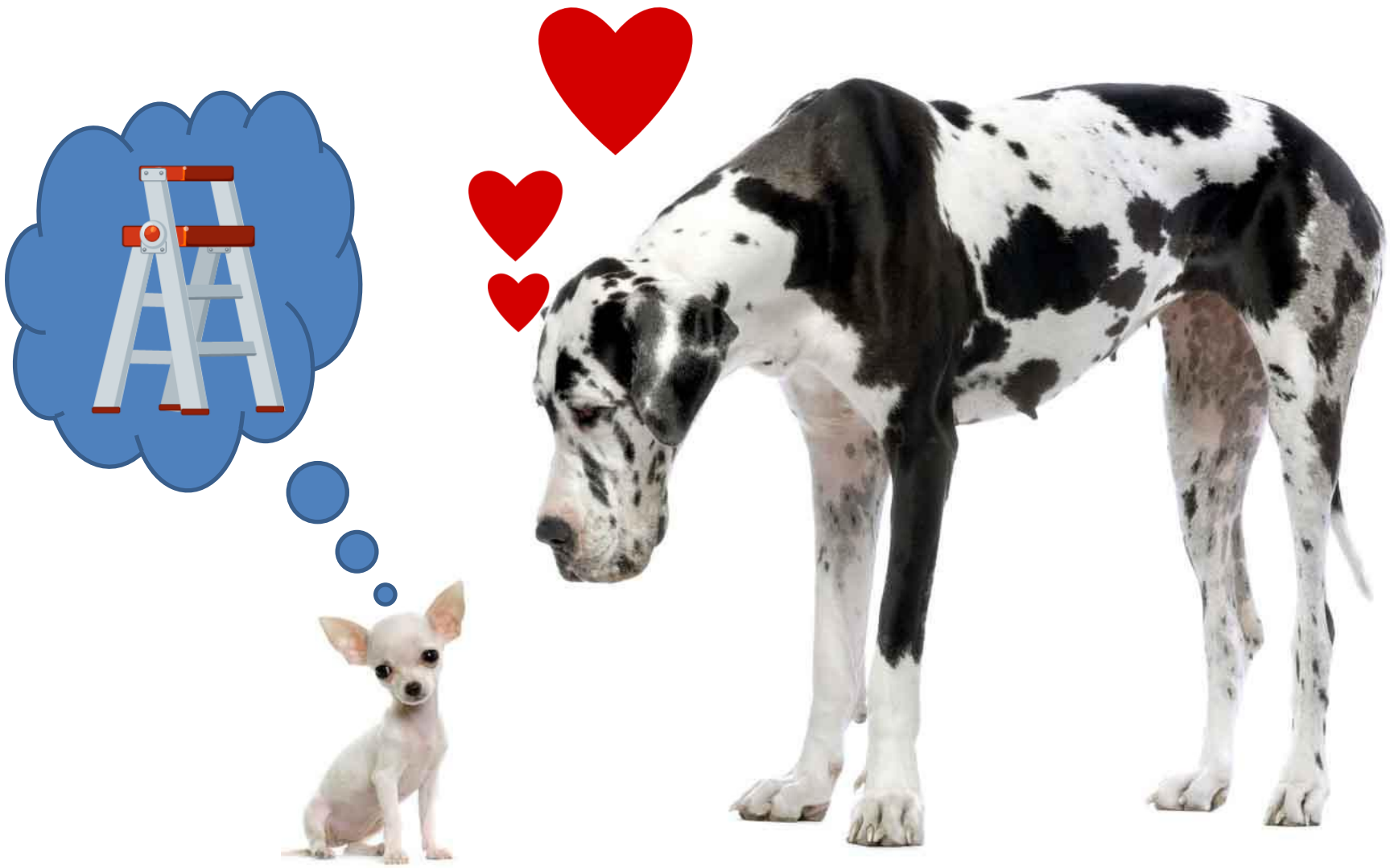
The search for the missing snowball in Eucalyptus

