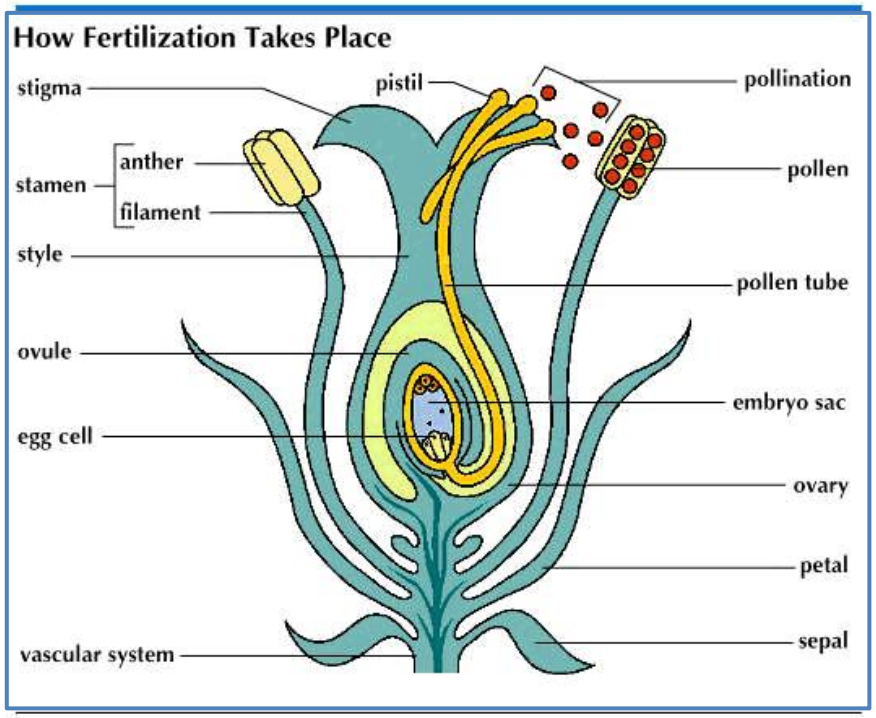
Phylogenetic patterns of reproductive isolation in *Eucalyptus*

Matthew Larcombe, **Dorothy Steane**, Rebecca Jones, Dean Nicolle, Barbara Holland, René Vaillancourt, Brad Potts

UTAS

Modes of Reproductive Isolation

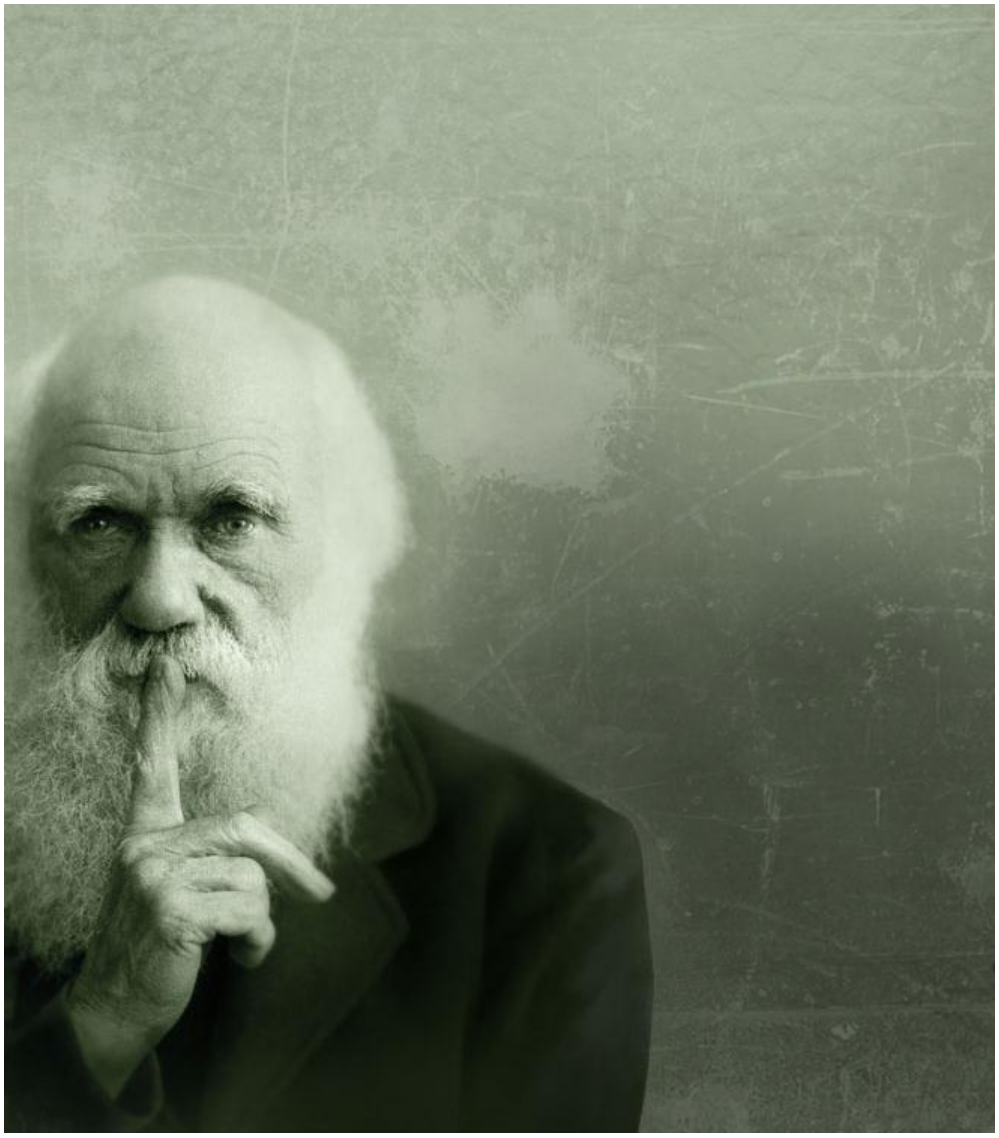
1. Pre-mating (e.g., species don't fancy each other to begin with; species are geographically isolated)
2. Post-mating
   A. Pre-zygotic → Embryo does not form (e.g., pollen tube does not reach ovum)

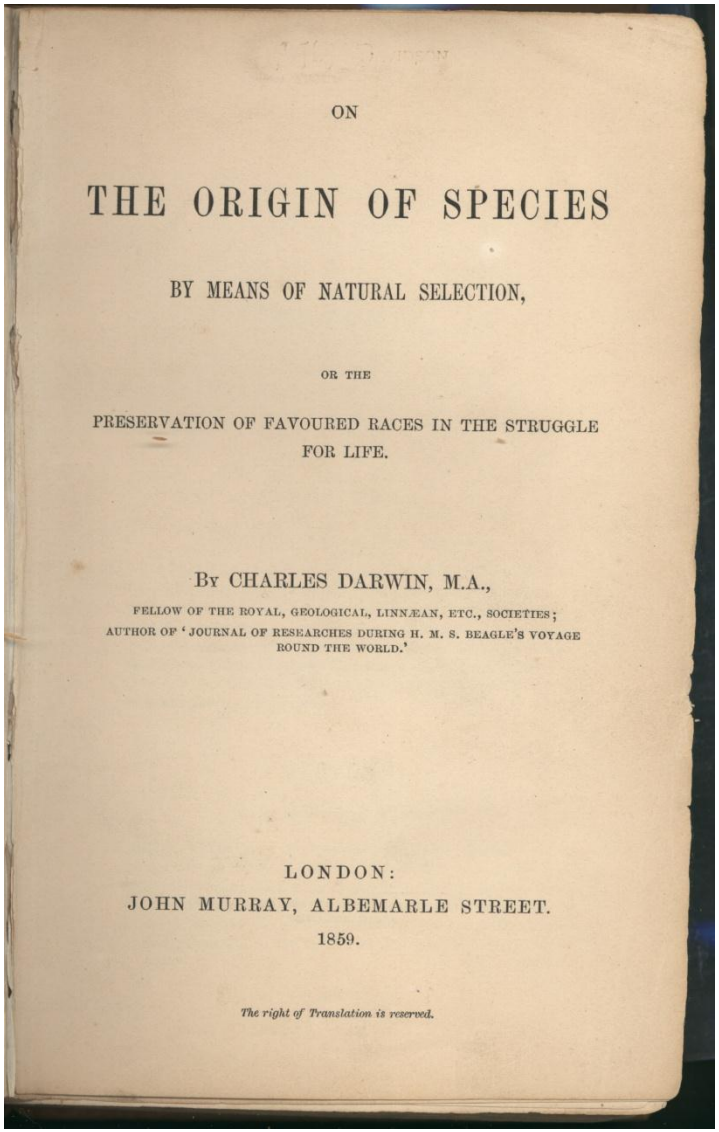


B. Post-zygotic

   i. Pre-dispersal (e.g., embryo aborts; no seed forms)
   ii. Post-dispersal (e.g., seedlings do not survive)

What causes speciation?
Darwin sorted that out didn't he?





