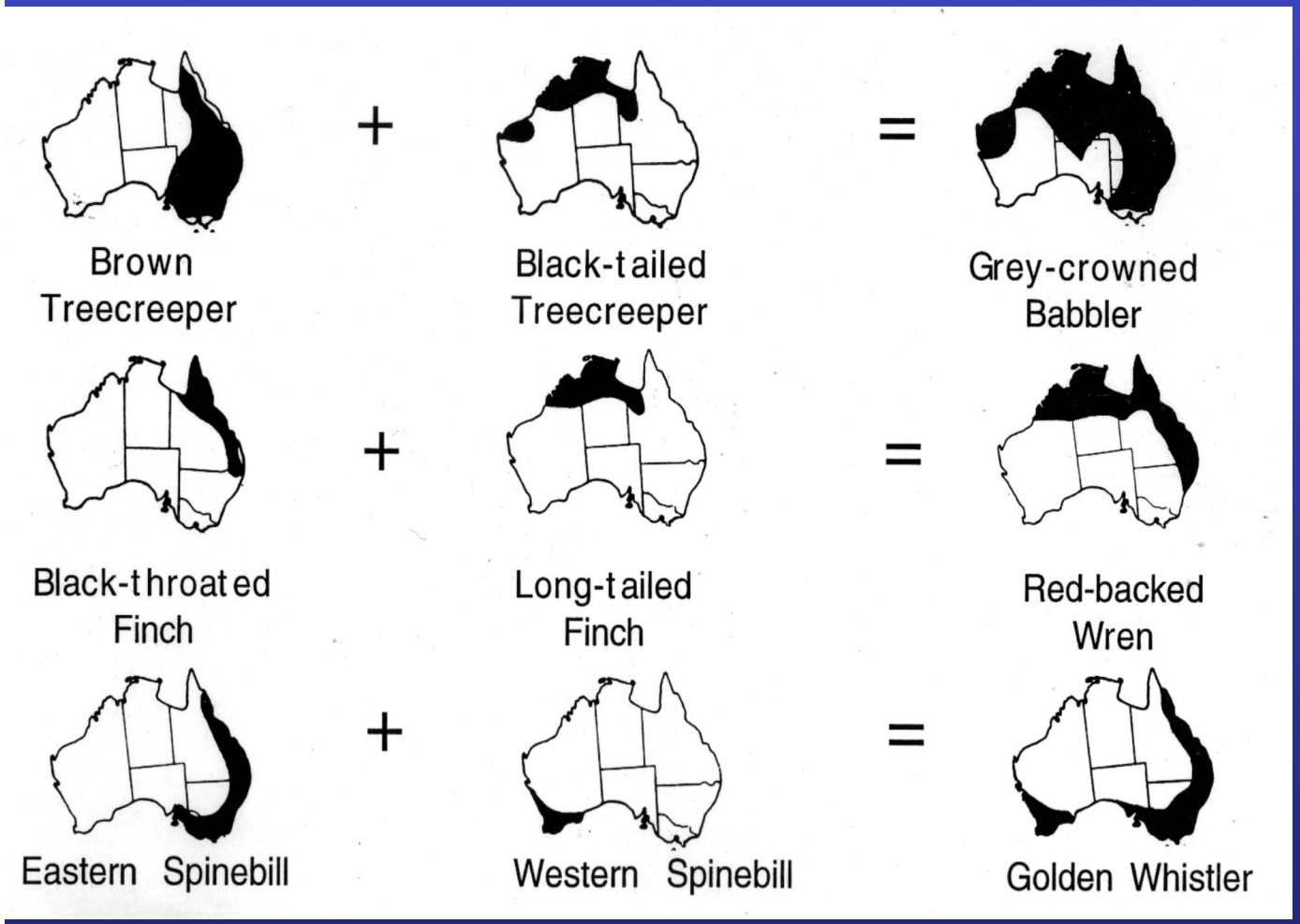
Overview:
Phylogeography of Australian birds

- *Molecular markers*
  - Advantages of sequence-based markers for phylogeography

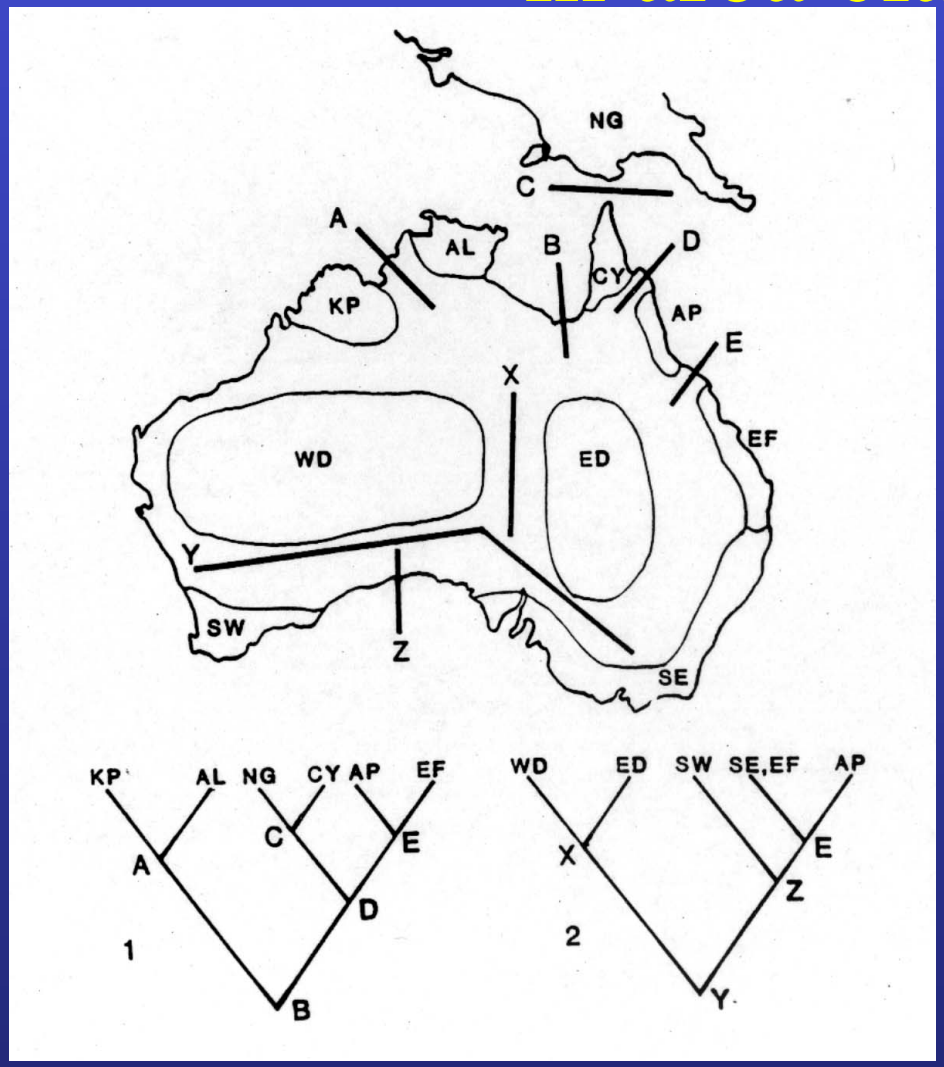
Overview : Phylogeography of Australian birds

- *Case studies*
  - Estimating phylogenies of closely related species
  - Estimating population structure on a continent-wide scale
  - Comparative phylogeography: estimating divergence times among recently diverged species
  - Estimating demographic histories using partially linked loci

Concordance of geographic ranges of Australian songbirds

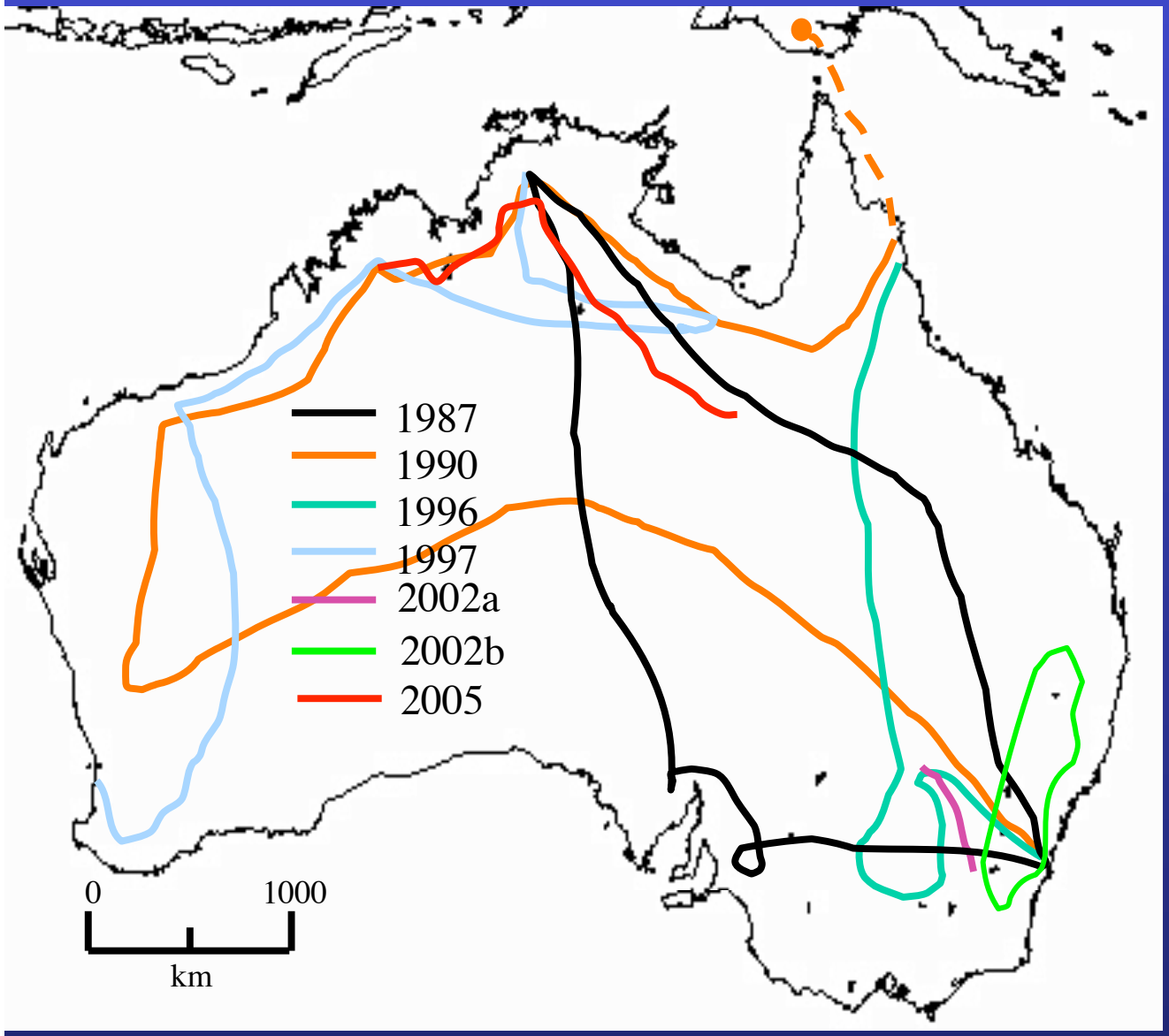


Carpentarian barrier (B) is deepest split in area cladograms



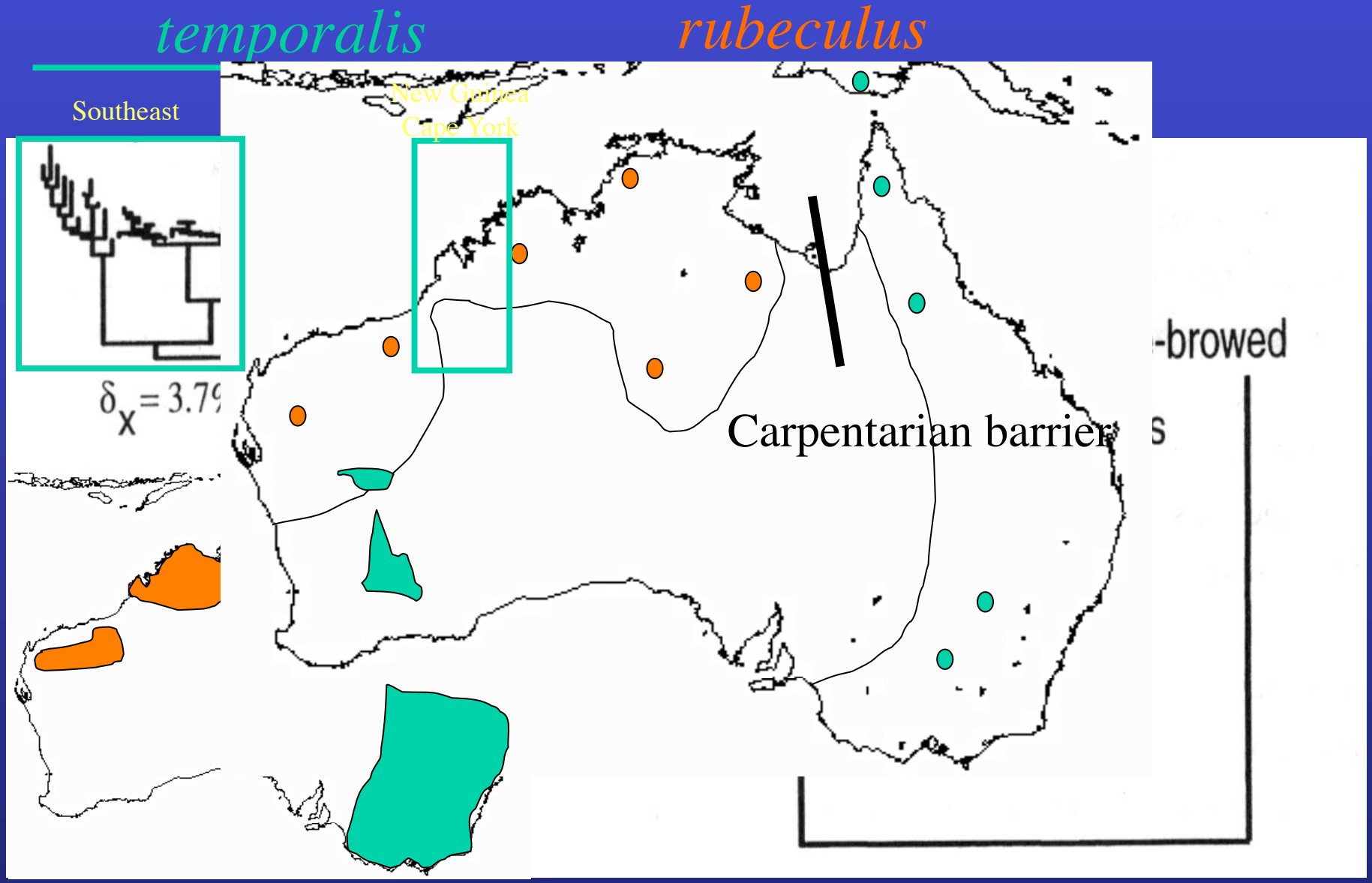
Cracraft J (1986) *Evolution* 40, 977-996.

