OEB 140 Genetics, Genomics and Evolution

Evolution in space and time:

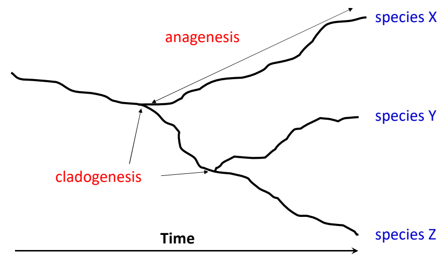
Population structure, gene flow, clines, hybrid zones

Spatial evolution across the geographic range of species

Importance for speciation

1

Phylogenetic tree with anagenesis and cladogenesis



anagenesis: evolution within lineages
vs.
cladogenesis: splitting of lineages, *speciation*

microevolution
vs.
macroevolution

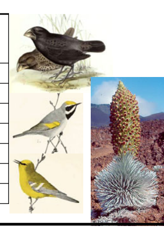
2

Speciation is hard to study. Why?

Because evolution is slow

The fossil record shows that morphological evolution is generally slow (although potentially fast under natural or artificial selection). *Speciation tends to be even slower!*

Taxon	Speciation interval (millions of years)
Galápagos finches	0.8-1.1
Dendroica warblers (New World)	0.8
Mammals	4.5
Primates	2.9-14.2
Ferns (Pteridophyta)	8.5-12.5
Flowering plants (Angiospermae)	11.2-13.0
Hawaiian flowering plants	0.5-5.0



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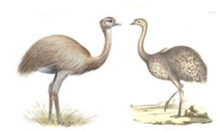
Clues to the study of speciation

A useful 'law' first enunciated by Alfred Russel Wallace

A.R. Wallace, 1855: "On the law which has regulated the introduction of new species." … "The following law may be deduced: –

Every species has come into existence coincident both in space and time with a pre-existing closely allied species."



By studying genetic variation and species in *space*, we may be able to understand a little more about genetic divergence and speciation *in time*.

4

"The law which has regulated the introduction of new species"

Why?

Plains Zebra, *Equus quagga burchelli* vs. Grévy's Zebra, *Equus grevyi*

Red Kangaroo, *Macropus rufus* vs. Eastern Grey Kangaroo, *Macropus giganteus*

Rhea americana vs. Rhea pennata

5

Clues to the study of speciation

"D.S. Jordan's Law" (1905) of geographic isolation

Jordan, a proponent of gradualistic Darwinism at a time when it was under attack from the Mendelians, argued that:

"Given any species in any region, the nearest related species is not likely to be found in the same region nor in a remote region, but in a neighboring district separated from the first by a [geographic] barrier of some sort"

In a sense Jordan's law seems like almost the opposite of Wallace's law, but by using "neighboring" he did not really disagree with Wallace.

Jordan knew of exceptions, but had fired the first shot in the debate over the importance of geographic isolation in speciation.

6

Geographic proximity of populations

Geographic relations can be classified into two major modes:

1. Local overlap, sympatry

Populations are said to be sympatric or in sympatry if they are in the same *neighborhood population*, because they overlap within *"cruising range,"* or *dispersal range.*
Example: Cardinals and Blue Jays in Cambridge, Mass.

2/10/2025 7

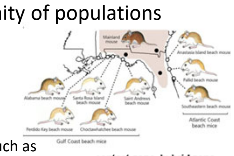
7

Geographic proximity of populations

2. Geographic separation

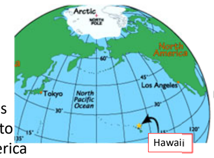
a) Parapatry

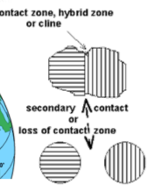
Populations in contact at edges, such as beach mice of Florida and Alabama



b) Allopatry

Populations are not in contact, such as island populations, as in Hawaii compared to mainland North America





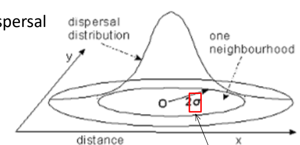
2/10/2025 8

8

Why does geography matter?

Because dispersal is limited! Dispersal and gene flow is often misunderstood, even by some evolutionists

Population geneticists often call dispersal *migration*, but do not mean the kind where birds return after migration to near their parents nest!