ON

THE ORIGIN OF SPECIES

BY MEANS OF NATURAL SELECTION,

OR THE

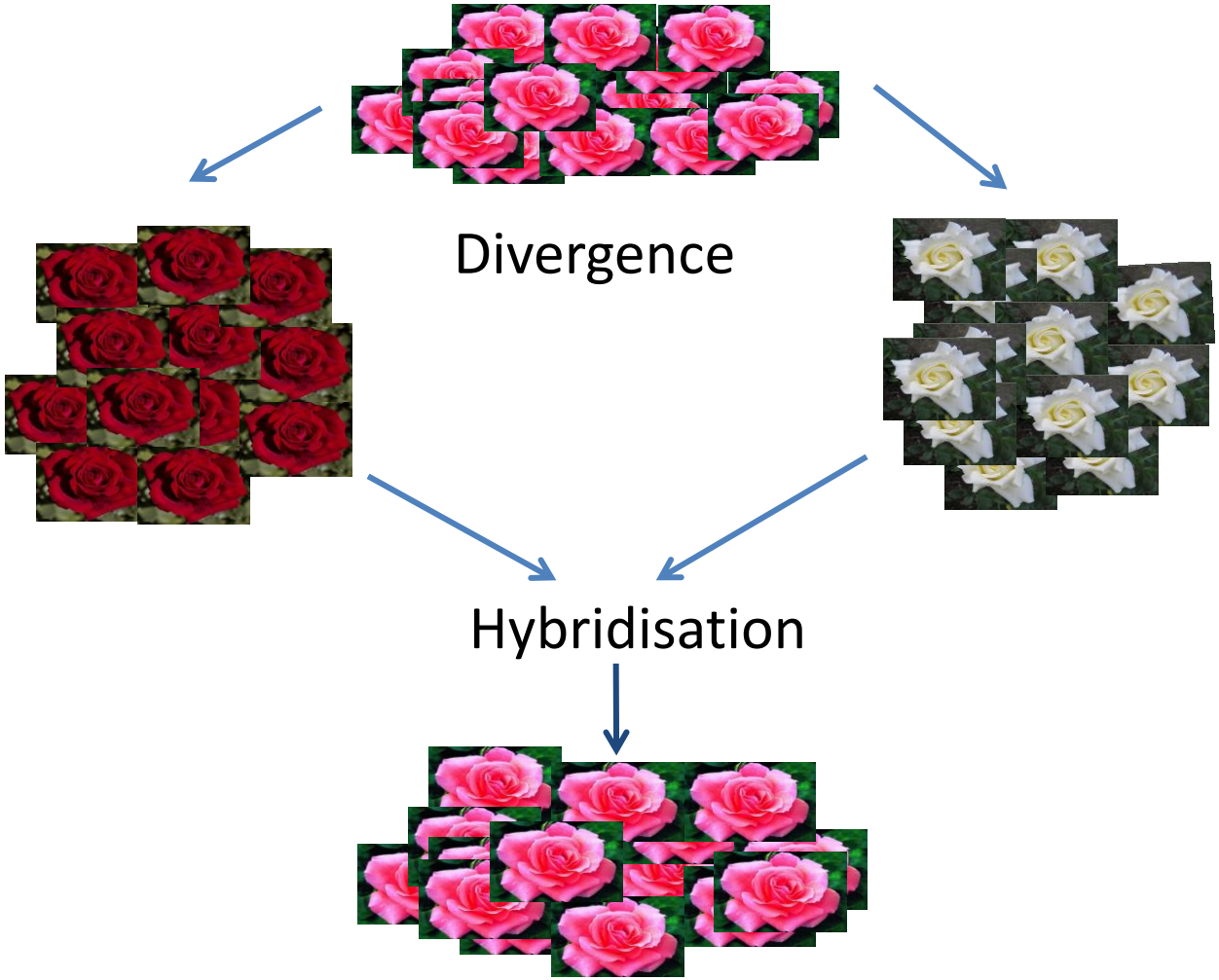
PRESERVATION OF FAVOURED RACES IN THE STRUGGLE FOR LIFE.

By CHARLES DARWIN, M.A.,

FELLOW OF THE ROYAL, GEOLOGICAL, LINNÆAN, ETC., SOCIETIES;
AUTHOR OF 'JOURNAL OF RESEARCHES DURING H. M. S. BEAGLE'S VOYAGE ROUND THE WORLD.'

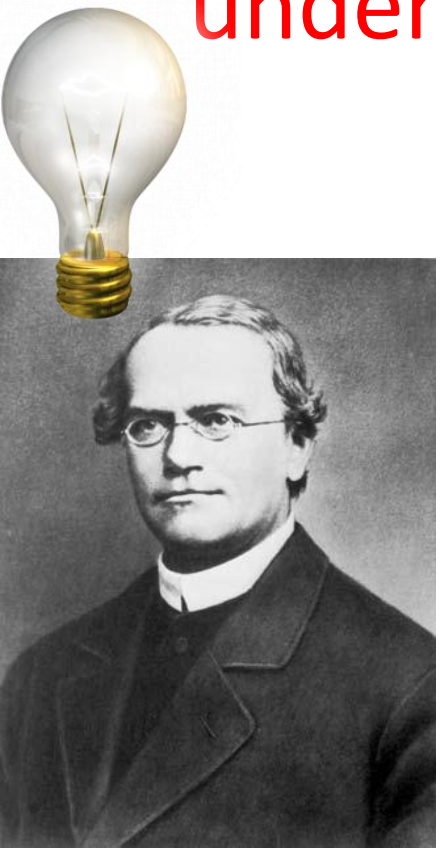
LONDON:
JOHN MURRAY, ALBEMARLE STREET.
1859.

Incomplete speciation can result in hybridisation => homogenisation

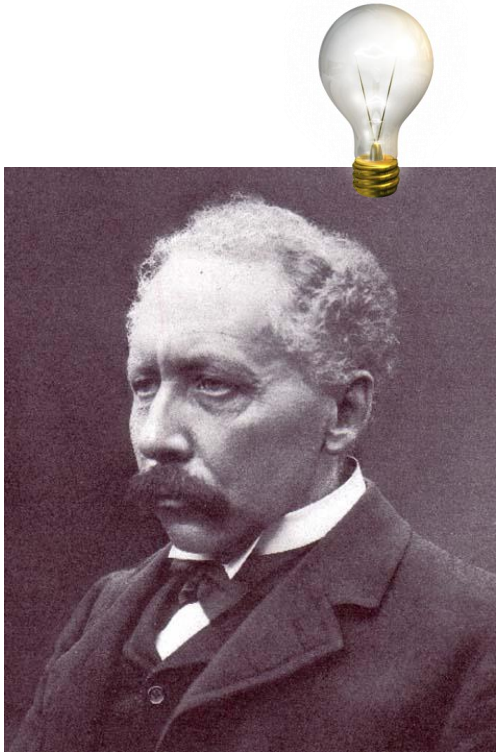


So, how do species become reproductively isolated?

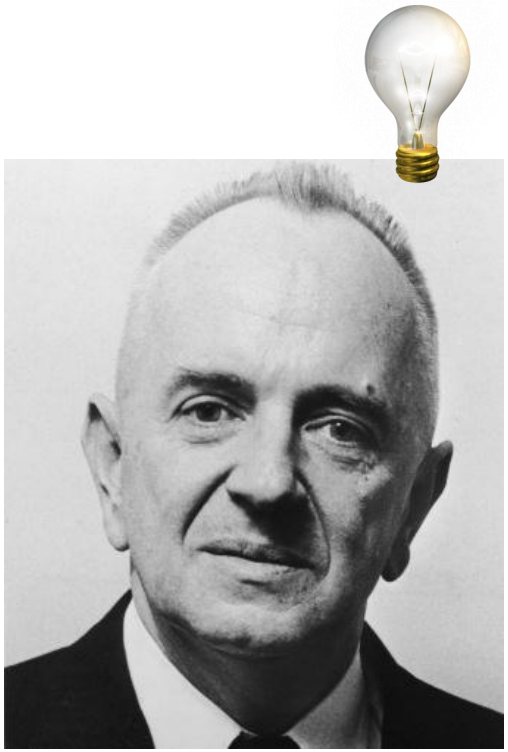
The missing piece of the puzzle was an understanding of genes and heritability



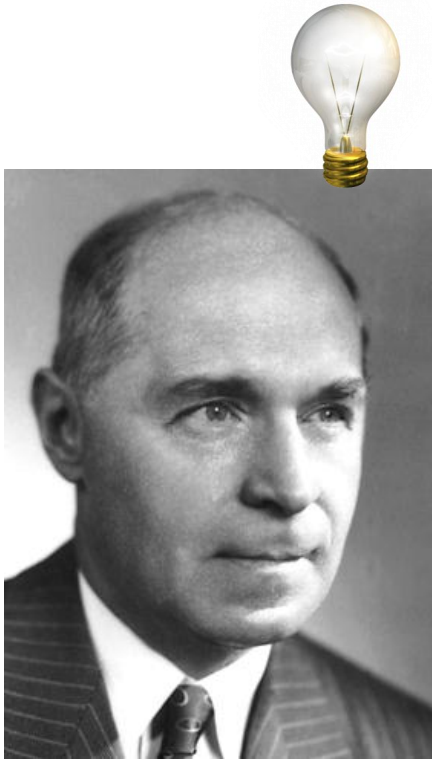
Mendel 1865



Bateson 1909



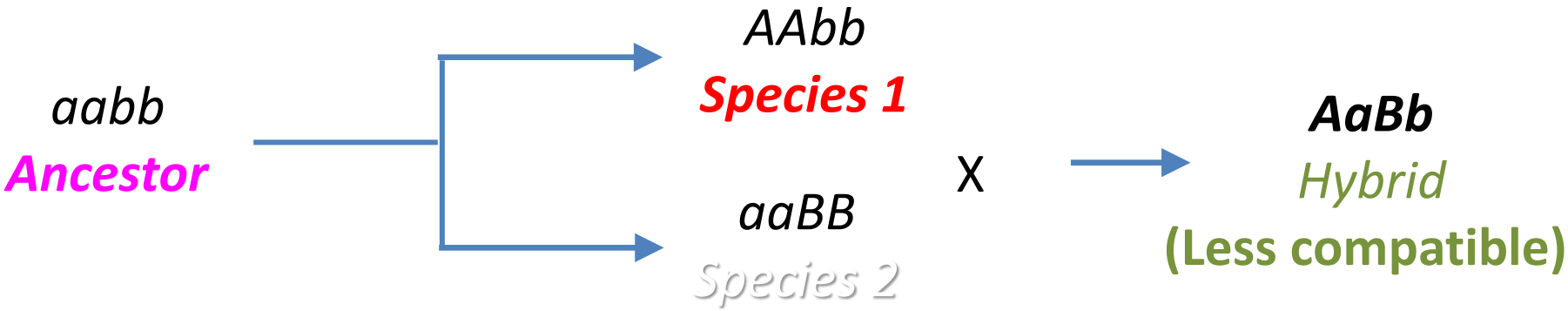
Dobzhansky 1937



Muller 1942

Reproductive isolation is a by-product of genetic incompatibility that arises via selection and drift