Australia expeditions, 1987 - 2005



Those welcoming Aussies…

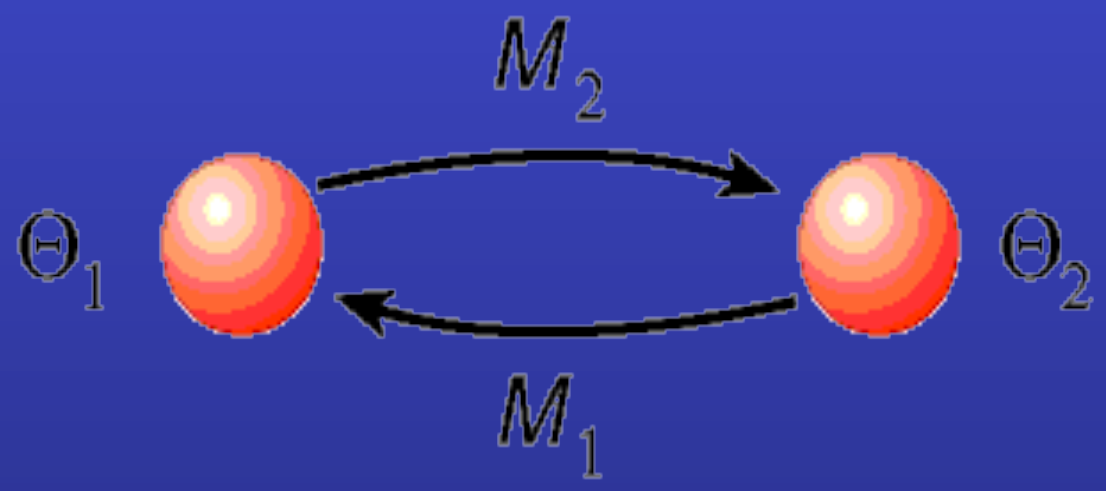
Mito Sampling localities for grey-crowned babblers



Edwards, S. V. (1993) *Proc. R. Soc. Lond. B* 252, 177-185.

Alternative models of population history

Population size: $\theta = 4N\mu$ Divergence time: $\tau=\mu t$ Gene flow: $M=m/\mu$

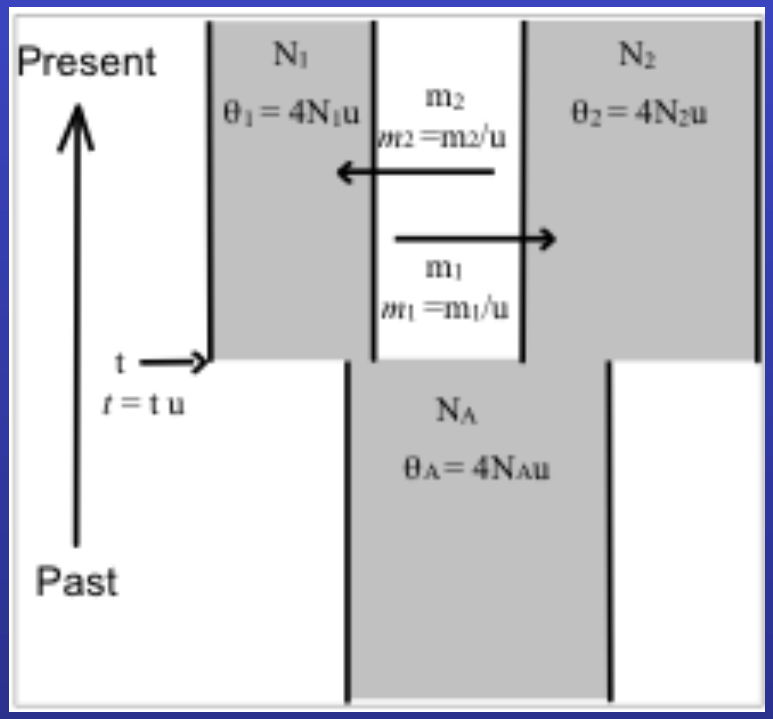


equilibrium migration model

MIGRATE: Beerli 2006 *Bioinformatics*

Alternative models of population history

Population size: $\theta = 4N\mu$ Divergence time: $\tau=\mu t$ Gene flow: $M=m/\mu$

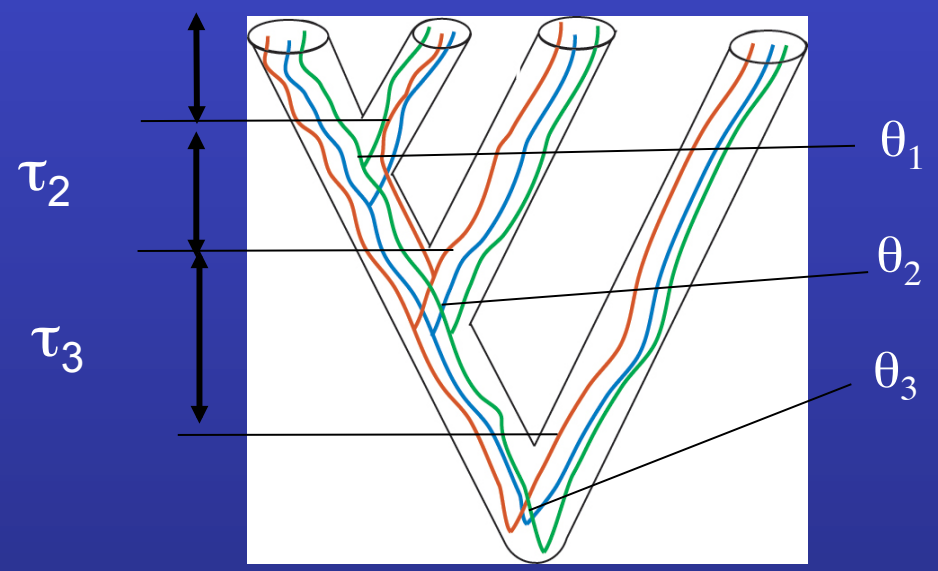


isolation-migration model

IM: Hey and Nielsen 2004 *Genetics*

Alternative models of population history

Population size: $\theta = 4N\mu$ Divergence time: $\tau=\mu t$ Gene flow: $M=m/\mu$



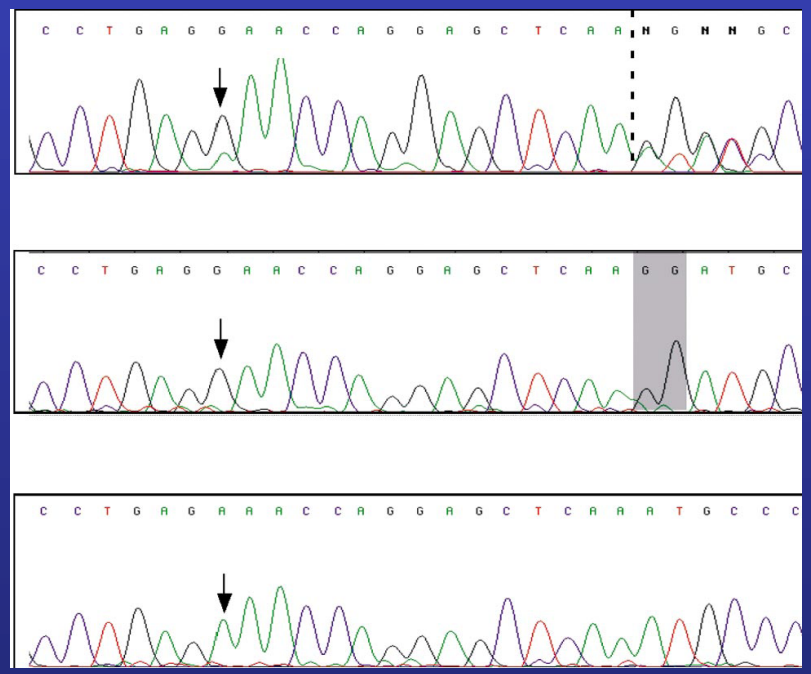
pure isolation
(phylogeny)

MCMCcoal: Rannala + Yang 2003 *Genetics*

BEST: Liu and Pearl, Syst. Biol. 56: 504-14

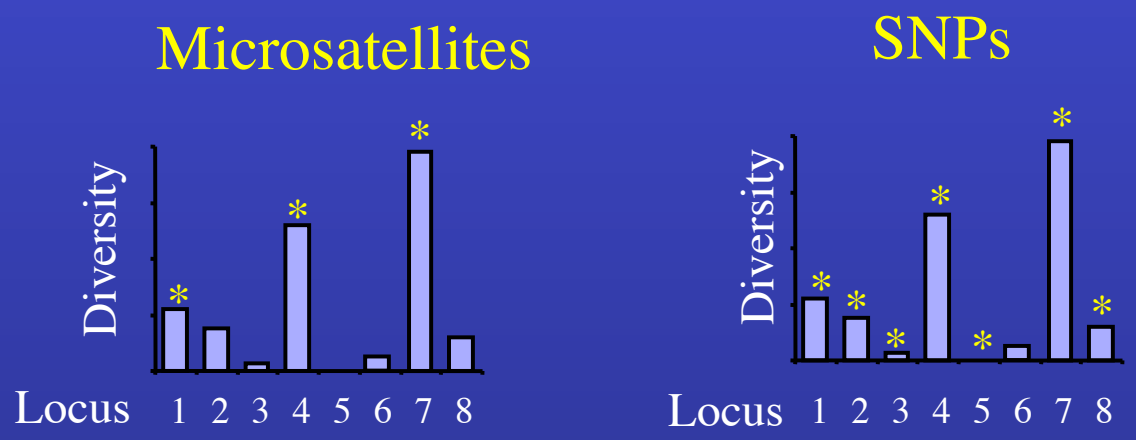
Anonymous loci: advantages over microsatellites

- Mutational scale directly comparable to mtDNA
- Mutational homoplasy is minimal
- Gene trees easily constructed
- Diversities easily compared across species

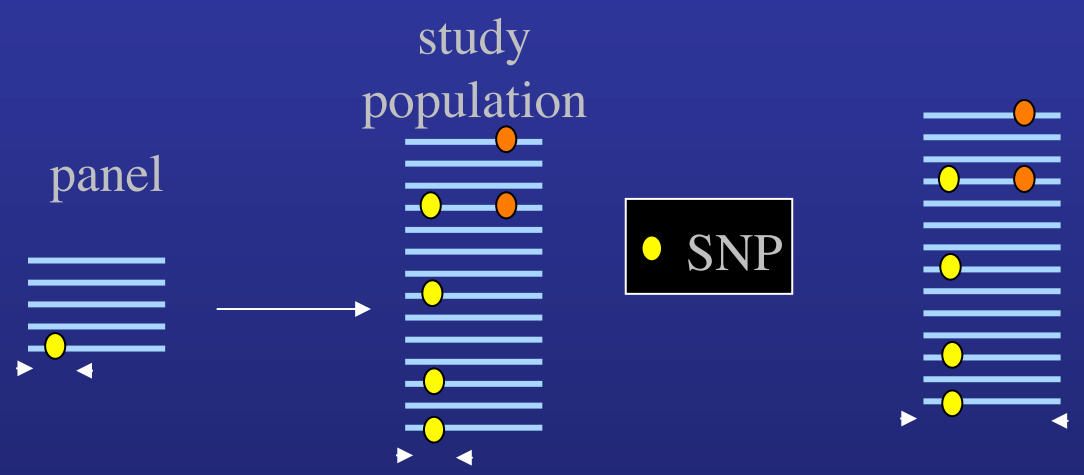


Brumfield R. et al. 2003 *TREE* 18, 249-256.

Ascertainment bias and sampling strategy for SNPs



* Locus chosen for phylogeographic survey

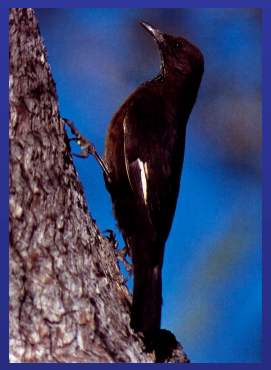


Brumfield R. et al. 2003 *TREE* 18, 249-256.