Dispersal by individuals leads to *gene flow* (though we usually mean *genotype flow*)

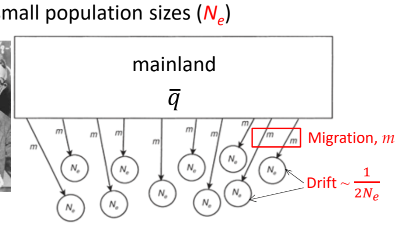
Gene flow can prevent divergence due to selection, drift

2/10/2025 9

9

Migration/drift balance in Sewall Wright's "island model" of population structure

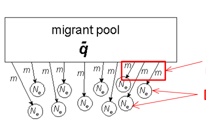
Migration (measured as a fraction *m* of each population per generation) from a "mainland" can balance drift on islands with small population sizes (N_e)



2/10/2025 10

10

Migration/drift balance: Sewall Wright's "Island model"



F measures identity by descent, and homozygosity

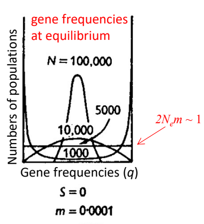
Migration, m, fraction of migrants in population

Drift ~ $\frac{1}{2N_e}$

At equilibrium: $F \approx \dfrac{1}{1+4N_e m}$

If $2N_e m \ll 1$ then $F \approx 1$
If $2N_e m \gg 1$ then $F \approx 0$

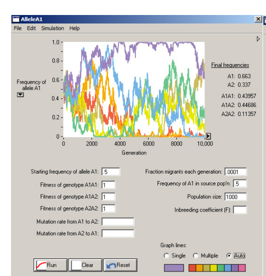
So: with no selection, *very approximately*, divergence is prevented if $2N_e m \approx 1$ - a migrant enters ea. population per gen., whatever the N_e

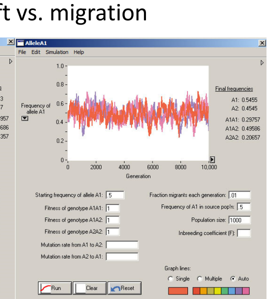


2/10/2025 11

11

Genetic drift vs. migration



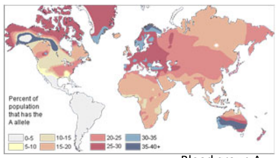


m << 1/2N_e : drift "wins," populations divergent

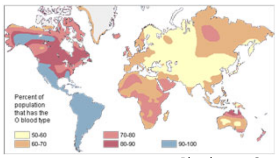
m >> 1/2N_e : migration "wins," populations are "swamped"

2/10/2025 12

12



Blood group A



Blood group O

ABO Blood groups in native human populations

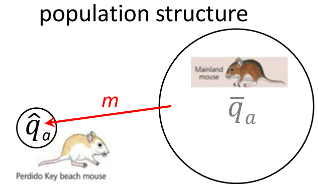
Although selection may be involved in maintaining the polymorphism, most of similarities and differences are due to migration (or lack of it)

http://anthro.palomar.edu/vary/

13

Migration/selection balance in Haldane's model of population structure

Additive selection* against *a* alleles, *s*



If $m \gg s$ then equilibrium $\hat{q} \approx \bar{q}$ -- "swamping!"

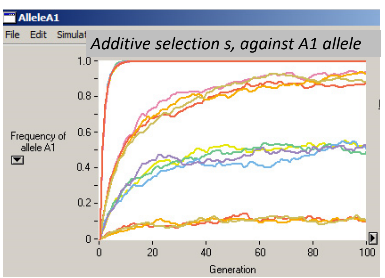
If $m \ll s$ then equilibrium $\hat{q} \approx \frac{m}{s}\bar{q}$ -- migration-selection equilibrium!