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

UTAS

Reproductive isolation is central to speciation



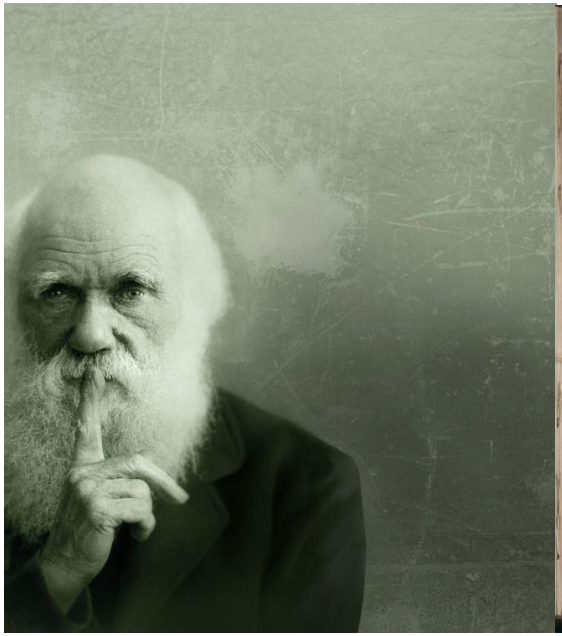
There is an obvious relationship between reproductive isolation and genetic divergence

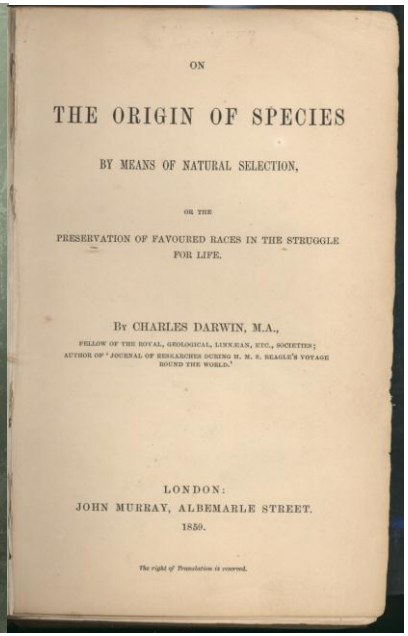
Low → **Reproductive isolation** → High

?

Low → **Genetic divergence** → High

One key question is what causes hybrid incompatibility





ON

THE ORIGIN OF SPECIES

BY MEANS OF NATURAL SELECTION,

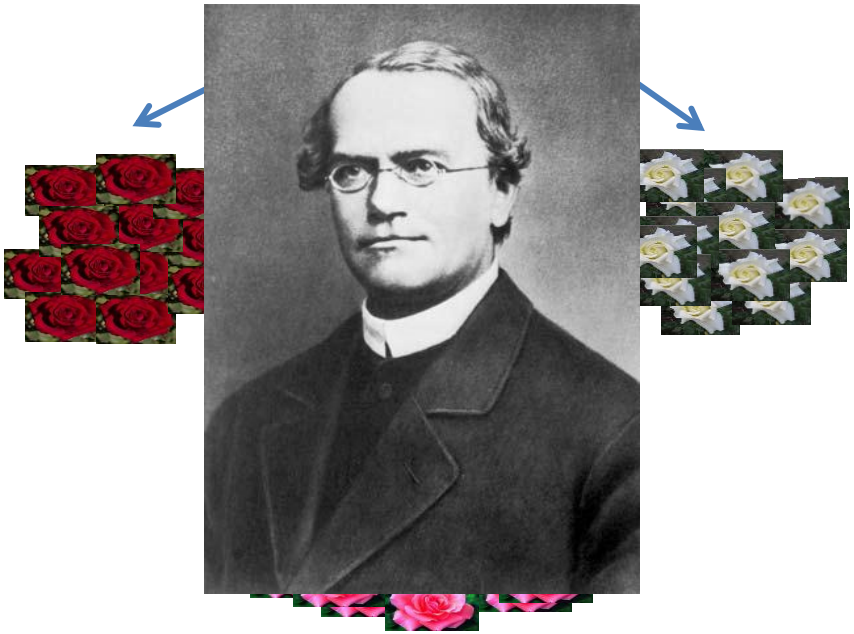
OR THE

PRESERVATION OF FAVOURED RACES IN THE STRUGGLE FOR LIFE.

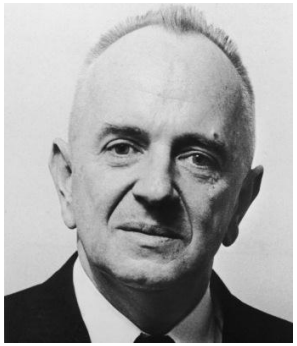
By CHARLES DARWIN, M.A.,

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

LONDON:
JOHN MURRAY, ALBEMARLE STREET.
1859.