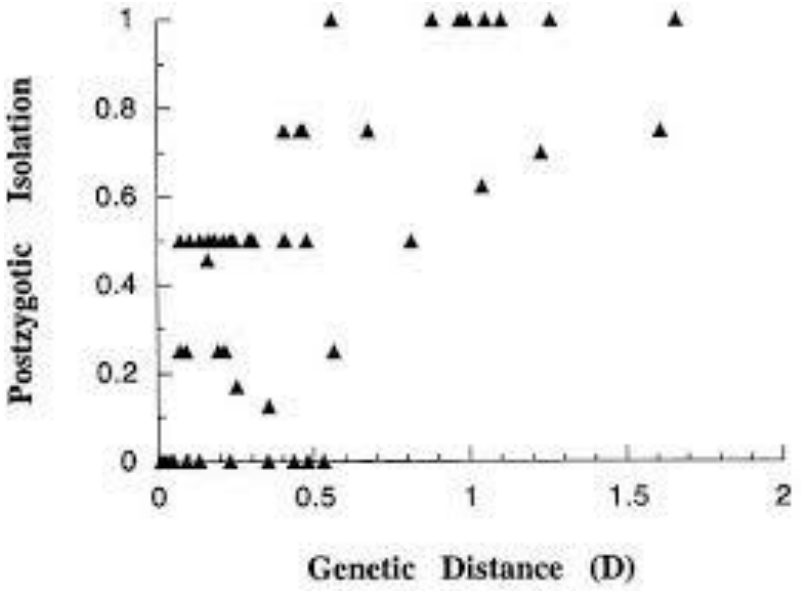
Bateson-Dobzhansky-Muller (BDM) model of incompatibility

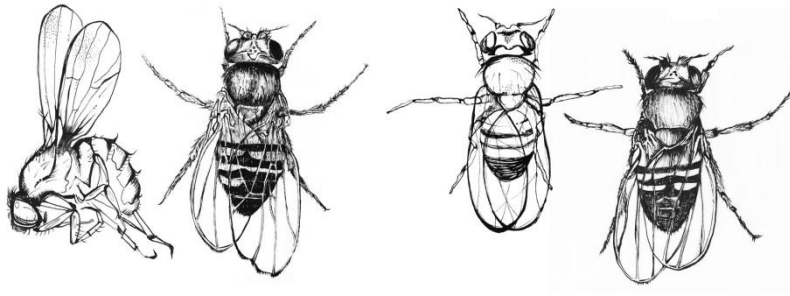


1. Minor allelic differences accumulate via drift
2. New allele combinations cause incompatibilities in hybrids
3. These accumulate over time (since divergence)
4. Ultimately lead to complete reproductive isolation

In animals, reproductive isolation increases with genetic distance

- Lots of evidence for BDM incompatibilities
- Male sterility involves hundreds of genes ('pre-zygotic isolation')
- Post-zygotic barriers evolve more slowly than prezygotic barriers





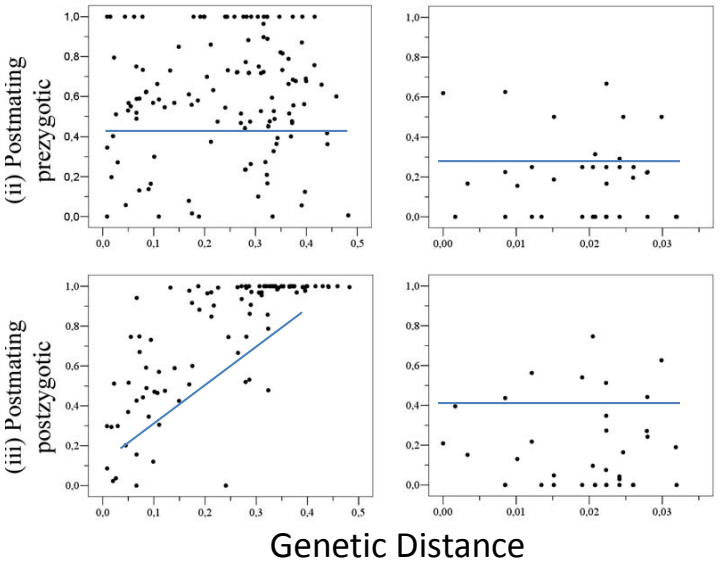
Drosophila spp.

Coyne and Orr
1989, 1997, 2004

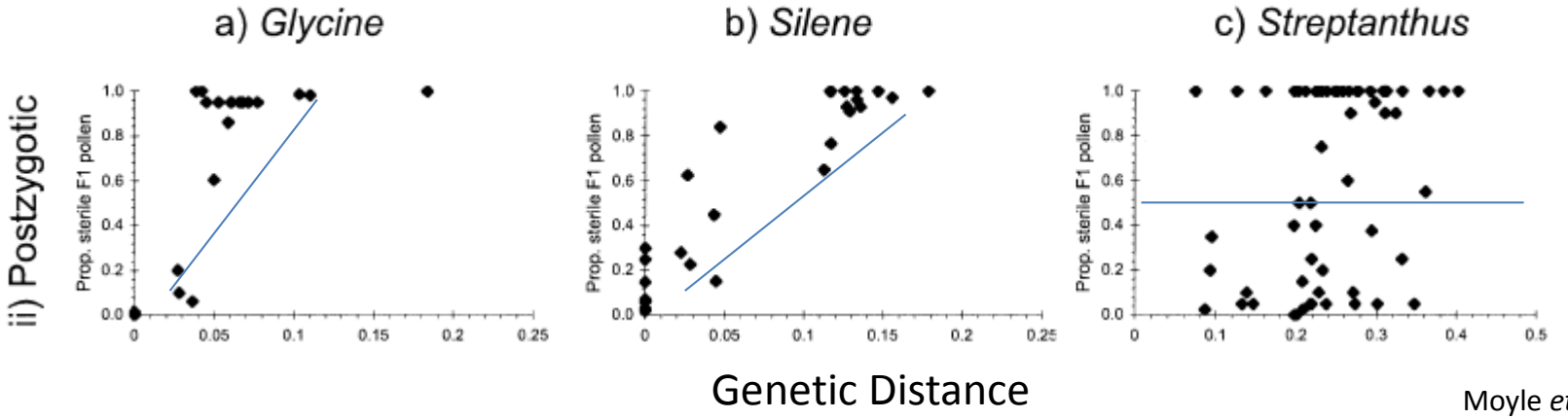
In plants, patterns of incompatibility are less clear

- Isolation sometimes increases with GD (but sometimes doesn't)
- No evidence that prezygotic barriers develop first

Orchids



Scopece et al. (2007)



Moyle *et al*. (2004)

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TARGET REVIEW

Hybridization and speciation*

R. ABBOTT[1], D. ALBACH[2], S. ANSELL[3], J. W. ARNTZEN[4], S. J. E. BAIRD[5], N. BIERNE[6], J. BOUGHMAN[7], A. BRELSFORD[8], C. A. BUERKLE[9], R. BUGGS[10], R. K. BUTLIN[11], U. DIECKMANN[12], F. EROUKHMANOFF[13], A. GRILL[14], S. H. CAHAN[15], J. S. HERMANSEN[13], G. HEWITT[16], A. G. HUDSON[17], C. JIGGINS[18], J. JONES[19], B. KELLER[20], T. MARCZEWSKI[21], J. MALLET[22,23], P. MARTINEZ-RODRIGUEZ[24], M. MÖST[25], S. MULLEN[26], R. NICHOLS[10], A. W. NOLTE[27], C. PARISOD[28], K. PFENNIG[29], A. M. RICE[30], M. G. RITCHIE[1], B. SEIFERT[31], C. M. SMADJA[32], R. STELKENS[33], J. M. SZYMURA[34], R. VÄINÖLÄ[35], J. B. W. WOLF[36] & D. ZINNER[37]

" the BDM model of hybrid incompatibilities requires a broader interpretation"

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The potential for gene flow from exotic eucalypt plantations into Australia's rare native eucalypts

Robert C. Barbour[a,b], Sascha L. Wise[a,b], Gay E. McKinnon[a], René E. Vaillancourt[a,b], Grant J. Williamson[a], Brad M. Potts[a,b,*]

If speciation is incomplete, then moving species around the landscape could result in:

- Interspecific gene flow
- Introgression
- Loss of genetic integrity
- Species replacement
- 'De-speciation'
- Maladaptation

