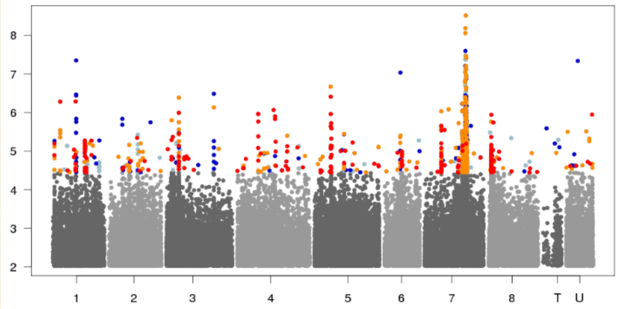
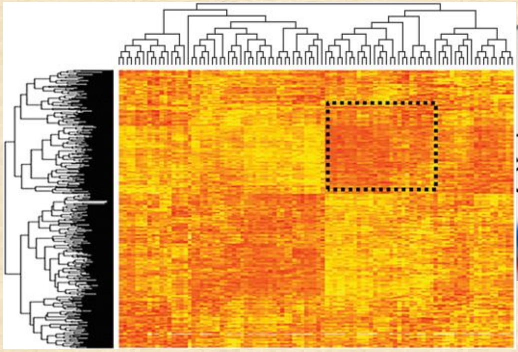




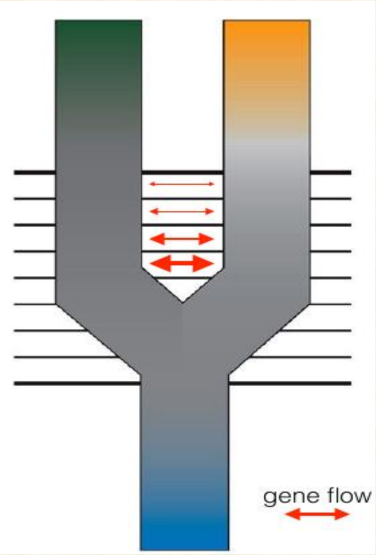
Genomics of speciation and adaptation: Polyploid speciation

02.04.2019, Filip Kolář

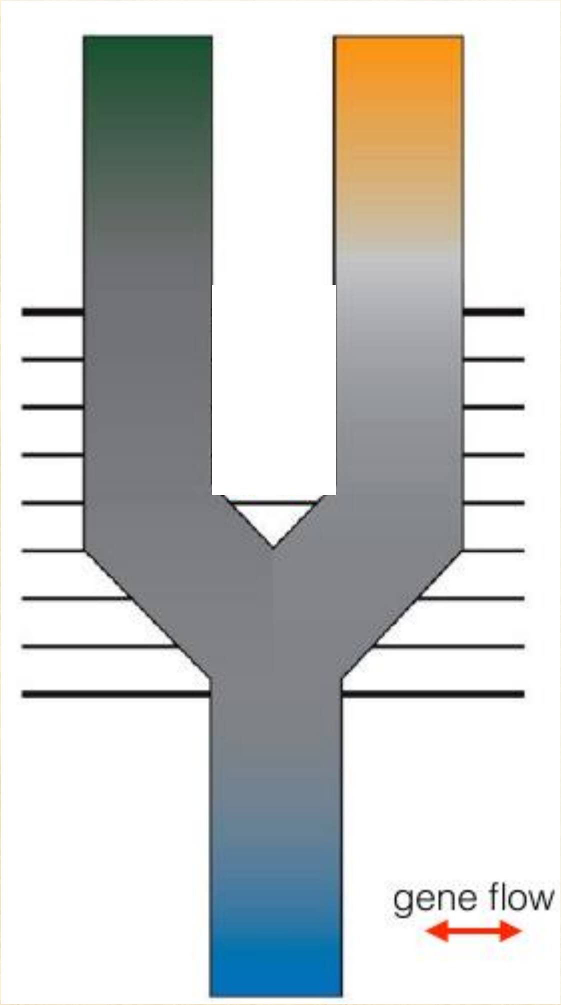




Where are we today?

The gray zone of speciation



The black-and-white zone of speciation



Big question in polyploidy

What is the role of whole genome duplication (WGD) in speciation?

- Driver of diversification or evolutionary dead-end?
- Importance outside plants?

Sympatric speciation

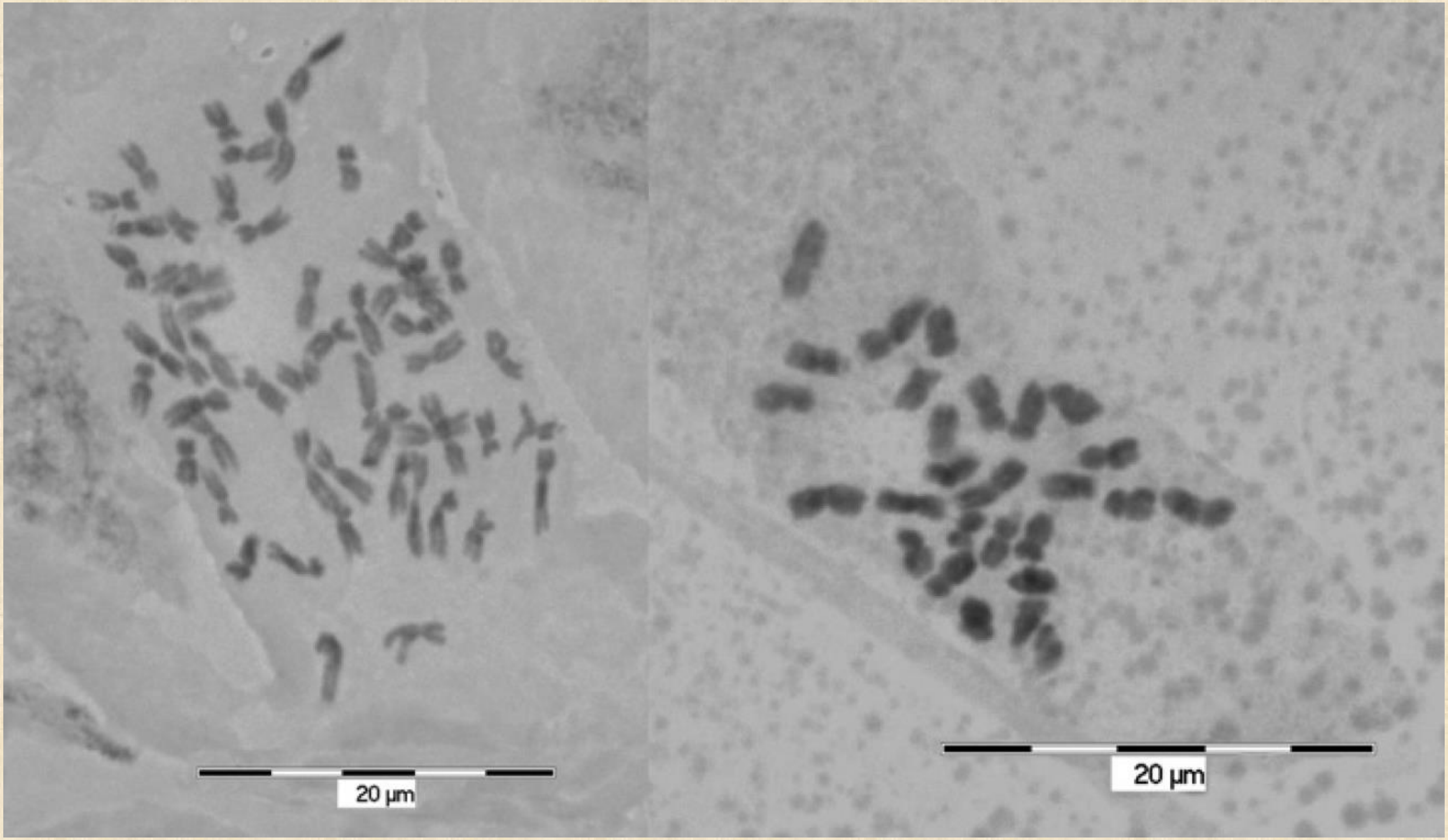
Role of WGD *per se* vs. later selection/drift

- Consequences of WGD *per se* (also prezygotic barriers)?
- Reinforcement?
- Does ploidy change population genomics of selection?

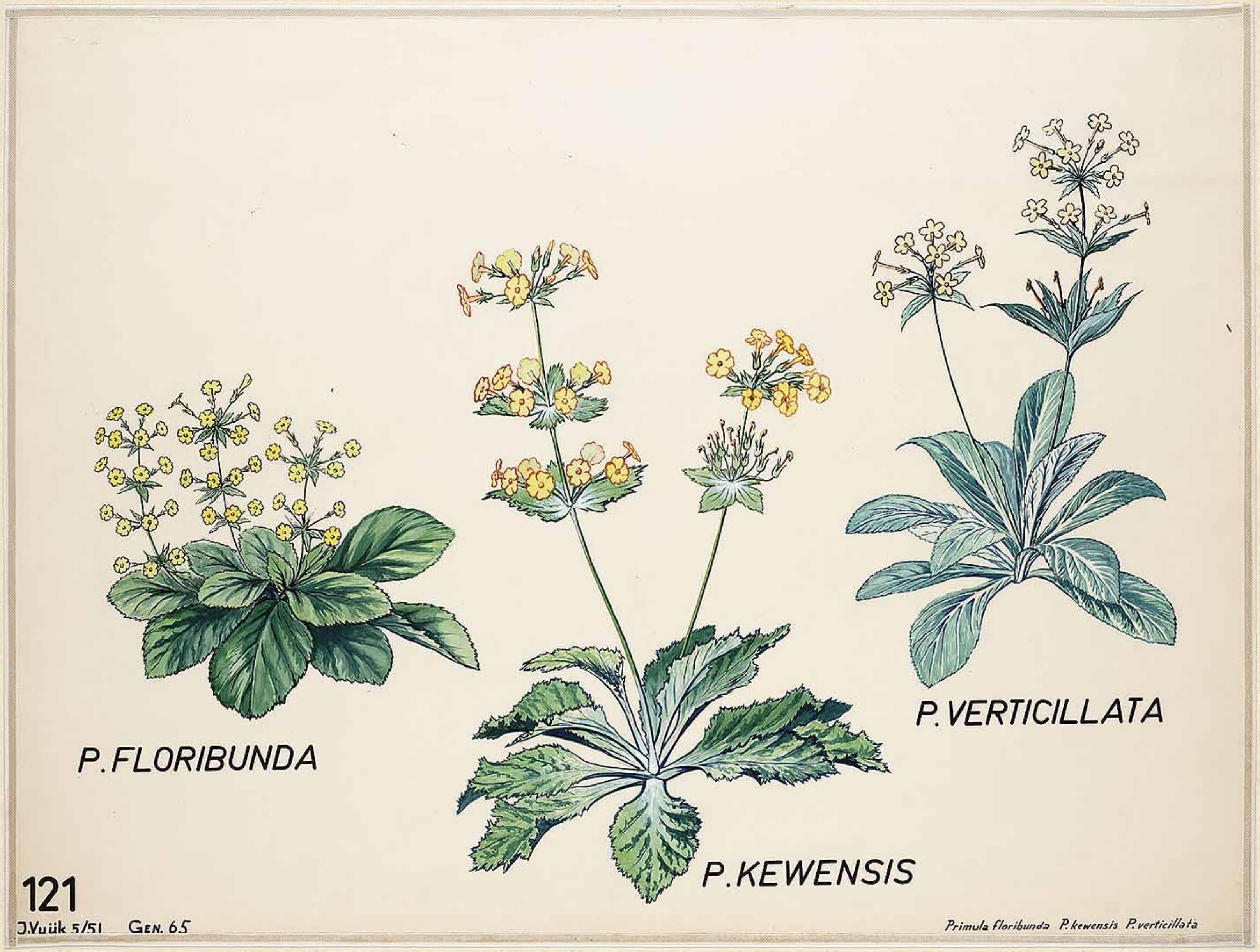
Inter-ploidy gene flow – how strong? Consequences?

Polyploidy

- the possession of more than two chromosome sets



Polyploidy


P. FLORIBUNDA
P. KEWENSIS
P. VERTICILLATA
121
J.Vuük 5/51
GEN. 65
Primula floribunda P. kewensis P. verticillata

Polyploidy

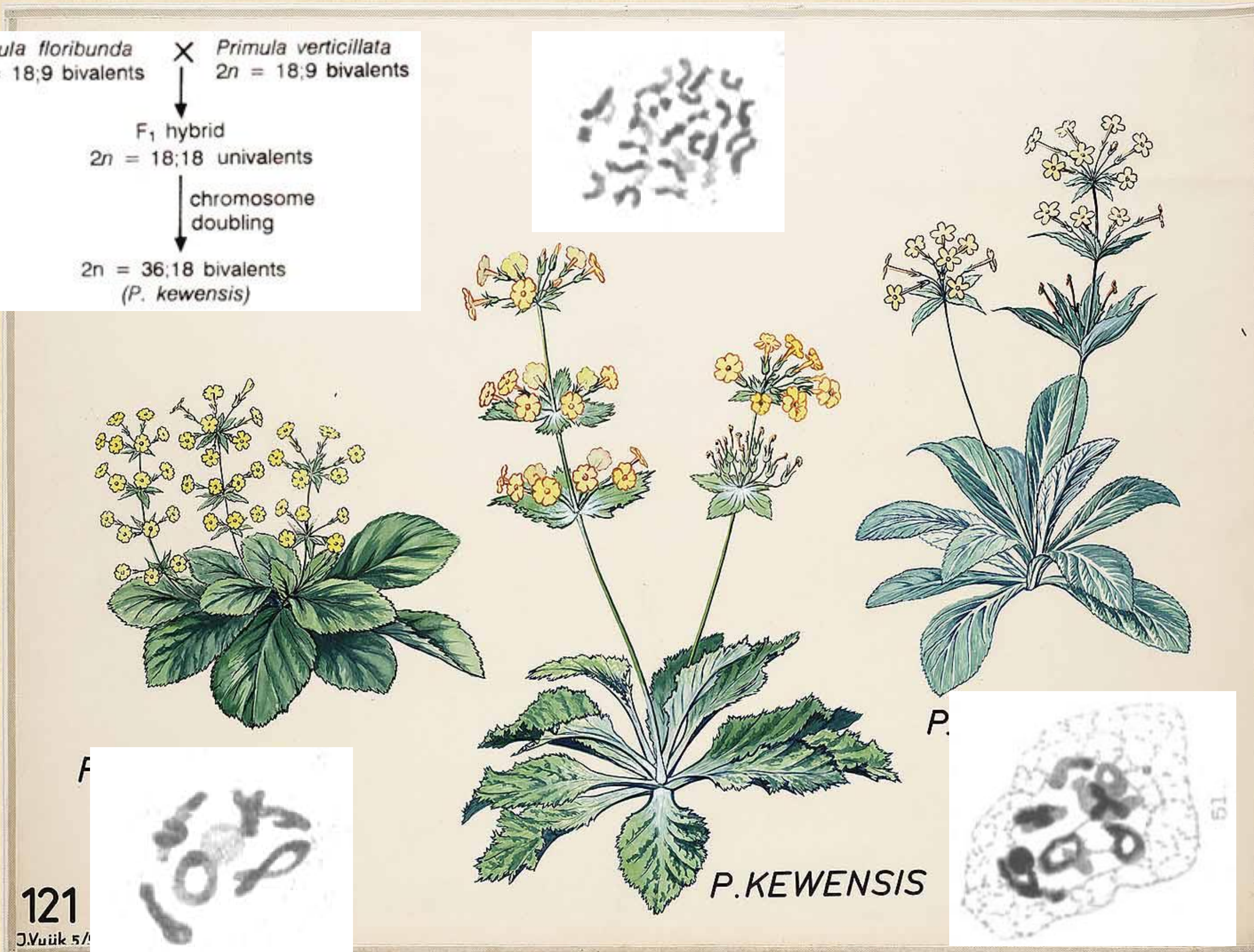
Primula floribunda × *Primula verticillata*
$2n = 18; 9$ bivalents — $2n = 18; 9$ bivalents

↓

F_1 hybrid
$2n = 18; 18$ univalents

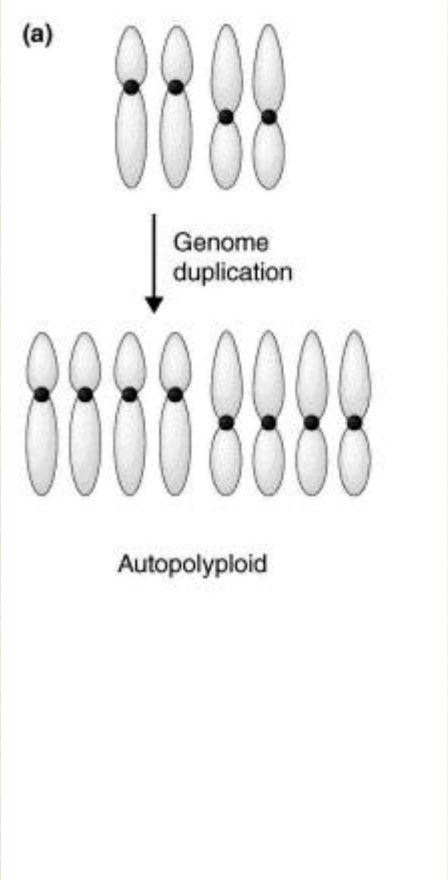
↓ chromosome doubling

$2n = 36; 18$ bivalents
(*P. kewensis*)

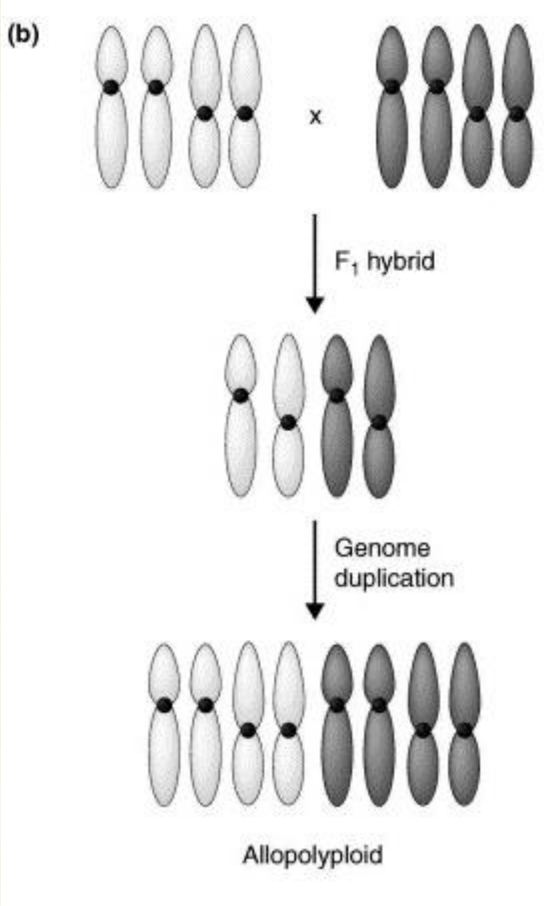


Polyploidy - mechanisms

- **autopolyploids** – intraspecific polyploids



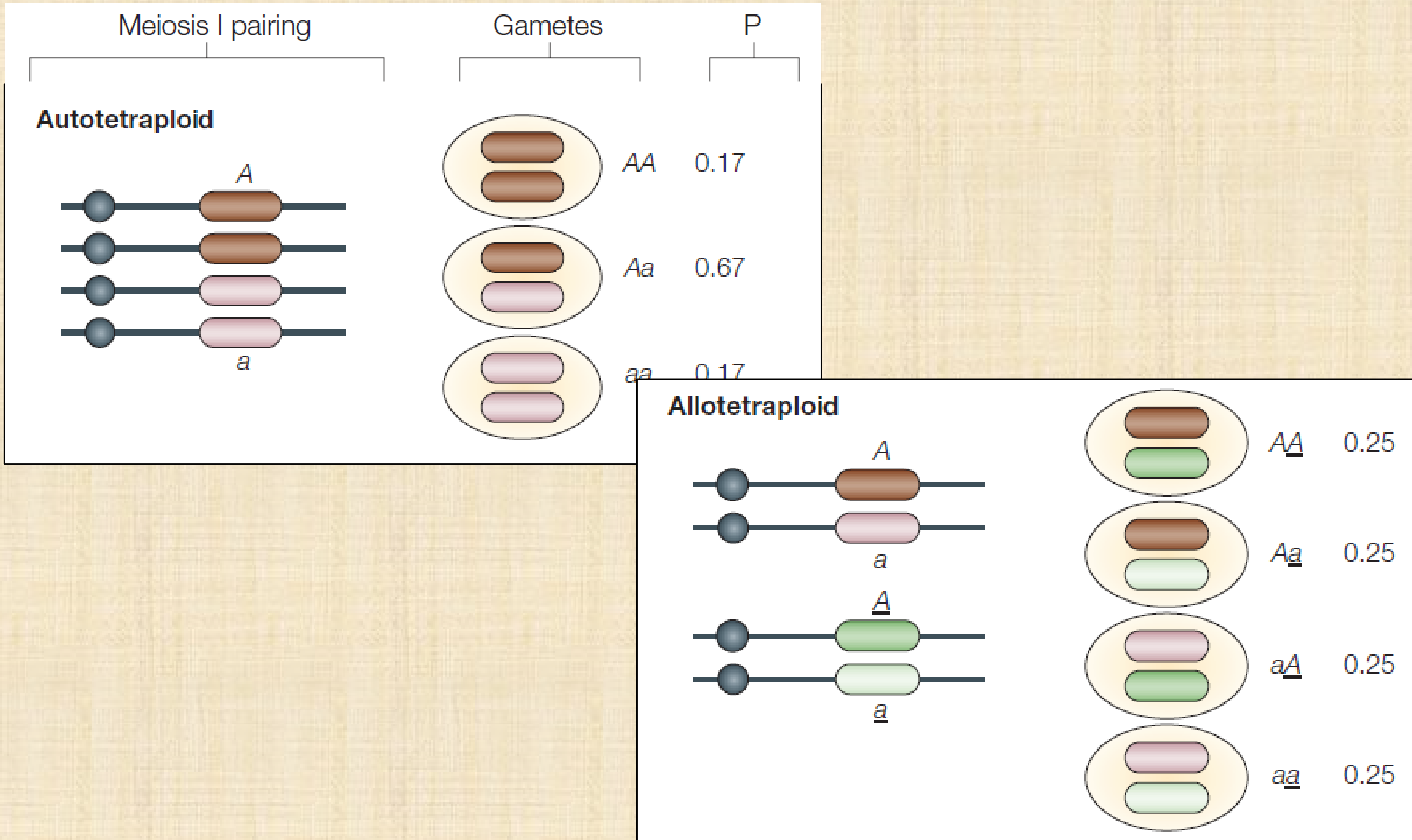
- **allopolyploids** – polyploid hybrids