AA Aa aa

* fitnesses are 1 : 1-*s* : 1-2s

14

Selection vs. migration



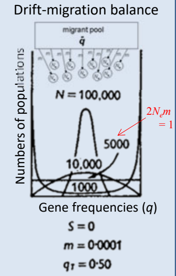
s = 0.1,
N_e = 1000, m>>1/(2N_e):
with ...
m = 0.5
m = 0.1
m = 0.05
m = 0.001

If *m* << *s* then *selection "wins," maintains divergence, q* $\approx$ *m/s*
If *m* >> s then *migration "wins", pops. are "swamped"*

15

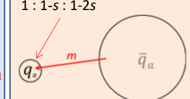
Genetic drift, selection, and migration

Drift-migration balance



Selection-migration balance

AA Aa aa
1 : 1-*s* : 1-2*s*



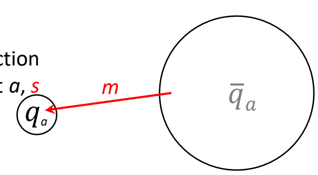
If $m \gg s$ then equilibrium $\hat{q} \approx \bar{q}$

If $m \ll s$ then equilibrium $\hat{q} \approx \frac{m}{s}\bar{q}$

16

But the previous models are rather unrealistic!

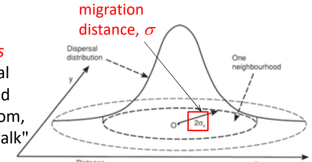
Selection against *a*, *s*



17

More realism!

migration distance, σ



Dispersal in *continuous populations.* If dispersal between birthplace and breeding site is ~ random, equiv. to "drunkards walk"

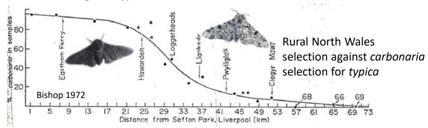
Same as passive diffusion: a *two-dimensional normal distribution.* Standard deviation, σ, of the dispersal distribution is a useful *measure of migration distance*

Sewall Wright developed this as a different model he called the "isolation by distance" model of population structure. A *"neighbourhood"* population consists of individuals who come from an area 2σ wide (86% of individuals originate < 2σ away.

18

Genetic variation across a geographic area: clines

Urban Liverpool
selection for *carbonaria*
selection against *typica*



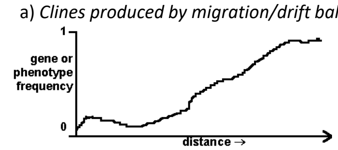
A *consistent* change in gene frequency, or heritable phenotype, across a geographical range is known as a *cline*

Clines occur because *dispersal* is limited: the whole region does not form a single *panmictic population*

19

Causes of clines

a) *Clines produced by migration/drift balance*



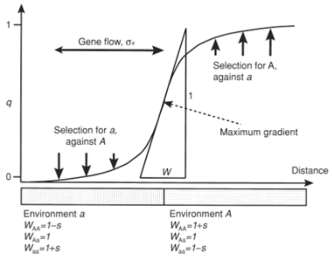
Random genetic drift : no consistent directional changes

Expect patchy polymorphic divergence

20

Clines due to migration/selection balance

b) Clines due to selection depending on environment, as in peppered moths). Selection favours different alleles in different areas; dispersal limited; frequencies may diverge → *cline*.

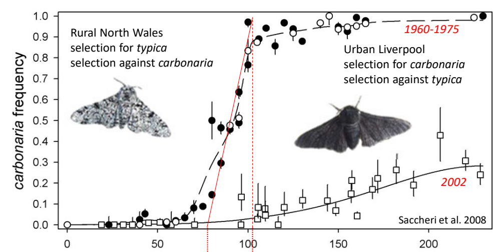


At equilibrium, the width *w* of a cline is proportional to dispersal σ divided by √(selection):

$$w = 1.7\frac{\sigma}{\sqrt{s}}$$

21

Cline in peppered moth melanism



$$w = 1.7\frac{\sigma}{\sqrt{s}}$$

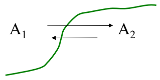
$w \approx 25$ km

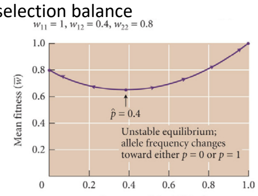
σ, dispersal est.	s, selection est.
2.0 km (Bishop)	0.14
13.6 km (Saccheri)	0.94

22

Clines due to migration/selection balance

c) *intrinsic selection*





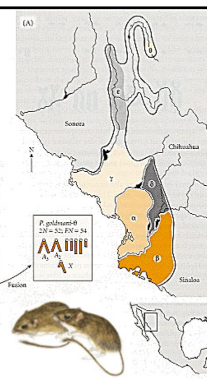
e.g. Heterozygous disadvantage
(*single locus*)