Case studies

Grassfinches (*Poephila*)
W. Bryan Jennings

Red-backed Wren
(*Malurus melanocephalus*)
June Lee



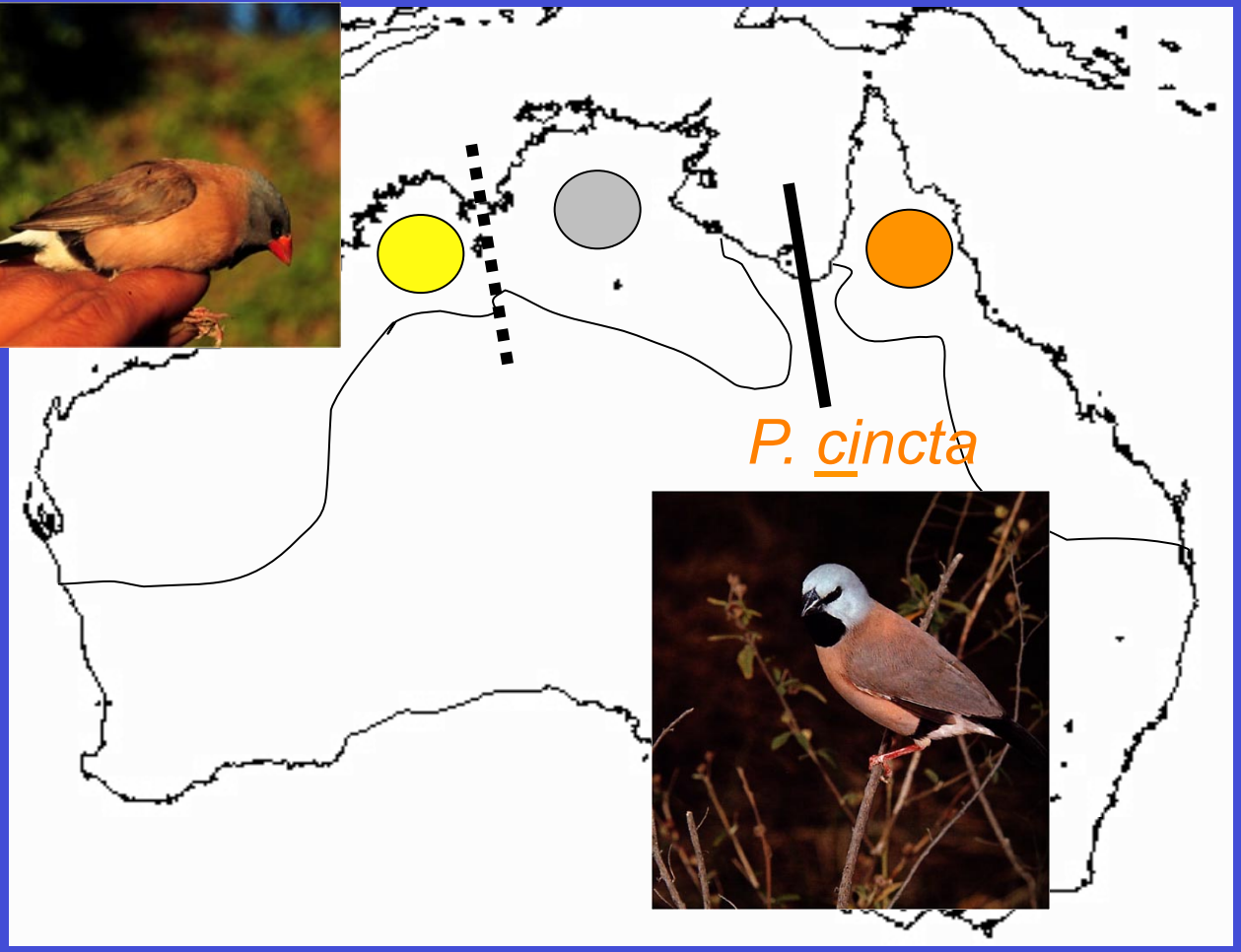
Treecreepers (*Climacteris*)
Nancy Rotzel

Zebra Finches
(*Taenopygia guttata*)
Chris Balakrishnan

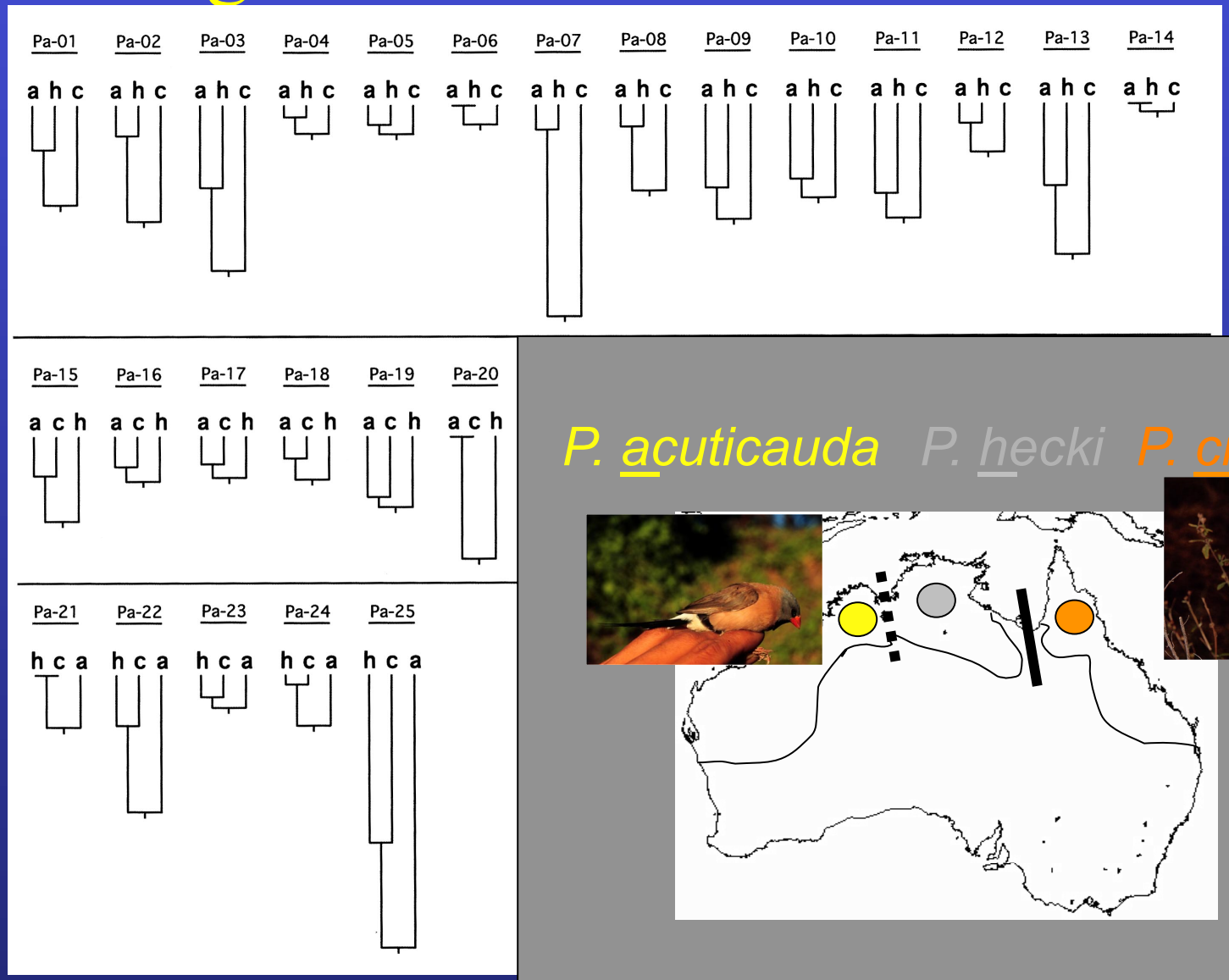
East-west pairs -- grassfinches (*Poephila*)

P. acuticauda

P. hecki



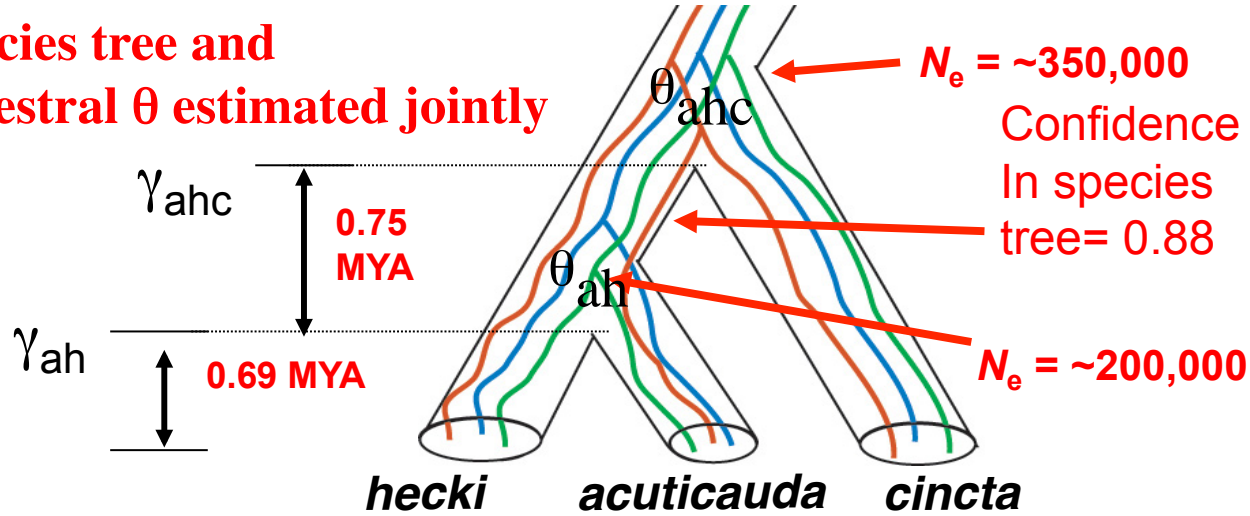
30 gene trees from Australian finches



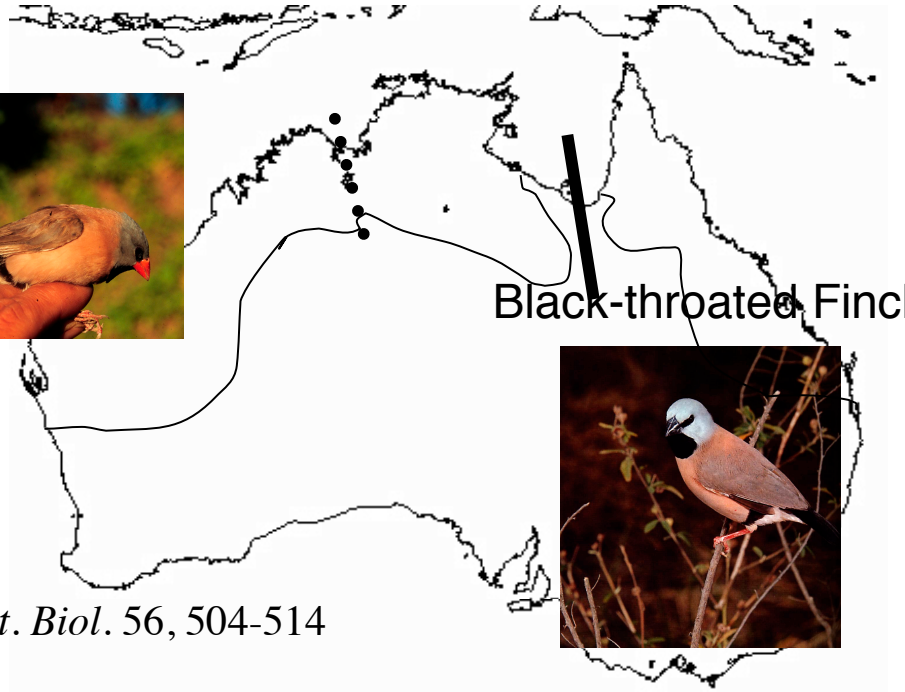
Jennings & Edwards (2005) *Evolution* **59,** 2033-2047.