Polyploidy - mechanisms

- **autopolyploids** – intraspecific polyploids
- random segregation – polysomic inheritance

- **allopolyploids** – polyploid hybrids
- preferential pairing – disomic inheritance



Polyploidy - example

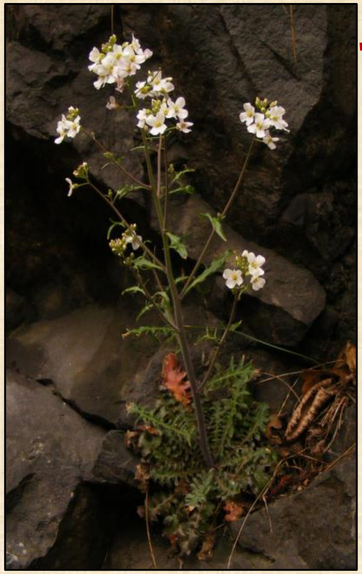
- allopolyploids – polyploid hybrids

A. thaliana **(2x, 4x)**

A. suecica (**4x**)

A. kamchatica (**4x**)

A. halleri **(2x)**



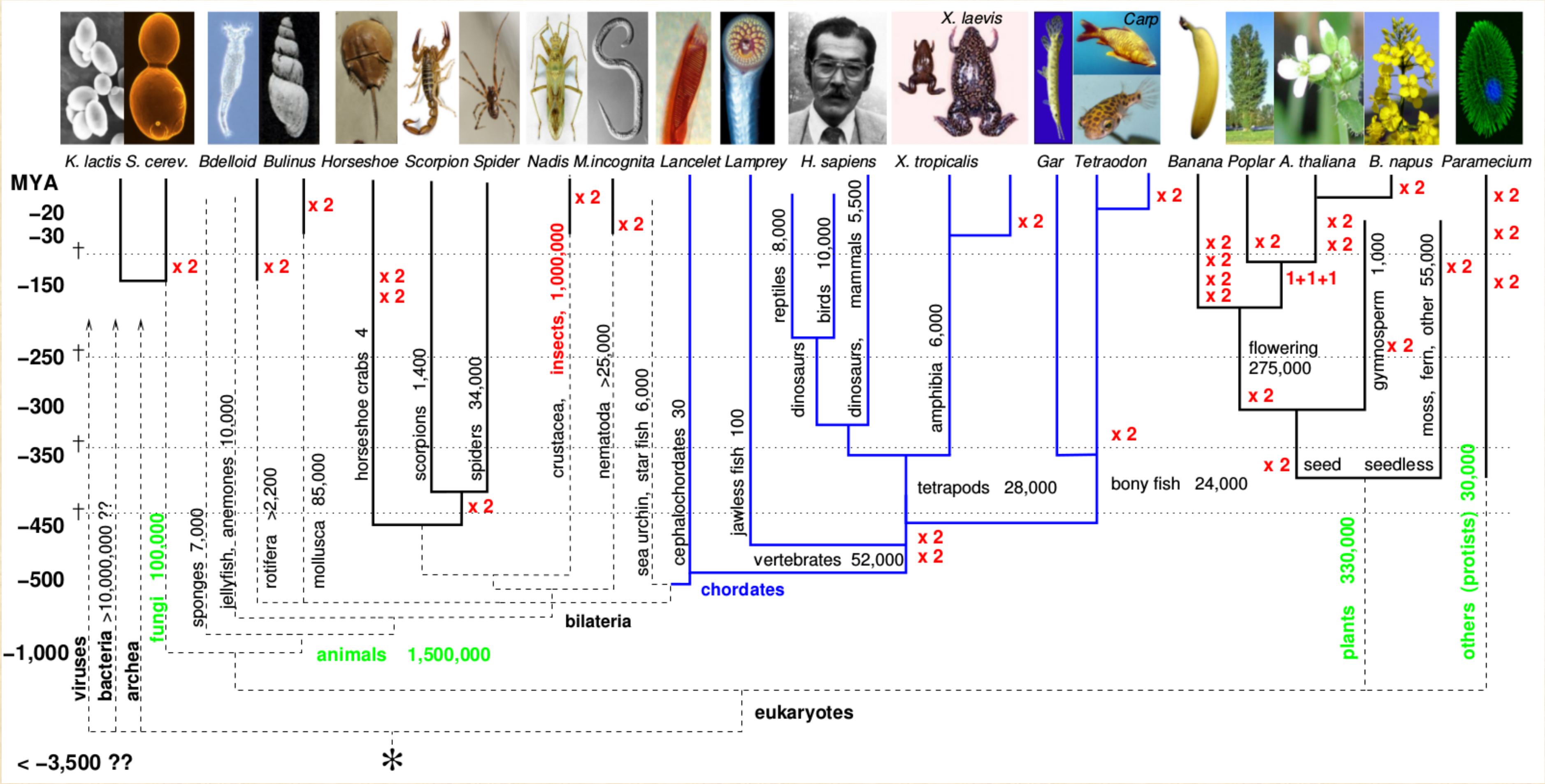
A. arenosa **(2x, 4x)**

A. lyrata **(2x, 4x)**

- autopolyploids – intraspecific polyploids

WGD in tree of life

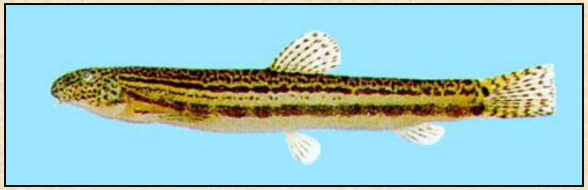
What is a diploid?



Eukaryotes

WGD in animals

Fishes > amphibians > reptiles > (birds, mammals)



Cobitis taenia

Saga pedo

Xenopus

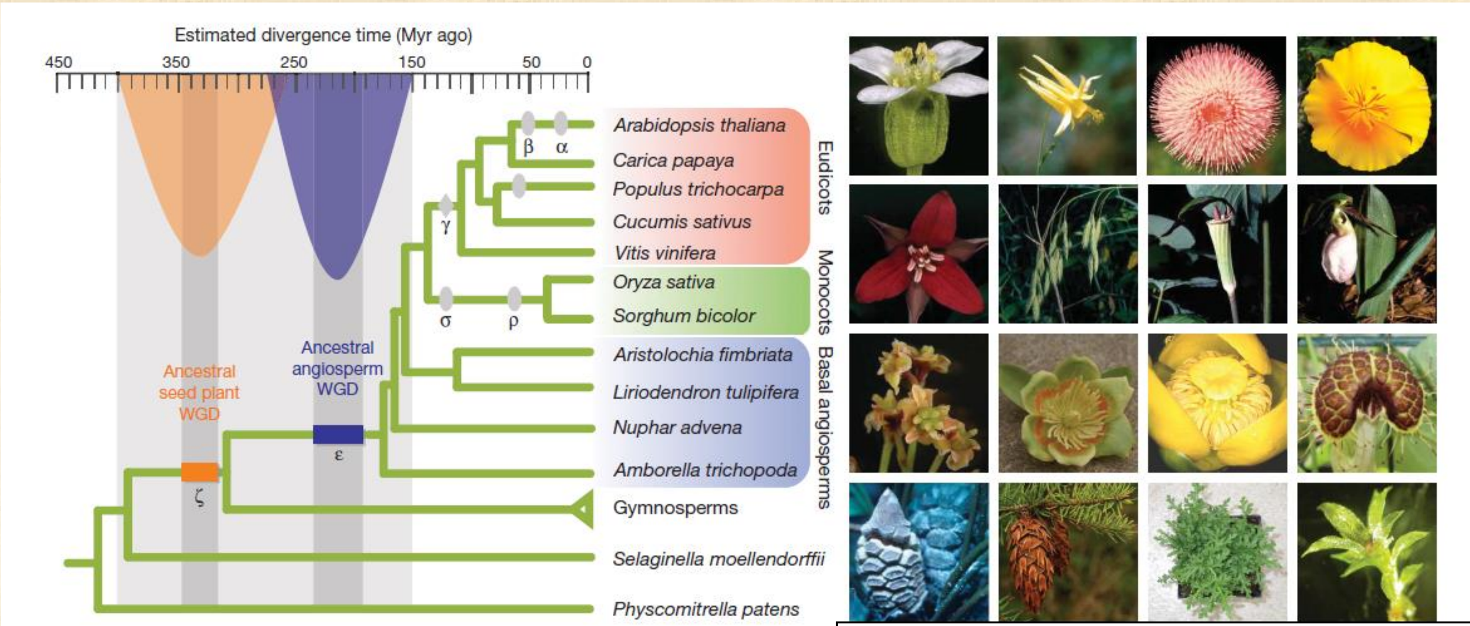
Tympanoctomys barrerae 2n = 4x = 102

H. versicolor

H. cinerea

WGD in tree of life

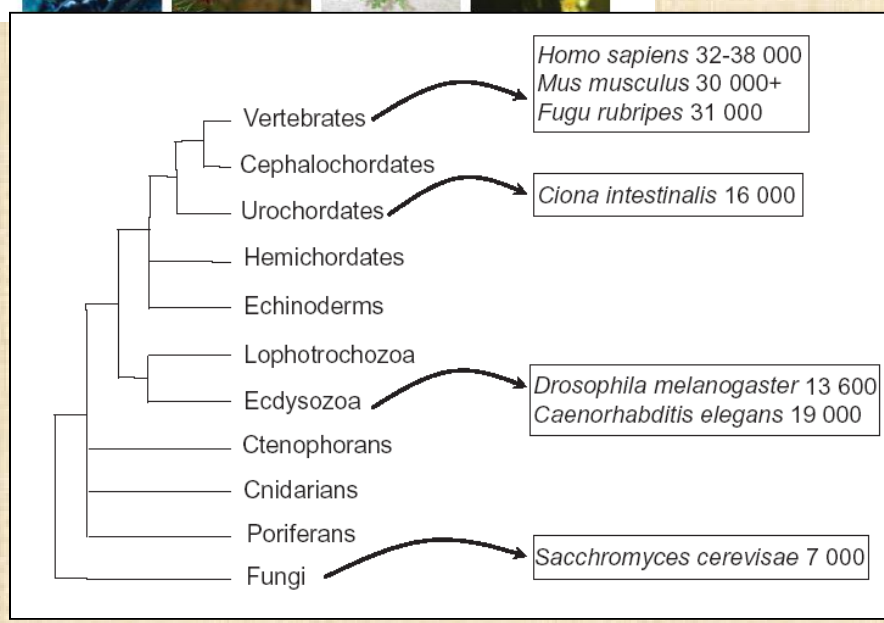
What is a diploid?



Seed plants (Jiao et al 2011 Nature)

N of genes

Duplicated genes (e.g. HOX)

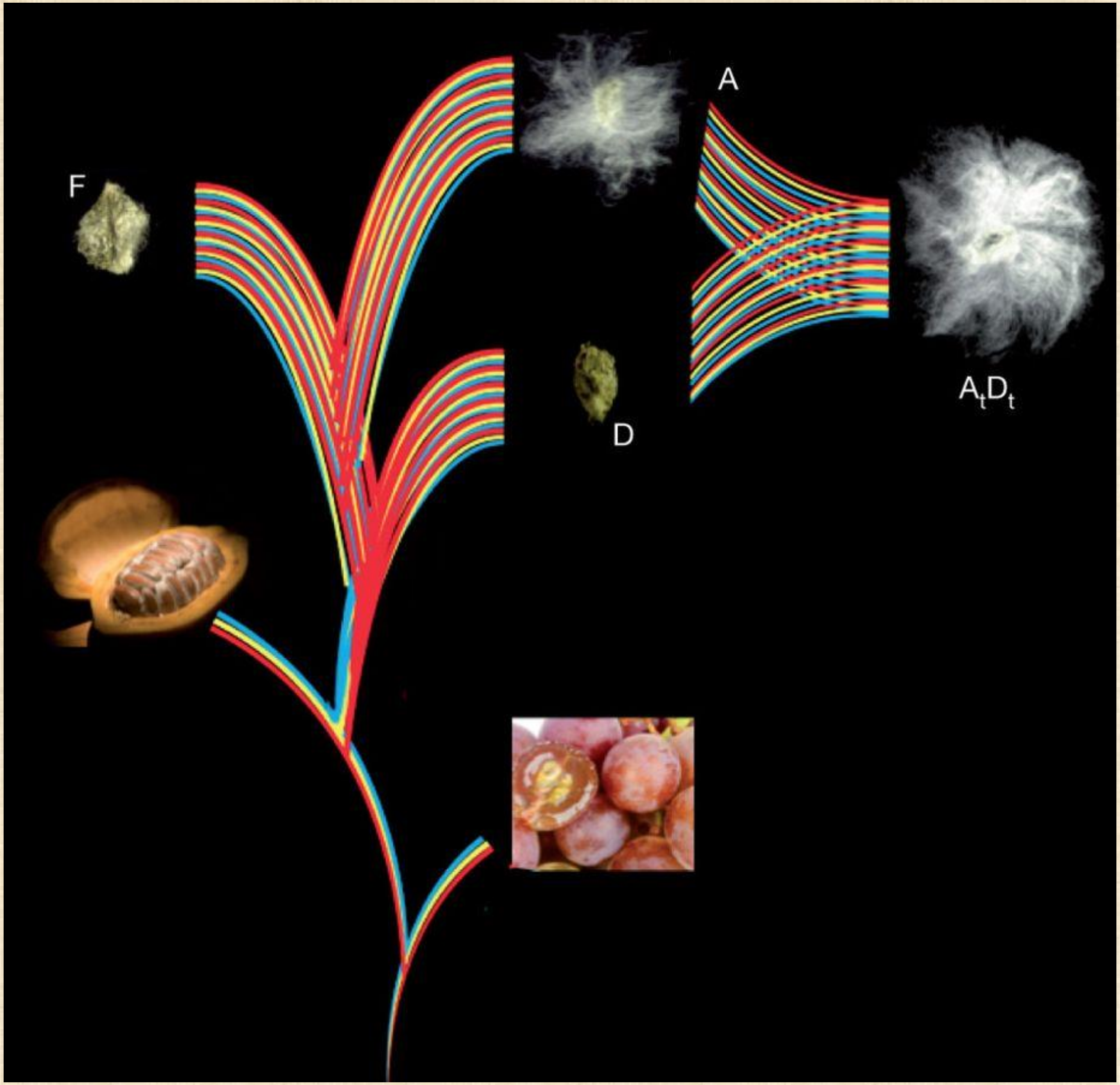


Vertebrates

WGD in tree of life

What is a diploid?

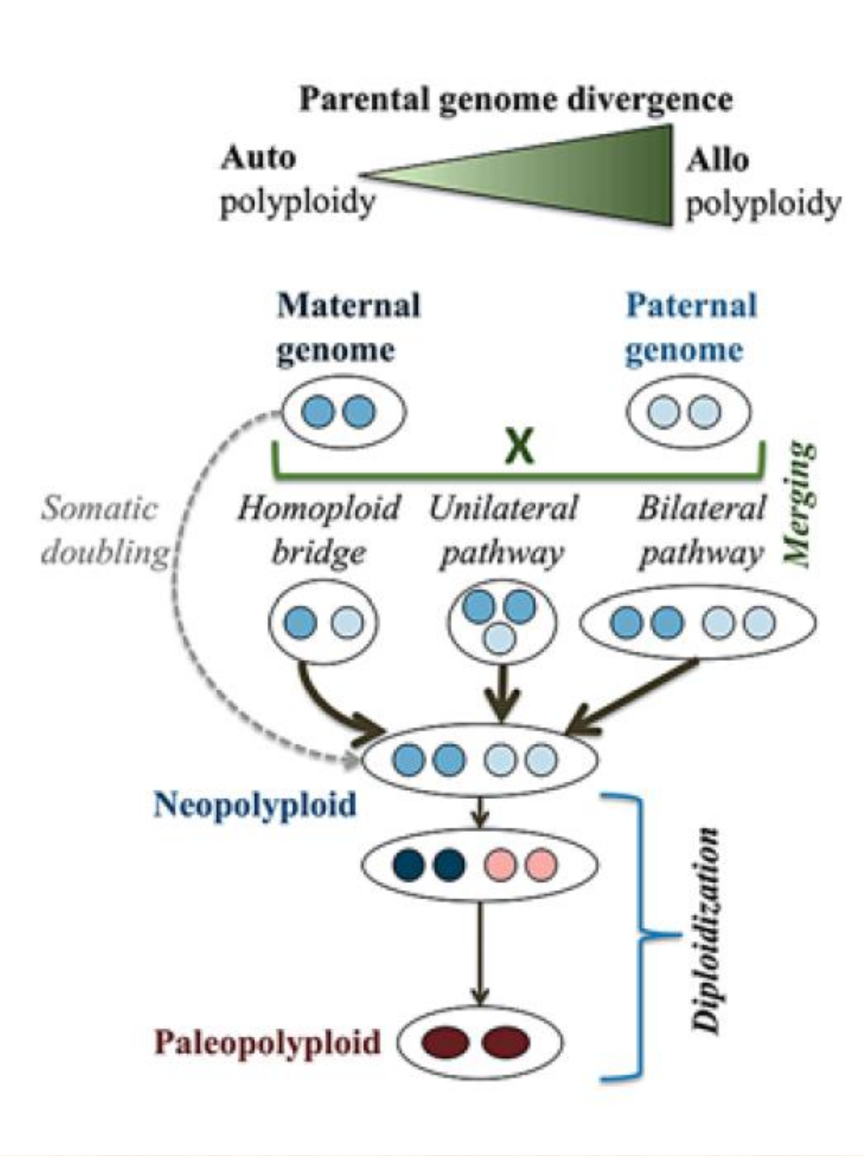
- cotton
- 30-36 duplications of ancestral angiosperm genome
- A: old world
- D: new world



Pathway to polyploidy

- 2 axes:
- time
- parental genome divergence

- difference auto vs. allo dissolves through time

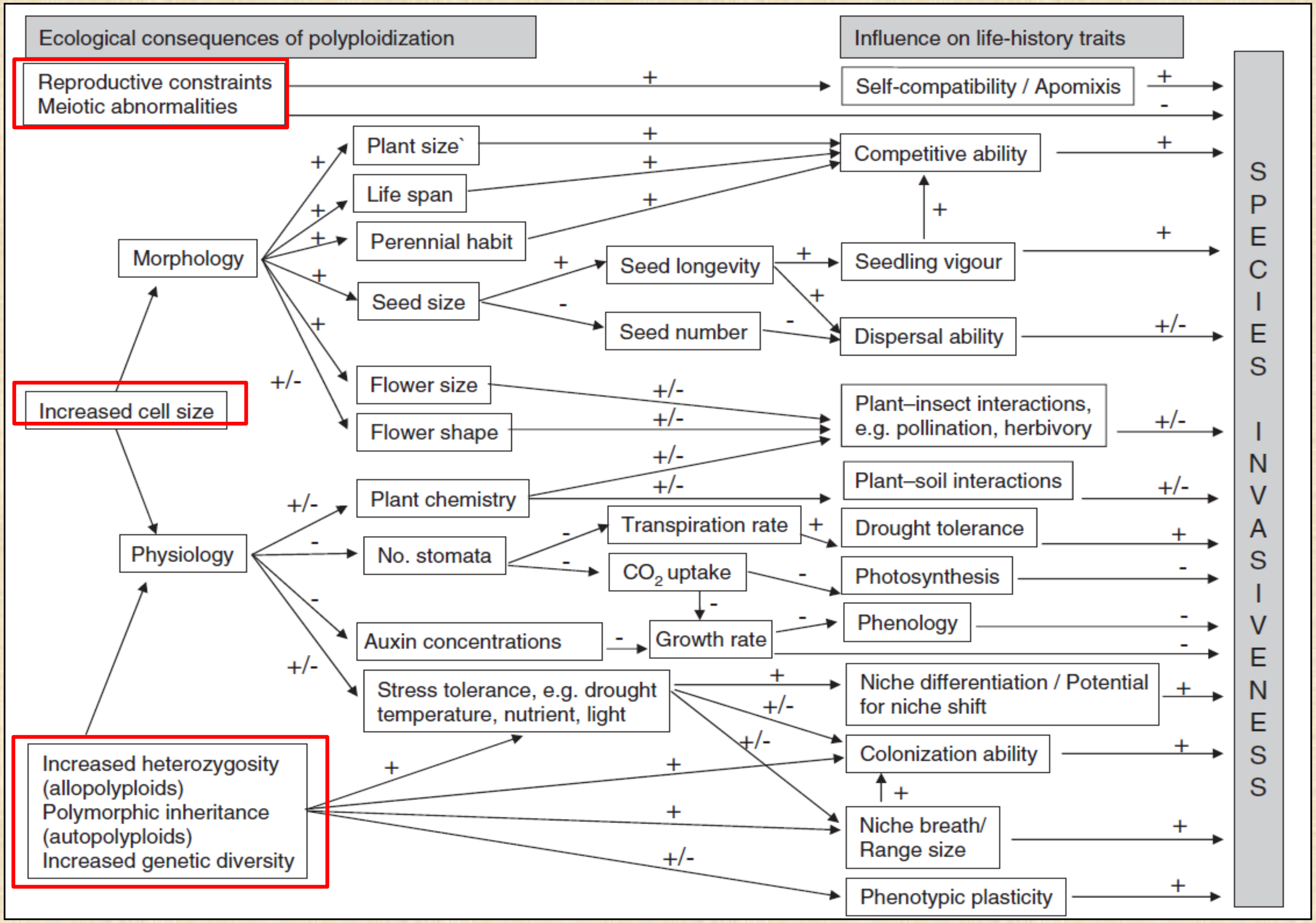


Tayale & Parisod 2013 CytGen Res

Polyploidy – double-edged sword

- „machos“ ...

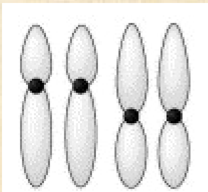
2x 4x
Chamerion angustifolium



polyploidy and invasive phenotype (te Beest et al. 2012 Ann Bot)

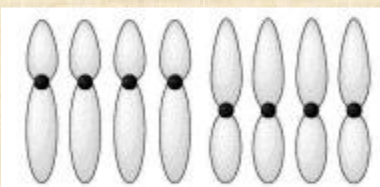
Polyploidy – road to success?