Review

Cell

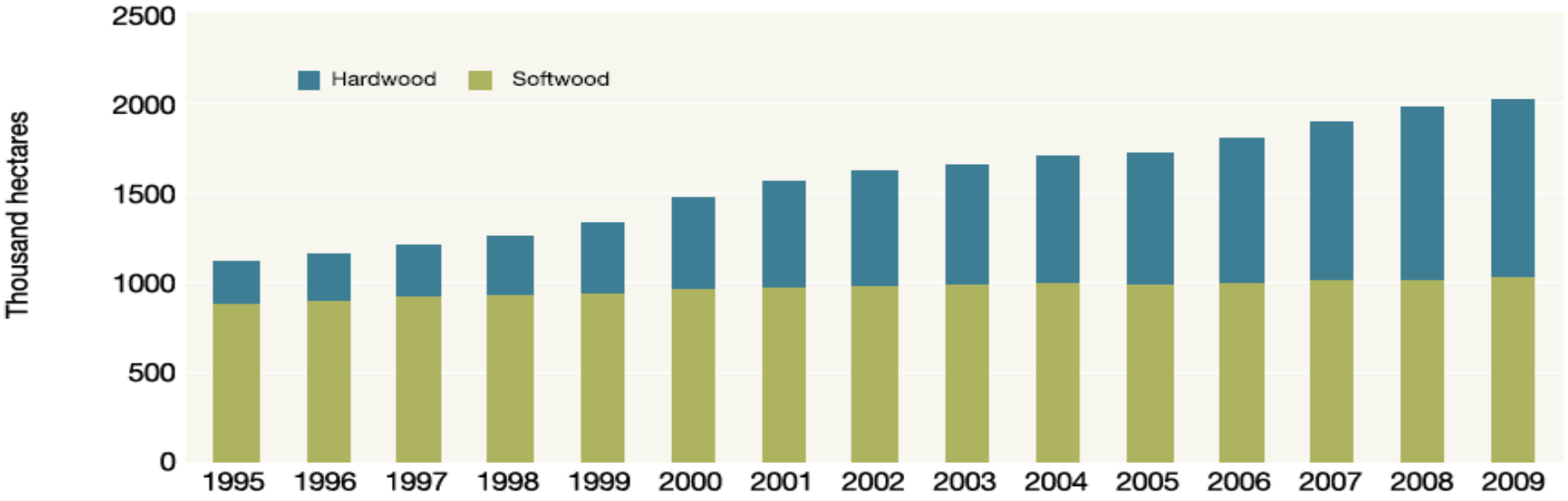
Compromising genetic diversity in the wild: unmonitored large-scale release of plants and animals

Linda Laikre[1], Michael K. Schwartz[2], Robin S. Waples[3], Nils Ryman[1] and The GeM Working Group[4]

[1] Department of Zoology, Division of Population Genetics, Stockholm University, S-10691 Stockholm, Sweden

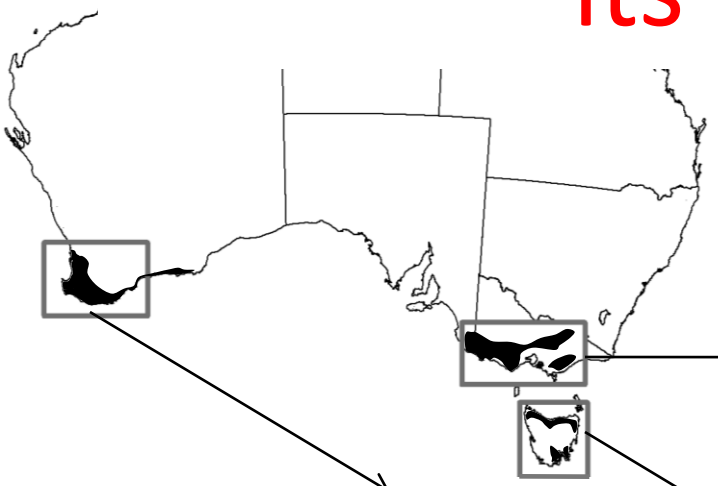
Eucalypt plantations in Australia

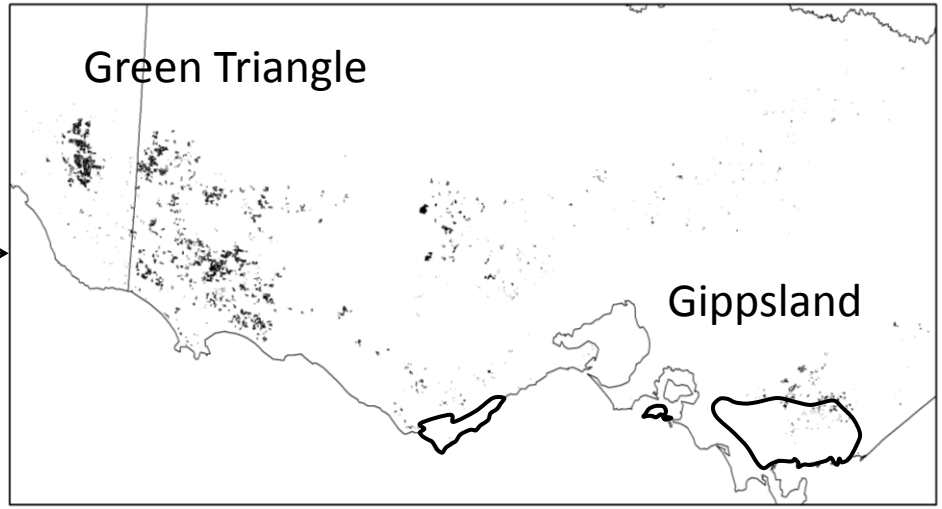
- The *E. globulus* estate reached 538, 000 ha in 2011
- total hardwood = 1,000,000 ha
- 150% increase since 2000

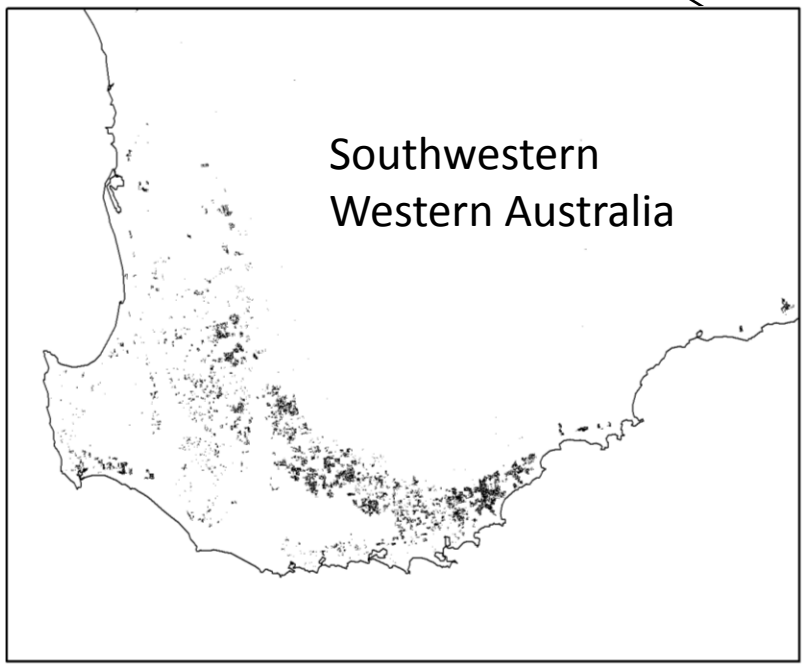


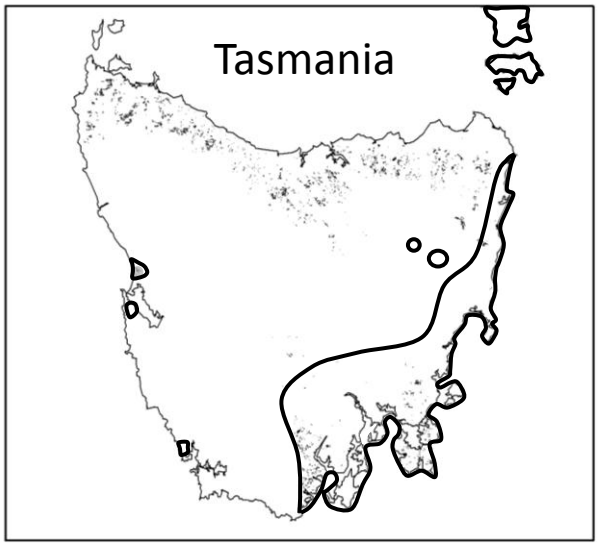
Gavran and Parsons (2011)