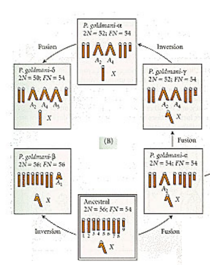
Here: $w = 2.8\frac{\sigma}{\sqrt{s}}$

Heterozygous disadvantage creates a kind of *disruptive selection*. Equilibrium gene frequency, $\hat{p} = \frac{t}{s+t}$ is unstable, selection prevents polymorphism

23

Narrow hybrid zones maintained by selection against chromosomal heterozygotes – e.g. *Perognathus* pocket mice





24

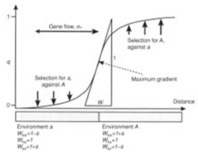
Summary of cline theory under selection

$$w = k\frac{\sigma}{\sqrt{s}} \ *$$

True for many kinds of selection, where *k* is about 1-3
"Widths of clines are a few multiples of dispersal distance"

EXTRINSIC selection – e.g. abiotic environment
INTRINSIC selection – such as:
i) heterozygote disadvantage
ii) frequency-dependent selection
iii) epistasis among genes

INTRINSIC selection includes the kinds of selection involved in incompatibilities among species, such as hybrid inviability or sterility

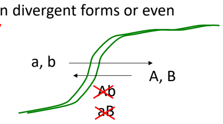


** Do not learn the equations, but do understand this!*

25

Hybrid zones

Narrow zones of contact between divergent forms or even species. "multiple narrow clines"



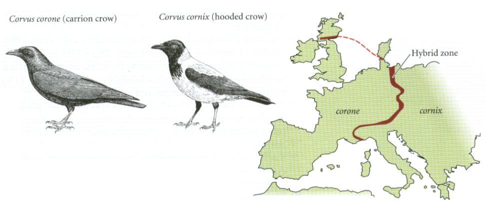
Hybrid zones :
few hybrids or many
hybrids themselves may
consist only of F_1 only,
or of F_1, F_2 and every kind of backcross.

Many species and/or races are distributed in parapatry, and have narrow hybrid zones between them.

Examples:
chromosomal races of mammals
warningly coloured butterflies
sexually selected birds

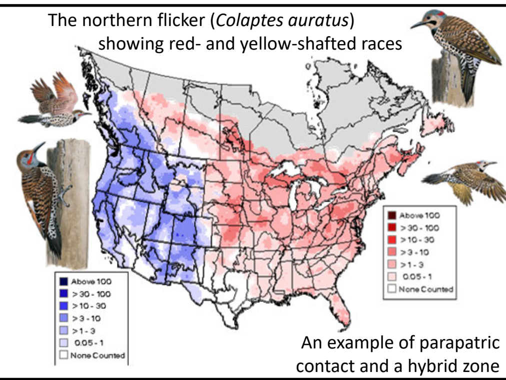
26

Hooded Crow vs. Carrion Crow (*Corvus* spp.) parapatric contact and hybrid zone in Europe



27

The northern flicker (*Colaptes auratus*) showing red- and yellow-shafted races



An example of parapatric contact and a hybrid zone

28

The fire-bellied/yellow-bellied toads (Bombina)

Meet in a narrow east-west hybrid zone stretching over a large part of eastern Europe.

Bombina bombina

Bombina variegata

29

enzyme locus clines

250 J. M. SZYMURA AND N. H. BARTON

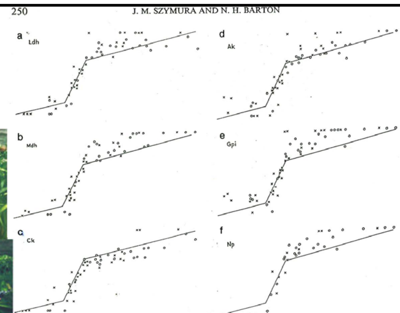


FIG. 3. Frequencies of the *variegata* allele at each enzyme locus (a, *Ldh-1*; b, *Mdh-1*; c, *Ck*; d, *Ak*; e, *Gpi*; f, *Np*). These are plotted on a logit scale, with fixed sites being set arbitrarily at $\log_e(p/q) = \pm 5$. Crosses: Cracow transect. Circles: Przemyśl transect. The clines are centered at $X = -0.19$ for the Cracow transect and $X = -2.60$ for the Przemyśl transect. The straight lines shown on each graph show the best fit to the whole data set, averaged across loci (see Fig. 4a for scale).