Diploid	Autotetraploid
Aa × Aa	AAaa × AAaa
AA Aa aa	AAAA AAAa AAaa Aaaa aaaa
1 : 2 : 1	1 : 8 : 18 : 8 : 1
	34



diploid

- new phenotypes
- genetic & epigenetic changes
- masking of load

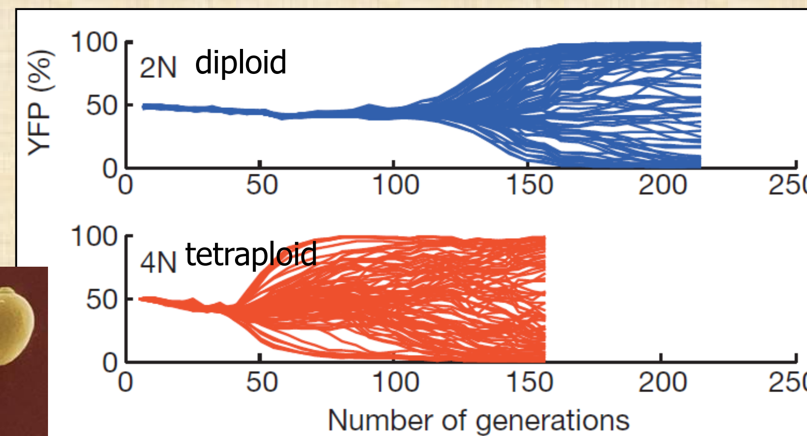


nascent polyploid

- large genetic diversity
- raw material for adaptation
- niche shift & expansion

established polyploid

diploid tetraploid

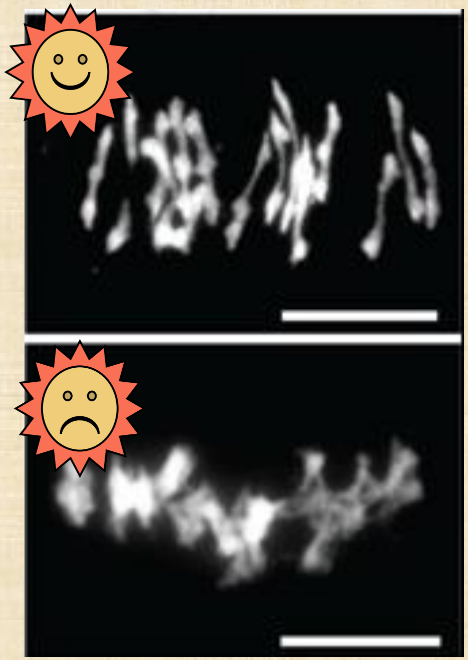


empirical rate of adaptation in yeast (Selmecki et al. 2015 Nature)

Polyploidy – double-edged sword

- ... or „monsters“

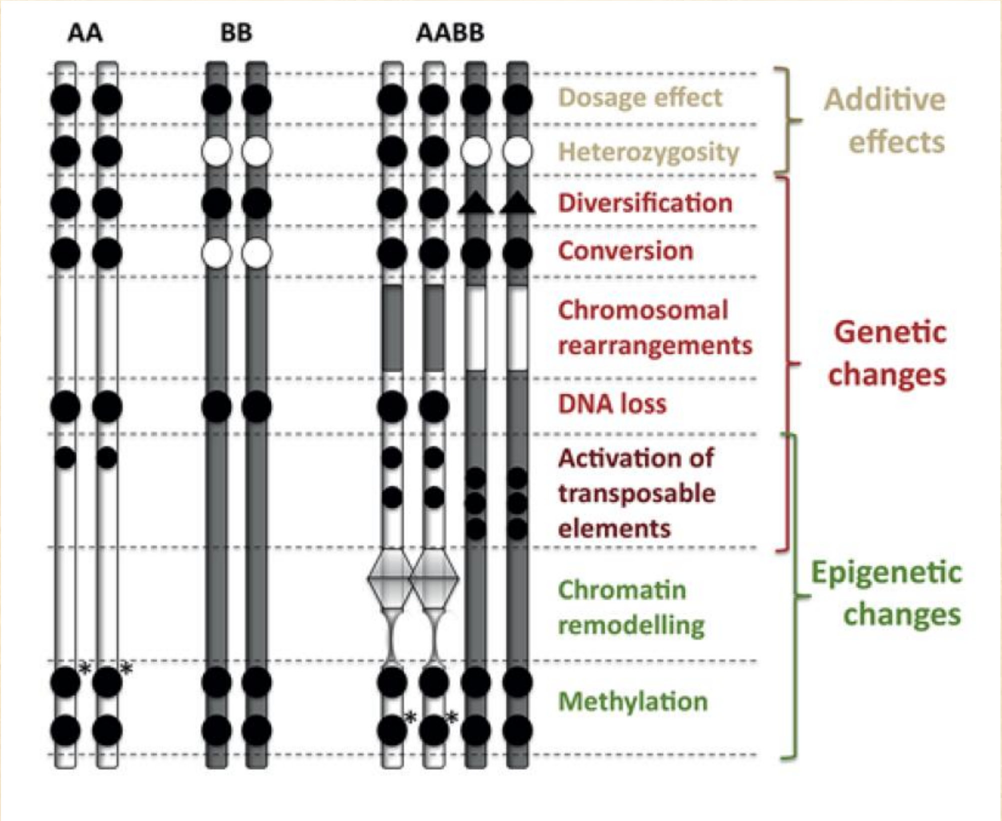
- **Individual-level effect**
- dosage problems
- cellular mis-management (2x volume vs. 1.6x surface: chromatin nuclear envelope relationship)
- meiosis problems (autopolyploids)
- “hybrid shock” (allopolyploids)



natural 4x

synthetic neo-4x

meiotic problems in synthetic but not established autotetraploids, *A. arenosa*, Yant et al. 2013 Curr. Biol.

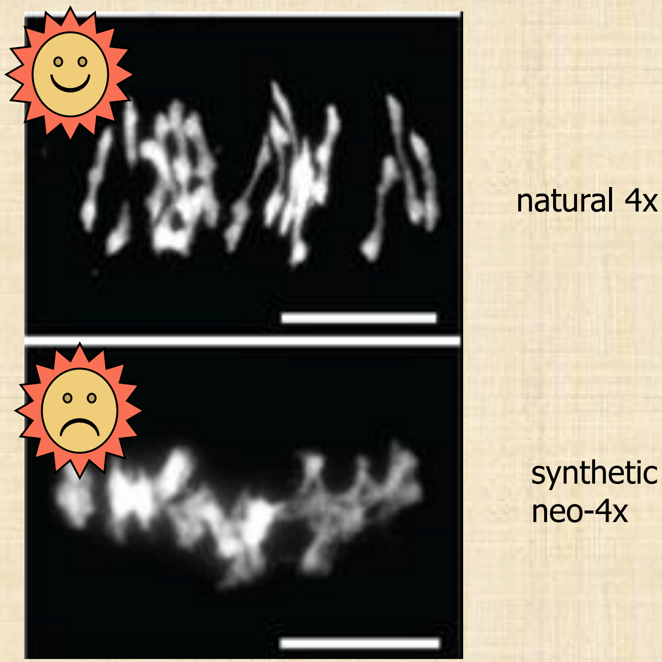


Changes after polyploidzation Tayale & Parisod 2013 CytGen Res

Polyploidy – double-edged sword

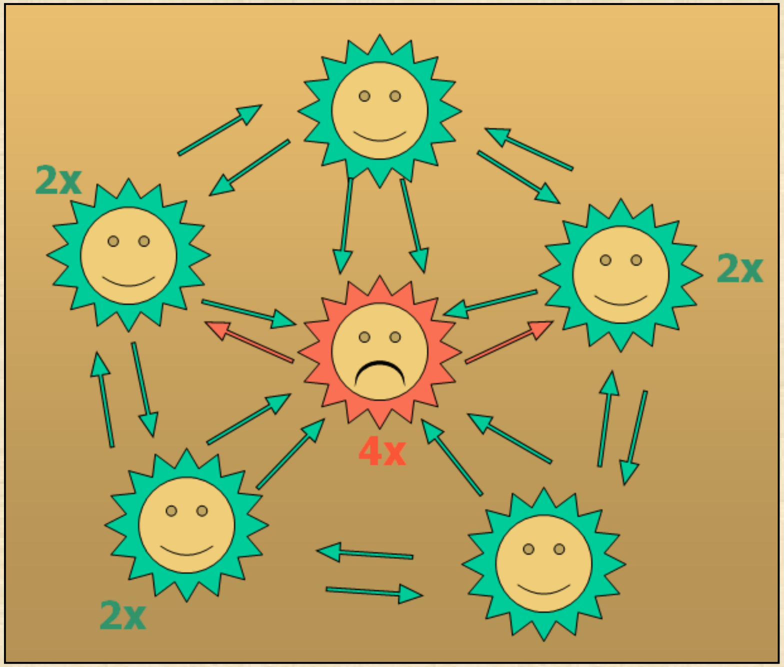
- … or „monsters"

- **Individual-level effect**
- dosage problems
- cellular mis-management meiosis problems (autopolyploids)
- "hybrid shock" (allopolyploids)



meiotic problems in synthetic but not established autotetraploids, *A. arenosa*, Yant et al. 2013 Curr. Biol.

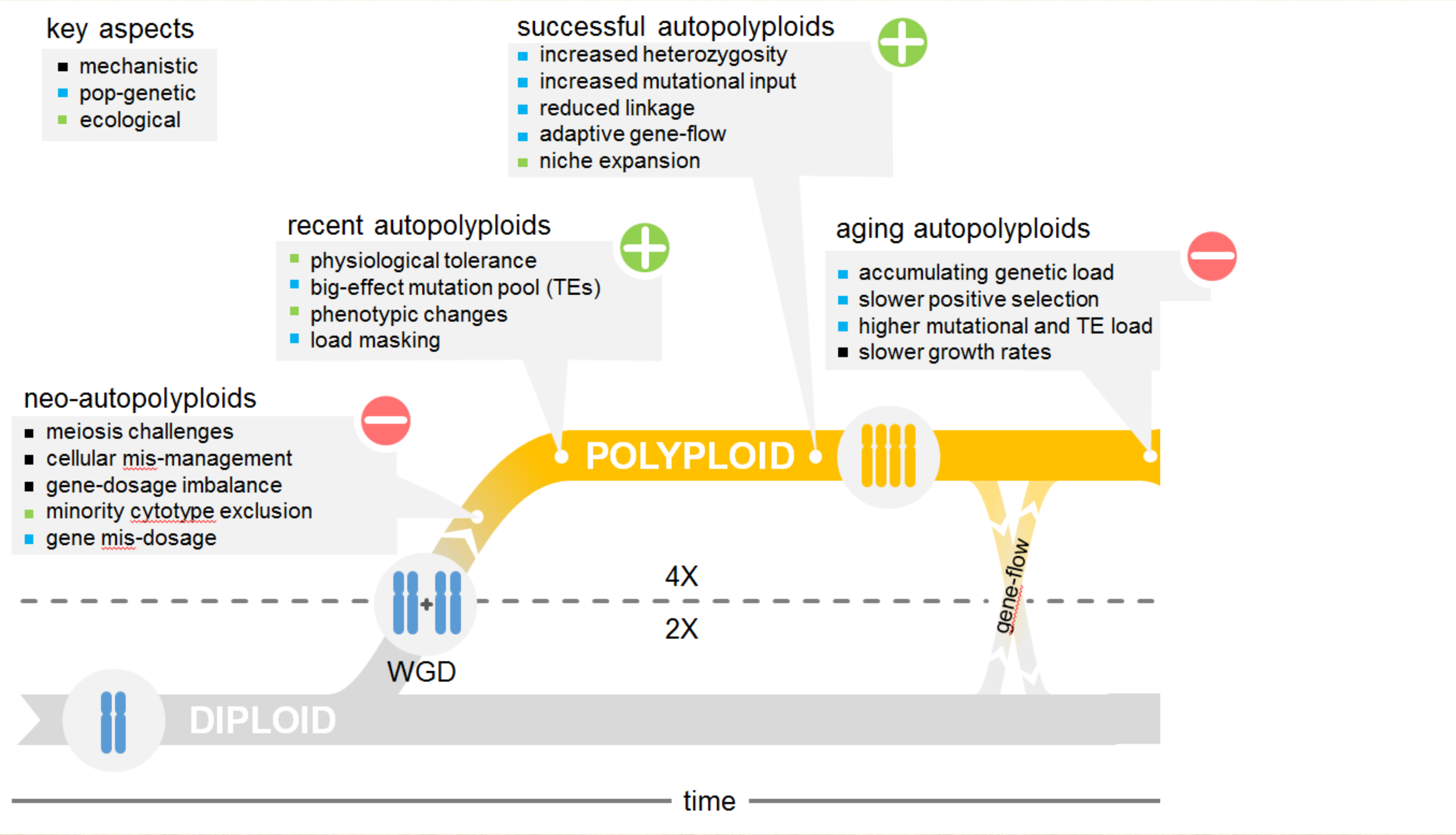
- **Population-level effect**
- competition
- demographic stochasticity
- frequency dependent selection



Minority cytotype exclusion, Levin 1975 Taxon

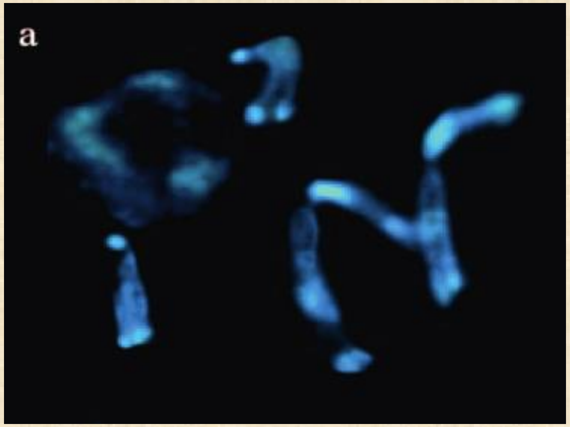
Polyploidy – double-edged sword

- multifarious challenges and potential advantages

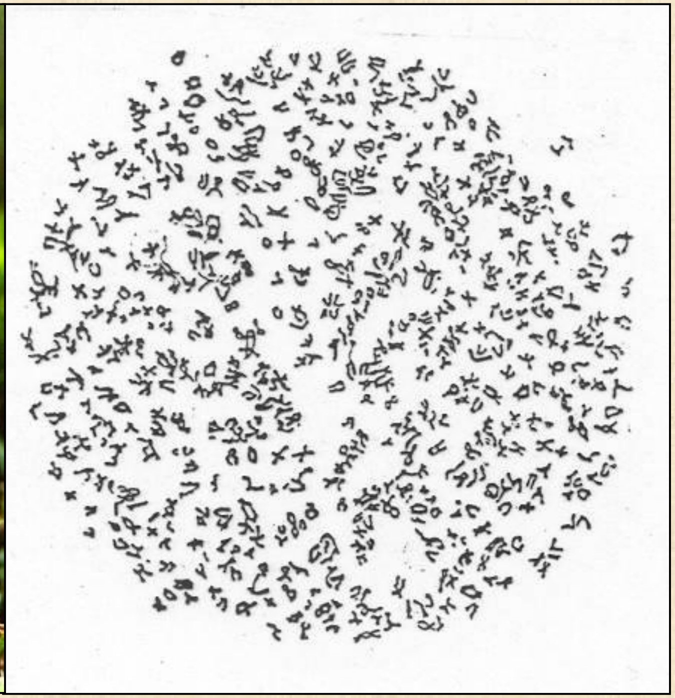


Baduel et al. 2018 Front Evol Ecol

Records

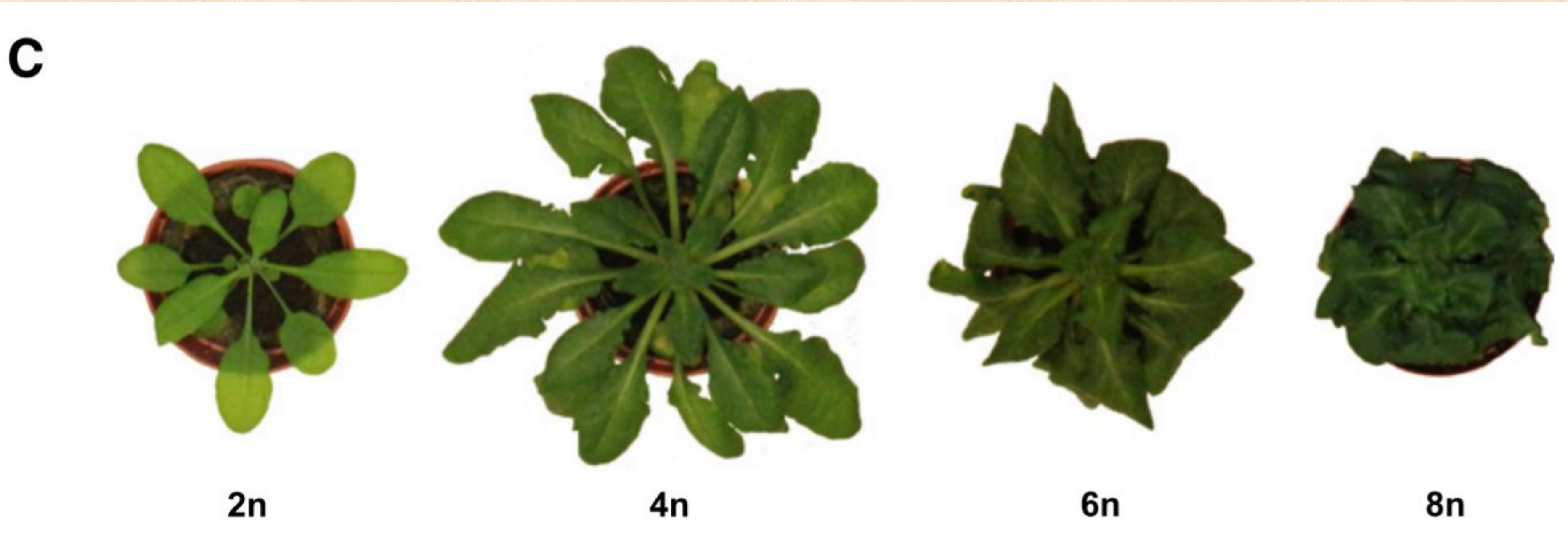


Haplopappus gracilis
2n = 4

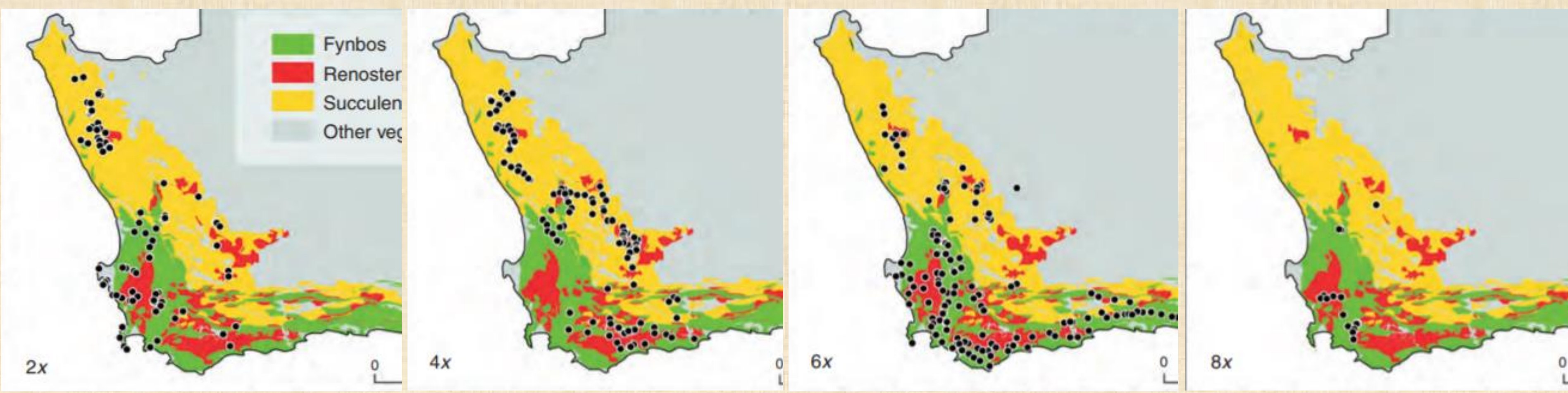


Ophioglossum reticulatum
2n = 96x = 1440,
Khandelwal (1990) Bot J Linn Soc

Are there limits?



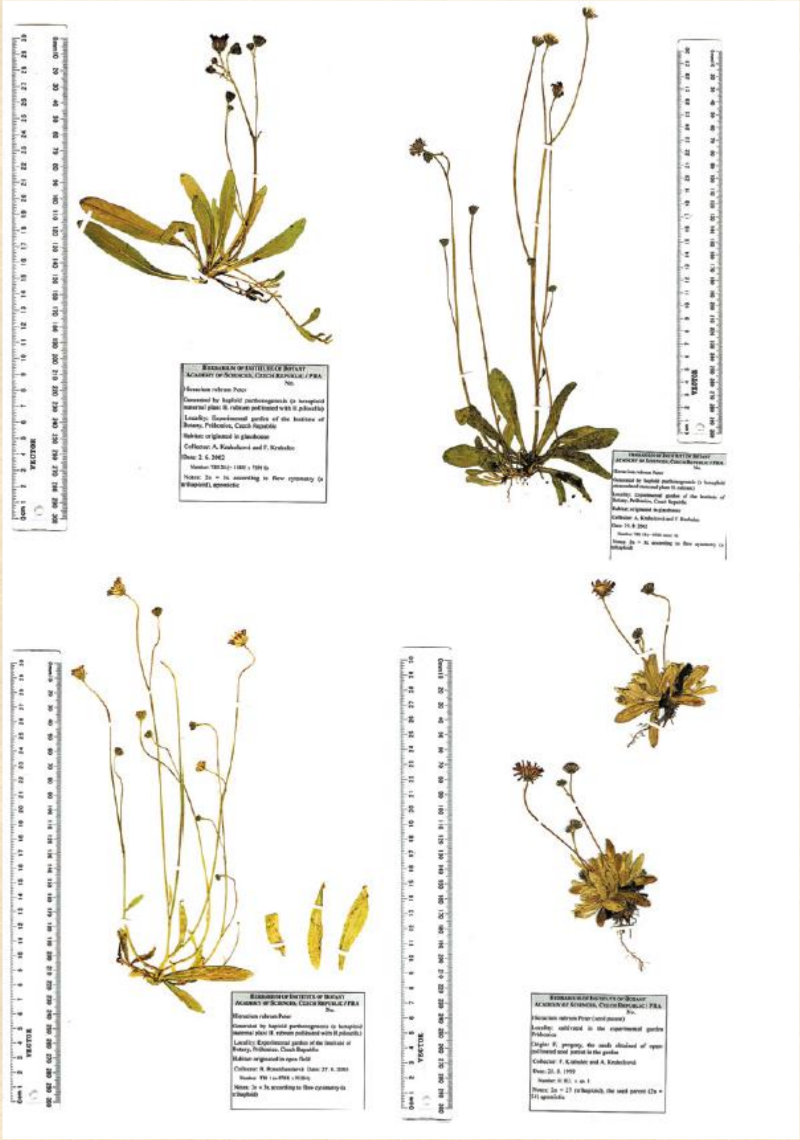
Arabidopsis thaliana (Corneille et al. 2019 Plant Physiol)
Slower development, delayed flowering



Oxalis obtusa in Cape (Krejcikova et al 2013 Ann Bot)

Can it go backwards?