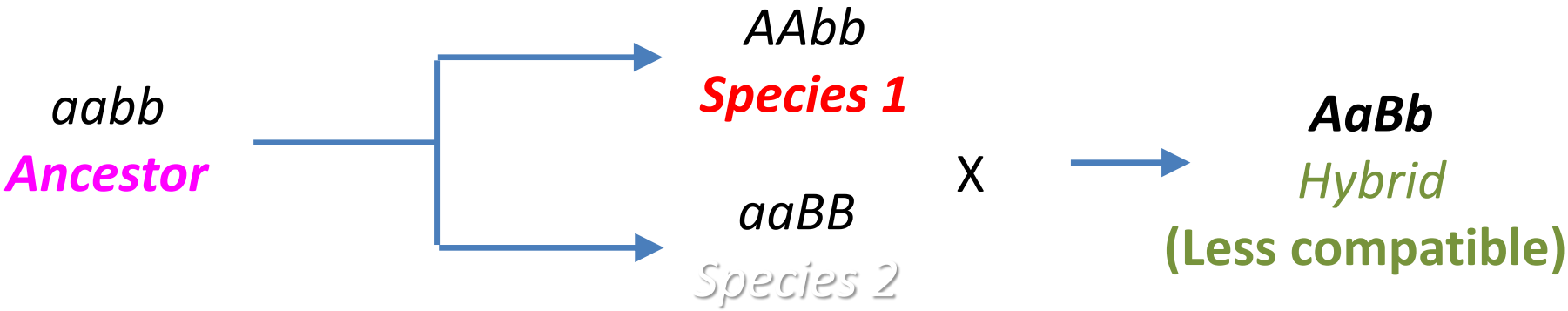
Bateson 1909



Dobzhansky 1937

Muller 1942

Bateson-Dobzhansky-Muller (BDM) model of incompatibility



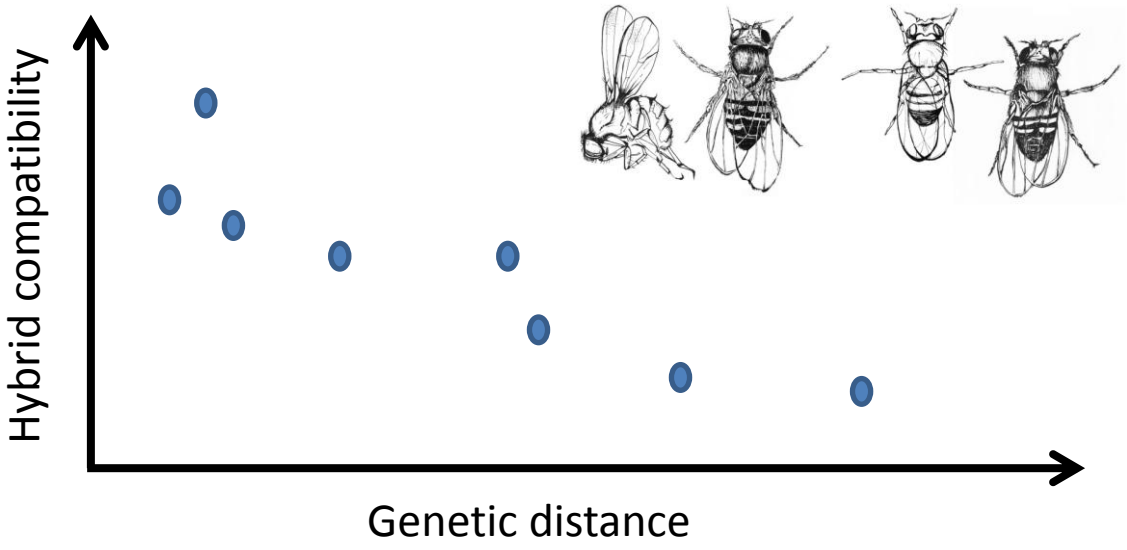
1. Minor allelic differences accumulate via drift
2. New allele combinations cause incompatibilities in hybrids
3. These accumulate over time (since divergence)
4. Ultimately lead to complete reproductive isolation

BDM model: predictions

1. Hybrid compatibility should decline with increasing divergence (genetic distance)
2. Intrinsic postzygotic barriers (BDM incompatibilities) should evolve more slowly than prezygotic barriers under selection
3. Due to negative epistasis the rate that hybrid incompatibilities accumulate should accelerate relative to the time since divergence leading a "**snowball effect**"