Species tree of *Poephila* grassfinches

Species tree and ancestral θ estimated jointly

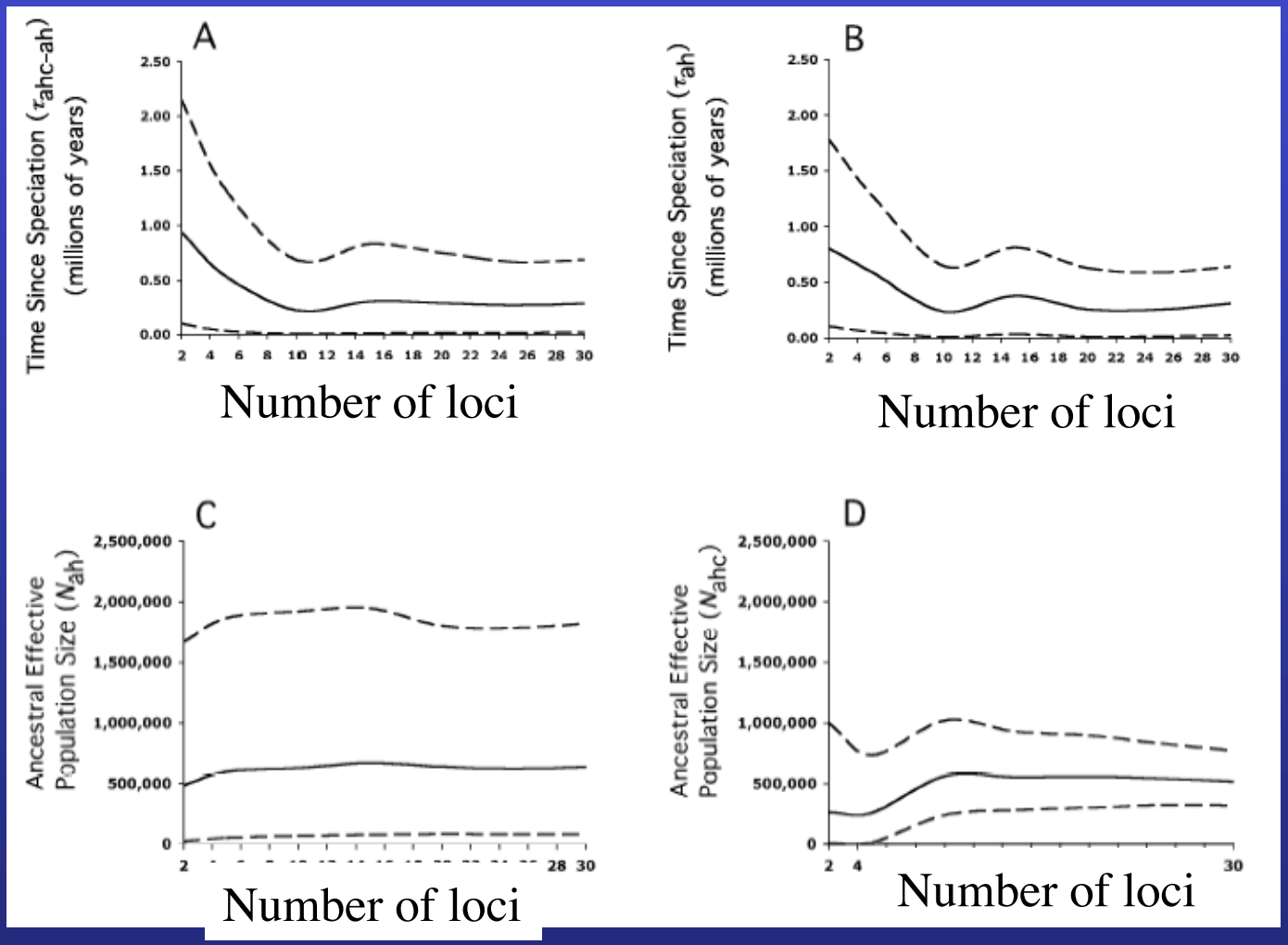


Long-tailed Finch



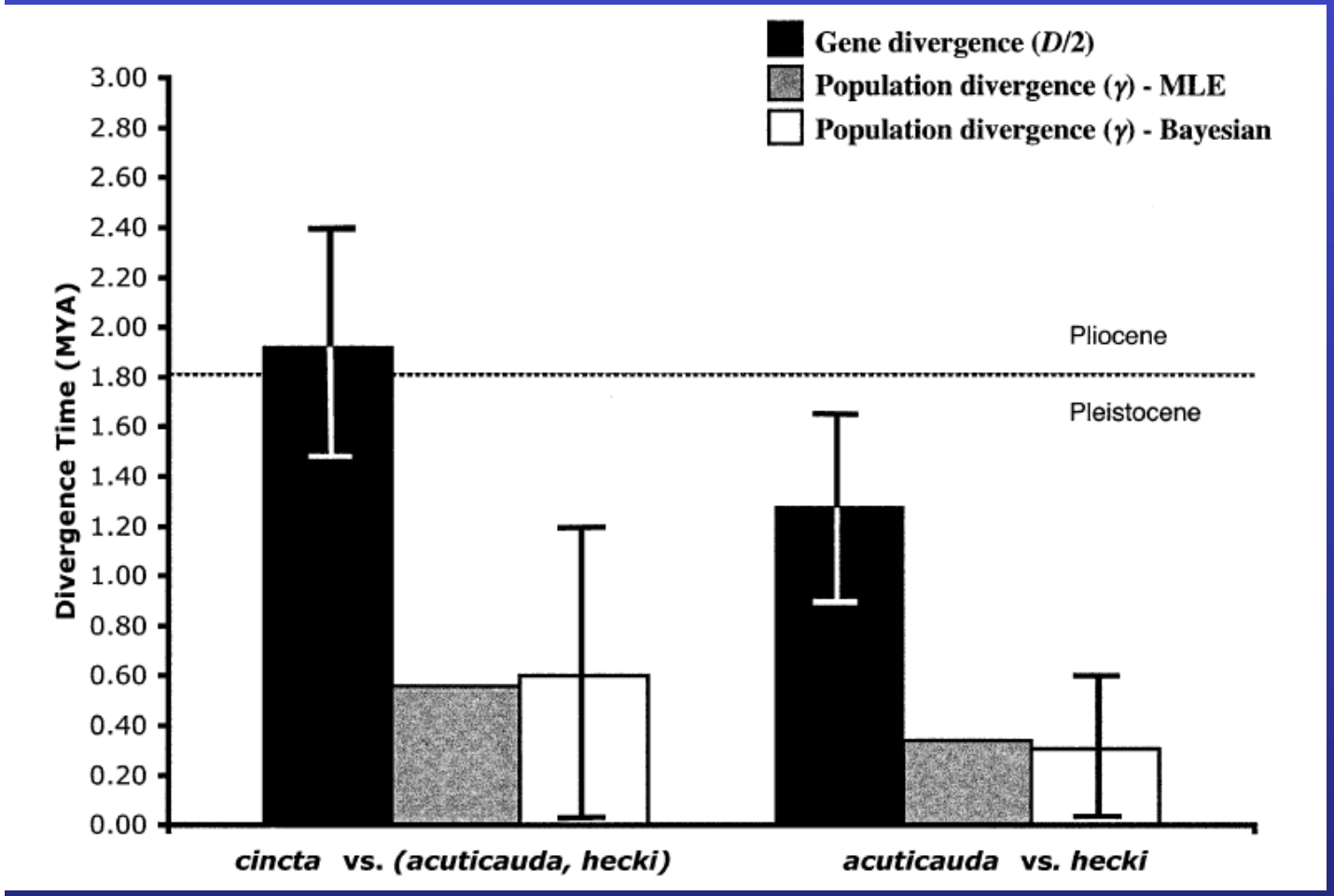
Liu and Pearl. 2007. *Syst. Biol.* 56, 504-514

Decreasing variance with increasing numbers of loci - mostly



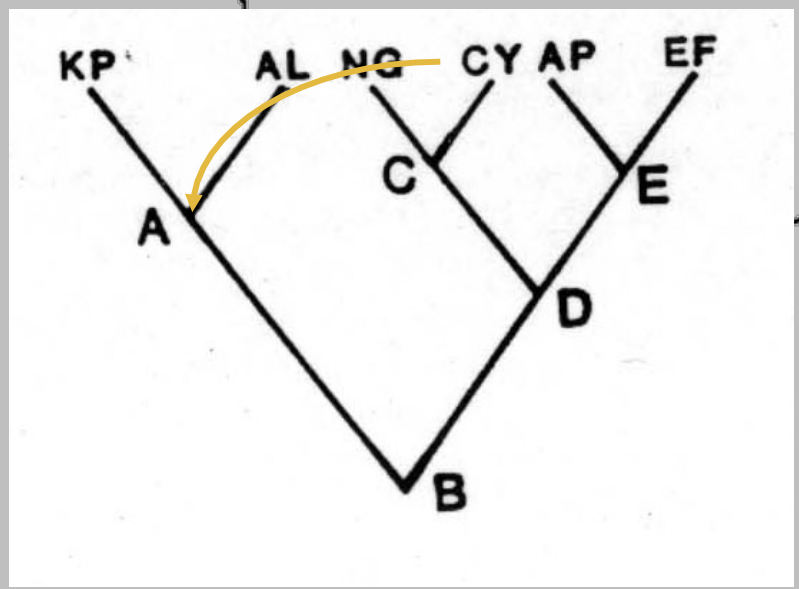
Jennings & Edwards (2005) *Evolution* **59,** 2033-2047.

Gene divergence substantially predates population divergence



Jennings & Edwards (2005) *Evolution* **59,** 2033-2047.

Red-backed Fairy wren - discordant subspecies boundaries



Arnheim Land
(AL)

Kimberley Plateau
(KP)

Cape York
(CY)

Atherton Plateau
(AP)

A

B

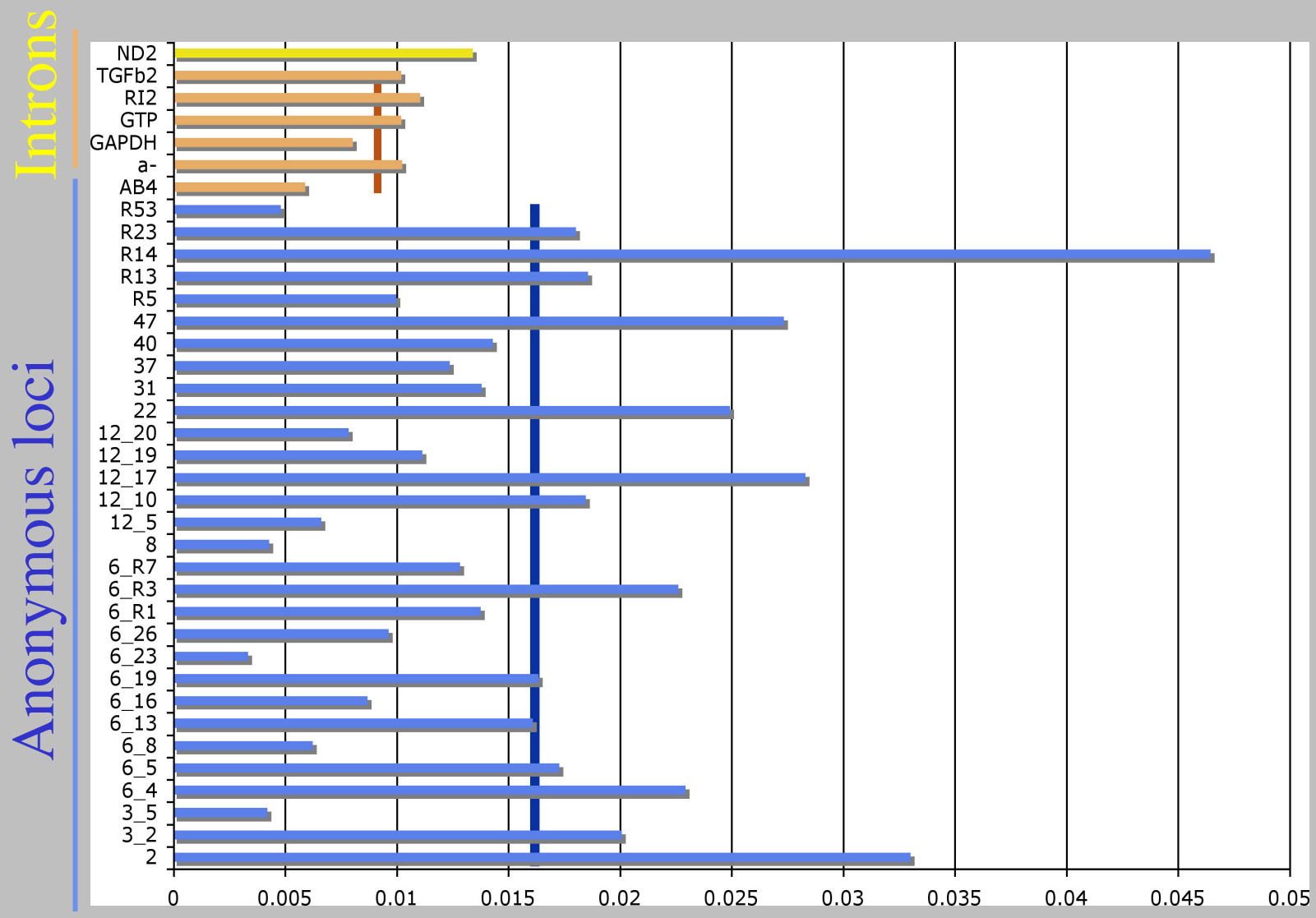
D

E

Eastern Forests
(EF)

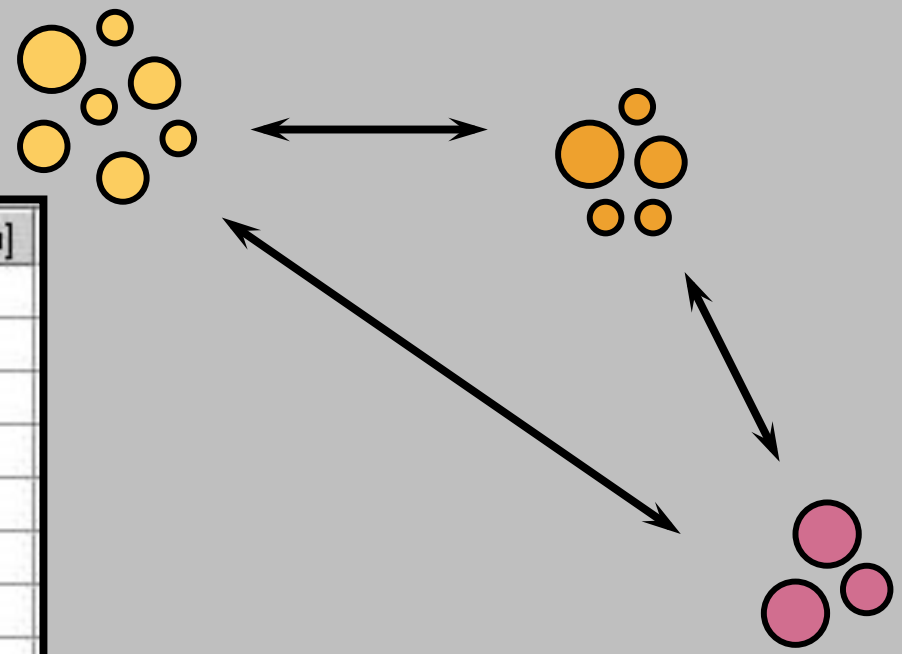
Modified from Cracraft *Evolution* 40: 977-996