E. globulus is planted well outside its natural range





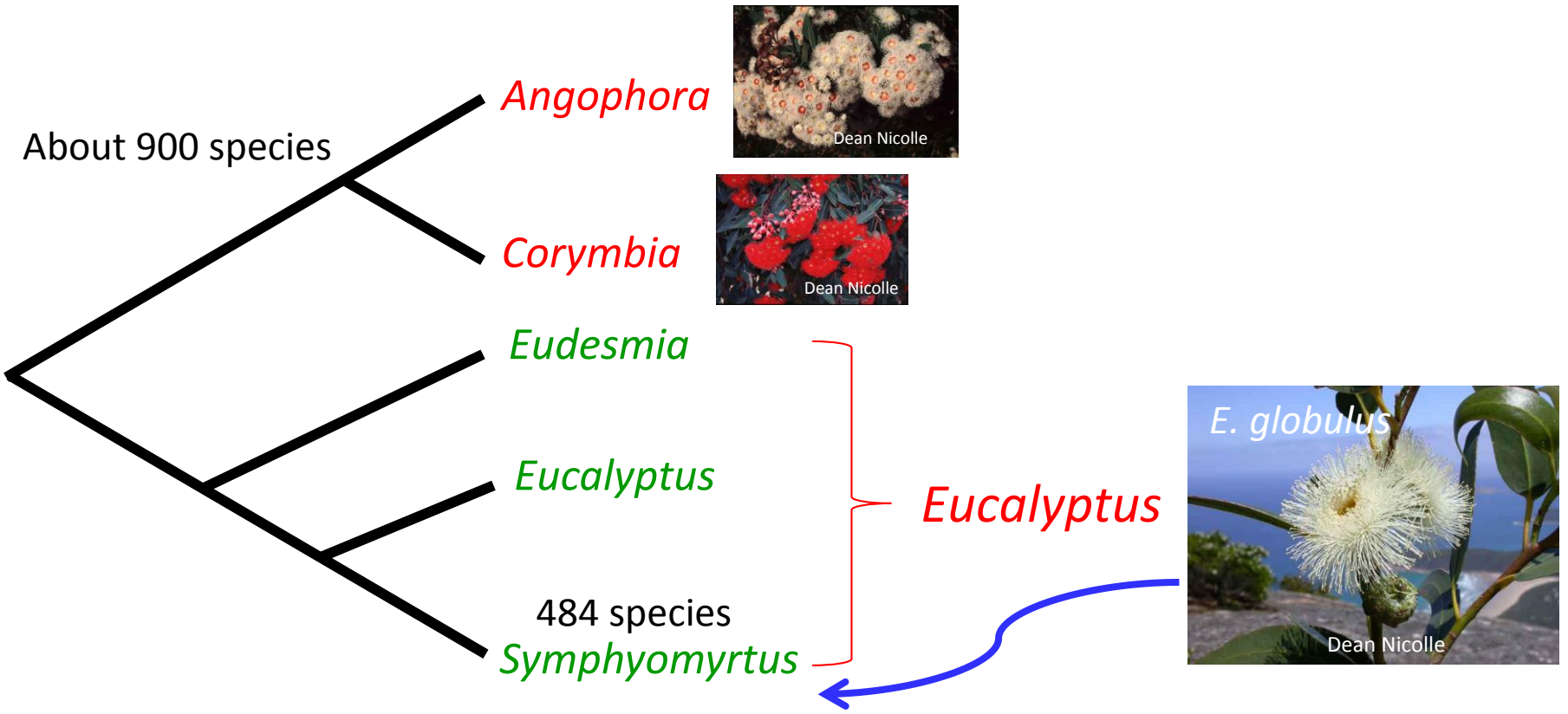




88% of plantations are adjacent to native eucalypt populations (n = 302)

Barbour *et al.* 2008, Biological conservation

Hybridisation occurs within eucalypt subgenera



- Hybridisation does not occur between genera/subgenera
- In theory, based on our current understanding of species compatibility, 484 species could be at risk of exotic gene flow from *E. globulus* plantations

We assessed patterns of post-mating isolation by combining controlled crossing and phylogenetics

Crossing:

- Currency Creek Arboretum (>900 taxa)
- > 7000 flowers crossed with *E. globulus* pollen
- 100 species
- 13 taxonomic sections
- Subg. *Symphyomyrtus* (96 spp.)
- Subg. *Eucalyptus* (2 spp.)
- Subg. *Eudesmia* (1 sp.)
- *Corymbia* (1 sp.)

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- *Corymbia* (1 sp.)

Phylogenetics:

Two datasets based on genome-wide DArT markers:

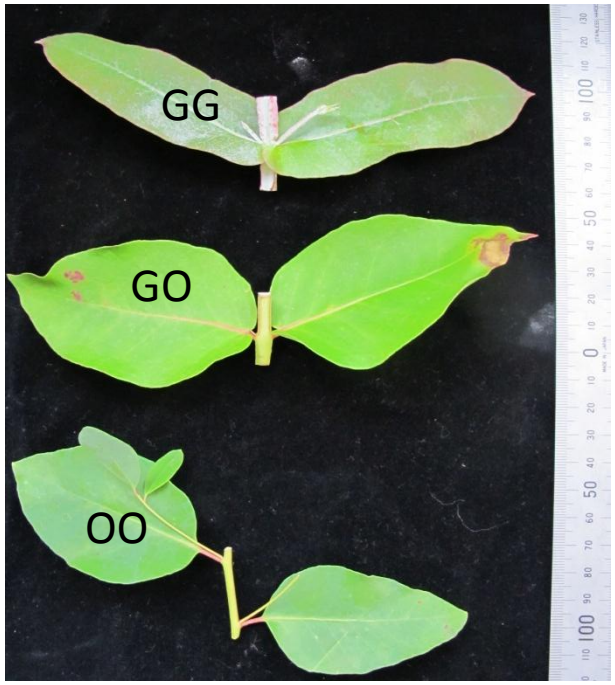
(1) 8350 markers covering all sections but not all species

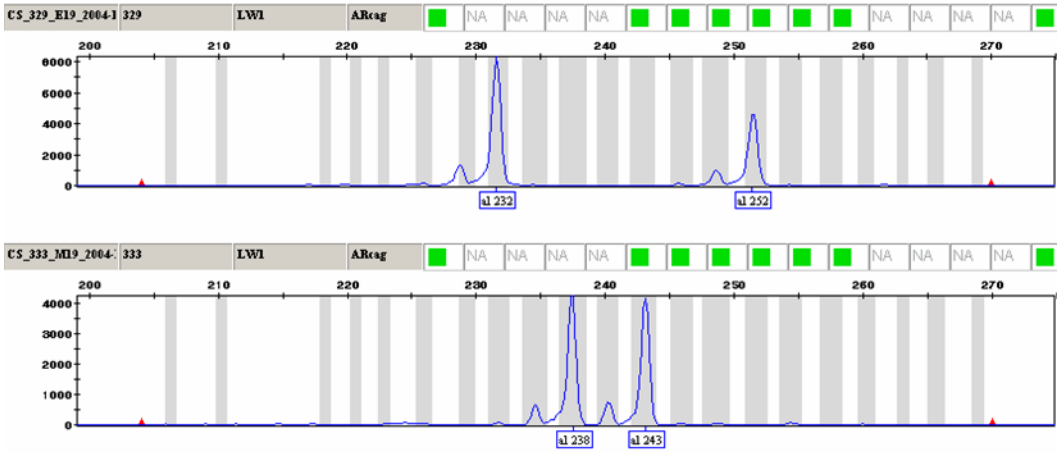
(2) 5050 markers covering ca. 200 spp. (Sections *Maidenaria*, *Latoangulatae* and *Exertaria*) including the 22 most closely related species in this study

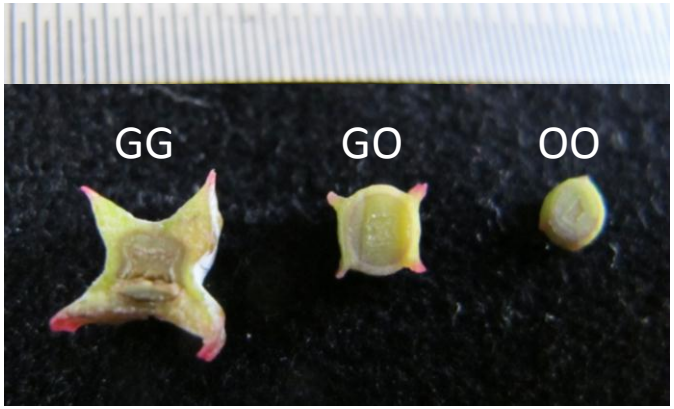
Two crossing approaches

- "**Supplementary**" pollination mimics natural pollination
- "**Cut-style**" pollination avoids (pre-zygotic) incompatibilities in the style and receptivity problems