Tests of the BDM model - comparative studies

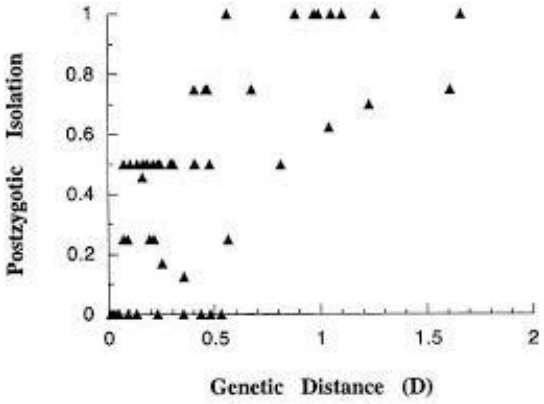
Comparative studies contrasting hybrid compatibility across linages with genetic distance are used to test the predictions of the BDM model



Lots of support for the first two BDM predictions

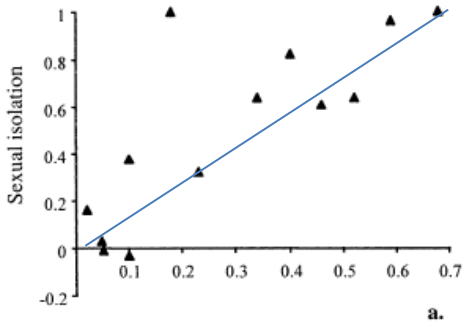
BDM prediction 1:

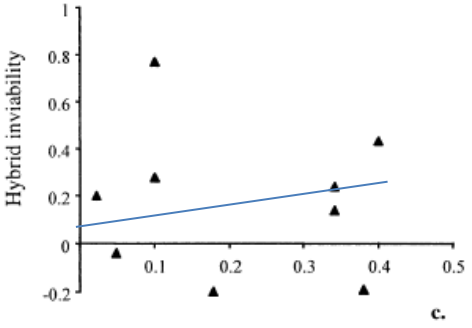
- Fruit fly's
- Birds
- Butterflies and moths
- Frogs
- Fish
- Orchids
- Catchfly
- Sunflowers
- .....



BDM prediction 2:

- Partridges
- Fruit flies
- Fish





But evidence for the third prediction is scarce

COMMENTARY

doi:10.1111/j.1558-5646.2009.0084

ARE SPECIES REAL? THE SHAPE OF THE SPECIES BOUNDARY WITH EXPONENTIAL FAILURE, REINFORCEMENT, AND THE "MISSING SNOWBALL"

Sébastien Gourbière[1,2] and James Mallet[3,4]

Dispatch
R1073

Speciation Genetics: Search for the Missing Snowball

Theory predicts that, as species diverge from one another, the number of genetic incompatibilities causing sterility or inviability in interspecies hybrids grows faster than linearly, or snowballs. Two new genetic analyses now provide the first empirical support for this snowball effect.

Daven C. Presgraves

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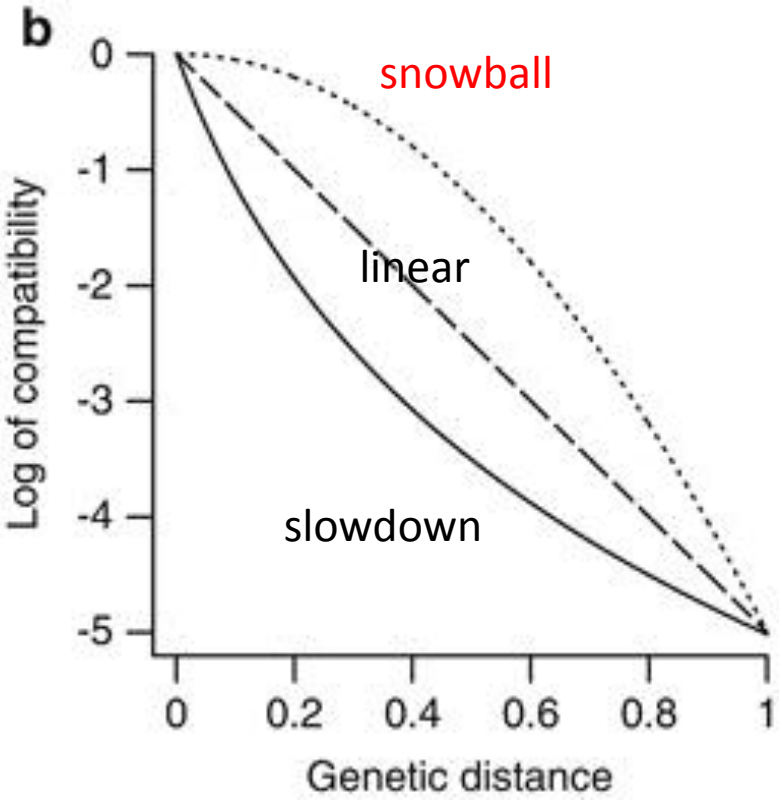
So where is the missing snowball?

