The unfolding of genomic divergence during ecological speciation in whitefish.

Louis Bernatchez
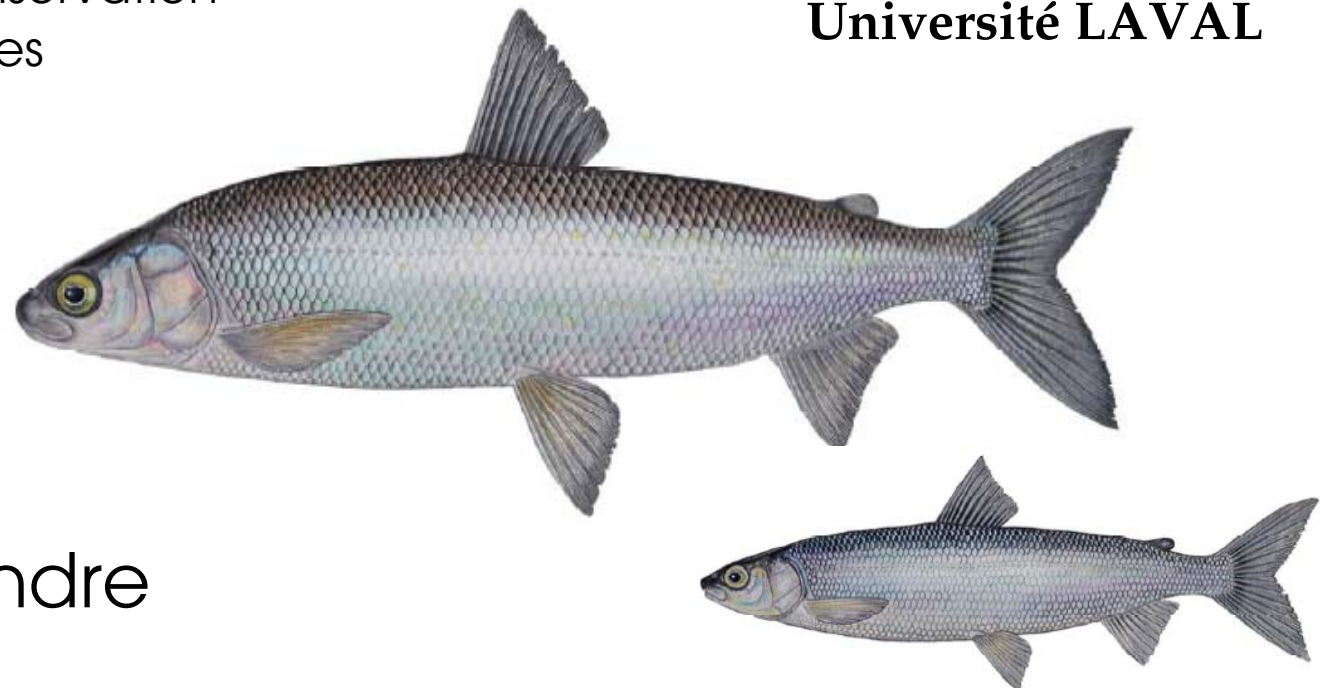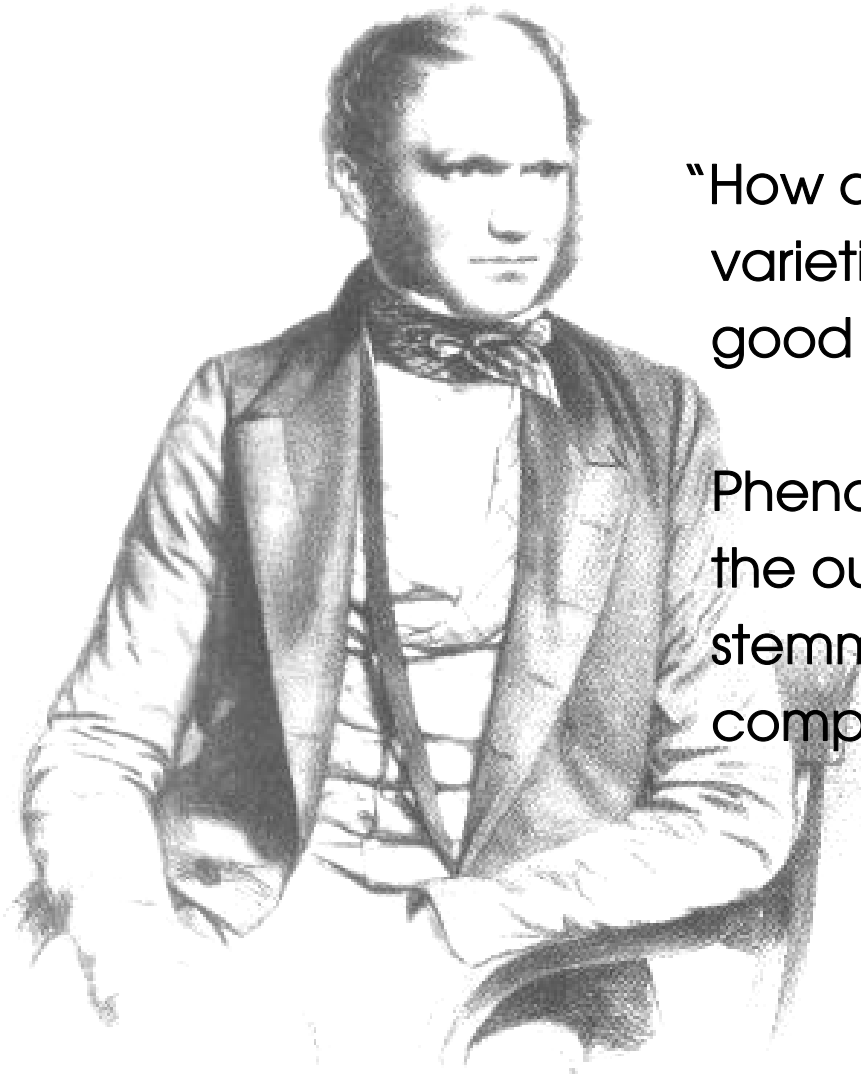
Genomics and Conservation of Aquatic Resources