Hybrids identified with morphology and validated with molecular markers



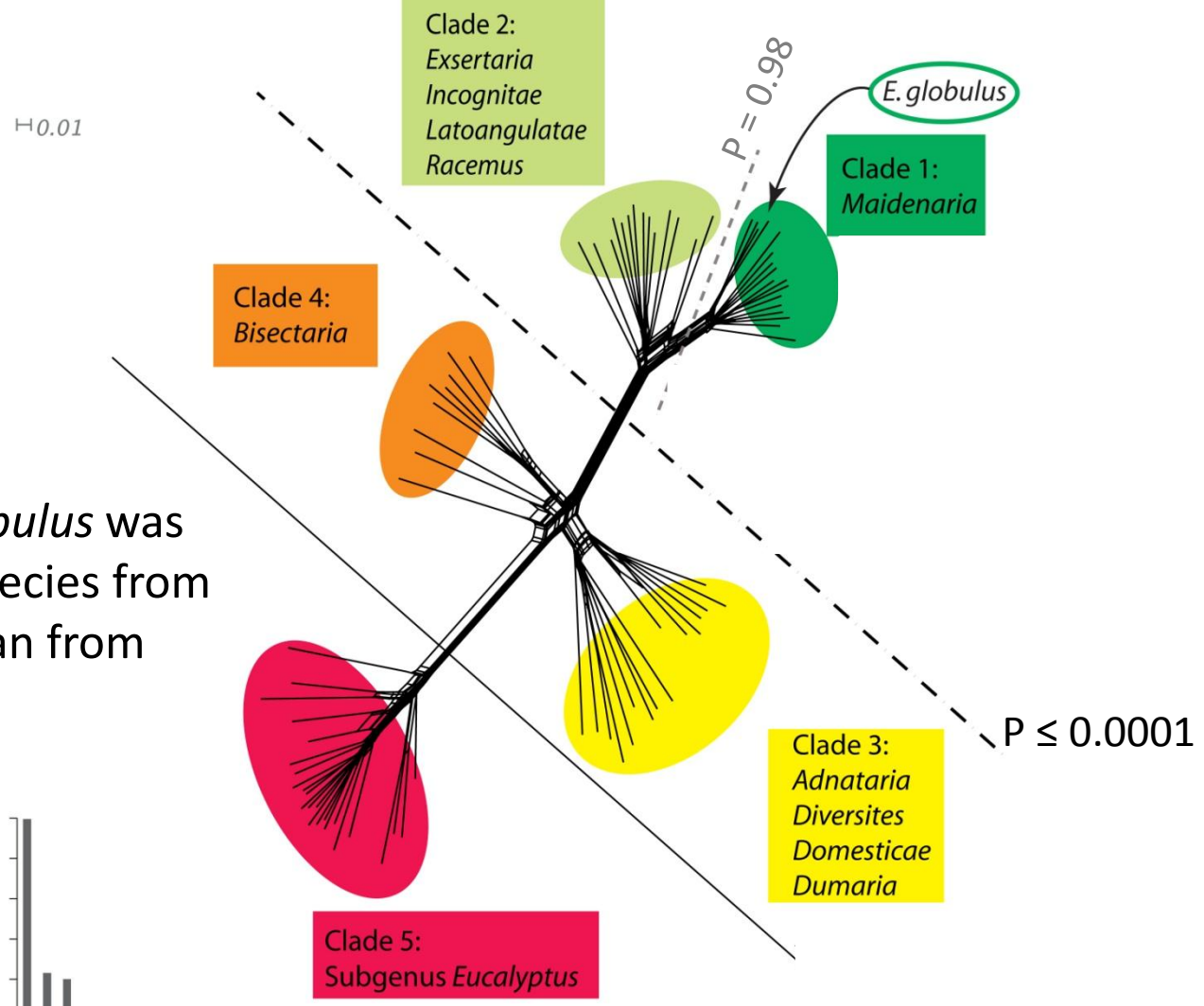


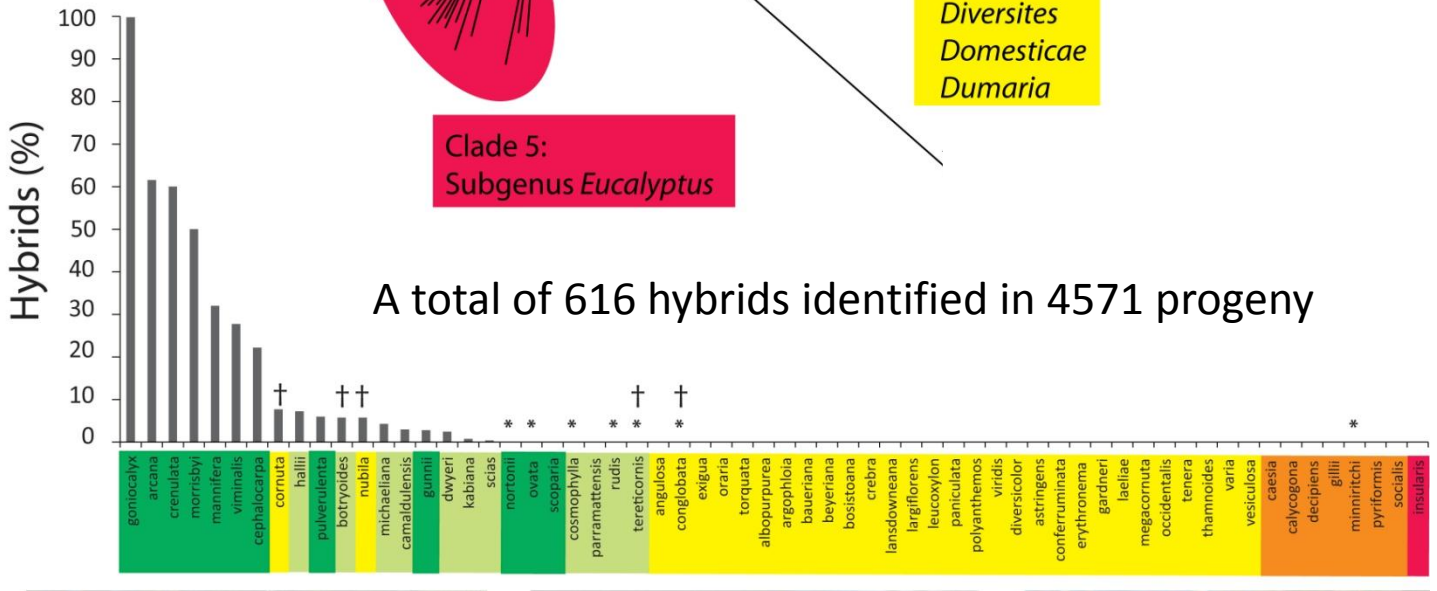


10 microsatellite loci were used to match alleles from each parent in hybrids

Hybrid success reflects phylogenetic relatedness

Hybridisation with *E. globulus* was more common among species from Clades 1 & 2 (22 spp.) than from Clades 3 & 4 (4 spp.)





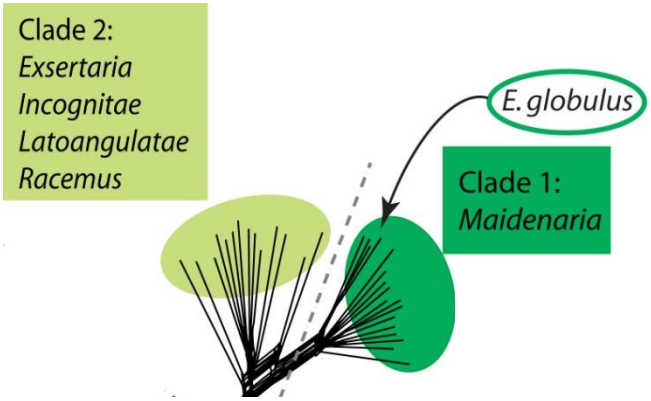
A total of 616 hybrids identified in 4571 progeny

* Hybrids from CS pollination only (not supplementary pollination)

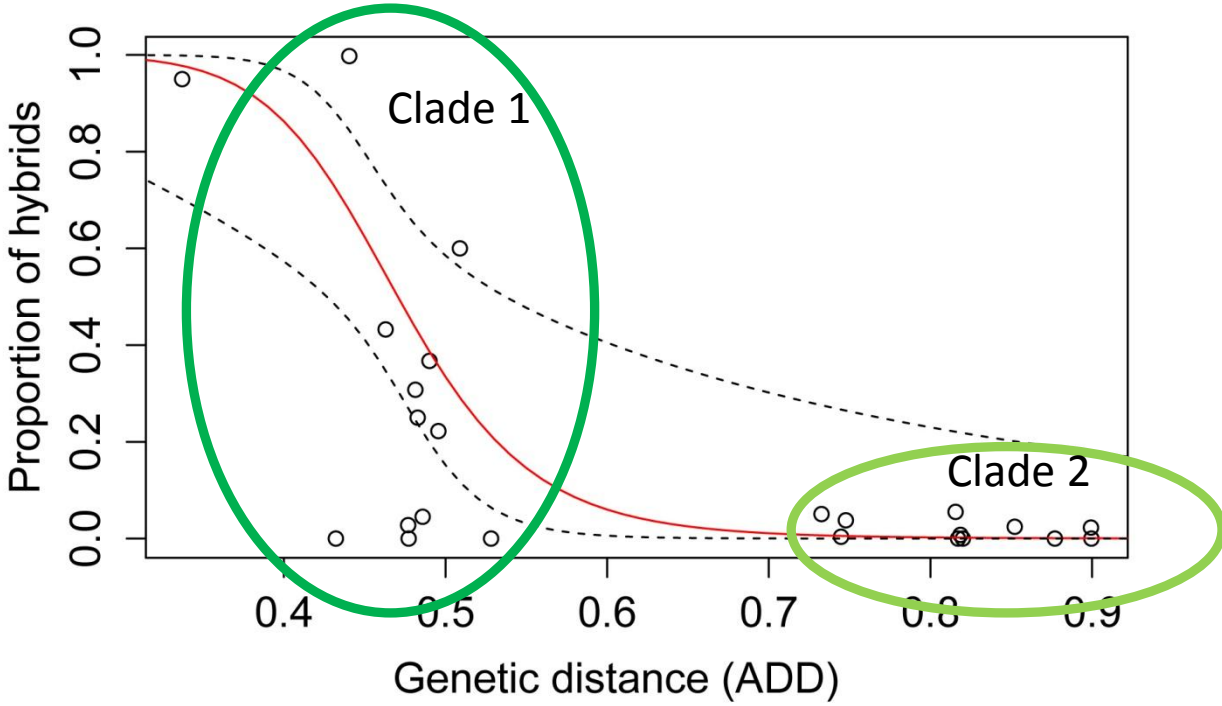
† Complete hybrid mortality

Hybrid success highest within Clade 1

- No difference between Clade 1 and Clade 2 in the *number of taxa* producing hybrids (*P* = 0.98)
- *Proportion* of hybrids produced (via supplementary pollination) is higher in Clade 1



Genetic distance explains 69 % of the variation (*P* = 0.01)