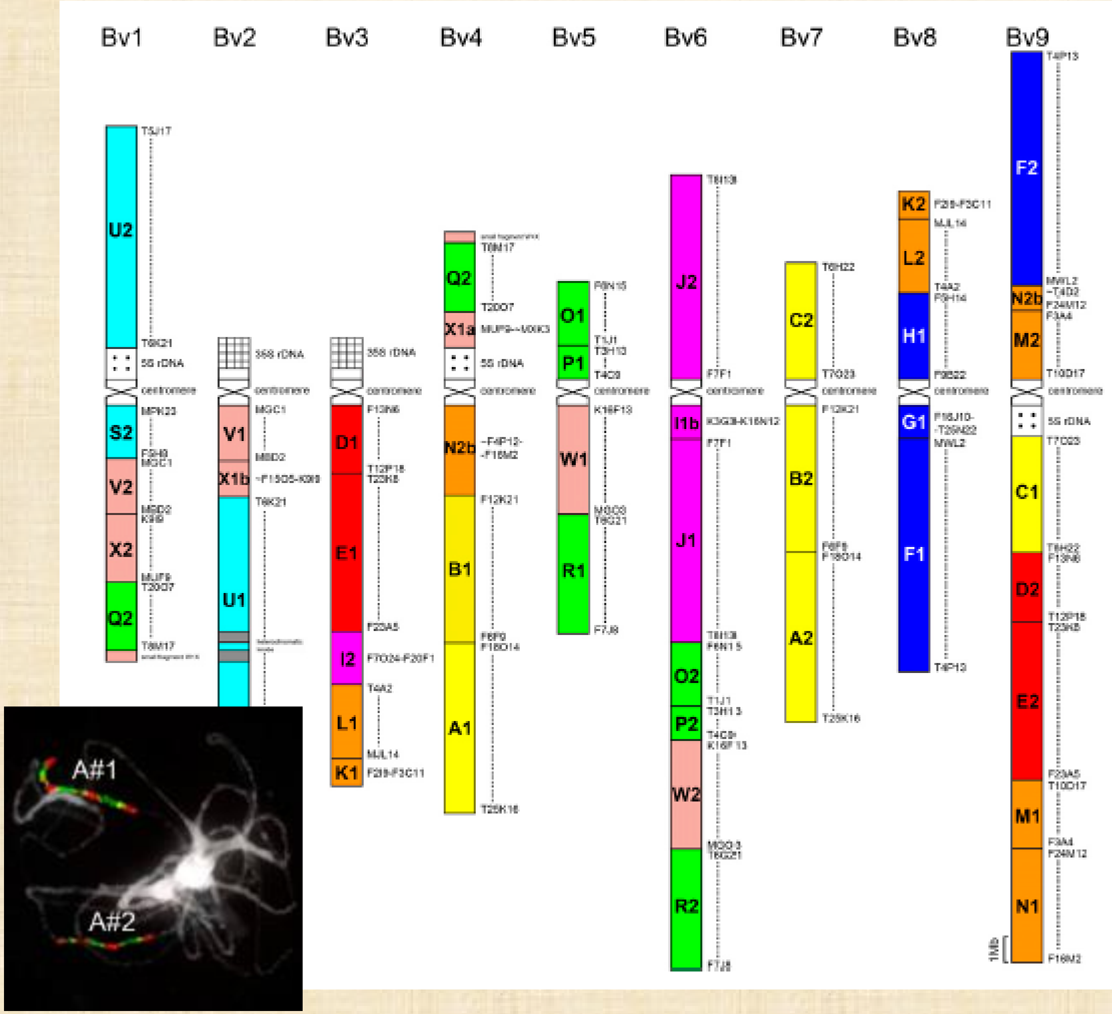
- polyhaploids
- rare, usually in apomictic complexes (haploid parthenogenesis)

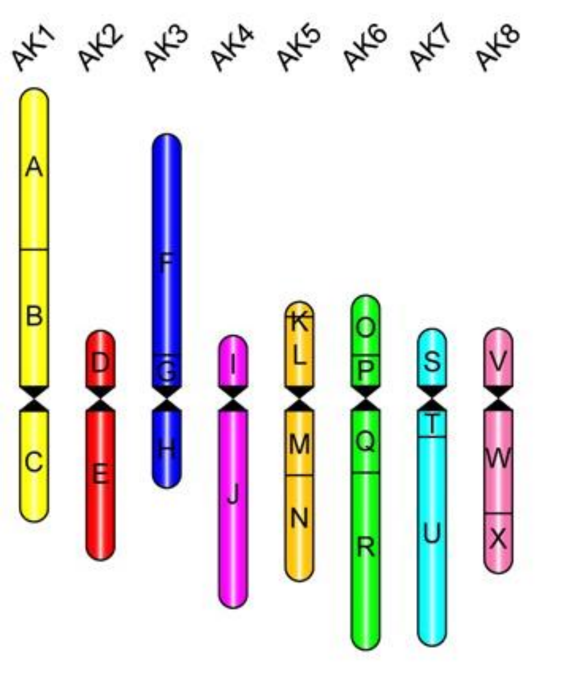


Trihaploid *Hieracium* subg. *Pilosellla* – up to 80% of progeny of hybrids

Can it go backwards?

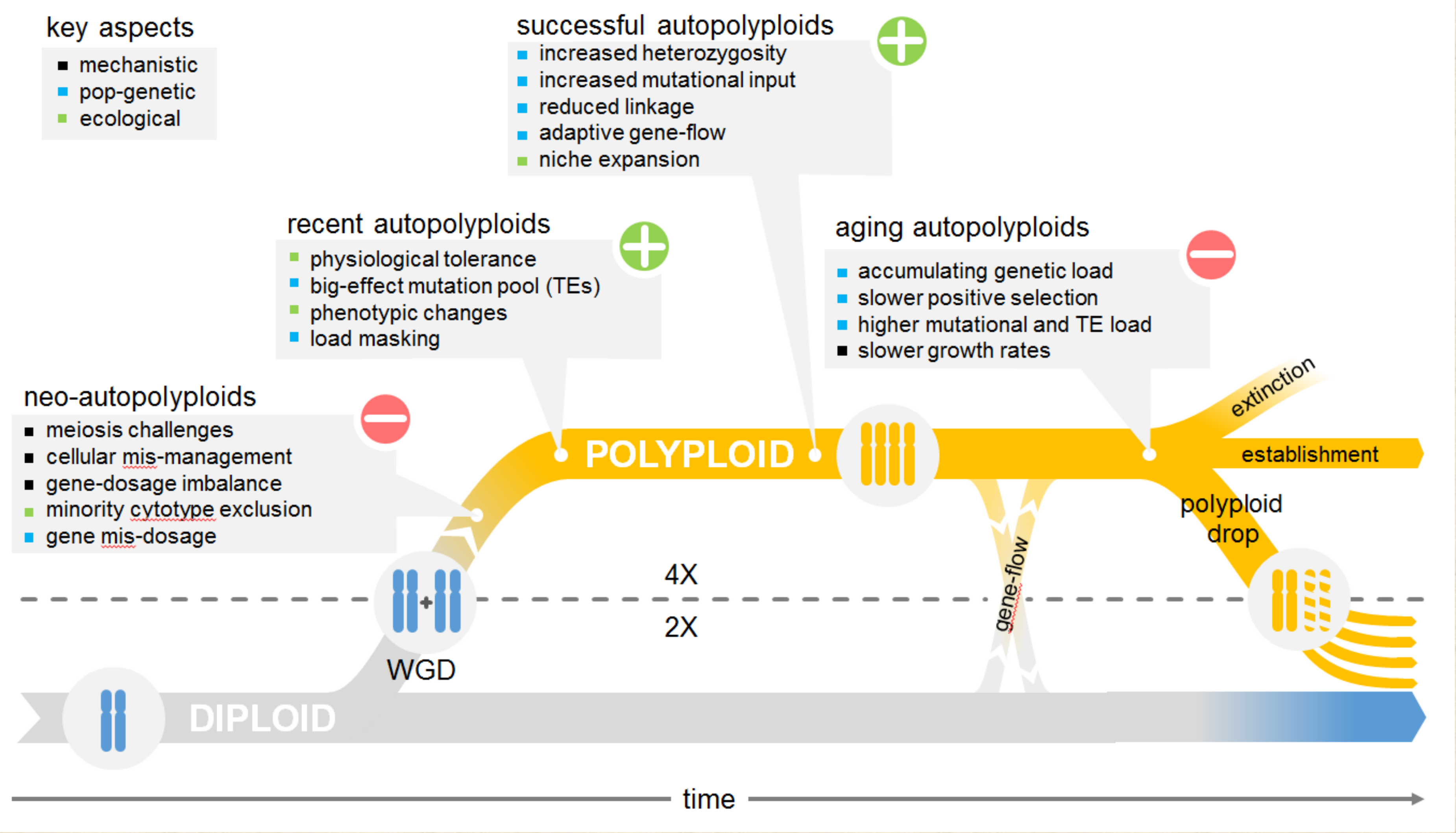
- *Biscutella* n = 9
- Brassicaceae ancestral karyotype n = 8



Polyploidy – double-edged sword

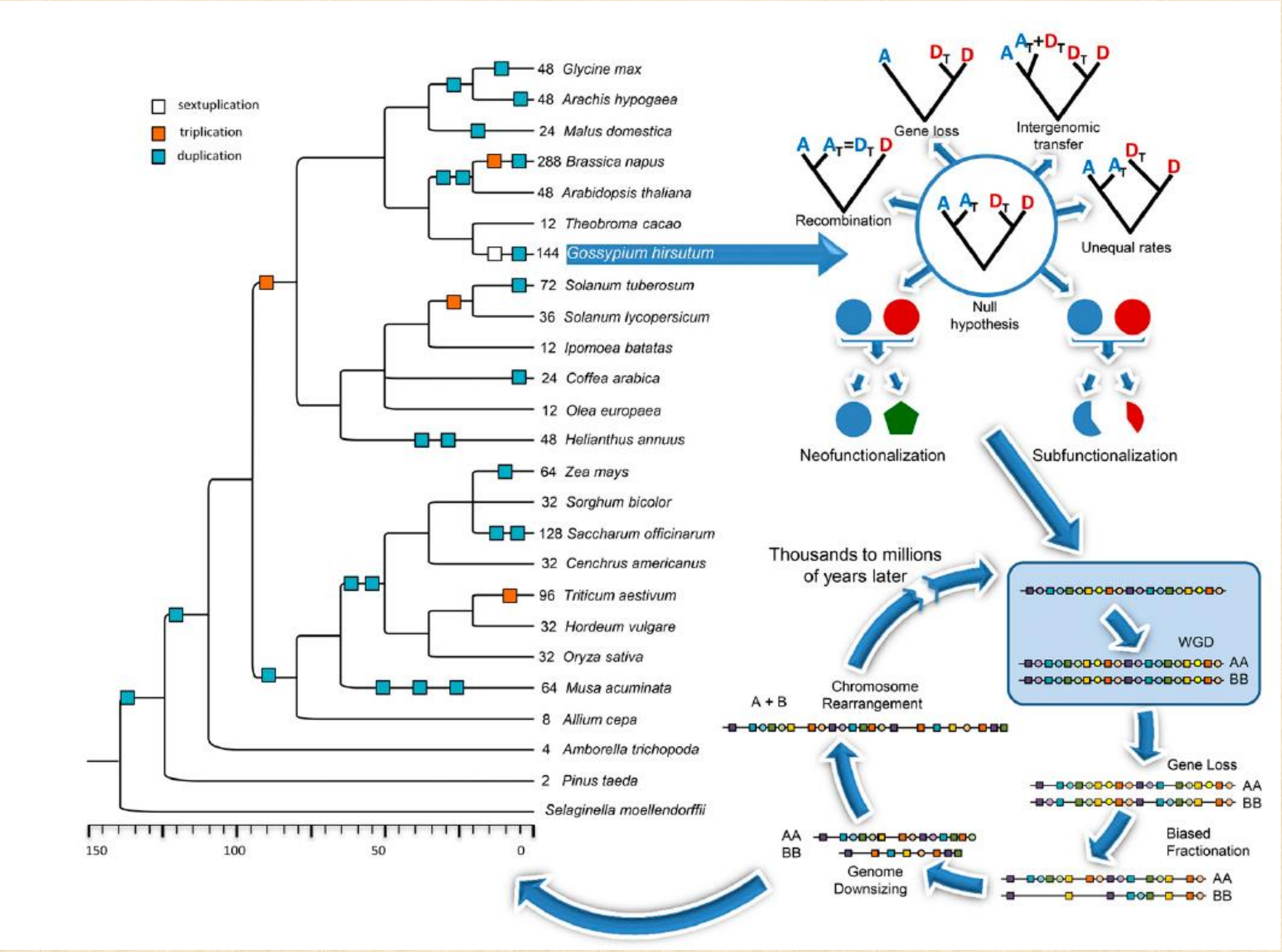
- Polyploid “hop”…
- … and “drop”



Baduel et al. 2018 Front Evol Ecol

Can it go backwards?

- Wondrous cycles

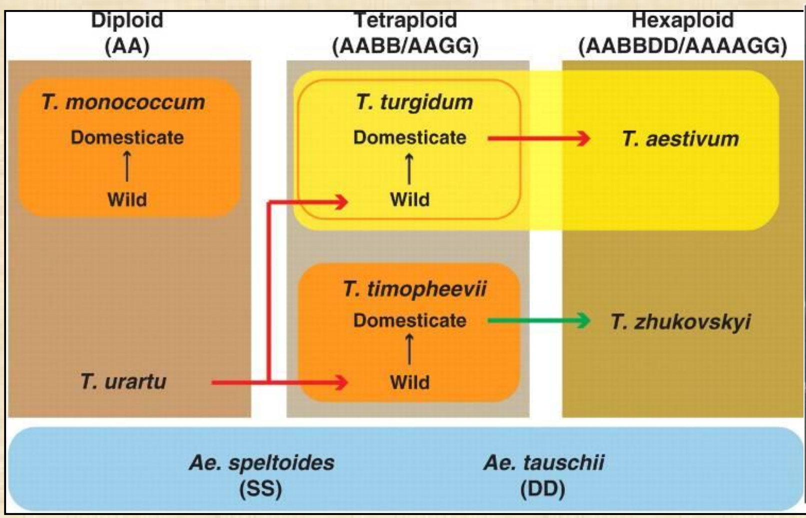


Wendel 2016 Am J Bot

Impact

- ancient WGDs
- Key innovations (vertebrates, flowering plants, …)

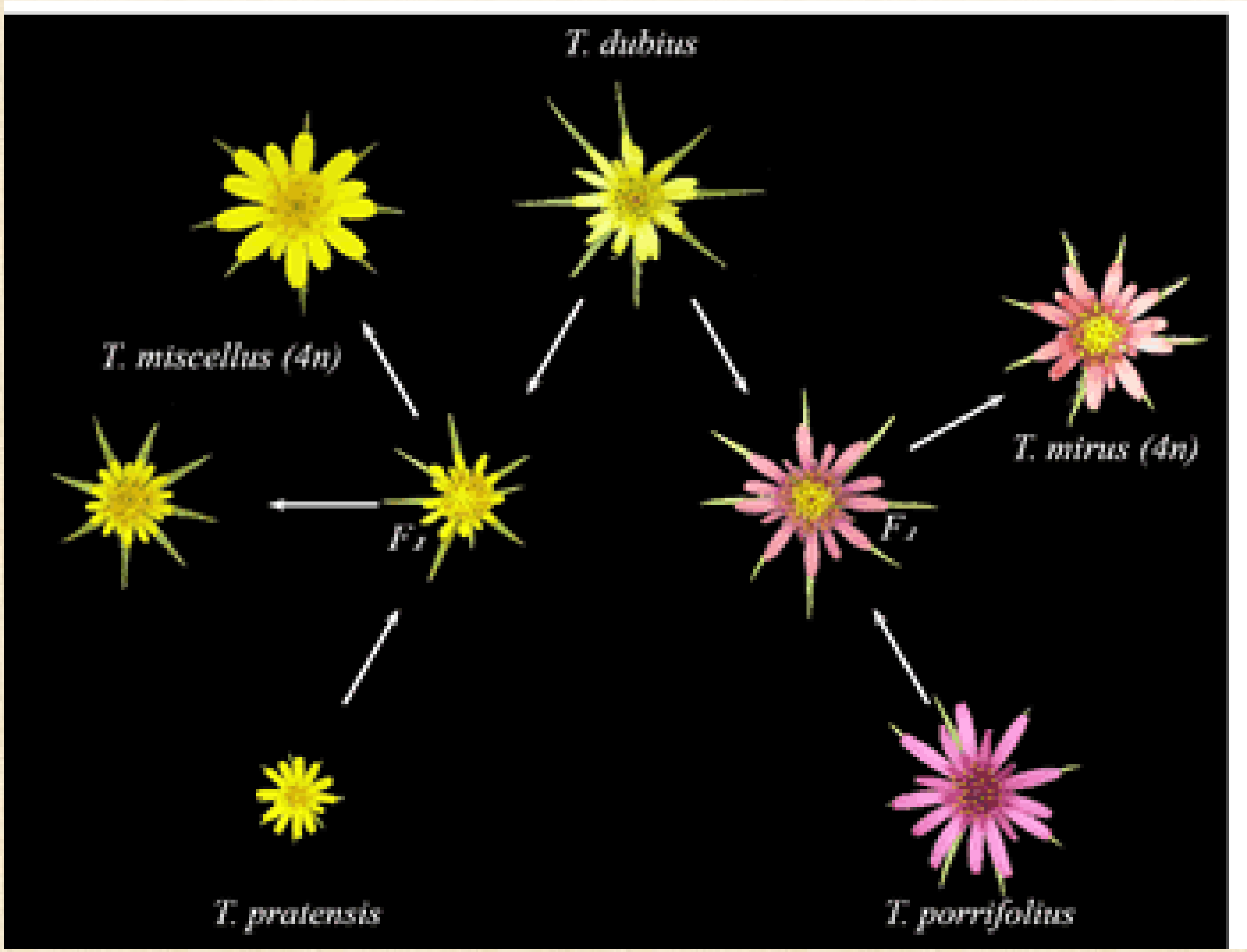
- **recent polyploids**:
- 71% crops (84% area), invasions, ...
- 90% of biomass are polyploids




Matsuoka et al 2011 *Triticum*

Polyploid speciation

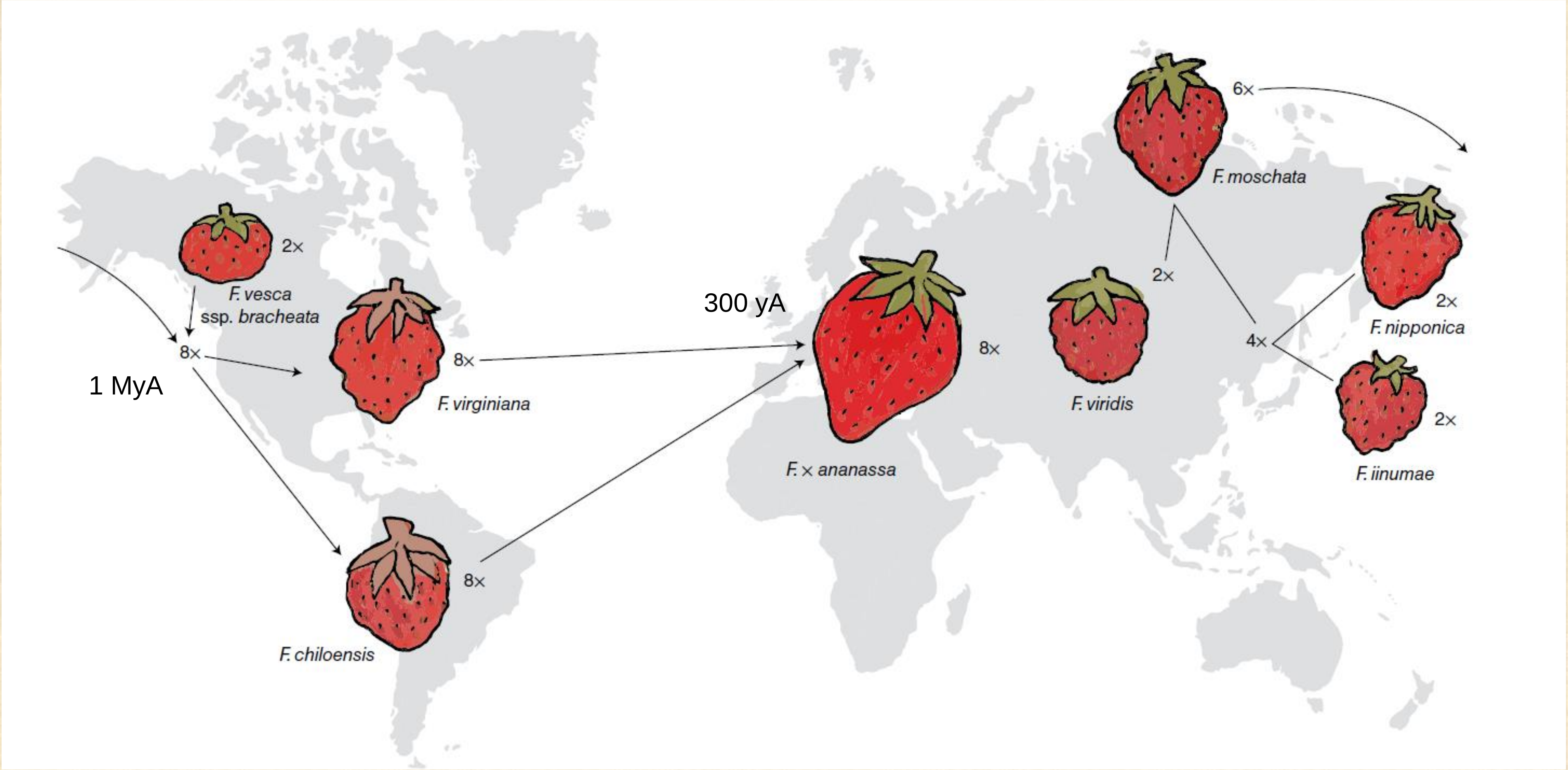
min. 21-times



min. 11-times

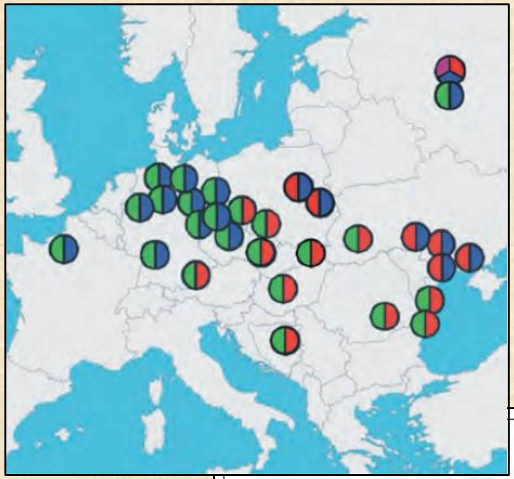
Kozí brada (*Tragopogon*) in USA – ca 100 years of evolution