30

The *Bombina* hybrid zone

	Bombina bombina	*Bombina variegata*
Habitat	Lowland	Hilly
Water bodies	Lakes, ponds	Temporary ponds, puddles
Skin thickness	Thin	Thick
Eggs (spawn)	Small, many	Large, fewer
Belly warning colour	Red and black	Yellow & black
Other differences	Male mating call	
	Hybrids develop less successfully	
	Immunological differences	
	Multiple allozyme differences	
	mtDNA differences	

Hybrid zones, then, are places where narrow gene frequency clines at multiple loci occur together

Held together by a mixture of extrinsic and intrinsic selection

31

Importance of hybrid zones, clines

Direct approach to the study of divergence in time via divergence in space

Hybrid zones separate forms that are "almost species."

Give us some idea of the sorts of traits that may be involved in the evolution of new species.

32

Importance of hybrid zones, clines

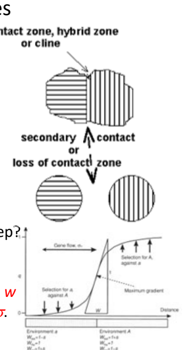
How did hybrid zones, clines originate?

Via allopatry then secondary contact?

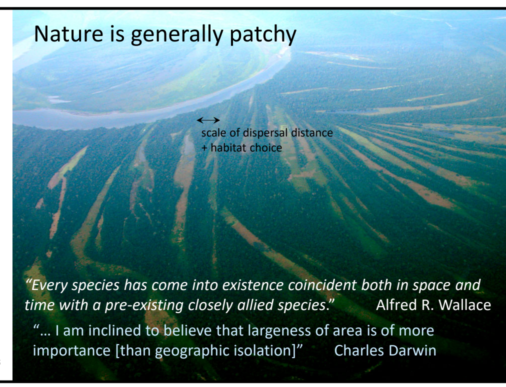
Or via divergence in parapatry?

Controversy in the understanding of speciation: Did species evolve in allopatry, parapatry or sympatry? Do hybrid zones between divergent races represent a first step?

Theory tells us that genetic differentiation can occur in parapatry, over short distances, w – a few multiples of the dispersal distance, σ.



33



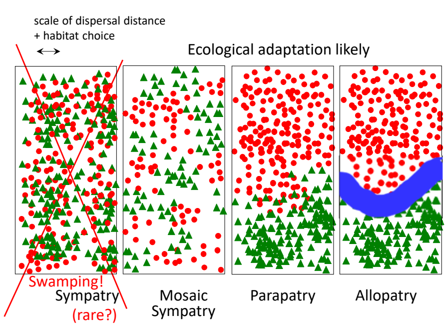
Nature is generally patchy

"Every species has come into existence coincident both in space and time with a pre-existing closely allied species." Alfred R. Wallace

"… I am inclined to believe that largeness of area is of more importance [than geographic isolation]" Charles Darwin

34

Rethink of sympatry vs. parapatry



35

Summary – drift, migration, selection

These results are fairly simple in outline:

Genetic drift vs. gene flow:

- If $m << 1/2N_e$ * then *drift "wins," populations divergent*
- If $m >> 1/2N_e$ * then *migration "wins", pops. are "swamped"*

Selection vs. gene flow:

- If $m << s$ * then *selection "wins," maintains divergence*
- If $m >> s$ * then *migration "wins", pops. are "swamped"*

More realistic continuous models:

- Width of cline with selection ~ a few dispersal distances σ *

Therefore, divergence, including speciation

- Is likely in *spite of gene flow*, provided selection or drift is strong enough, and gene flow is not "swamping."