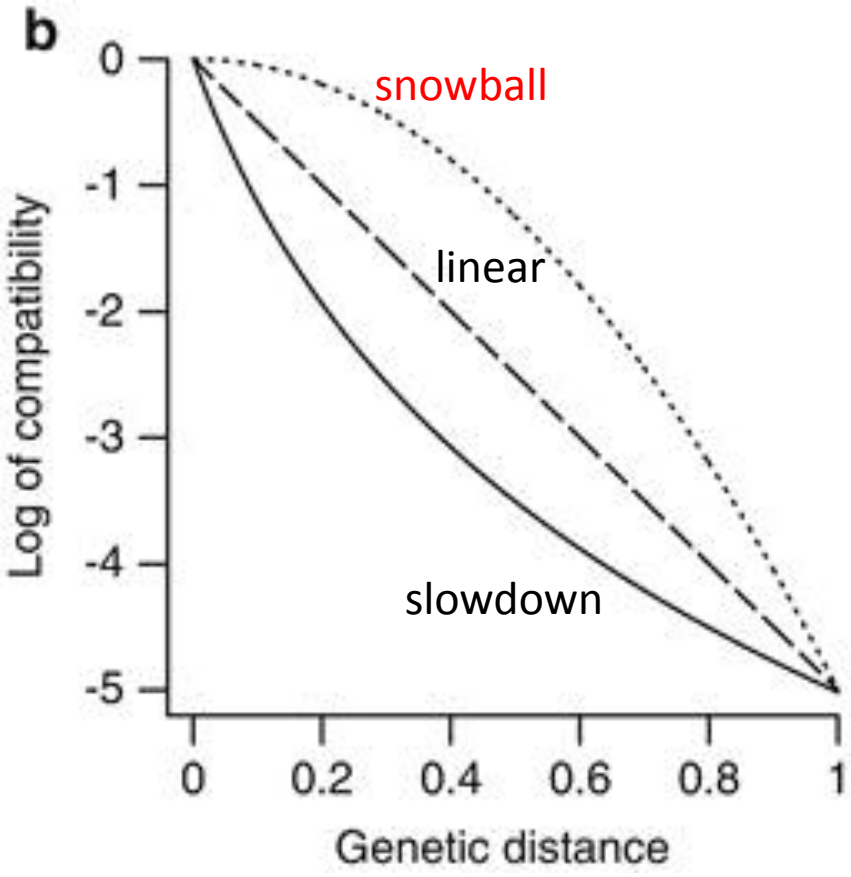


Do the results fit the Bateson-Dobzhansky-Muller (BDM) model?

BDM= “snowball model” – isolation accelerates with increasing divergence (DRIFT)

Genomic rearrangements = “linear model”

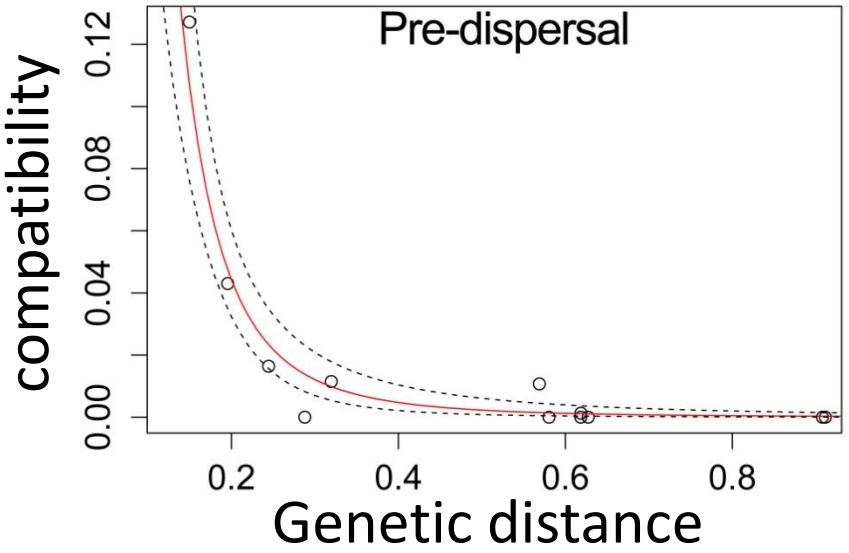
Reinforcement = “slowdown model” (SELECTION)



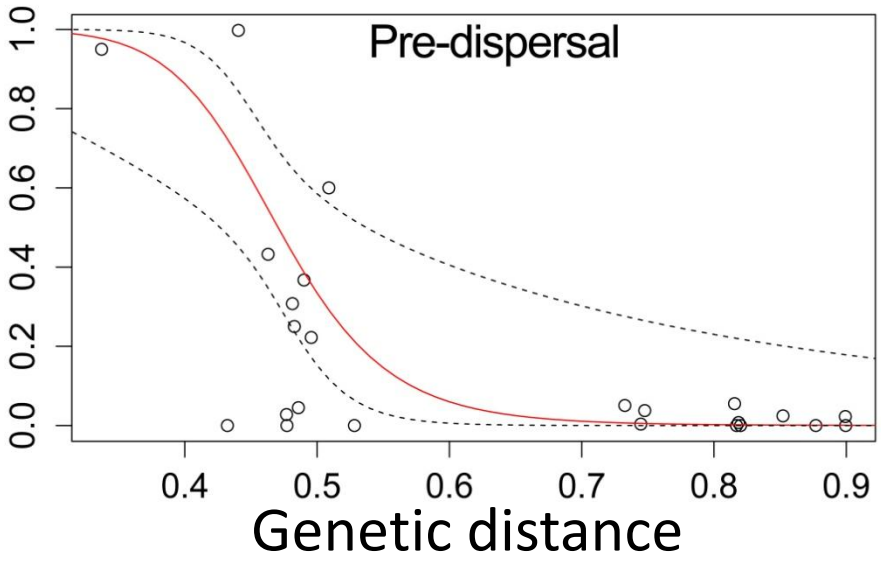
Pre-dispersal: Eucalypts do not conform to BDM model

- Opposite to what would be expected under BDM
- Consistent with a ‘slowdown’ model
- Selection acting to form pre-zygotic barriers
- Pollination and fertilisation may occur but seed is not formed
- Prevents formation of unfit hybrids

All clades



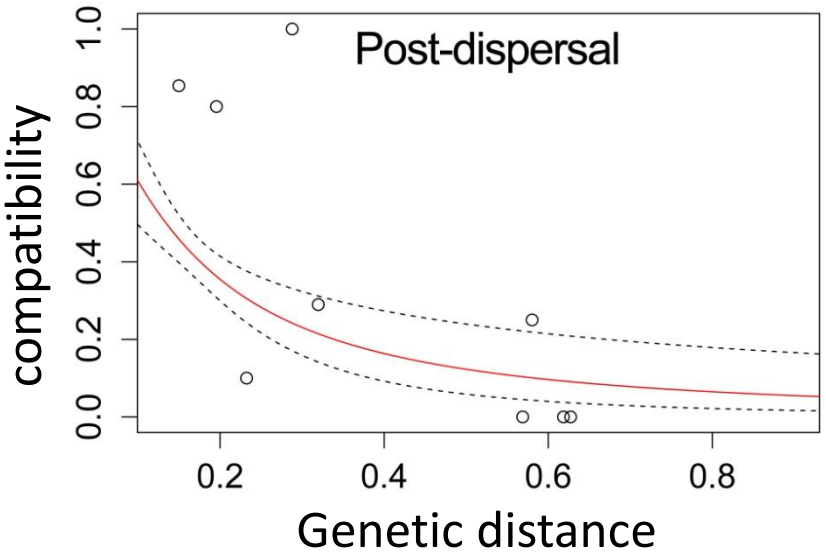
Clades 1 and 2



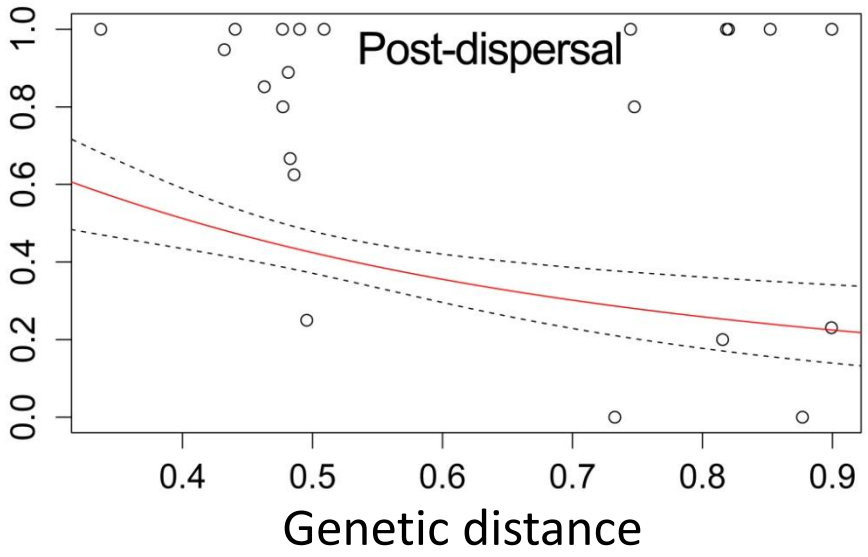
Post-dispersal:
Eucalypts still don't conform to BDM model …

- Measured as survival at one year.
- More linear (?) pattern of compatibility could suggest genomic rearrangement model … ??? (more likely 'slowdown' model?)
- Few studies have found 'snowball' effect (BDM)
- BDM model may be too simplistic