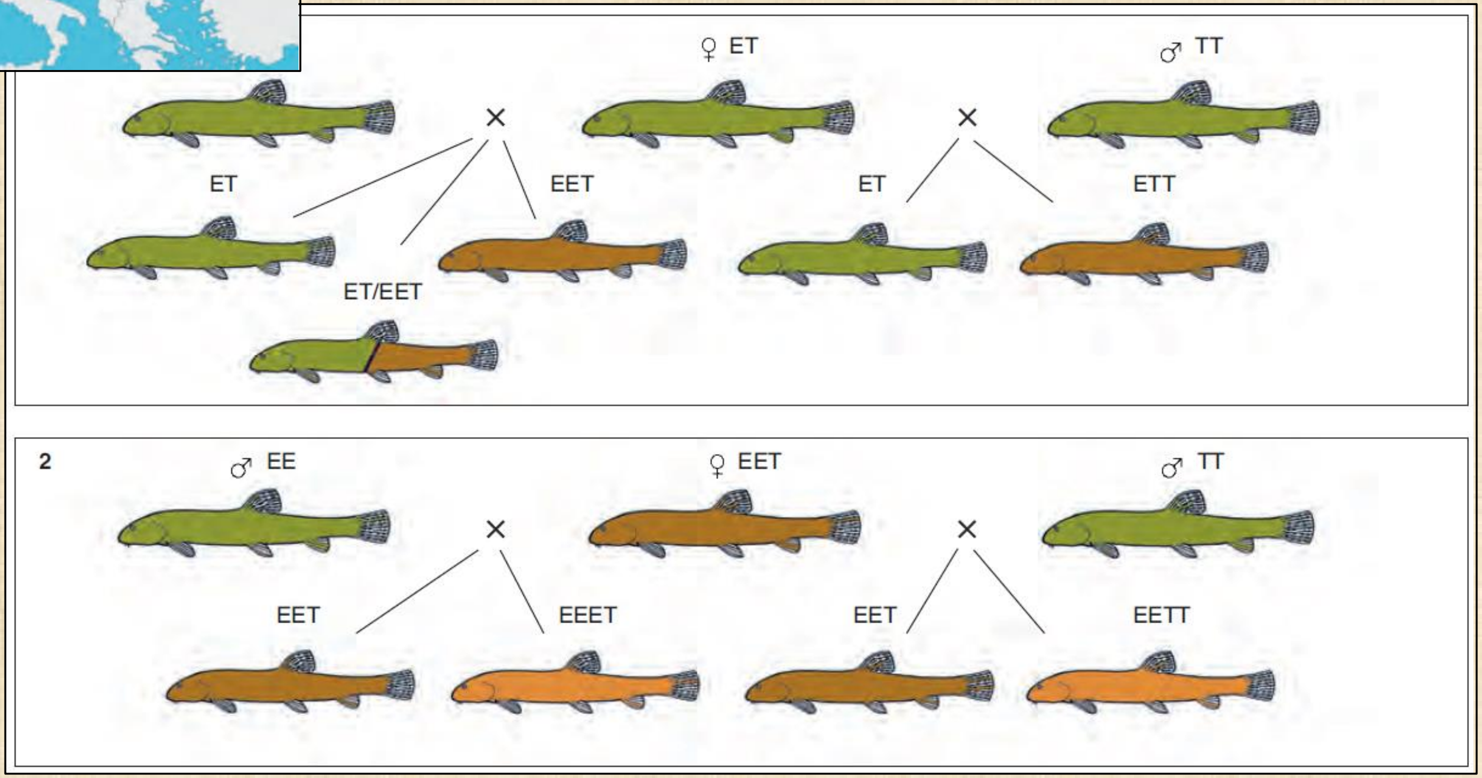
Polyploid speciation



Spatio-ploidal evolution of strawberry (*Fragaria*) (Bertioli 2019 Nat. Genet.)

Polyploid speciation

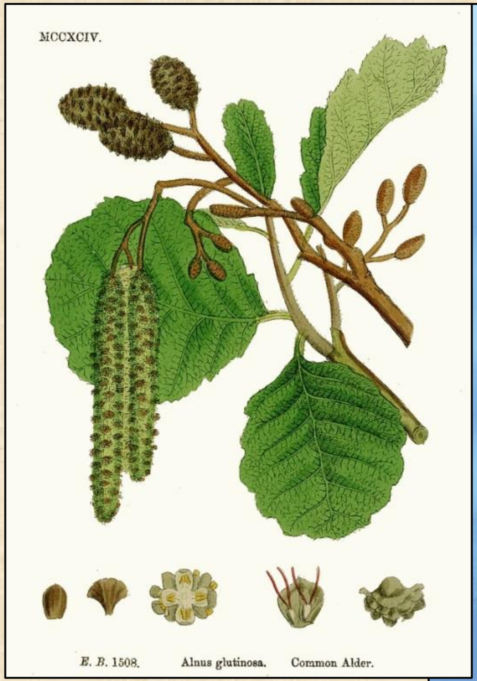


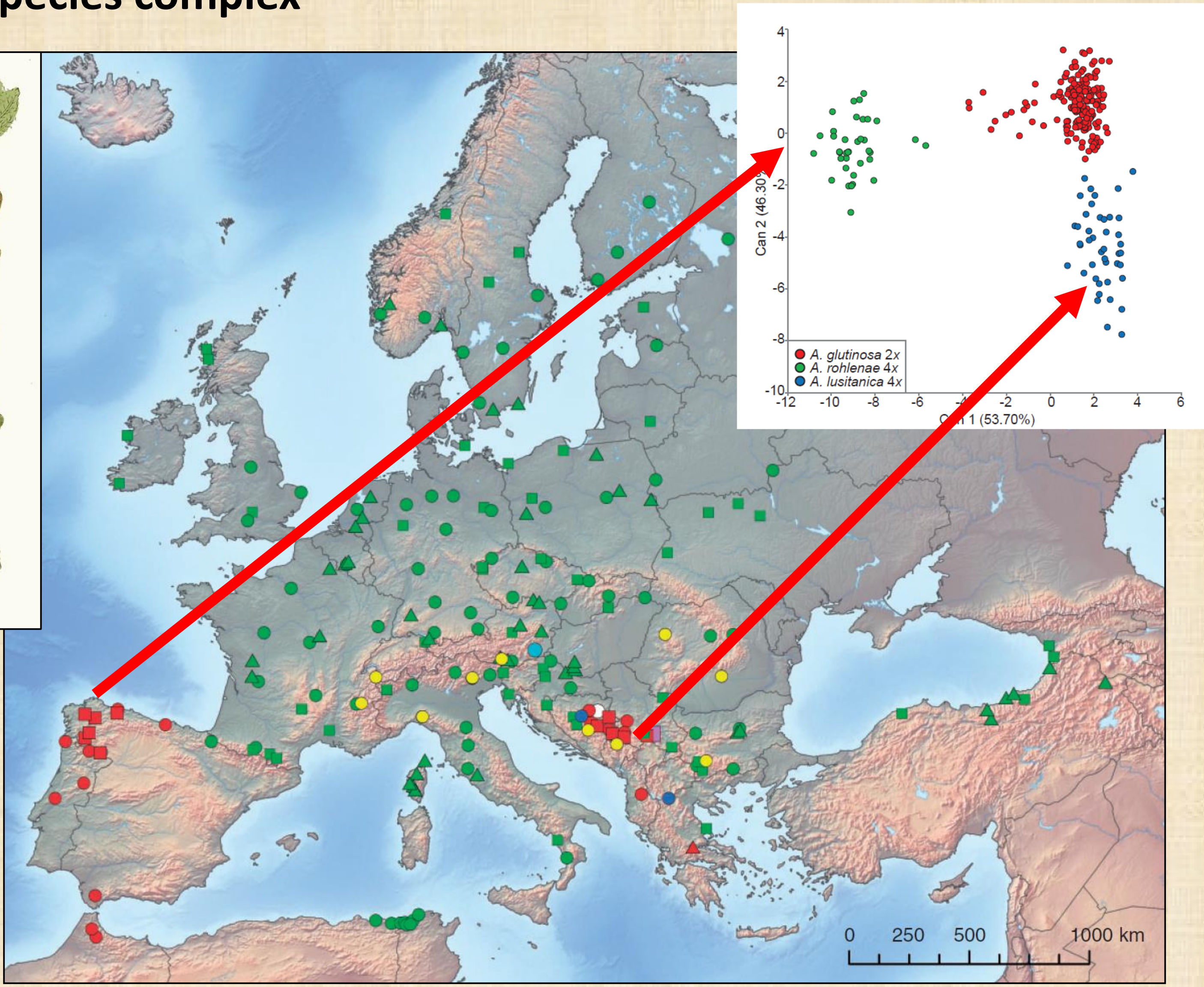


Cobitis taenia (TT) and C. elongatoides (EE) and their hybrids that reproduce further asexually/unisexually, despite they need males to start the oocyte development (Rab et al. 2003 Ziva)

Autopolyploid speciation

Autopolyploid **species complex**





Alnus glutionsa (2x, green), *Alnus rohleane* (4x, red), *Alnus lusitanica* (Mandak et al 2016 Ann Bot, Vit et al. 2017 Taxon)

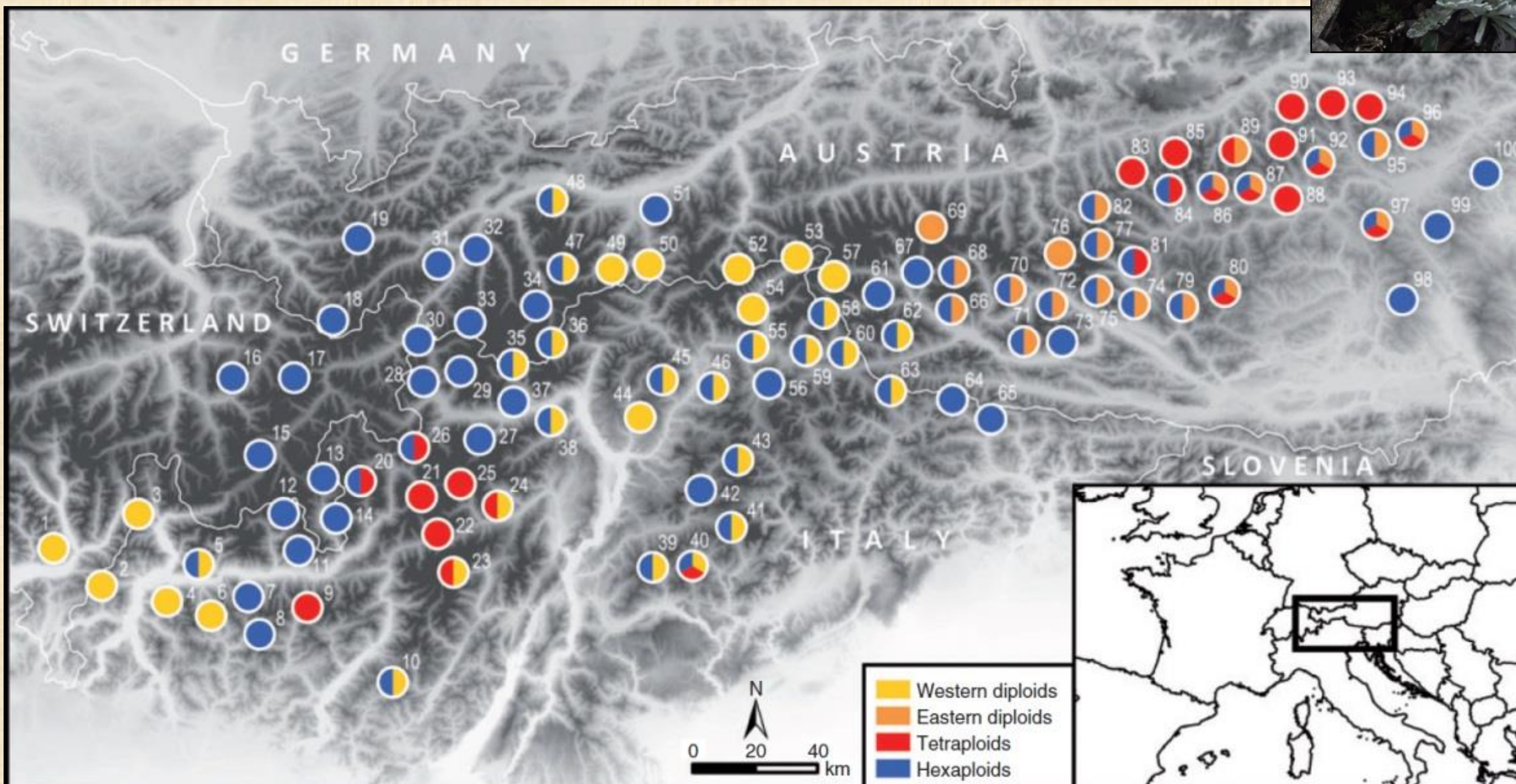
Underestimated diversity?

Autopolyploid

-2006 (chromosome counts): 6x

2007 (flow cytometry 380 samples: 2x, 4x, 5x, 6x, 7x

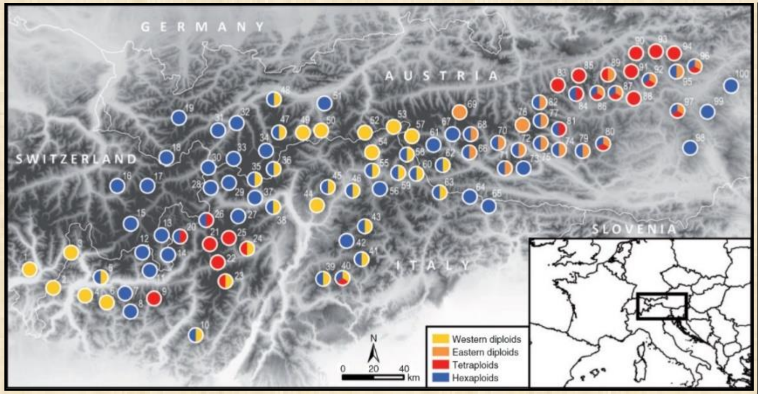
2010 (flow cytometry of 5033 indivs.: 2x, 3x, 4x, 5x, 6x, 7x, 8x, 9x

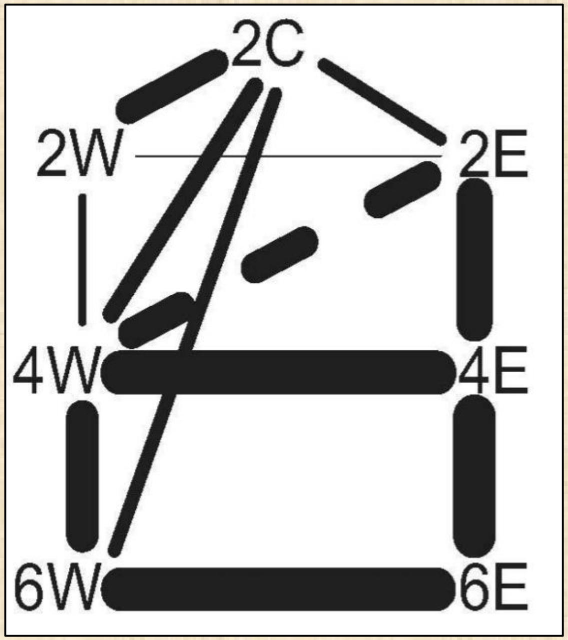


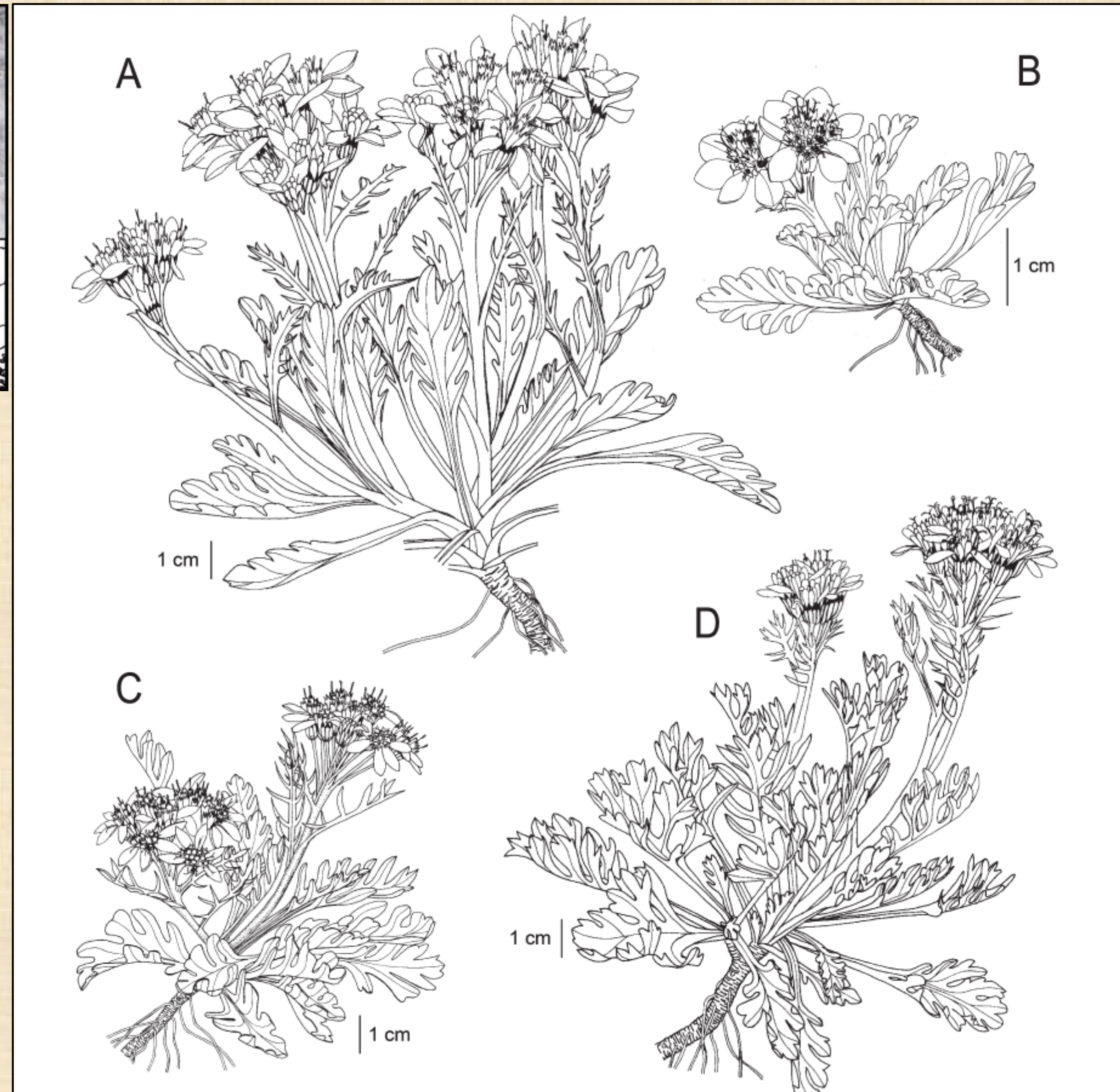
Senecio carniolicus complex (2x – 9x) Suda et al. 2017 Am J Bot, Sonnleitner et al. 2011 Ann Bot.