Genetic Diversity among loci - θ

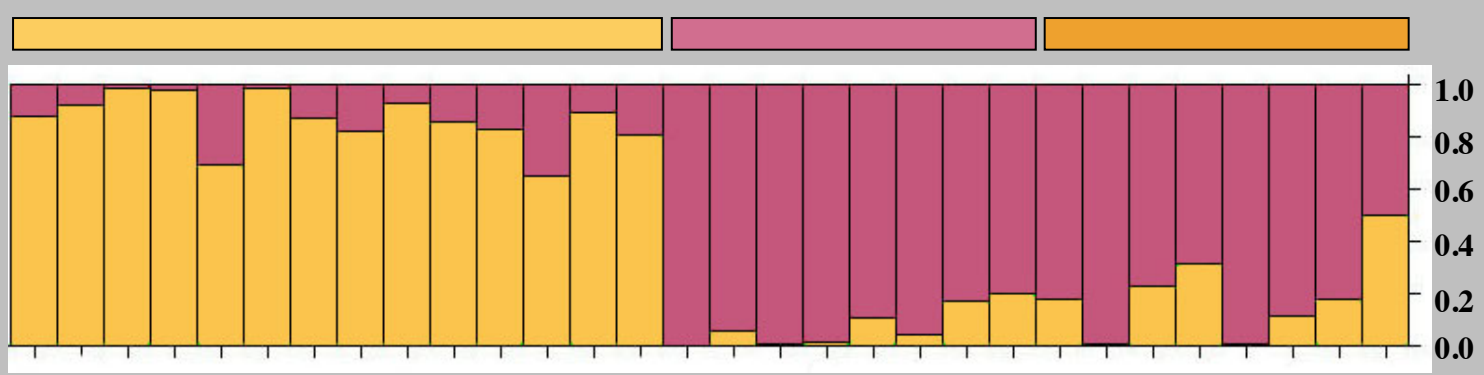


Lee & Edwards. 2008. Evolution 62: 3117-3134.

Population Assignment - Structure



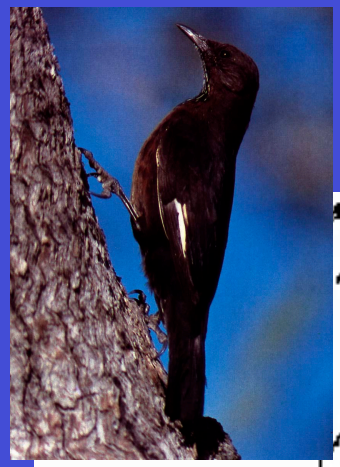
K	Ln P(D)	Var[LnP(D)]
1	-22842.8	805.2
1	-22847.2	813.6
1	-22844.8	809.7
2	-22062.8	2148.2
2	-22077.3	2176.7
2	-22060.1	2135.9
3	-28951.7	14967.9
4	-26786.3	10266.9
5	-32129.0	22148.8



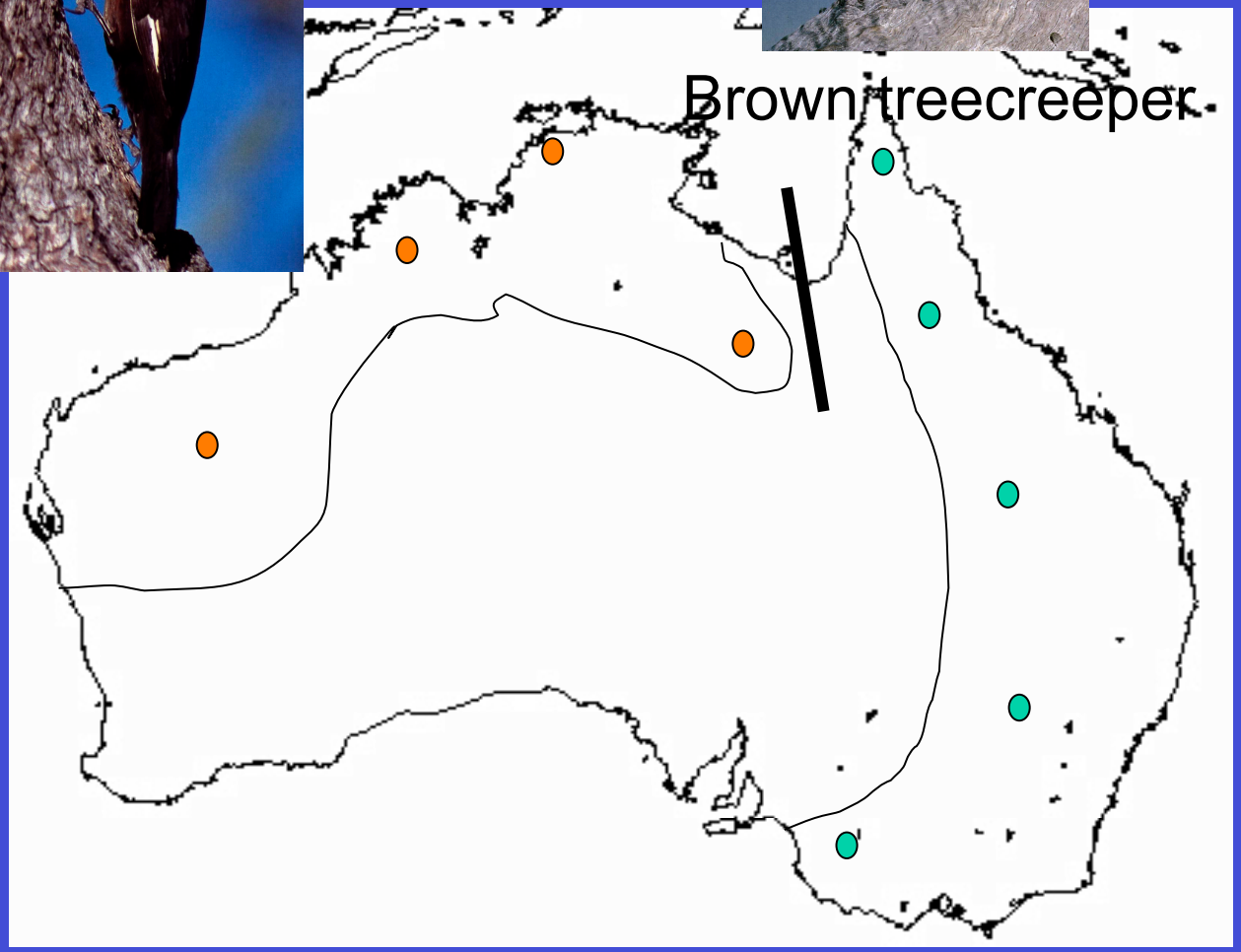
Lee & Edwards. 2008. Evolution 62: 3117-3134.

Treecreepers (*Climacteris*)

Black-tailed treecreeper



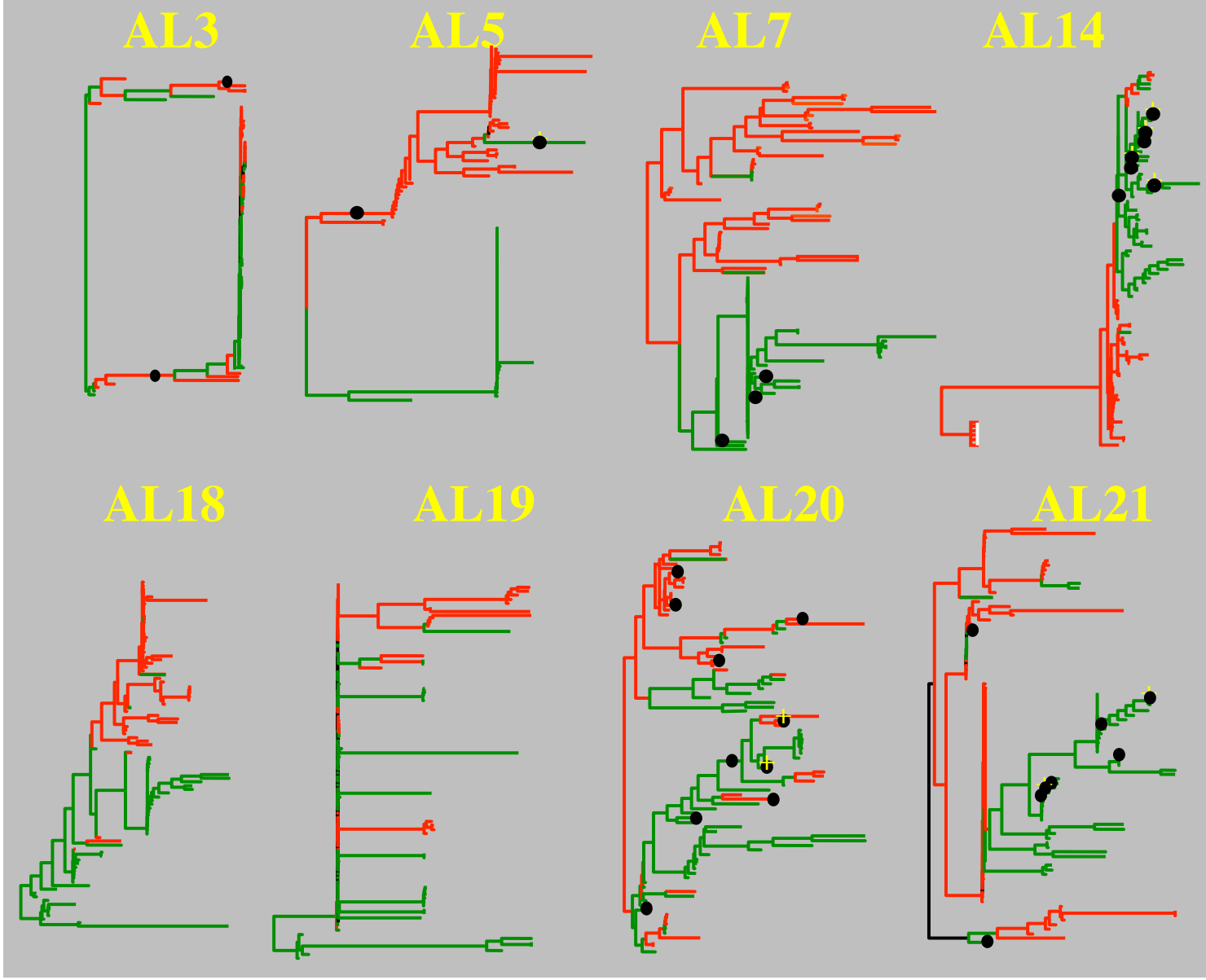
Brown treecreeper



8 gene trees in Australian treecreepers

Black-tailed (western) Treecreeper lineages

Brown Treecreeper (eastern) lineages



Maximum likelihood/Bayesian approaches: Advantages for estimating gene flow

- Parsimony approach
  - Assumes complete certainty of gene tree
  - Statistical testing of different hypotheses of gene flow is cumbersome
  - Confidence limits reflect only uncertainty in *s*

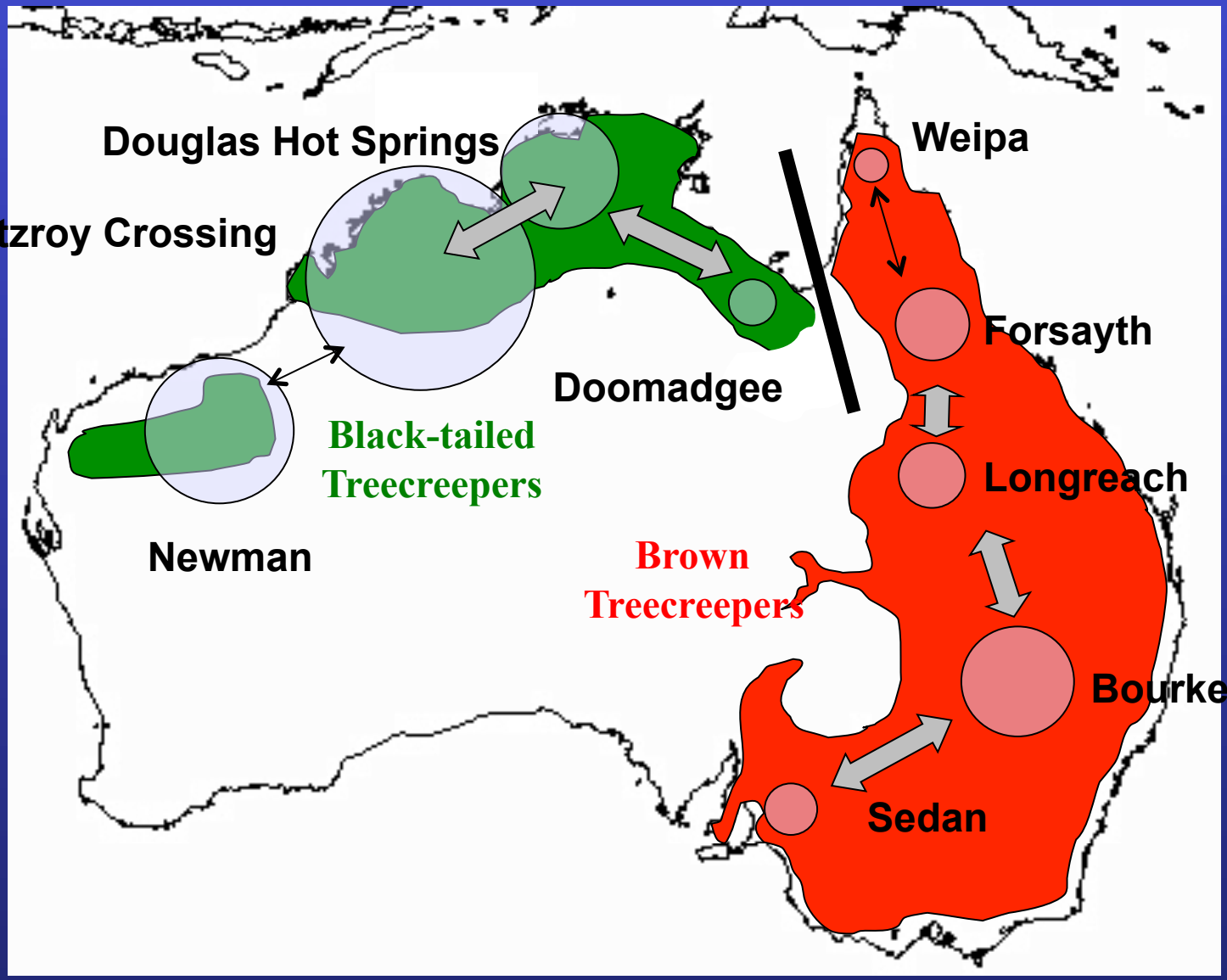
Maximum likelihood/Bayesian approaches: Advantages for estimating gene flow