All clades

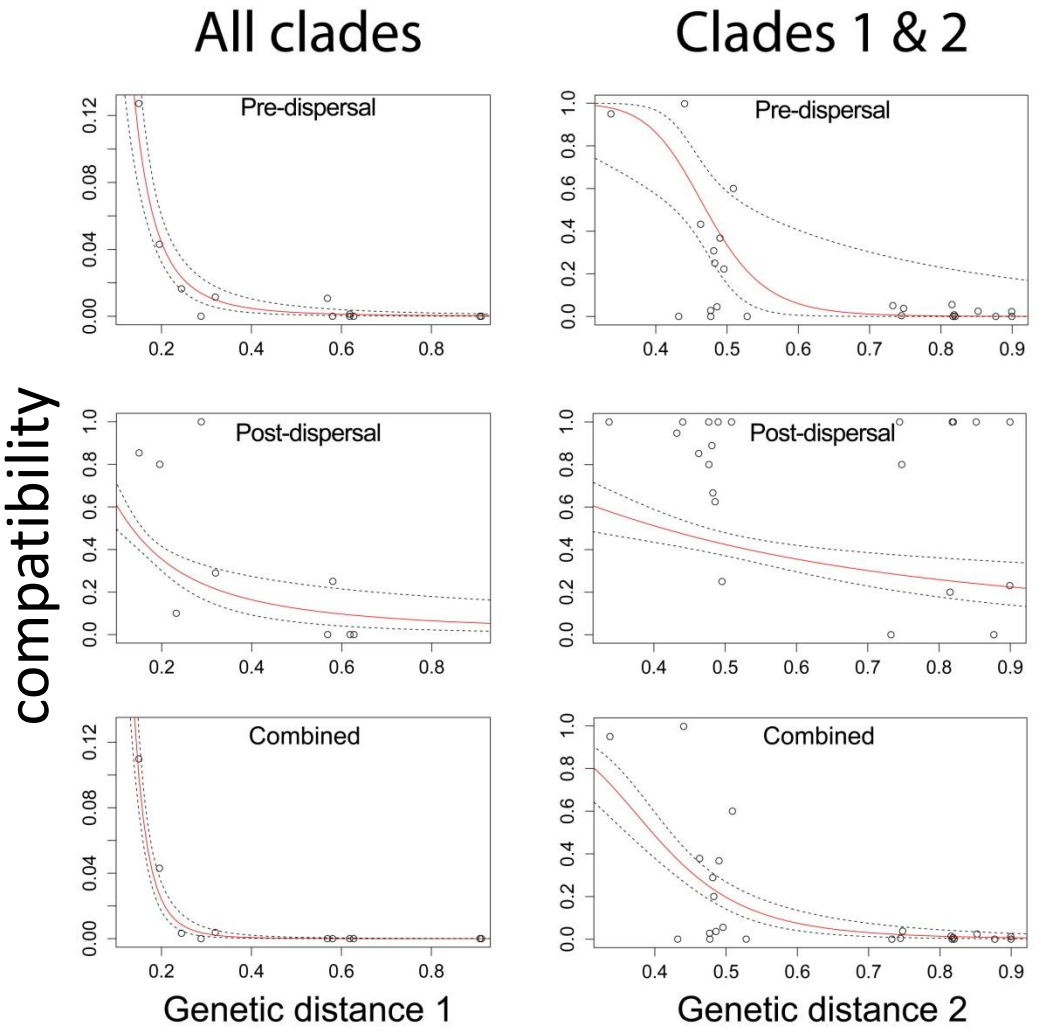


Clades 1 and 2



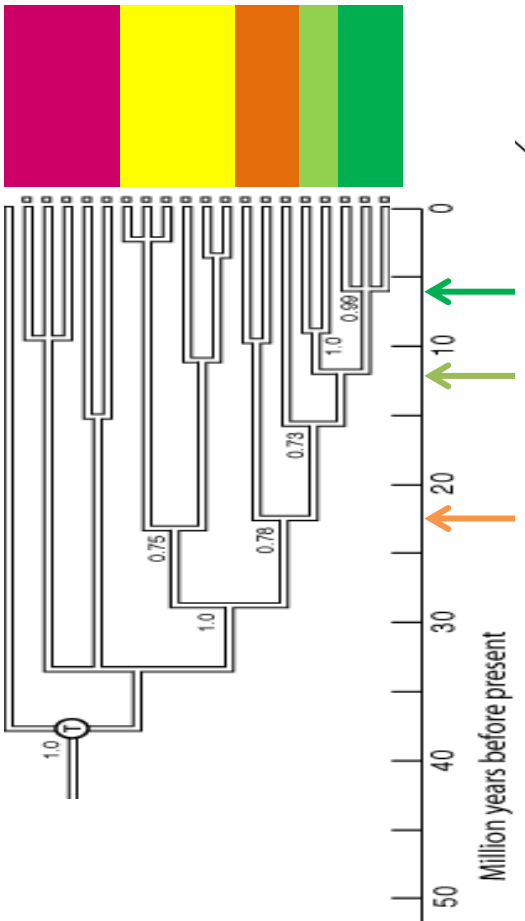
Overall, eucalypts display a ‘slowdown’ (reinforcement) model of hybrid compatibility

- Natural selection on traits that affect reproductive success should evolve faster than reproductive barriers developing via drift (BDM)



What is the timeframe for reproductive isolation in *Eucalyptus*?

Dated eucalypt phylogeny (Crisp *et al.* 2011)



Clade 2:
Exsertaria
Incognitae
Latoangulatae
Racemus

E. globulus

Clade 1:
Maidenaria

← Crossability = 0.546 (0.464)
50% takes 3-10 mya

Clade 4:
Bisectaria

← Crossability = 0.045 (0.036)
95% takes 10-15 mya

← Crossability = 0.006 (0)
100% takes 21-31 mya

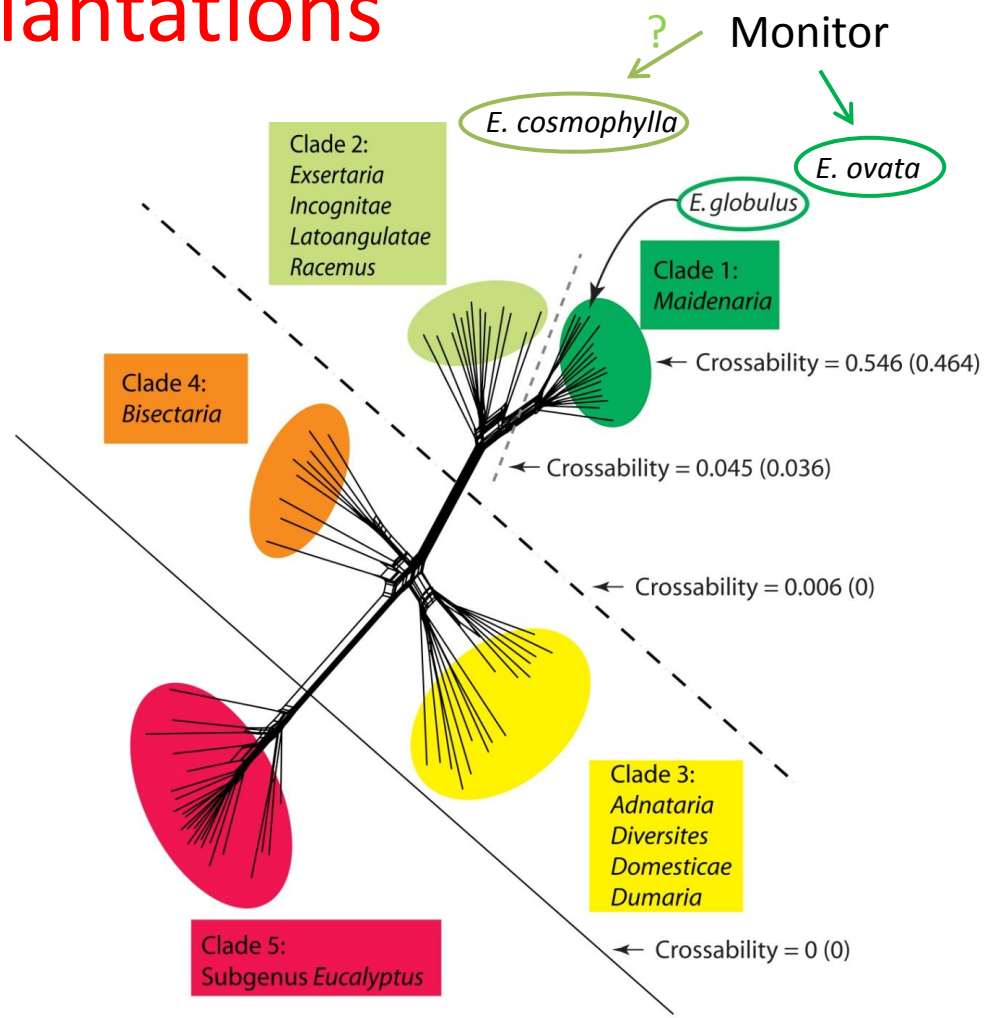
Clade 3:
Adnataria
Diversites
Domesticae
Dumaria

Clade 5:
Subgenus *Eucalyptus*

← Crossability = 0 (0)

The risk of exotic gene flow from *E. globulus* plantations

- Previously 484 'at risk' species (within Subg. *Symphyomyrtus*)
- Clades 3 & 4 are isolated, leaving 138 'at risk' species
- The 70 species in Clade 2 have a 45% lower risk than the 68 species in clade 1



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