G&M 2010 propose two alternative modes of evolution and a method for comparing :

1. Snowball = drift with epistasis

2. Linear = drift without epistasis

3. Slowdown = selection (reinforcement) without epistasis



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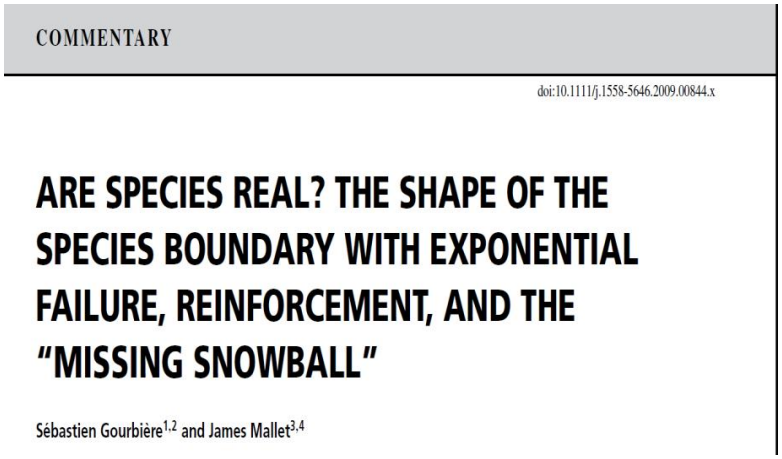

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The G&M approach has been tested in:

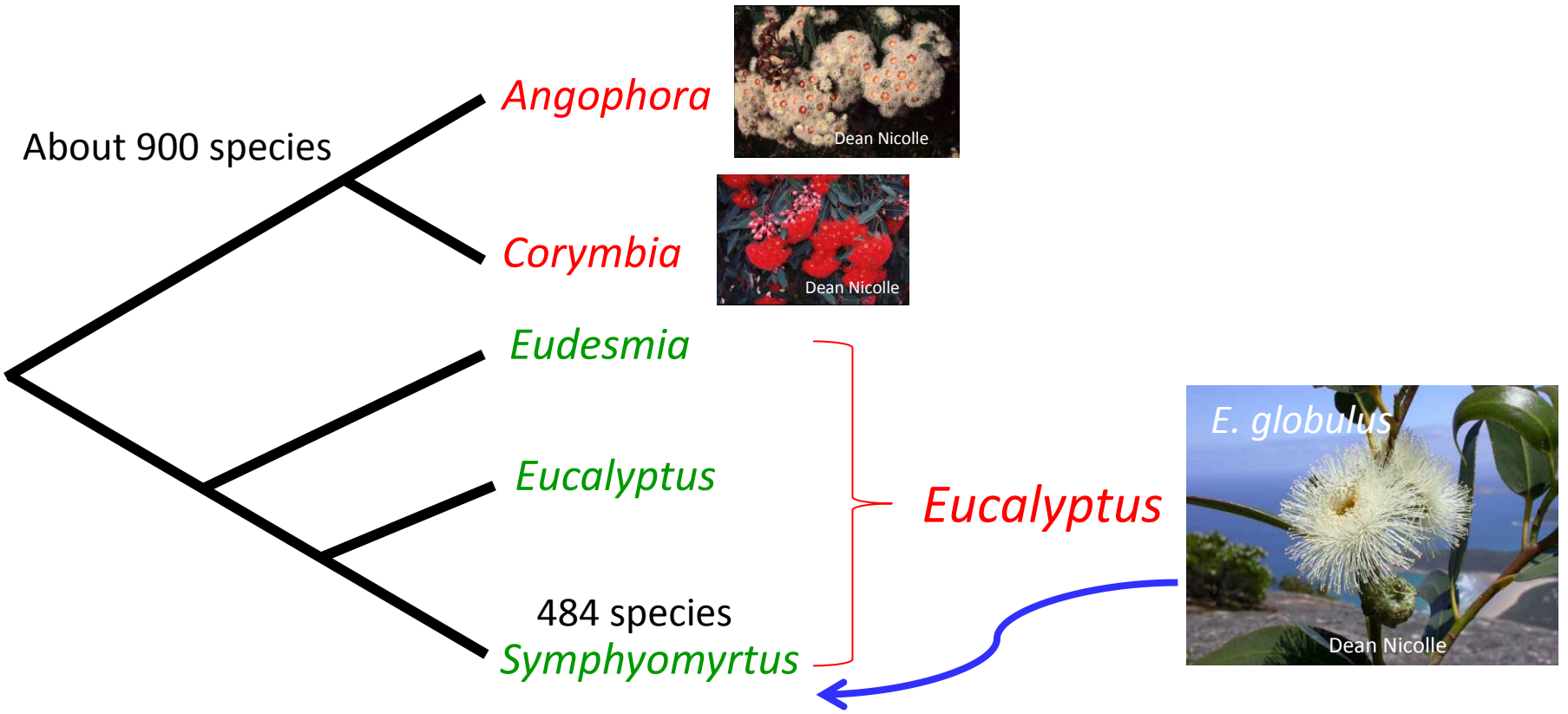
- Bacteria
- Fungi
- Fruit fly
- butterflies
- Shrimps
- Starfish
- Frogs
- Birds