Polyploid speciation

Autopolyploid **species complex**



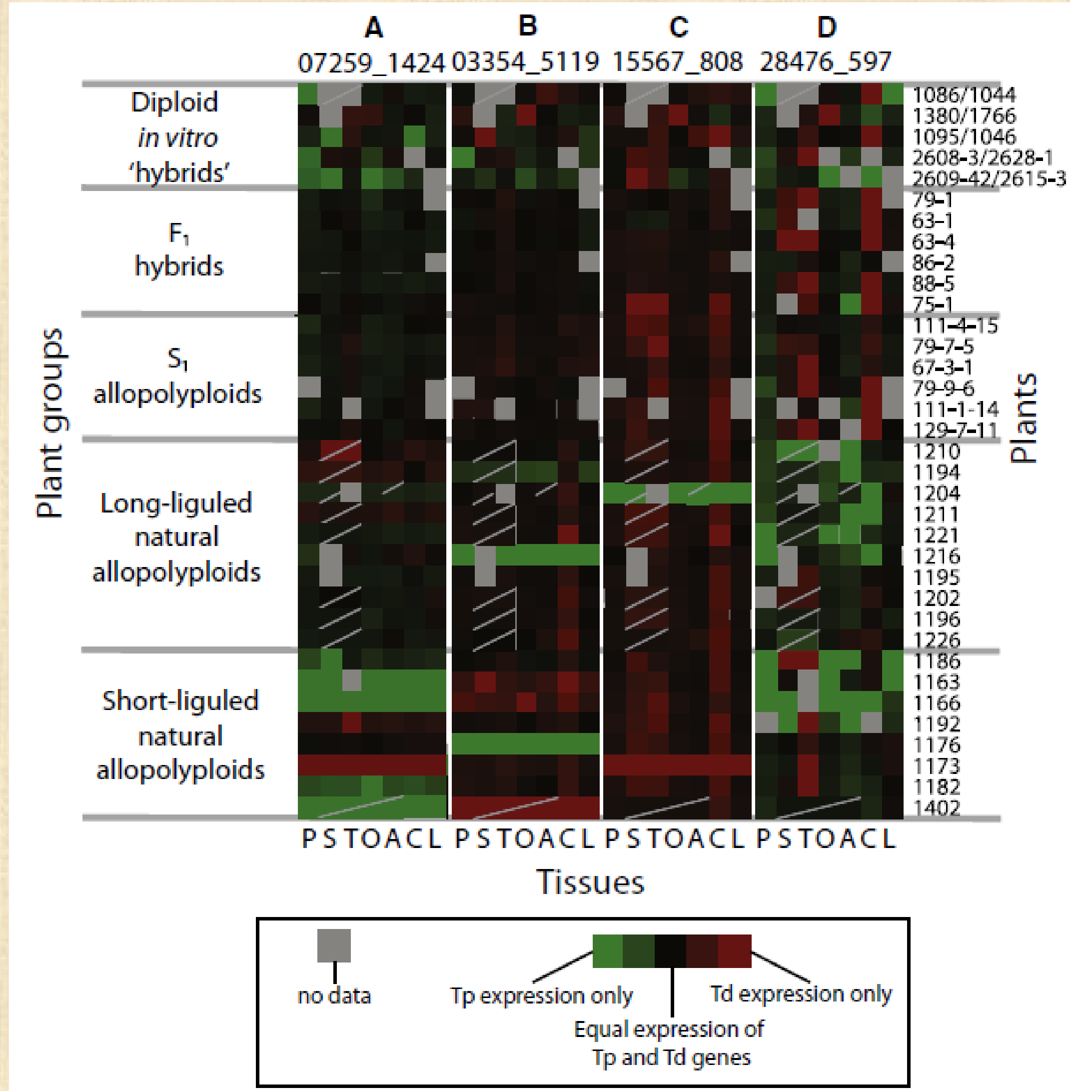




Senecio carniolicus complex (2x – 9x) Flatscher et al. 2015, Winkler et al. 2018 Mol Ecol res.

Polyploid speciation

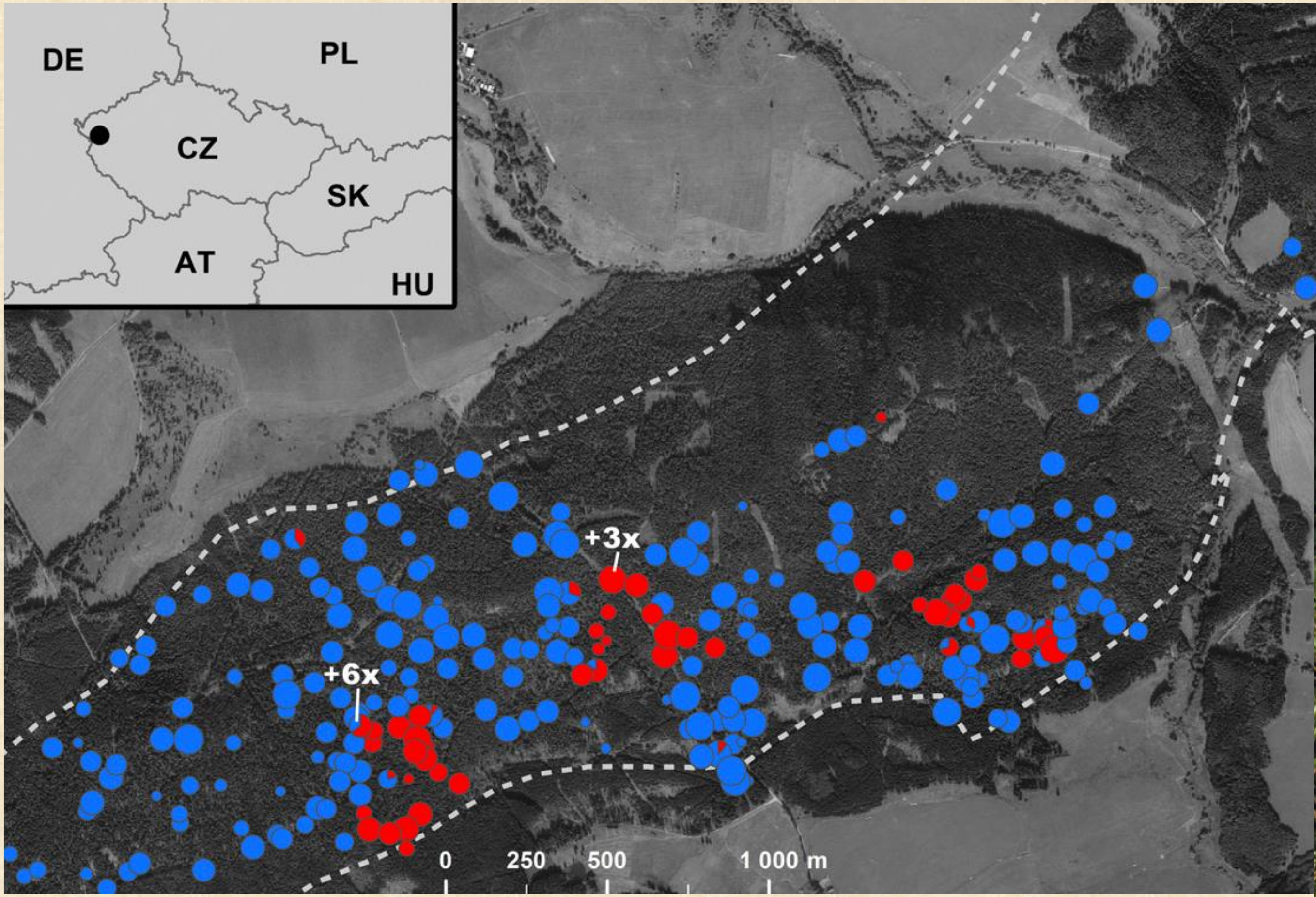
Does evolution repeat itself?



Buggs et al 2011 Curr Biol – subfunctionalization in allopolyploid *Tragopogon*

Polyploid speciation

Mixed-ploidy species: Natural laboratories of polyploidy speciation (16% of species – in those on average 16% mixed pops)



Knautia serpentinicola Hanzl et al 2014 Am J Bot

Polyploid speciation

Barriers

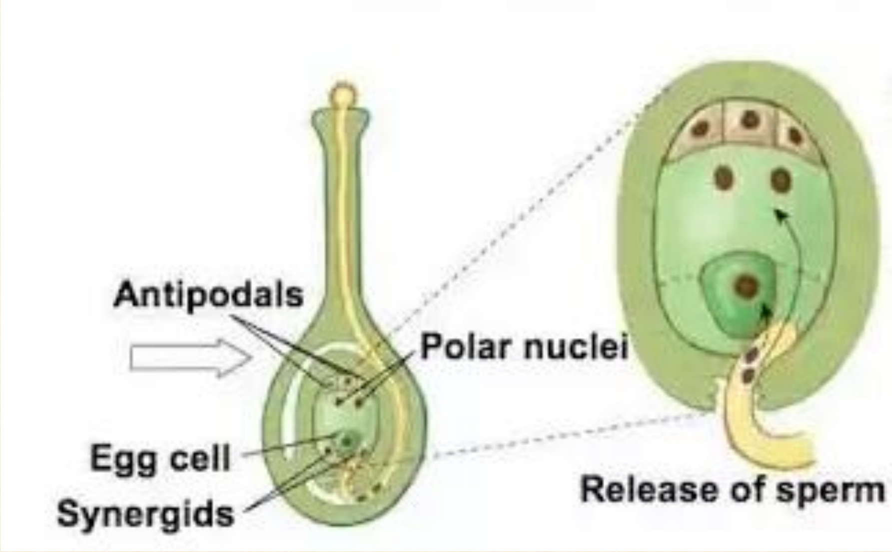
- Prezygotic
- **Postzygotic**

Postzygotic barriers

Triploid block

- Triploid seed – inviable / reduced viability
- Maternal : Paternal ratio in endosperm

- 2x mom + 2x dad =
- 4x mom + 4x dad =
- 2x mom + 4x dad =
- 4x mom + 2x dad =



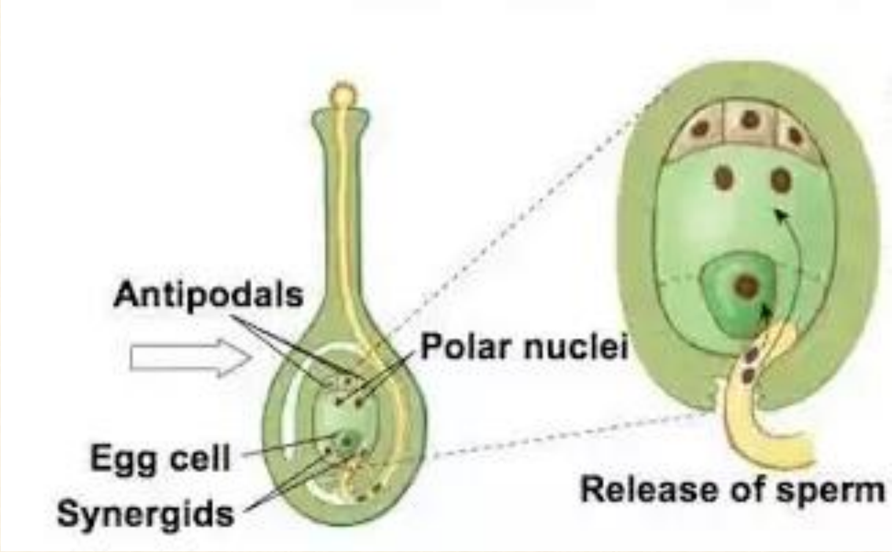
Double fertilization

Postzygotic barriers

Triploid block

- Triploid seed – inviable / reduced viability
- Maternal : Paternal ratio in endosperm

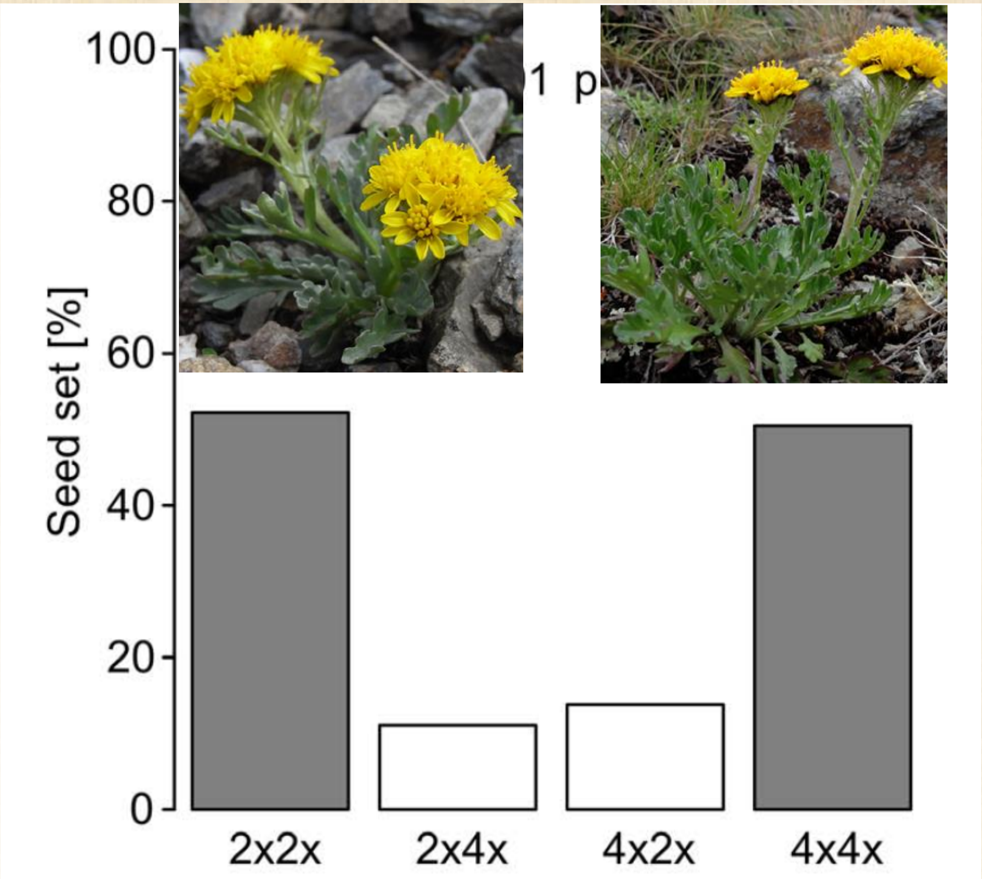
- 2x mom + 2x dad = 2:1
- 4x mom + 4x dad = 2:1
- 2x mom + 4x dad = 2:2
- 4x mom + 2x dad = 4:1



Double fertilization

Postzygotic barriers

Strong triploid block



Experimental crossings

Senecio carniloicus agg. (Sonnleitner et al 2013 PloS ONE, Huelber et al. 2015 Ecol Evol)

Postzygotic barriers

Triploid block

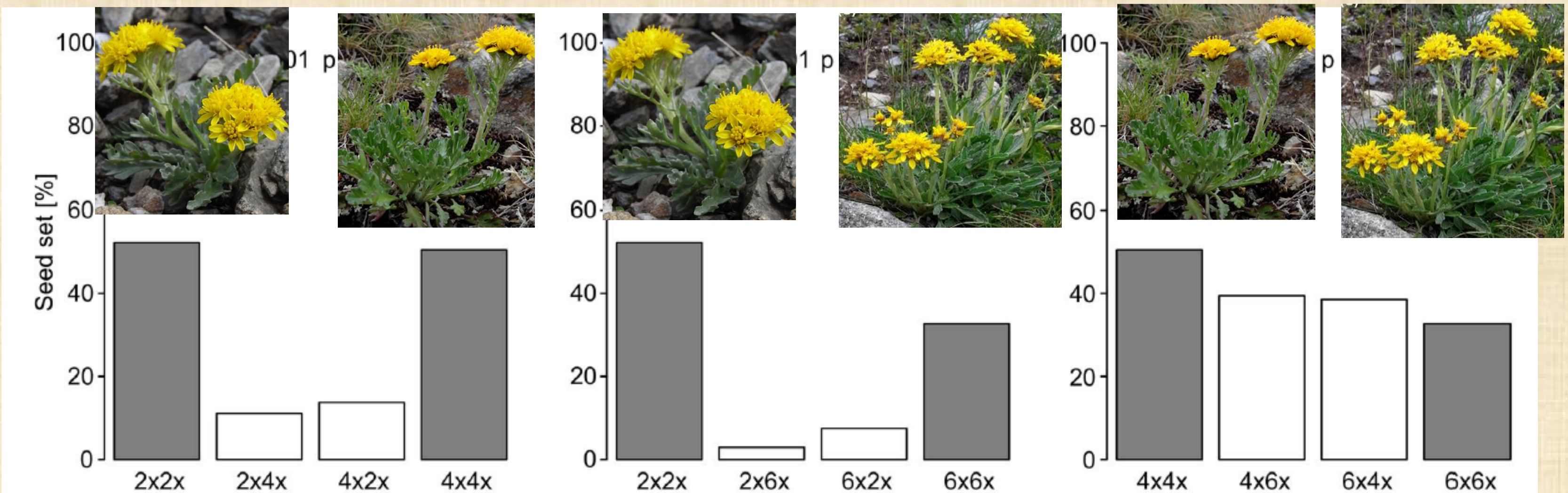
- Triploid seed – inviable / reduced viability
- Maternal : Paternal ratio in endosperm

- 2x mom + 2x dad = 2:1
- 4x mom + 4x dad = 2:1
- 2x mom + 4x dad = 2:2
- 4x mom + 2x dad = 4:1

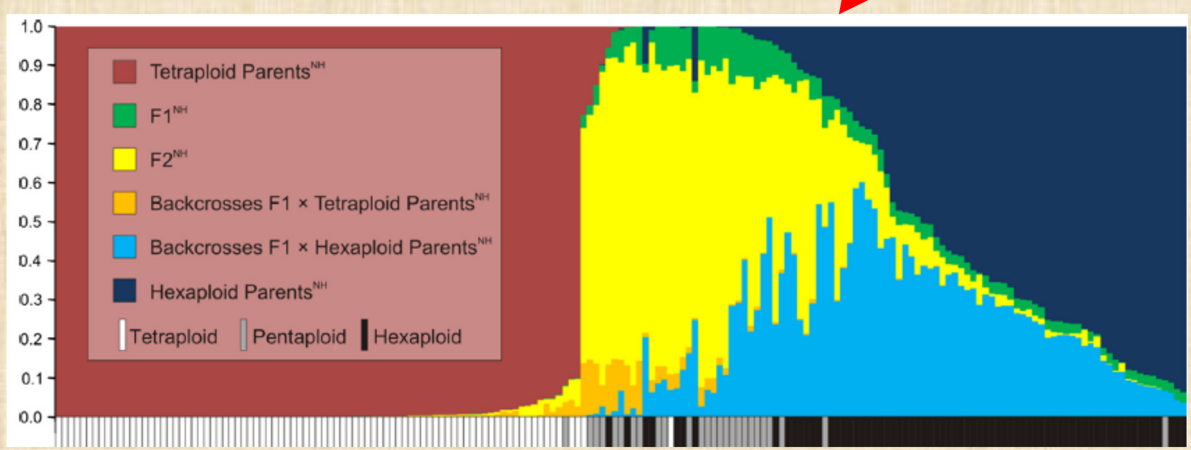
- **4x mom + 6x dad = 4:3**
- **6x mom + 4x dad = 6:2 = 3:1**

Postzygotic barriers

Strength of the barriers vary by ploidy



Experimental crossings



Natural population

Senecio carniloicus agg. (Sonnleitner et al 2013 PloS ONE, Huelber et al. 2015 Ecol Evol)

Postzygotic barriers

Lower triploid fitness

- Rare 3x in field vs. common 3x in experiments
- Cummulative fitness:

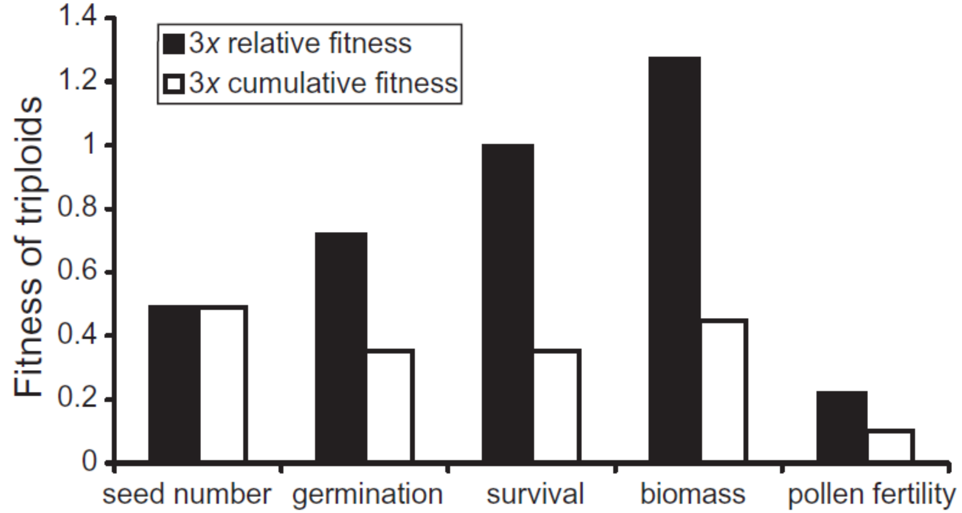


Figure 4. Relative fitness (by stage) and cumulative fitness of triploids ($2x \times 4x$ crosses) compared with diploids for five successive life stages in *Chamerion angustifolium*, based on a greenhouse study (Burton & Husband, 2000). Seed number refers to the fertility of the cross, not to seed number of triploid plants.