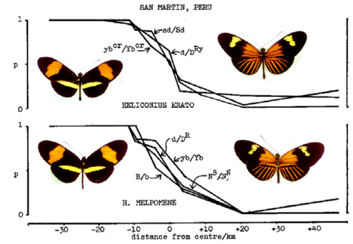
** Do not learn equations, but do learn these basic ideas!*

36

2/10/2025 37

37

Frequency-dependent selection explains narrow hybrid zones

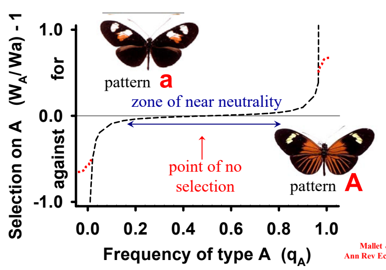


Warning colour: rare forms non-adaptive because predators learn commoner colour pattern

Mallet et al. 1990. Genetics 124:921

38

Novel warning colour or mimicry pattern: frequency dependent selection



Mallet & Joron 2000. Ann Rev Ecol Syst 30:201

39

Part III

How might mimicry diverge geographically?

- Warning colour/Müllerian theory
- How do totally novel patterns evolve?
  - Individual selection?
  - Kin selection?
  - Kin-founding? – a chromosomal model
  - Shifting balance? – a general model for adaptation

A classic evolutionary ecology problem

40

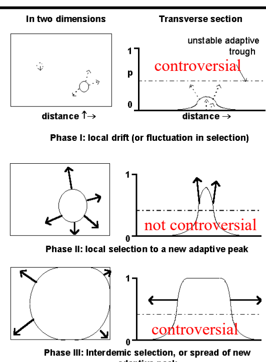
Possible mechanism: “the shifting balance”

Wright 1930, 1931 etc.

today, considered somewhat controversial

but must explain some

chromosomal evolution?
warning colour?
multilocus adaptation?

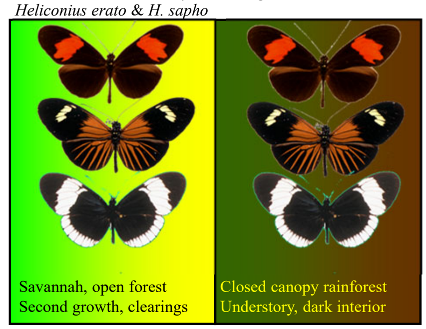


Mallet 2010. Ecol Ent 35 (Suppl. 1): 90

41

Some maybe ecological traits…

Heliconius erato & H. sapho



Mallet 2010. Ecol Ent 35 (Suppl. 1): 90

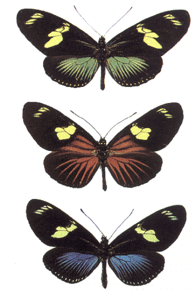
42

Phase I: local genetic drift?

species	author	date	location	F_{ST}	est. *Nm*
erato	Mallet	1986	Peru	0.013	19.0
melpomene	Mallet	1986	Peru	0.032	7.6
erato	Silva &c	1994	Brazil	0.025	9.8
erato	Jiggins &c	1997	Ecuador	0.006	41.4
himera	Jiggins &c	1997	Ecuador	~0.000	~ ∞
charithonia	Kronforst &c	2001	Florida	~0.000	~ ∞
various	Kronforst &c	2008	Costa Rica	0.040	6.0
various	Kronforst &c	2008	Costa Rica	0.125	1.8

If *Nm* < 1 then Phase I likely

43

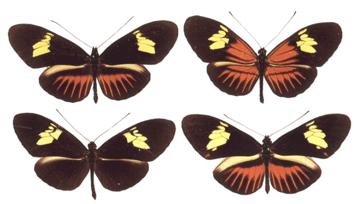


Phase I: local polymorphism
Heliconius (Laparus) doris

Mallet 2001. Evol Ecol 13: 777

44

Phase I: Local polymorphism
Heliconius timareta



Mallet 2001. Evol Ecol 13: 777

45

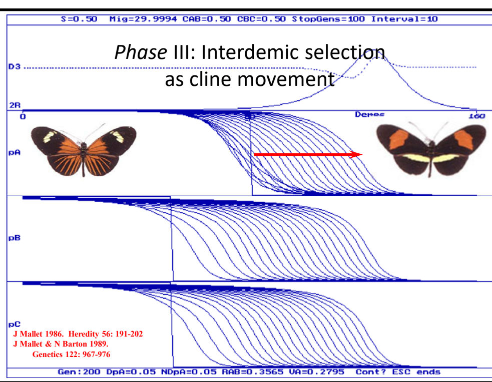
Phase II: Ordinary natural selection: mimicry