- ML approach (MIGRATE)
  - Integrates the two sources of uncertainty
    - Accommodates uncertainty in trees by integrating over all trees
    - Accommodates the range of *Nm* given these trees
  - Hypothesis testing easier

Treecreeper populations are connected but variable in size (MIGRATE)

10,000 individuals

1-2 migrants per generation

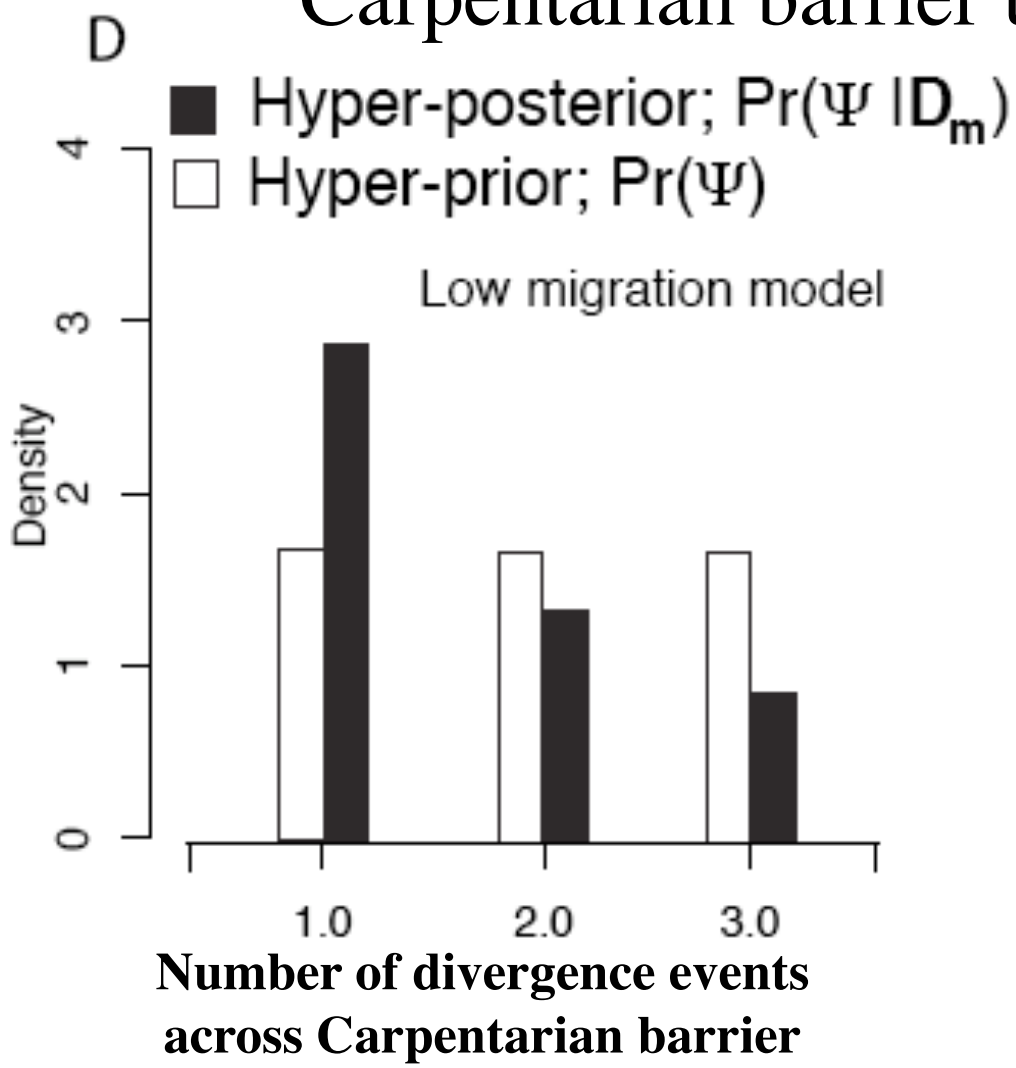


Rotzel, Edwards and Beerli, unpubl. data

Carpentarian speciation occurred well within the Pleistocene*

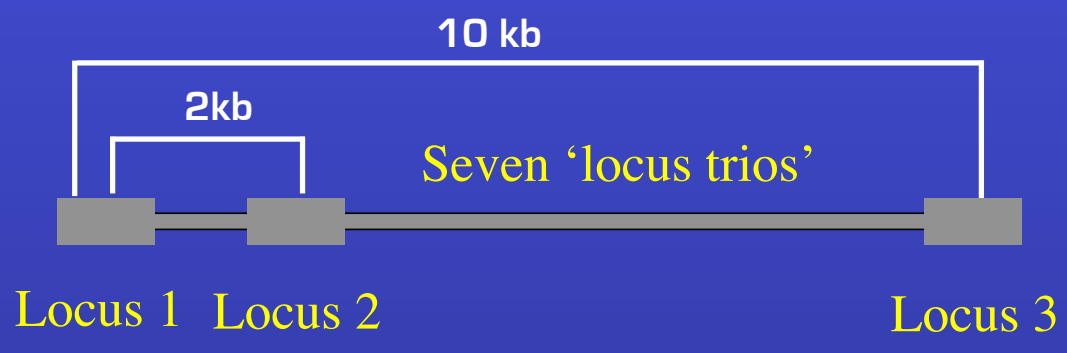
*Assuming a long term mutation rate of 3.6 X 10^{-9} per site per year

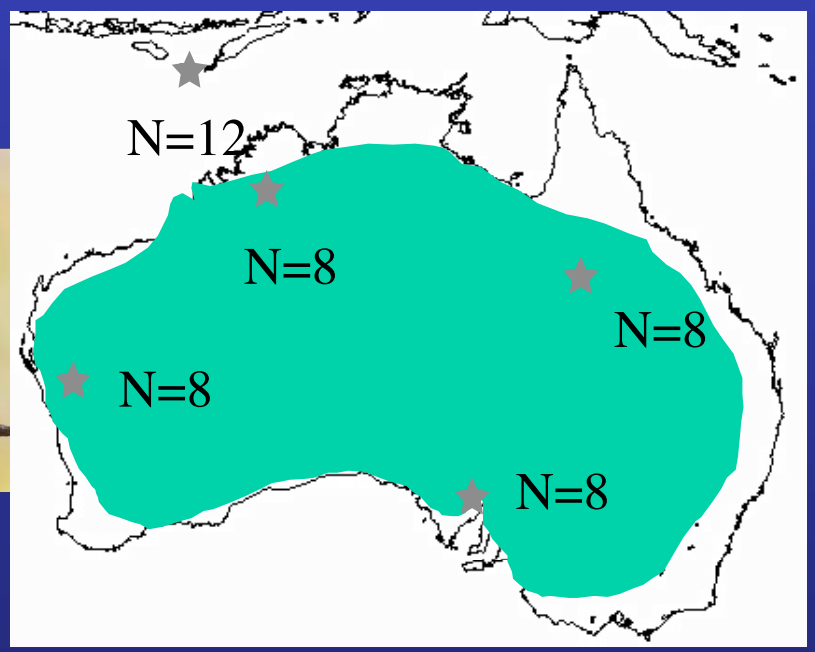
Test of contemporaneous divergence across Carpentarian barrier using msBayes



Huang et al. 2011. BMC Bioinformatics 12

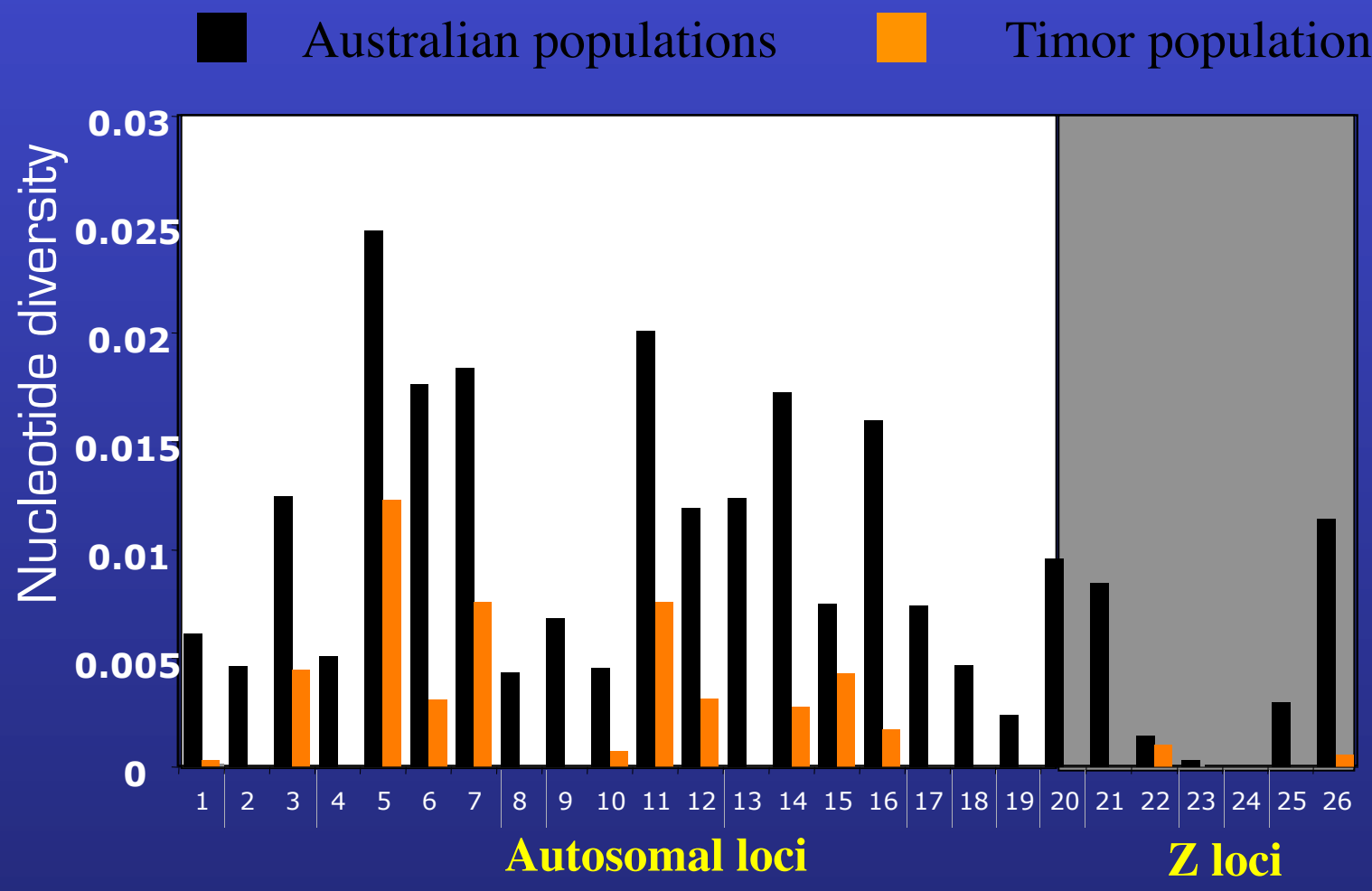
Zebra Finch: a population genomics model system