Only minor support for the snowball effect in butterflies

But G&M noted some potential issues with their least-squares modelling approach:

- Uses log-compatibility meaning zeros need replacing
- Uses proportions so doesn't account for variation in effort
- Assumes normally distributed residual errors
- It is difficult to test differences between un-nested models

Hybridisation in eucalyptus



- Hybridisation does not occur between genera/subgenera but can occur within subgenera

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.)

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

Crossing:

Dorothy Steane

- Curren… …tum
- > 7000 …d
- 100 sp…
- 13 taxonomic sections
- Subg. S… …(96 spp.)
- Subg. E… …p.)
- Subg. E…
- *Corymb*…

Rebecca Jones

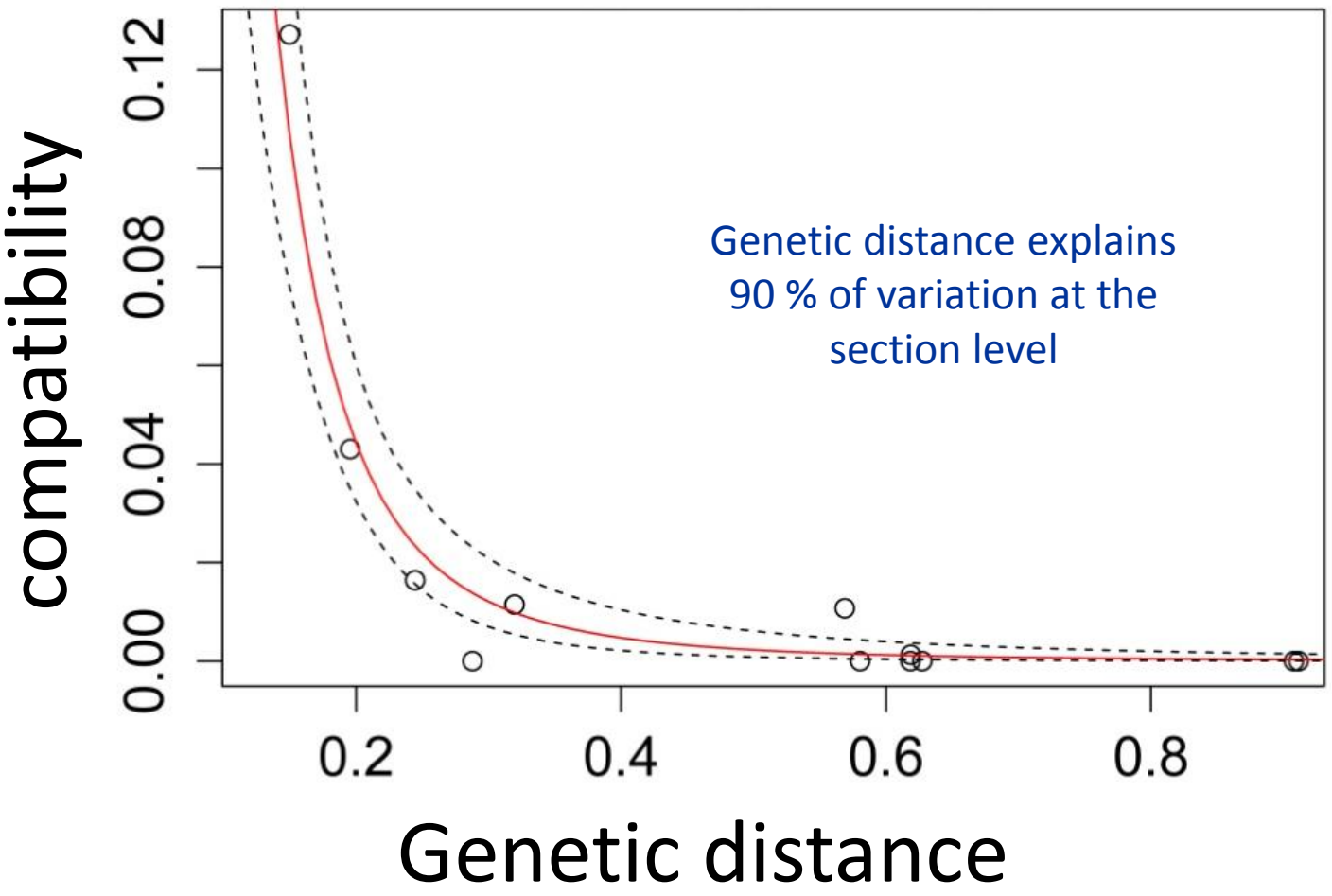
Phylogenetics:

Genome-wide DArT markers:

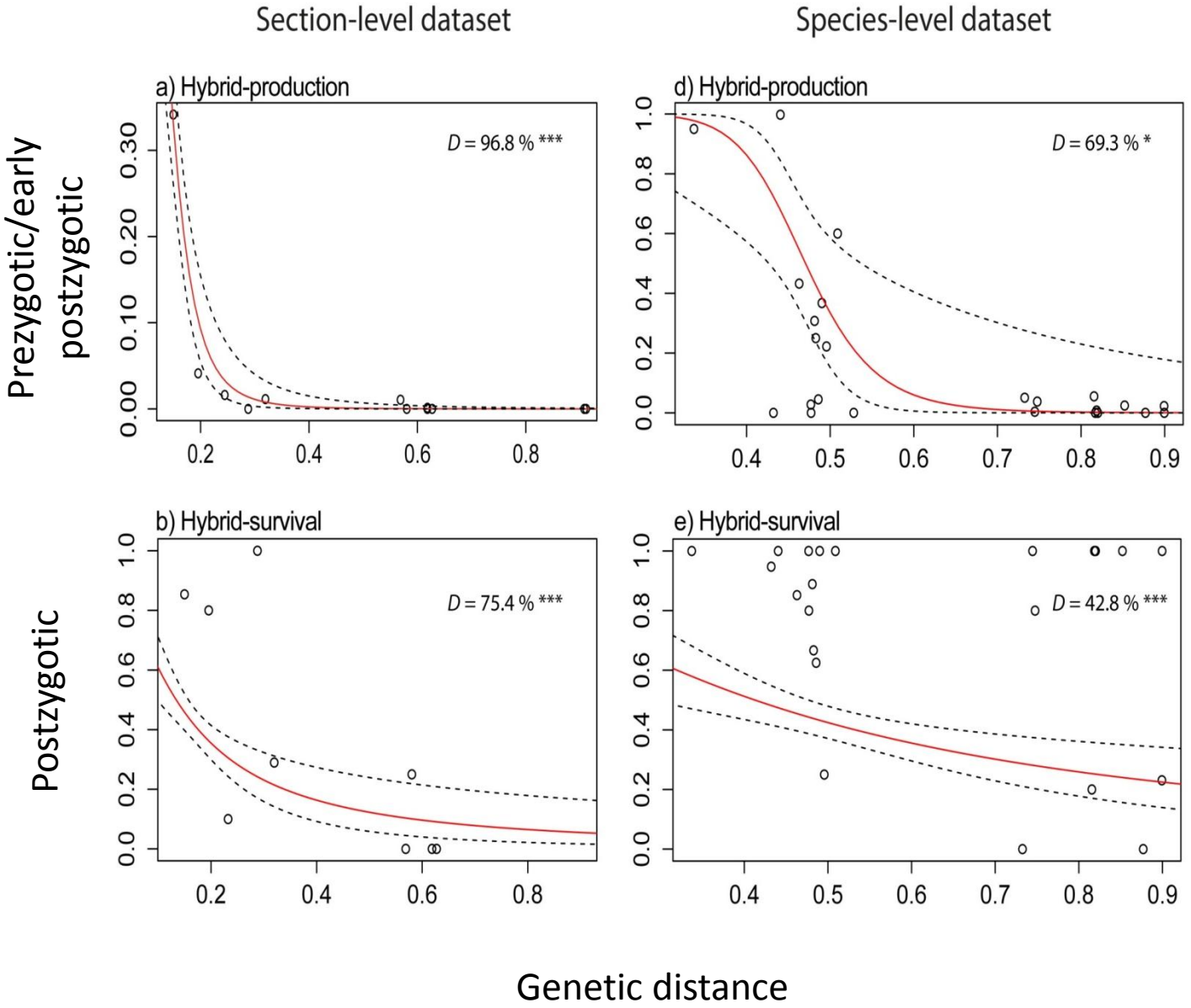
(1) 8350 markers covering all sections but not all species