Chamerion angustifolium (Husband 2004)

Postzygotic barriers

Reduced triploid fertility

- Problems with chromosome pairing in meiosis

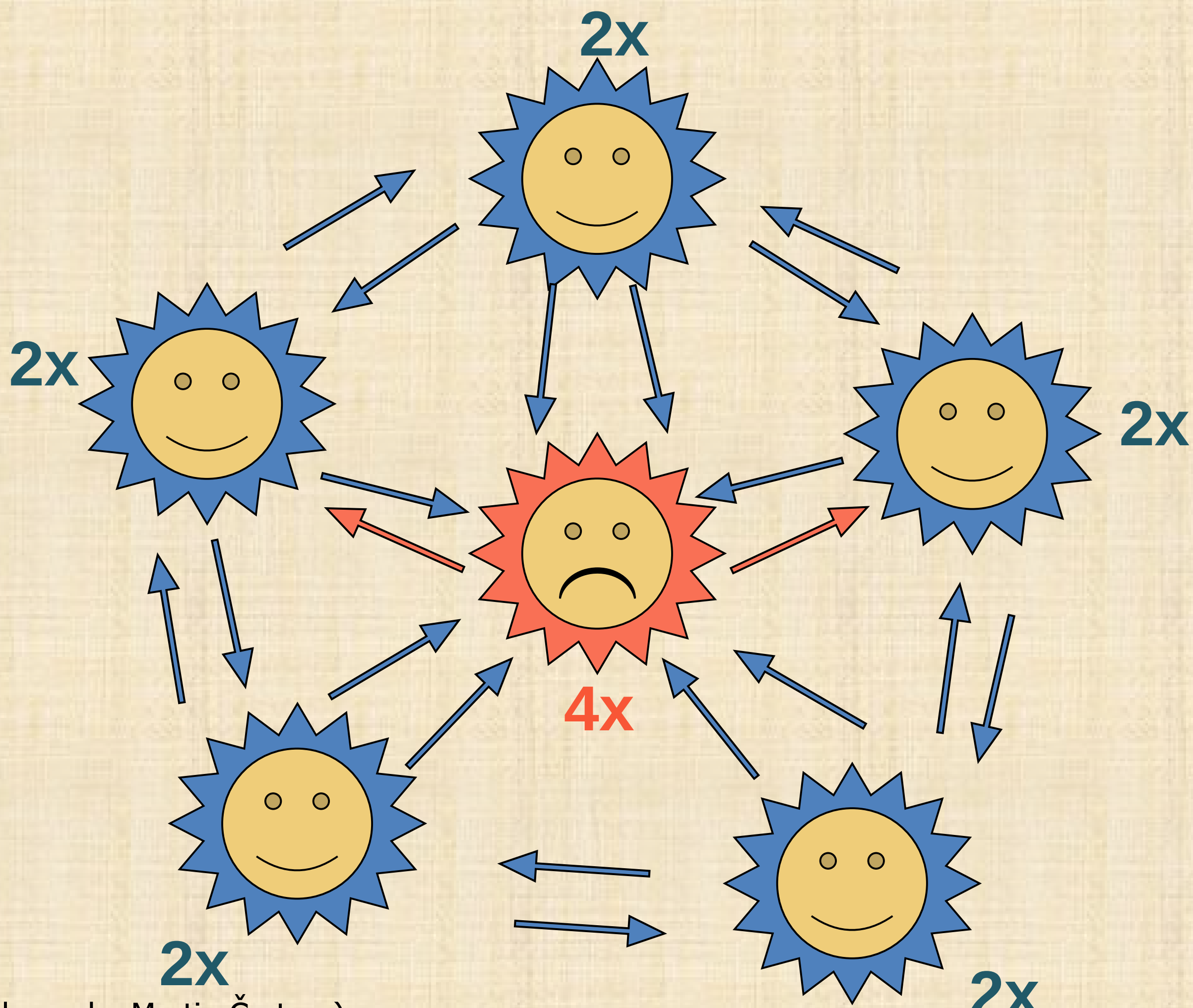
Polyploid speciation

Barriers

- **Prezygotic**
- Postzygotic

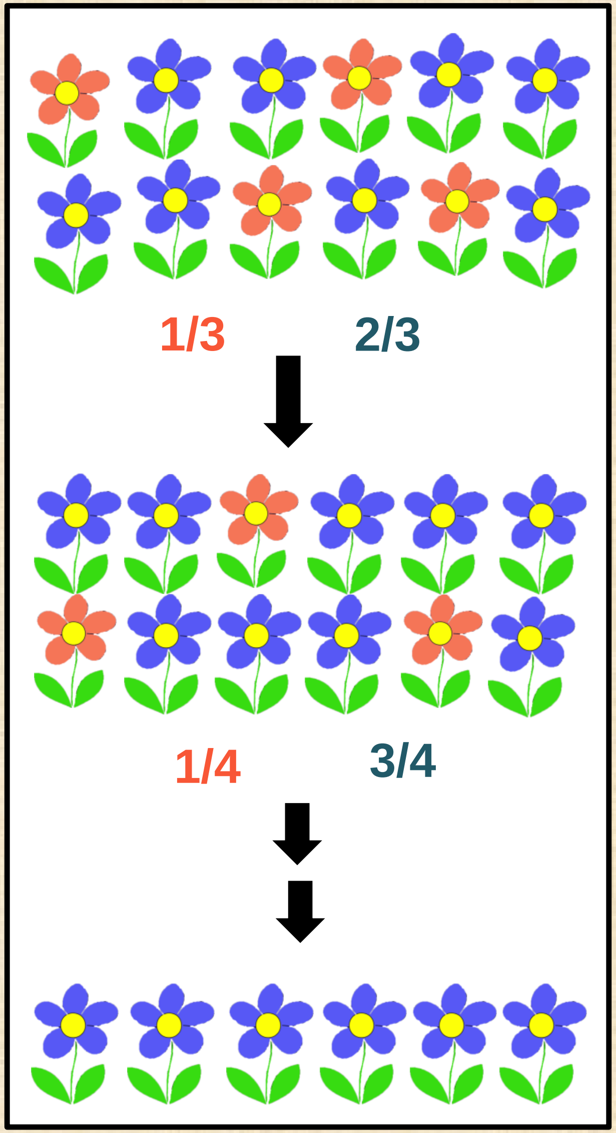
Prezygotic barriers – trigger

Minority cytotype exclusion



(drawn by Martin Čertner)

Levin 1975 Taxon
40% freq polyploid excluded in 4 generations

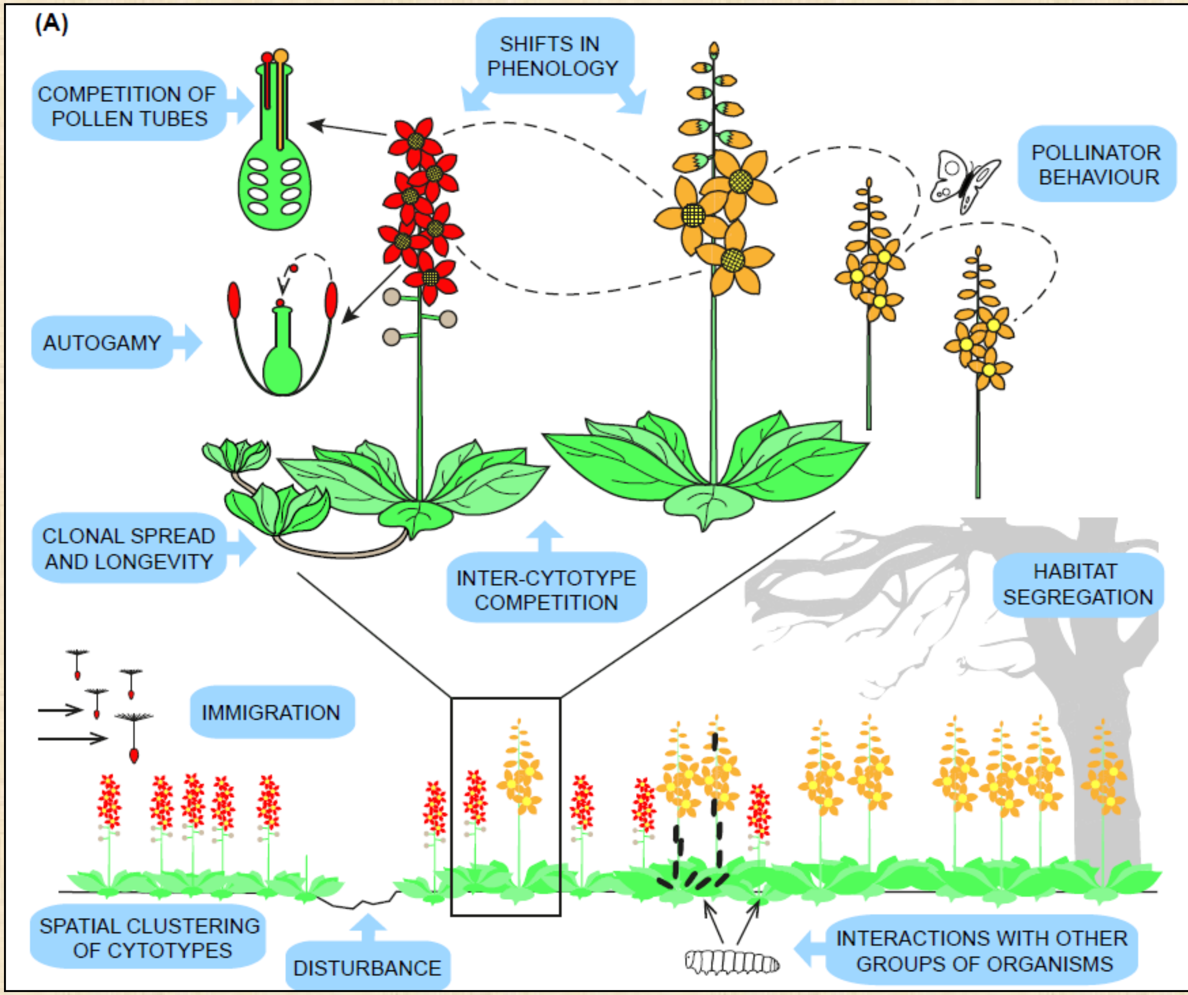


Prezygotic barriers

Barriers

- **Prezygotic**
- Spatial arrangement
- Flowering time
- Pollen competition
- Repro-system shift (autogamy, apomixis)
- Niche shift
- Pollinator preference
- Mycorrhizal association

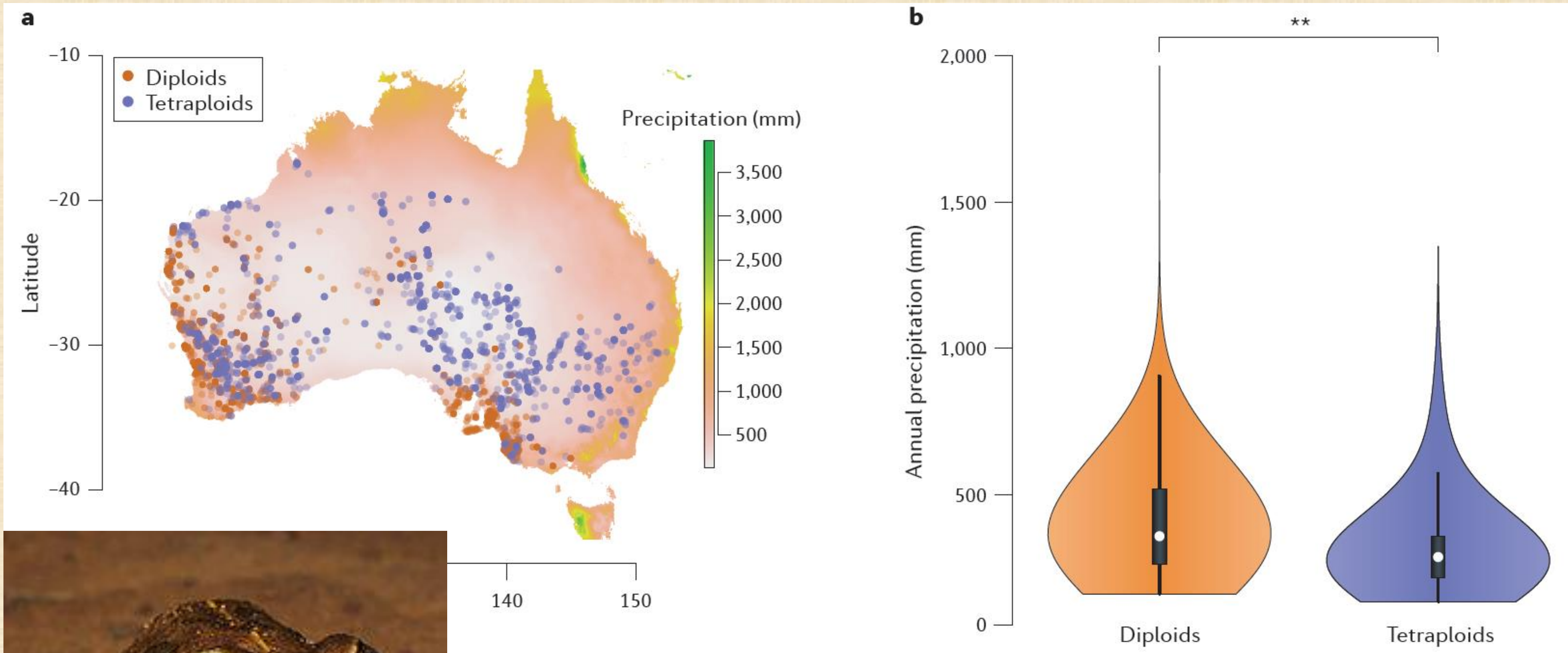
- Postzygotic



Kolar et al 2017 Trend Plant Sci

Prezygotic barriers

Ecological divergence

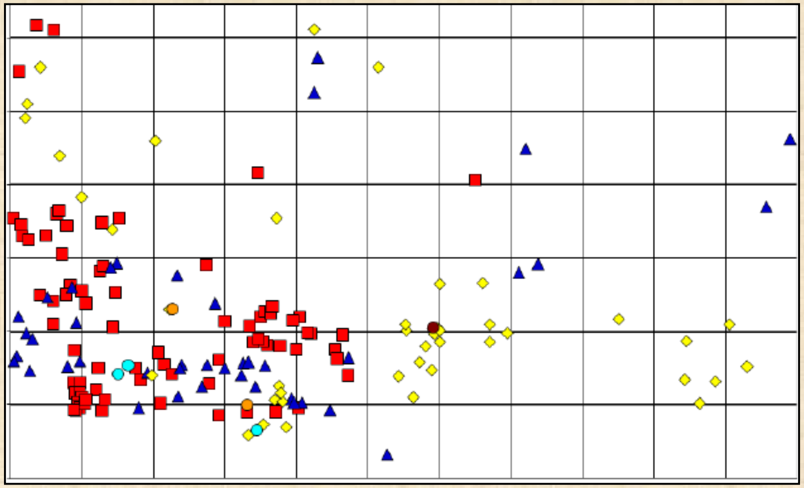


Neobatrachus (van de Peer et al 2017 Nat Rev Genet)

Prezygotic barriers

Prezygotic barriers?

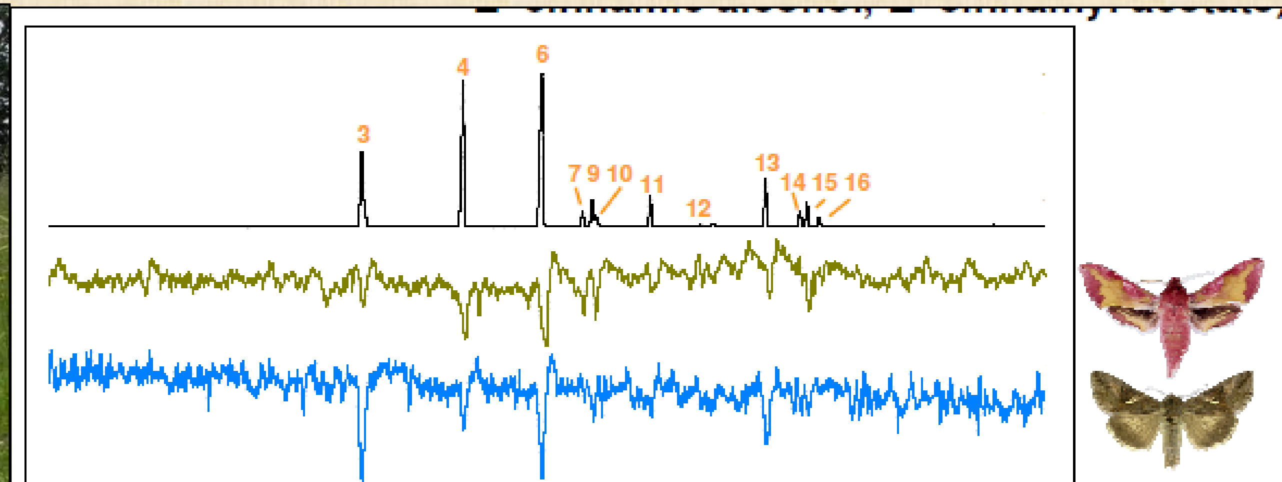
Gymnadenia – 5 ploidies in one population

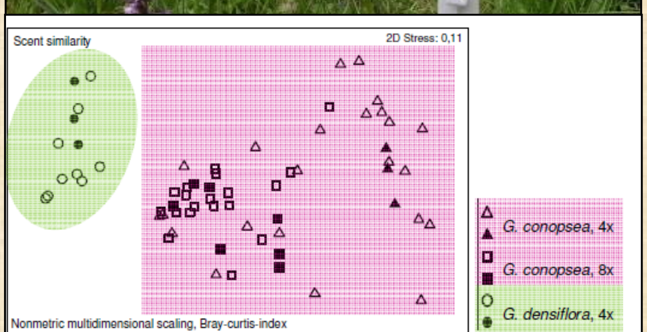


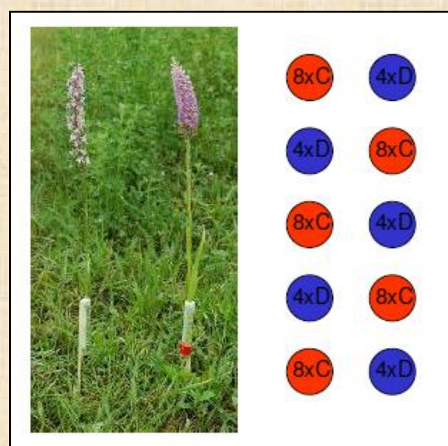
Gymnadenia conopsea agg. (2x,3x,4x,5x,6x),
Trávníček et al. 2011 AnnBot

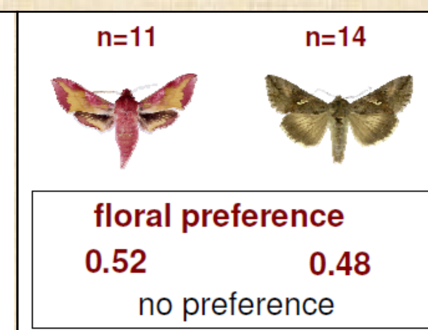
Prezygotic barriers

Prezygotic barriers? – pollinator shift





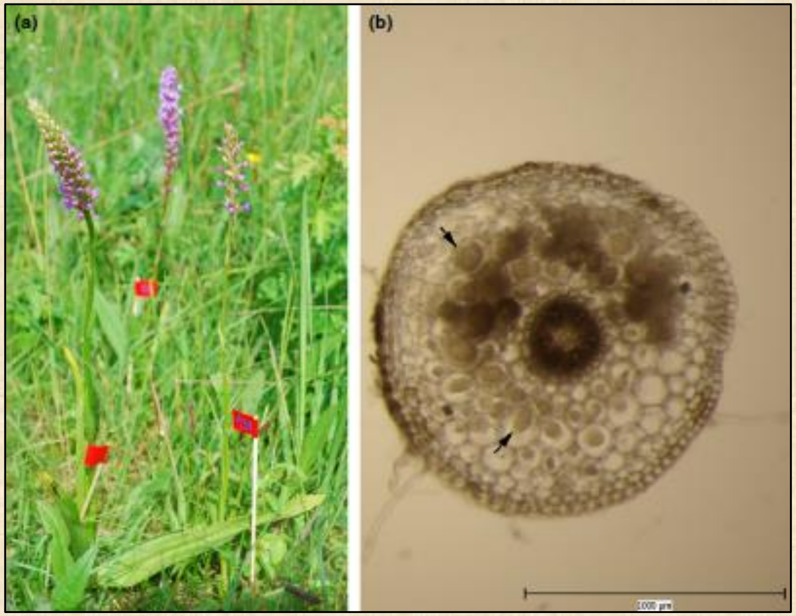




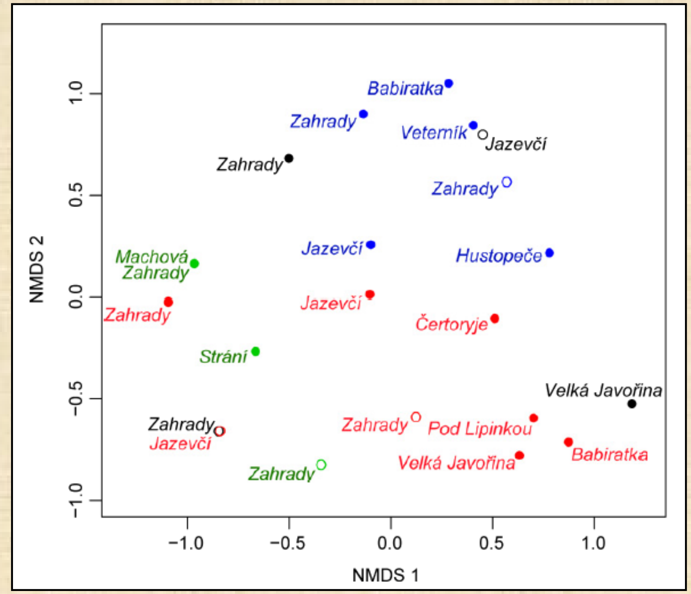
Gymnadenia conopsea agg.
(Jersáková et al. 2010 Evol Ecol)