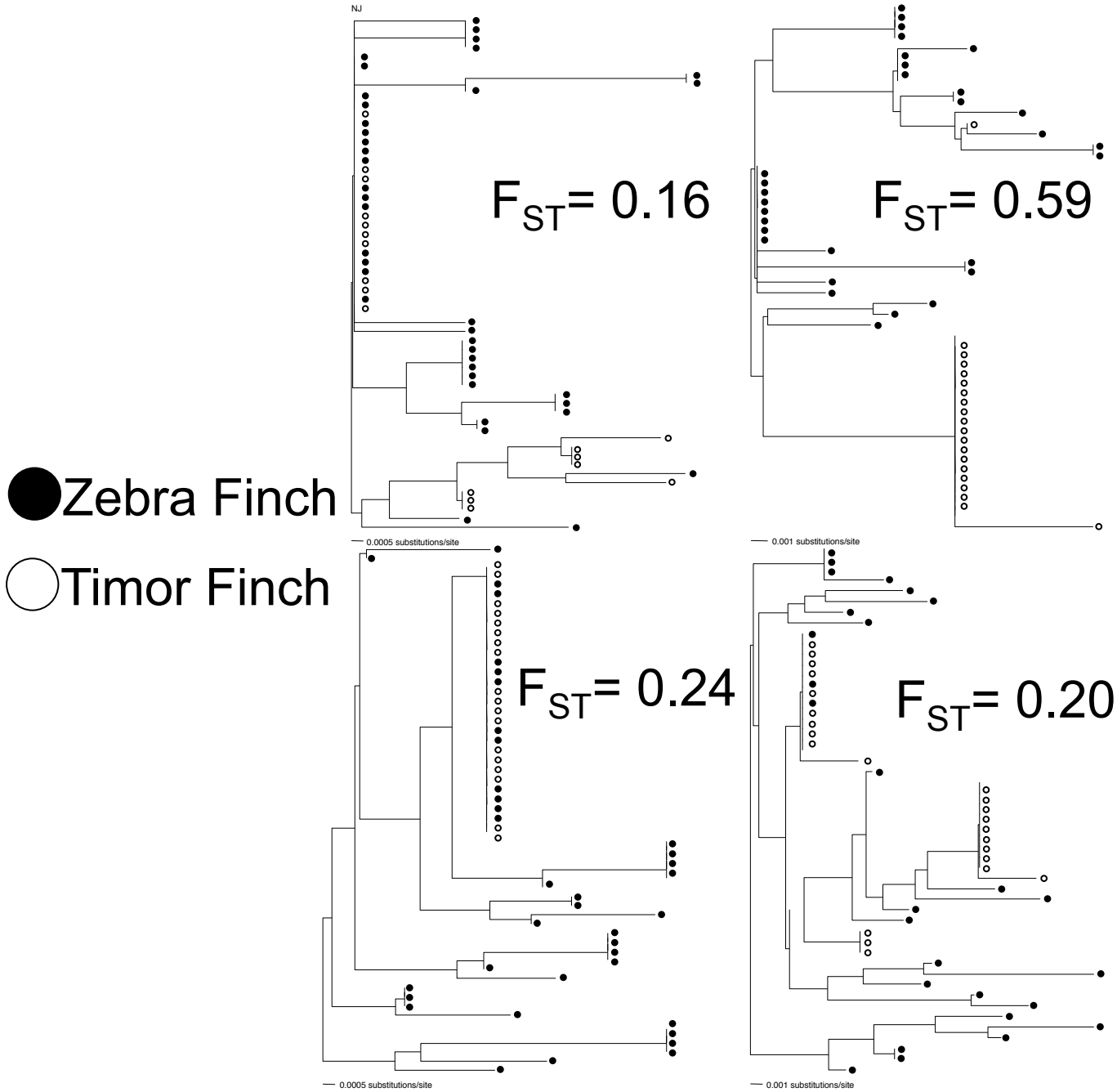
Balakrishnan, C.B. & Edwards, S. V. 2009. *Genetics* 181: 645-660