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

Compatibility declines as genetic distance increases



Postzygotic barriers develop more slowly than prezygotic barriers



Improved modelling approach to test for the snowball effect

Barbara developed an equivalent modelling approach G&M, but using maximum likelihood instead of least-squares, that:

- took into account variation in hybridisation attempts
- could cope with zeros
- could cope with non-normal residual errors
- and enabled more simple model comparison through AIC

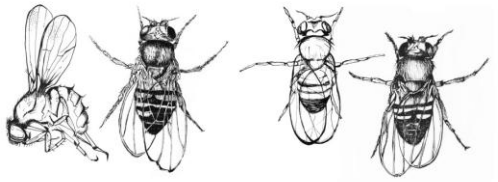
It seems we found the snowball!

Comparison/dataset	Model	AIC	w_i
Prezygotic/section-level	linear	2017.2	0.000
	snowball	**1754.0**	**1.000**
	slowdown	1952.0	0.000
Postzygotic/section-level	linear	214.9	0.000
	snowball	**197.4**	**0.997**
	slowdown	208.9	0.003
Combined/section-level	linear	1812.7	0.000
	snowball	**1508.1**	**1.000**
	slowdown	1741.4	0.000
Prezygotic/species-level	linear	2019.5	0.000
	snowball	**1556.7**	**1.000**
	slowdown	1574.7	0.000
Postzygotic/species-level	linear	209.8	0.000
	snowball	**190.7**	**0.754**
	slowdown	192.9	0.246
Combined/species-level	linear	1995.1	0.000
	snowball	**1491.0**	**0.996**
	slowdown	1502.3	0.004

The *number* (as apposed to the strength) of incompatibilities has been shown to snowball

A Test of the Snowball Theory for the Rate of Evolution of Hybrid Incompatibilities

Daniel R. Matute, Ian A. Butler, David A. Turissini, Jerry A. Coyne



Hybrid Incompatibility "Snowballs" Between *Solanum* Species

Leonie C. Moyle[1] and Takuya Nakazato[1,2]

The number and the strength are not the same thing

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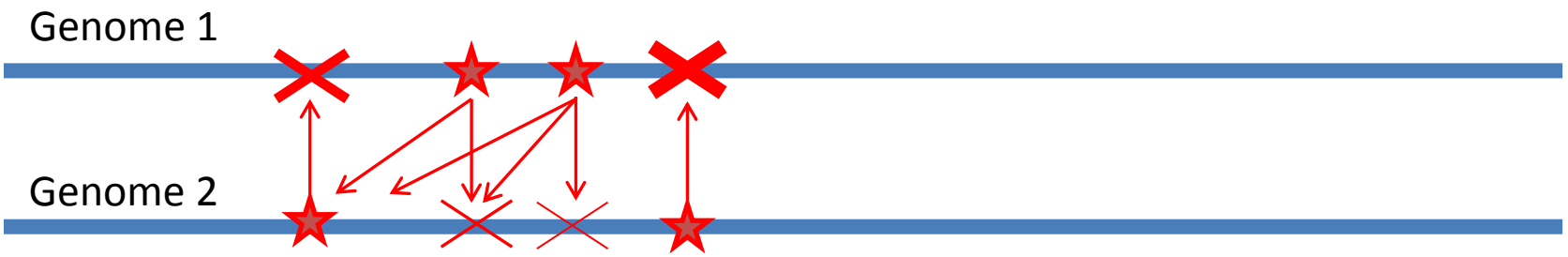

Strength is a poor proxy for the number of incompatibilities

Conclusion

- We have shown that the strength as well as the number of incompatibilities can snowball with divergence.
- Which may suggest, that in *Eucalyptus,* divergence is driven by many genes of small effect, in line with the BDM model.

Thanks to:
Forest and Wood Products Australia,
Cooperative Research Centre for Forestry
Guy and Simone Roussel and
James worth

The effect of Zeros, number of hybridisation attempts