Prezygotic barriers

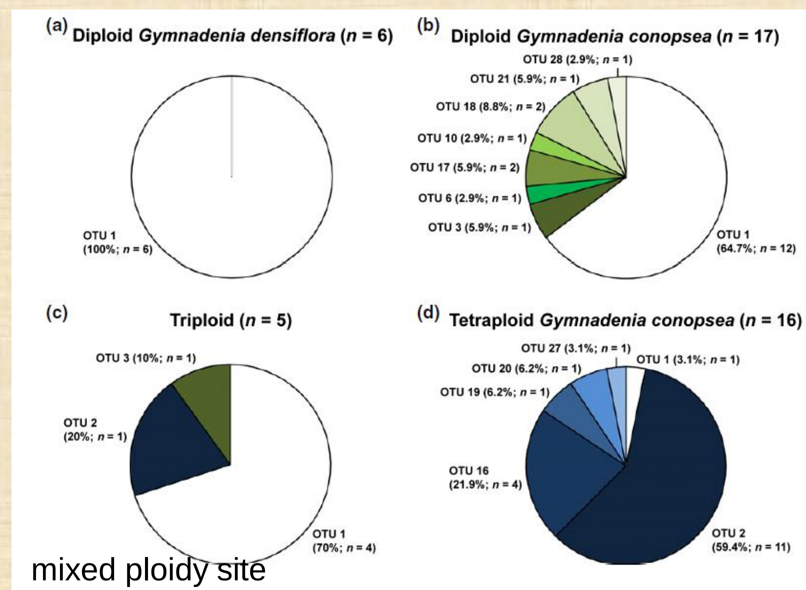
Prezygotic barriers? - mycorrhiza



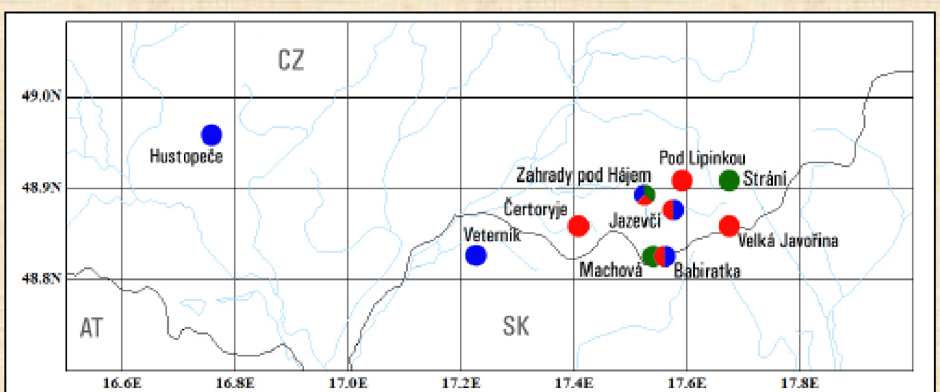
Gymnadenia conopsea agg. Těšitelová et al. 2013 New Phytol



fungi OTUs, among pop*cytotypes all sites

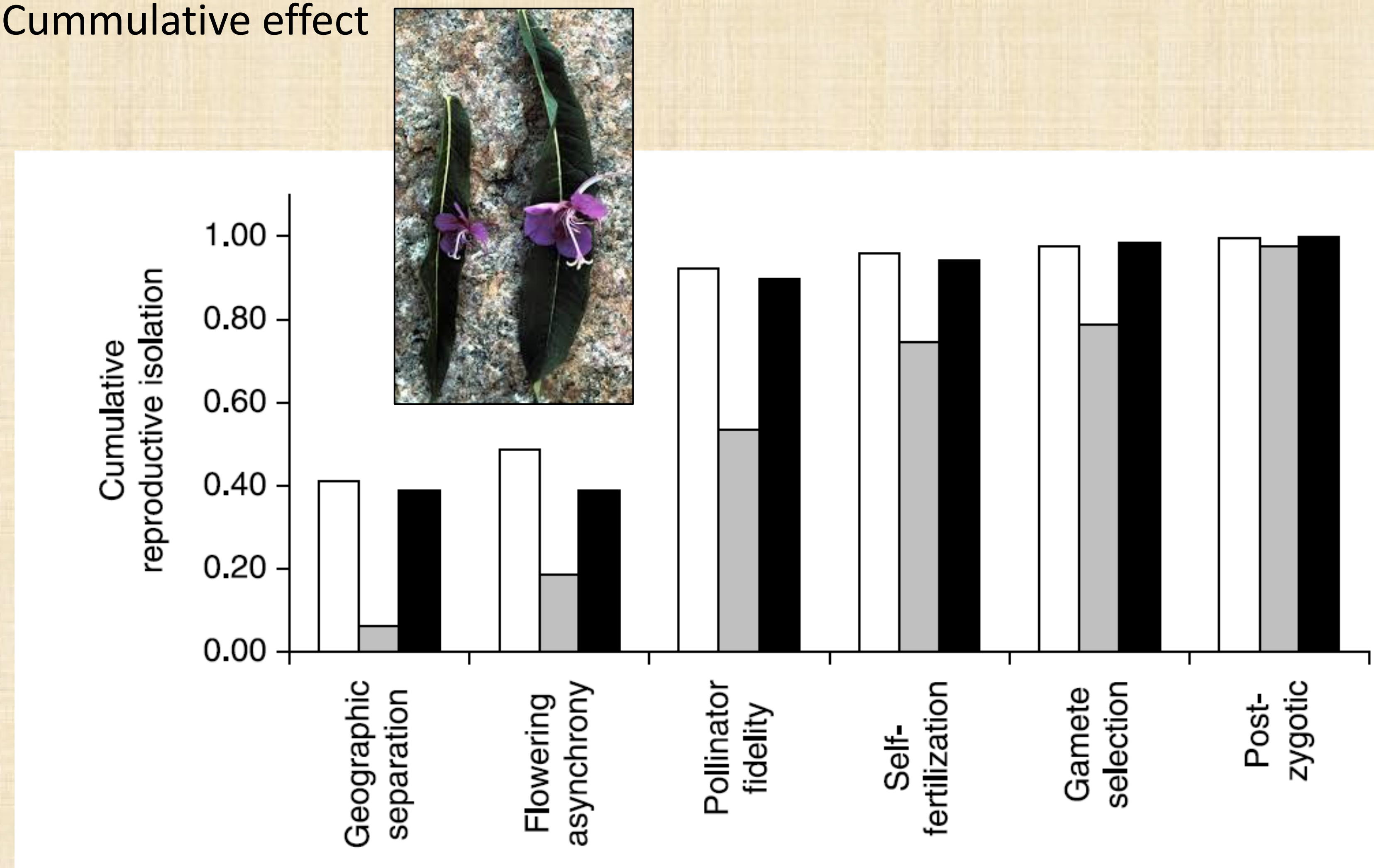


mixed ploidy site



Prezygotic barriers

Cummulative effect



Chamerion angustifolium (2x,3x,4x), Husband & Sabara 2004 New Phytol
Overall (white), 2x-specific (gray), 4x-specific (black)

Interploidy gene flow

- ploidy – might be a porous barrier

Neobatrachus sutor (2x) mating *N. kunapalari* (4x) (photo S. Mahony)

Genome-wide admixture signal
Arabidopsis arenosa (2x, 4x) Monnahan et al. 2019 Nat Ecol Evol

Does cross-ploidy gene flow facilitate or constrain adaptation and speciation?

Interploidy gene flow

- if 3x sterile – there is still a workaround
- unred2x + red 4x -> 4x

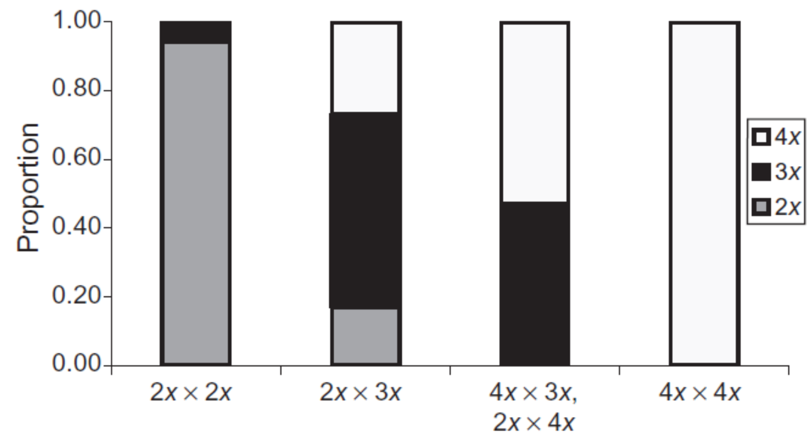
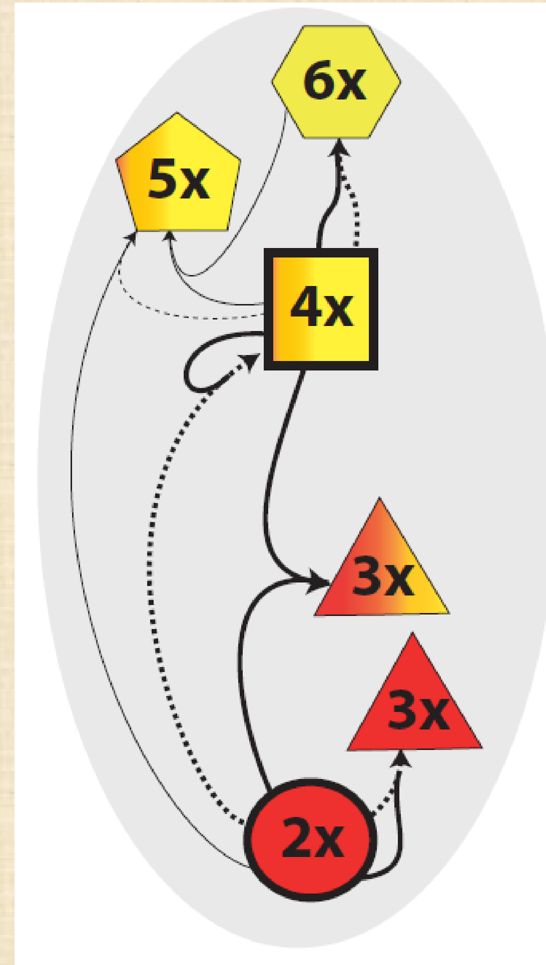


Figure 5. Proportions of diploid (grey), triploid (black) and tetraploid (white) offspring produced in five different between-ploidy crosses. Cross-type with similar offspring composition are pooled. Redrawn and modified from Burton & Husband (2001).

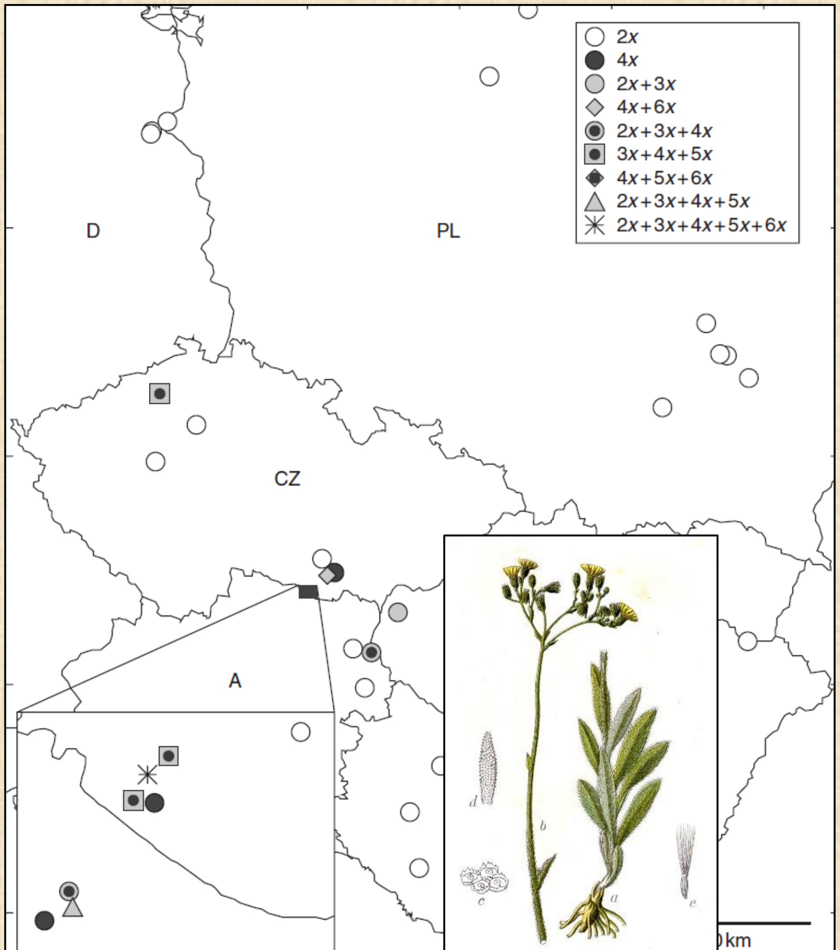


Chamerion angustifolium (Husband 2004)

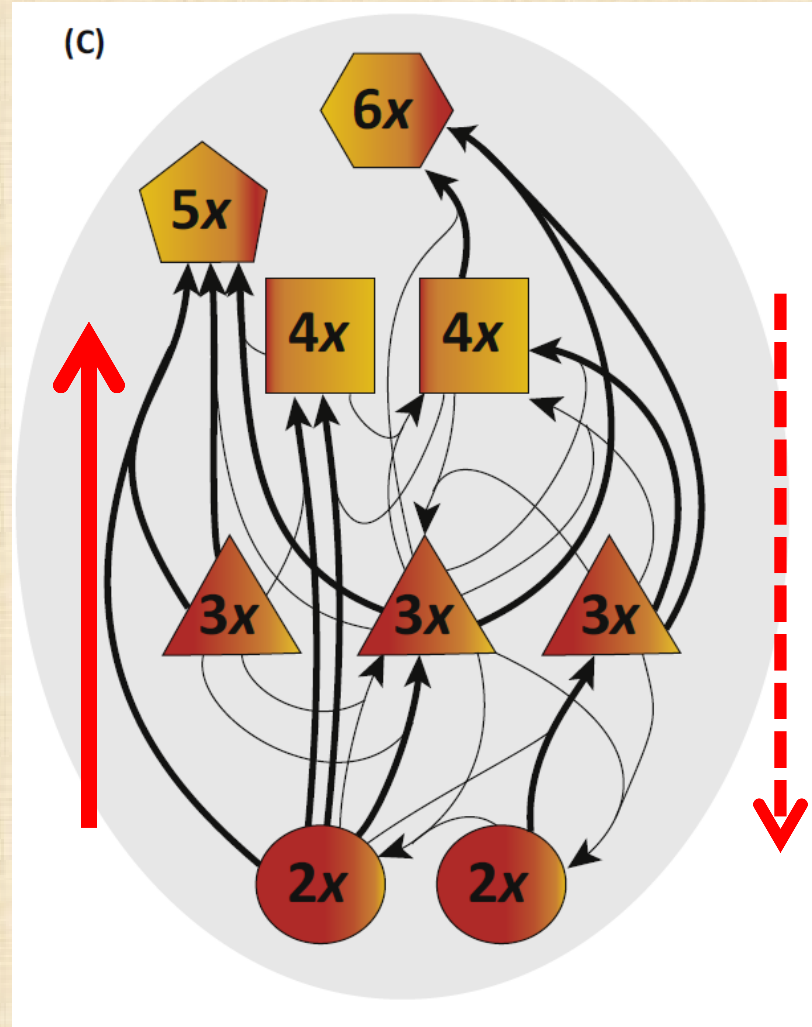
Dashed line = unreduced gamete,
solid line = reduced gamete

Interploidy gene flow

- if 3x fertile
- generators of diversity



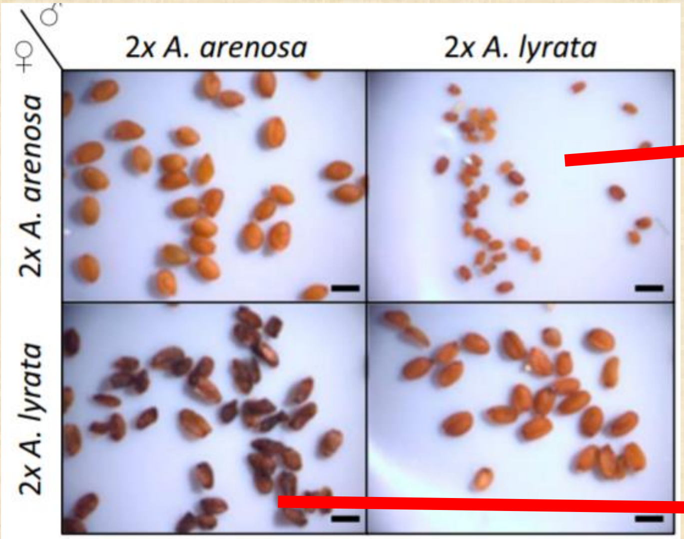
Pilosella echioides Trávníček et al. 2011 Ann Bot



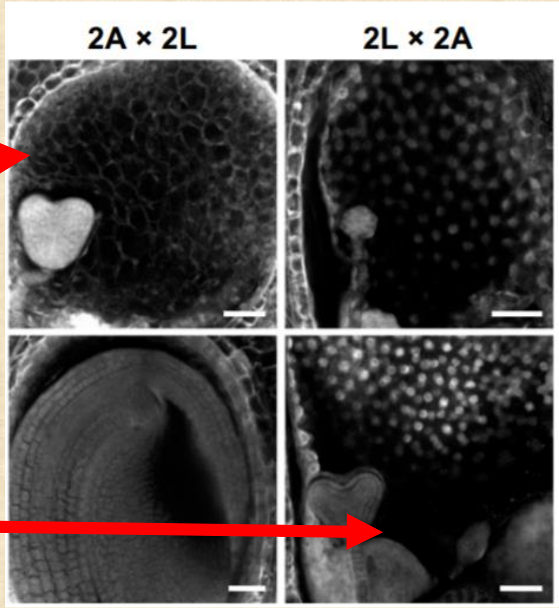
Thick line = unreduced gamete, thin line = reduced gamete (Kolář et al. 2017, Trends Plant Sci)

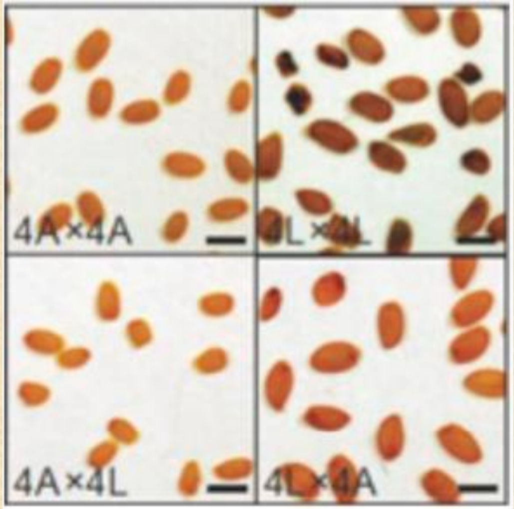
Polypoloidy & barrier breakdown

Crossess **between** species: *Arabidopsis arenosa* vs. *Arabidopsis lyrata*



DIPLOIDS





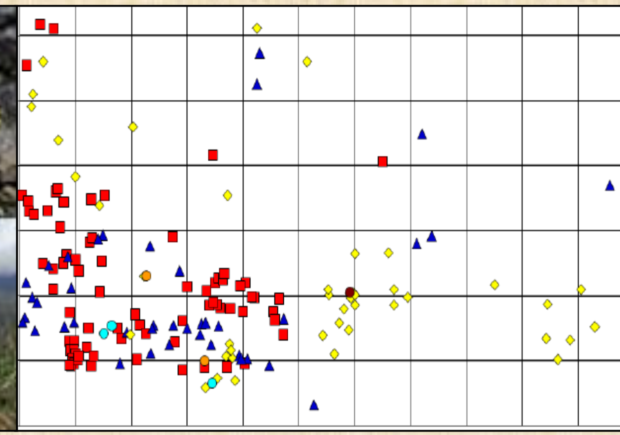
TETRAPLOIDS

Lafon Placette et al 2017 PNAS

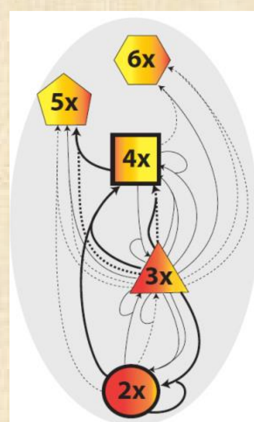
Polyploidy - summary

- key innovarion or dead-end?

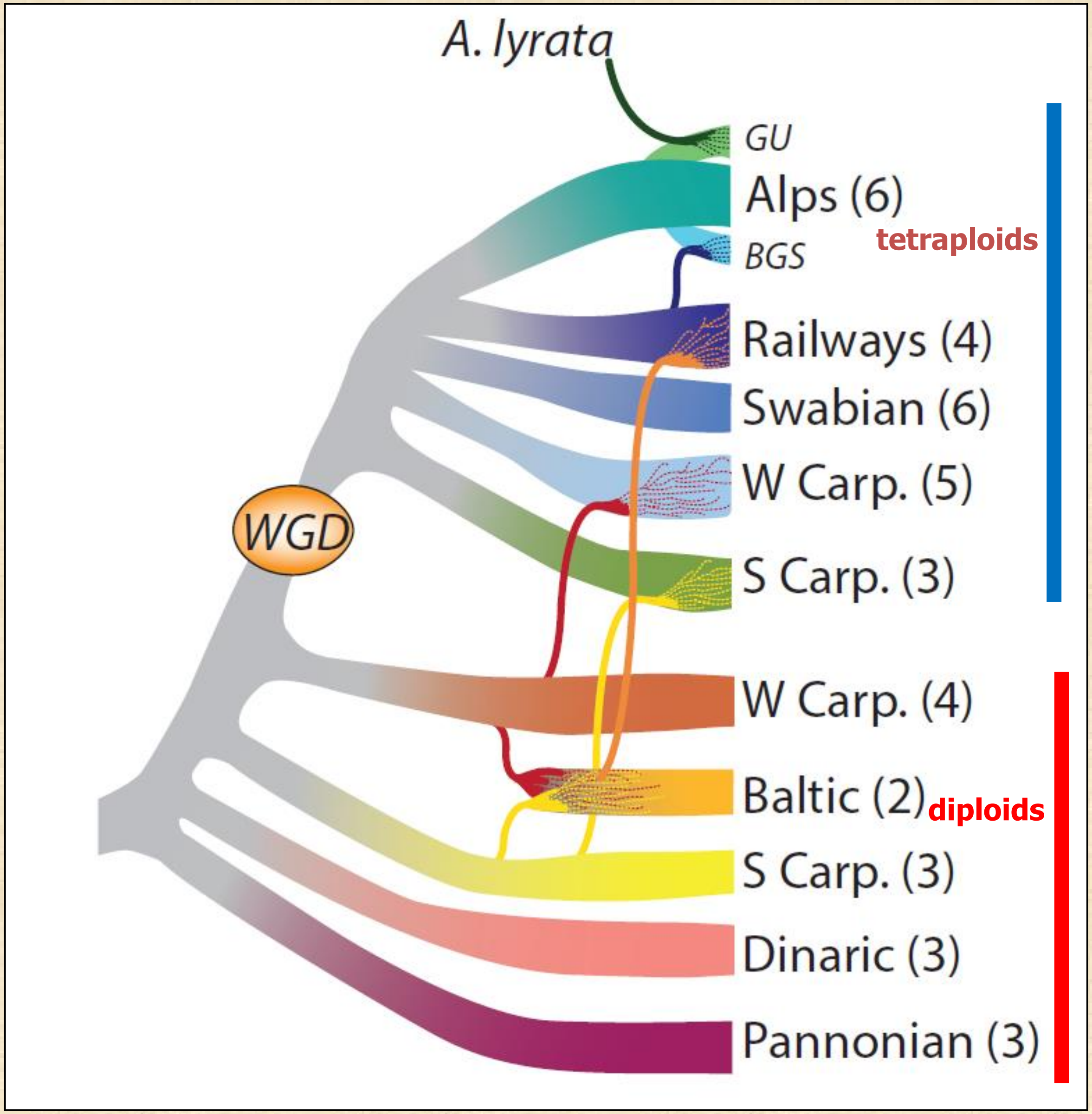

- huge variation

- sympatric speciation vs. gene flow



Polyploidy



A. arenosa (2x, 4x)

Arabidopsis arenosa
Yant & Bomblies 2017 Curr. Opin. Plant Sci