Dramatically reduced polymorphism in Timor Finches

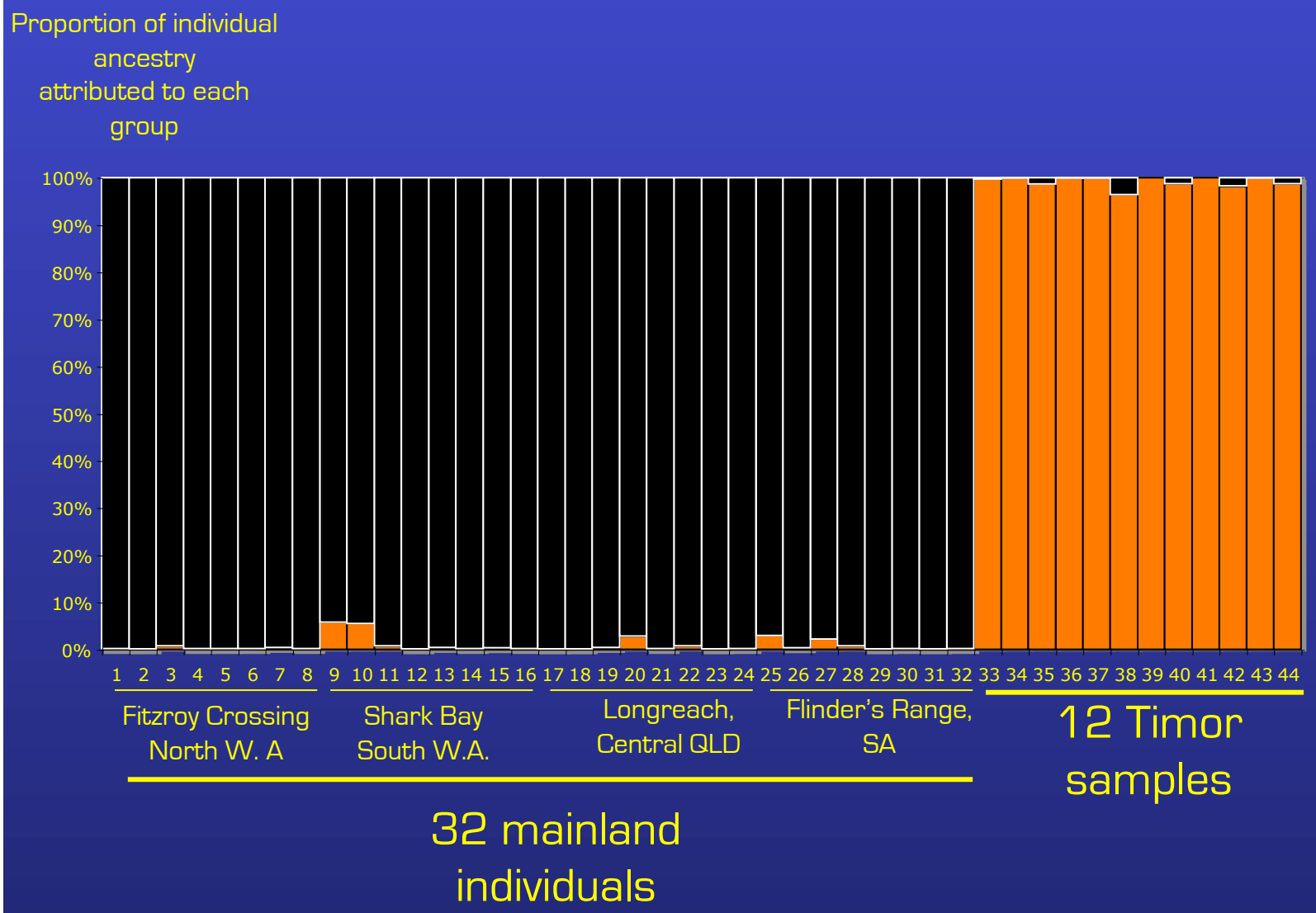


Balakrishnan, C.B. & Edwards, S. V. 2009. *Genetics* 181: 645-660

Linked locus pair: 182 35

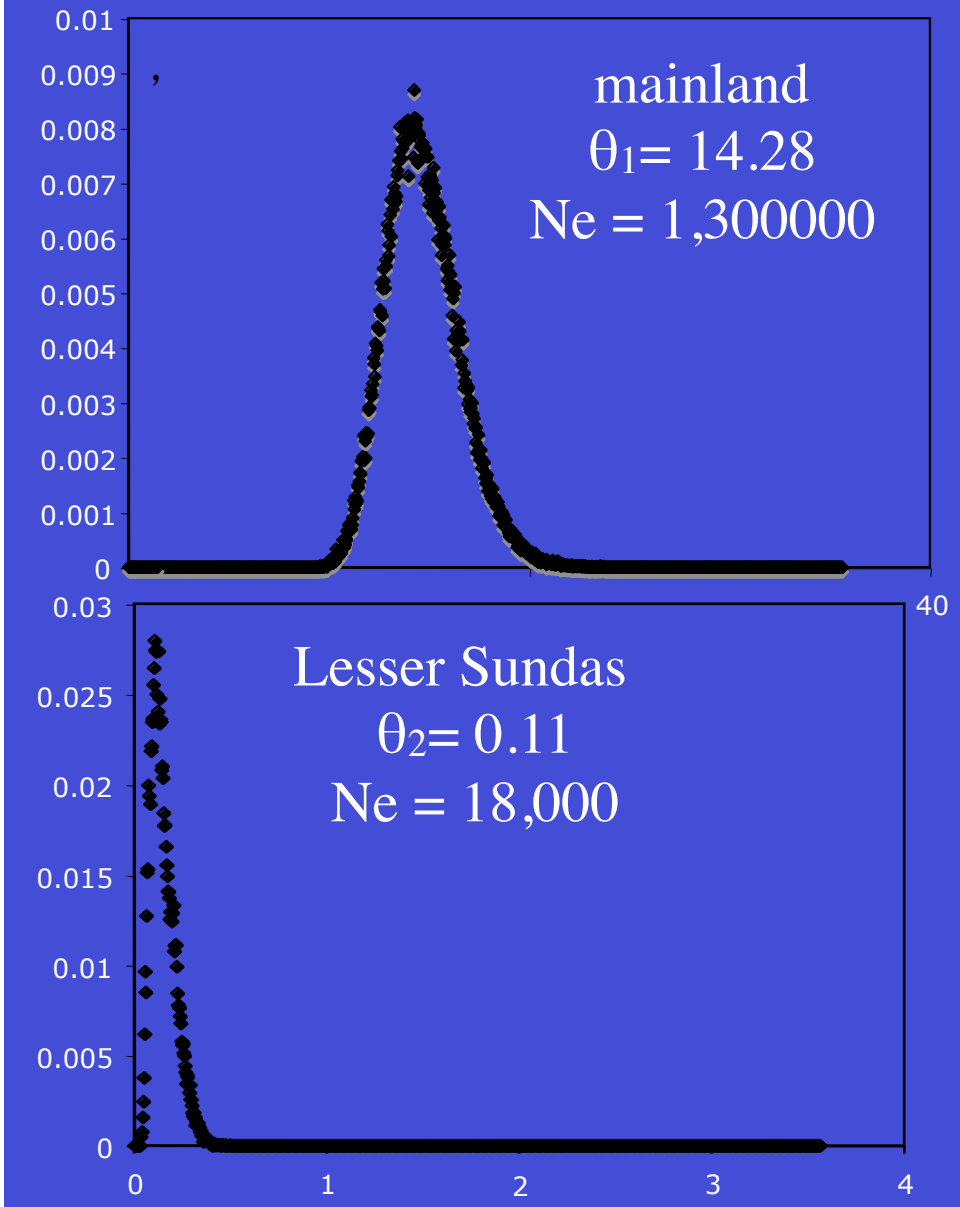


Strong differentiation of mainland and island finches

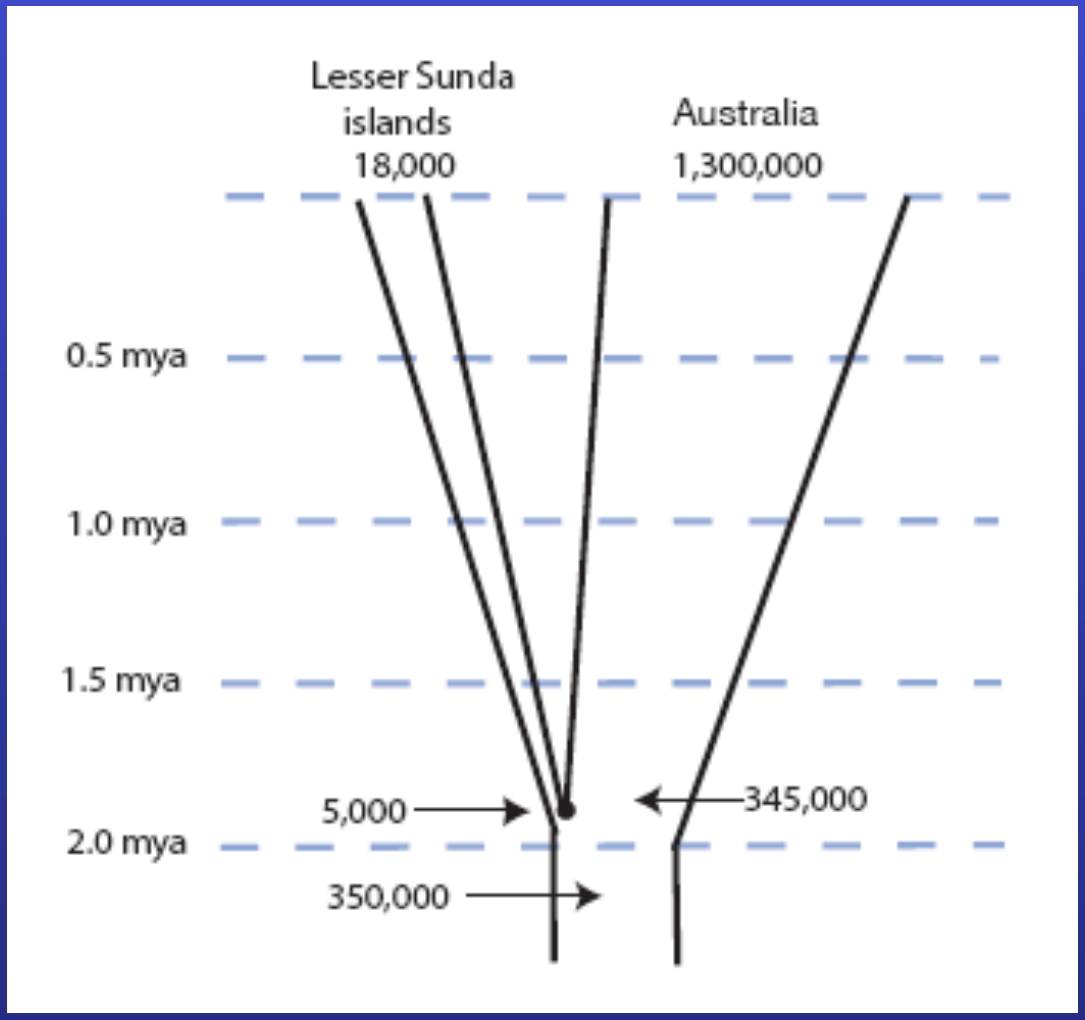


Balakrishnan, C.B. & Edwards, S. V. 2009. *Genetics* 181: 645-660

Population growth in mainland but not island finch populations

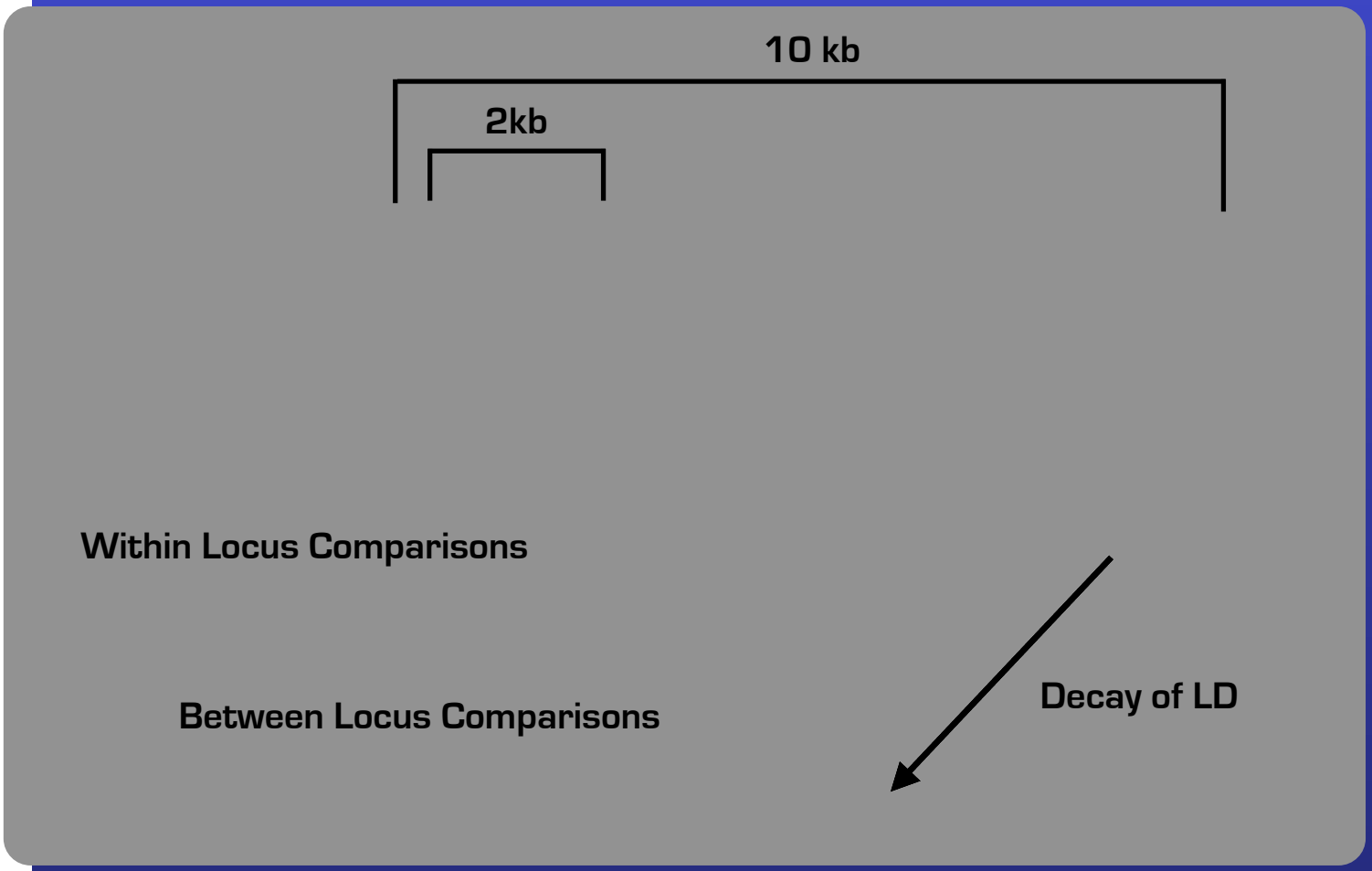


Demographic scenario for Zebra Finch



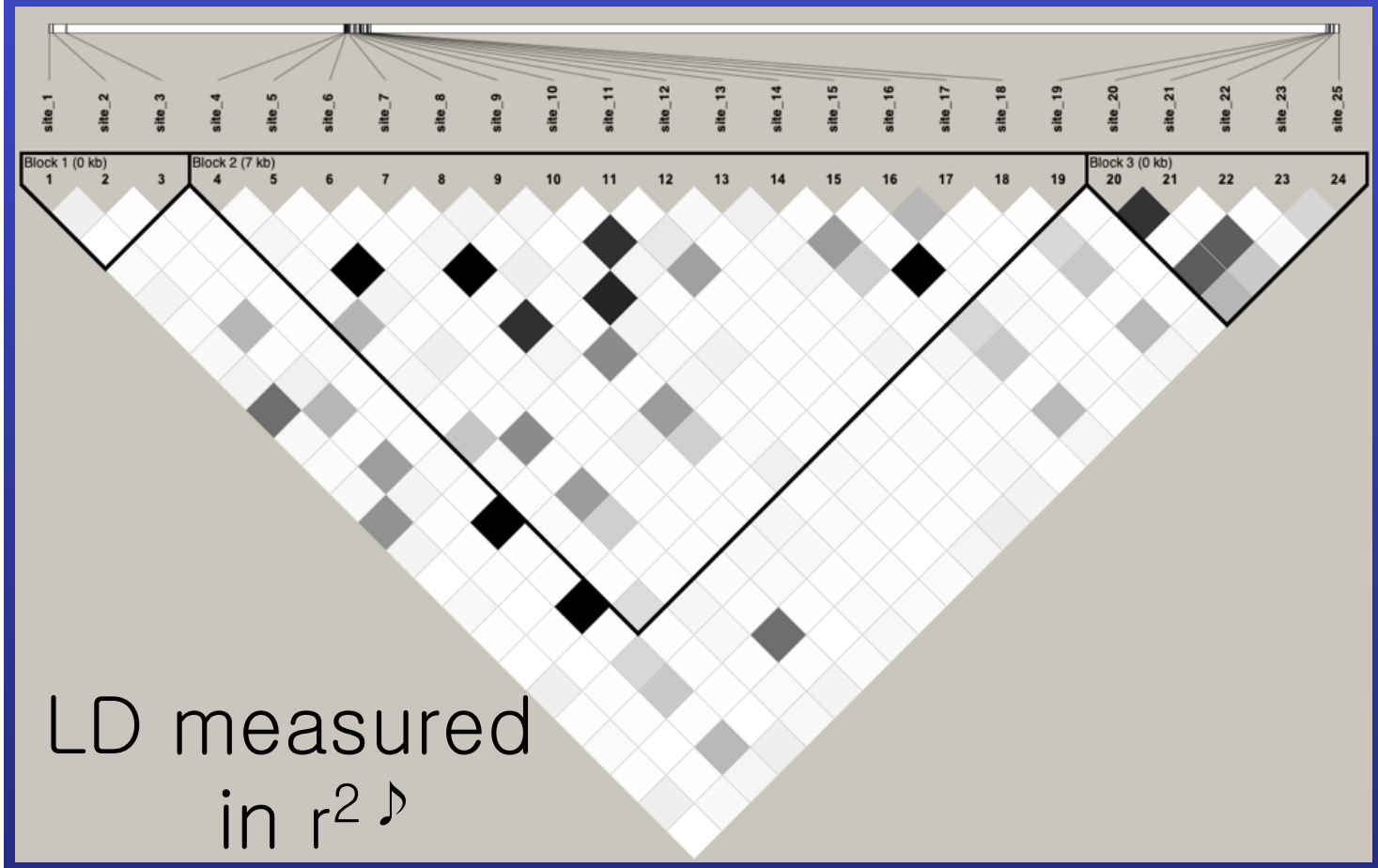
Balakrishnan, C.N., Lee J. Y. and Edwards, S. V. 2010. Pp. 65-88
In: *In Search of the Causes of Evolution: From Field Observations to Mechanisms*.
(Eds., Peter and Rosemary Grant), Princeton University Press, Princeton, NJ.

Test of linkage disequilibrium: locus trios



Balakrishnan, C.B. & Edwards, S. V. 2009. *Genetics* 181: 645-660

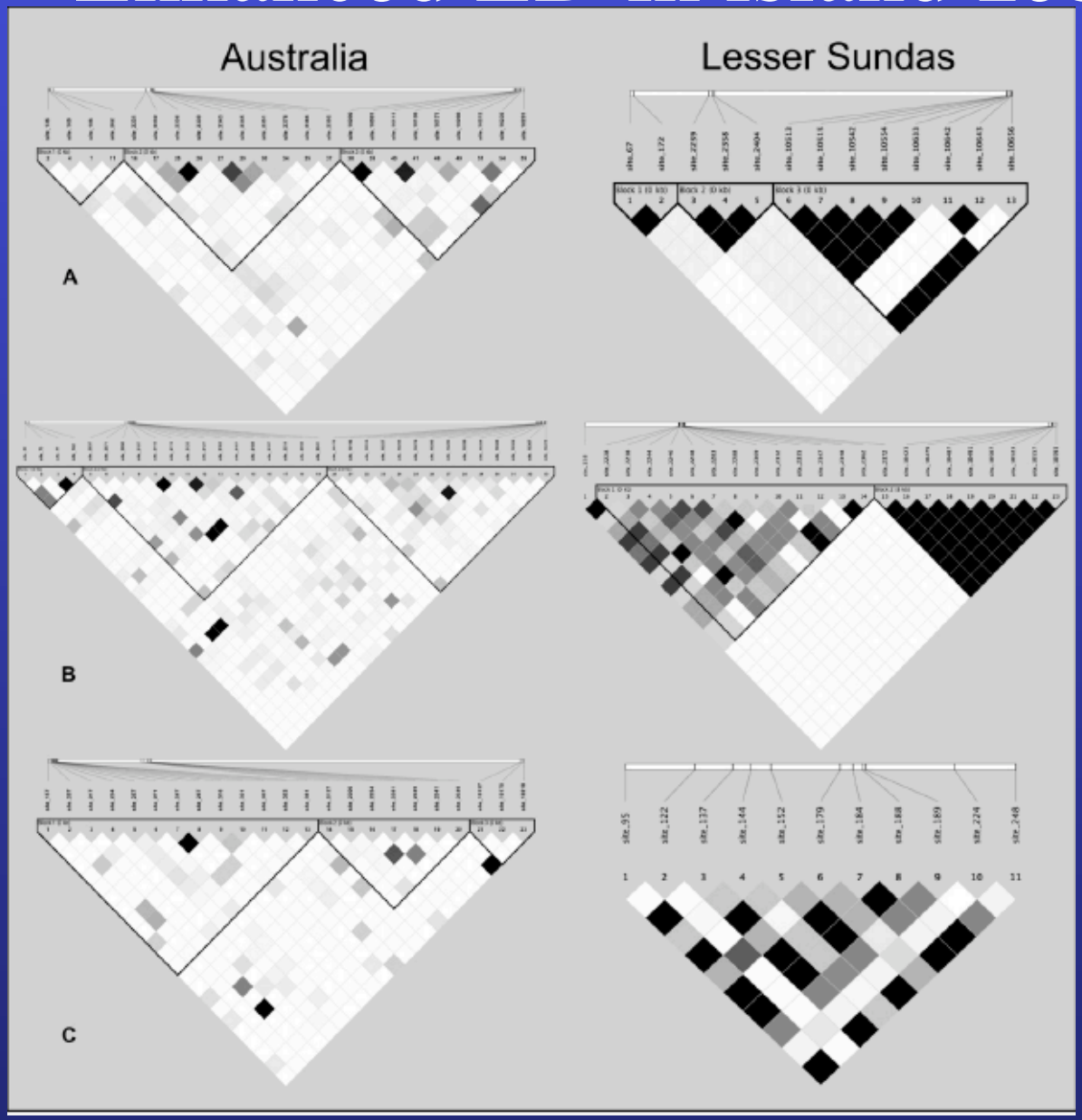
Low levels of linkage disequilibrium in mainland birds♪



LD measured in r^2 ♪

Balakrishnan, C.B. & Edwards, S. V. 2009. *Genetics* 181: 645-660

Enhanced LD in island zebra finches



Balakrishnan, C.B. & Edwards, S. V. 2009. *Genetics* 181: 645-660

Founder effect speciation?

- May 1942: "Genetic Revolution"
  - Following colonization, gene frequencies may change rapidly due to drift
  - Induces linkage disequilibrium
  - New gene combinations
  - New environment imposes new selective regime

Australian Zebra Finch

Lesser Sundas Zebra Finch

Conclusions:

- Multilocus analysis focuses attention on the population level aspects of phylogeography and reduces variance of parameter estimates

- Discordance among gene trees can be reconciled with unique population histories - even phylogeny

- Australian bird speciation is characterized by high levels of incomplete lineage sorting, suggesting recent divergence and large population sizes, despite significant population structure

Acknowledgments

Grassfinches/Statistics

- Bryan Jennings, Harvard (--> Humboldt State)
- Liang Liu, Harvard
- Dennis Pearl, Ohio State

Treecreepers

- Nancy Rotzel
- Peter Beerli
- Burke Museum (University of Washington)

Wrens

- June Lee
- Leo Joseph and Australian
- National Wildlife Collection (ANWC)

Zebra Finches

- Dave Runciman (LaTrobe U.)
- Museum of Comparative Zoology, Harvard

Fieldwork - Logistics

- Walter Boles, Australian Museum
- Nate Rice, Philadelphia Academy of Sciences
- Angus Emmott, numerous private landholders

Funding

- NSF