Heliconius erato

Heliconius melpomene

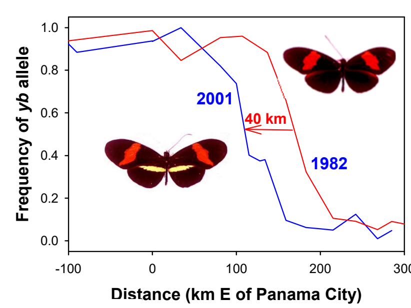
2/10/2025 46

46



47

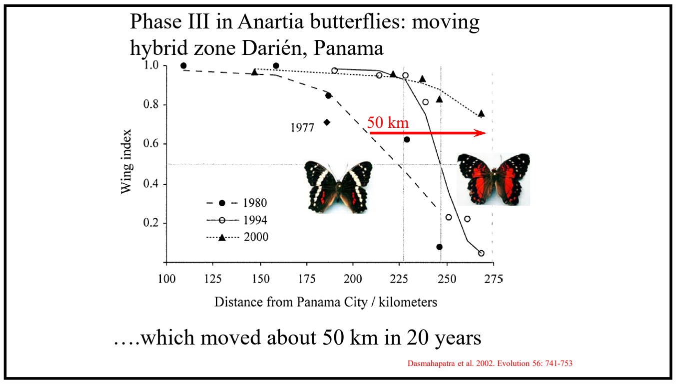
Heliconius erato hybrid zone – Phase III



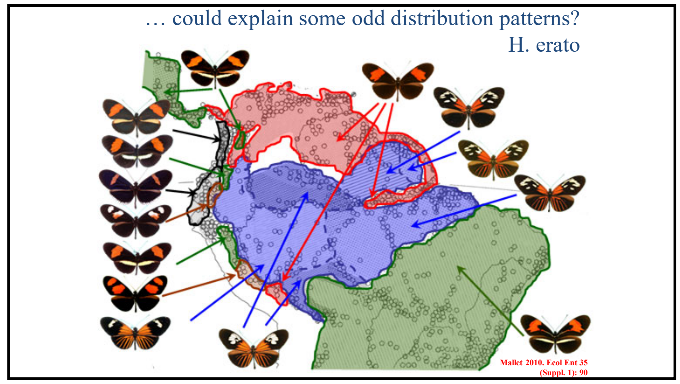
Darién, Panama

MJ Blum 2002. Evolution 56: 1992-1998

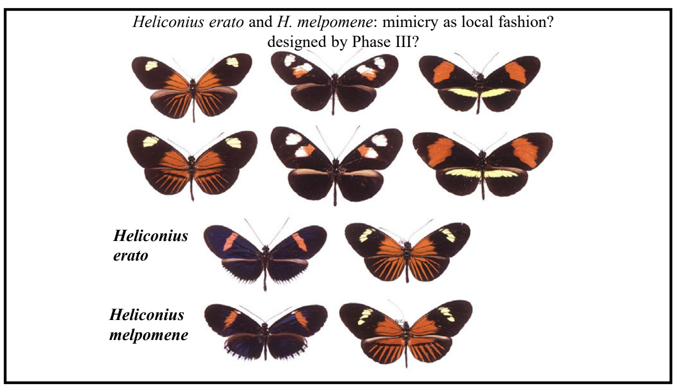
48



49



50



51

Summary – drift, migration, selection

These results are fairly simple in outline:

Genetic drift vs. gene flow:

- If $m << 1/2N_e$ * then *drift "wins," populations divergent*
- If $m >> 1/2N_e$ * then *migration "wins", pops. are "swamped"*

Selection vs. gene flow:

- If $m << s$ * then *selection "wins," maintains divergence*
- If $m >> s$ * then *migration "wins", pops. are "swamped"*

More realistic continuous models:

- Width of cline with selection ~ a few dispersal distances, σ *

Therefore, divergence, including speciation

- Is likely in *spite of gene flow*, provided selection or drift is strong enough, and gene flow is not "swamping."

** Do not learn equations, but do learn these basic ideas!*

2/10/2025 52

52