Pierre-Alexandre Gagnaire

On the Origins of species ...

"How does the lesser difference between varieties become ultimately converted into good and distinct species? ..."

Phenotypic divergence and speciation are the outcomes of divergent natural selection stemming from environment diversity and competition (the struggle for existence).
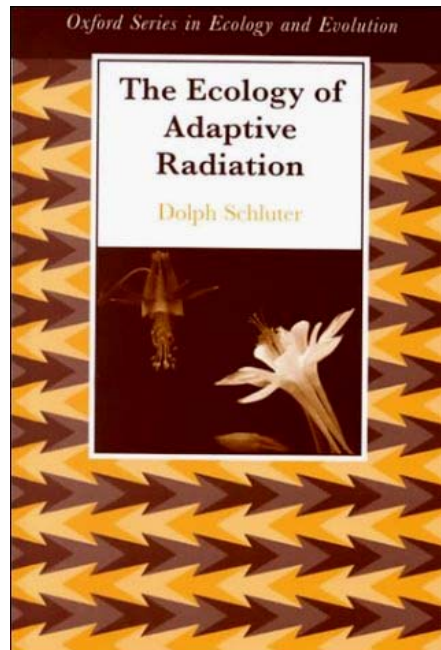
Darwin, 1859

On the Origins of species …

Knowledge on the ecological causes of speciation has made substantial leaps …
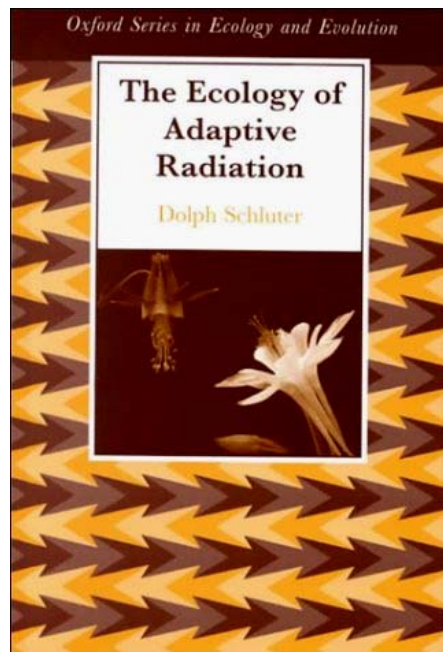
Dolph Schluter, 2000

On the Origins of species ...

...Ten years later ...

« One of the most glaring deficiencies is the almost complete absence of information on the genetics of ecological speciation. »

Schluter & Conte, 2009

The unfolding of genomic divergence during ecological speciation

. Most progress has been made in detecting individual "speciation genes" causing or enhancing reproductive isolation.

(Pesgraves 2010; Nosil & Schluter 2011)

. Until recently, little empirical investigation of genome wide patterns of divergence during the speciation process.

. Yet, some of the most important issues pertain to genome wide patterns of divergence…
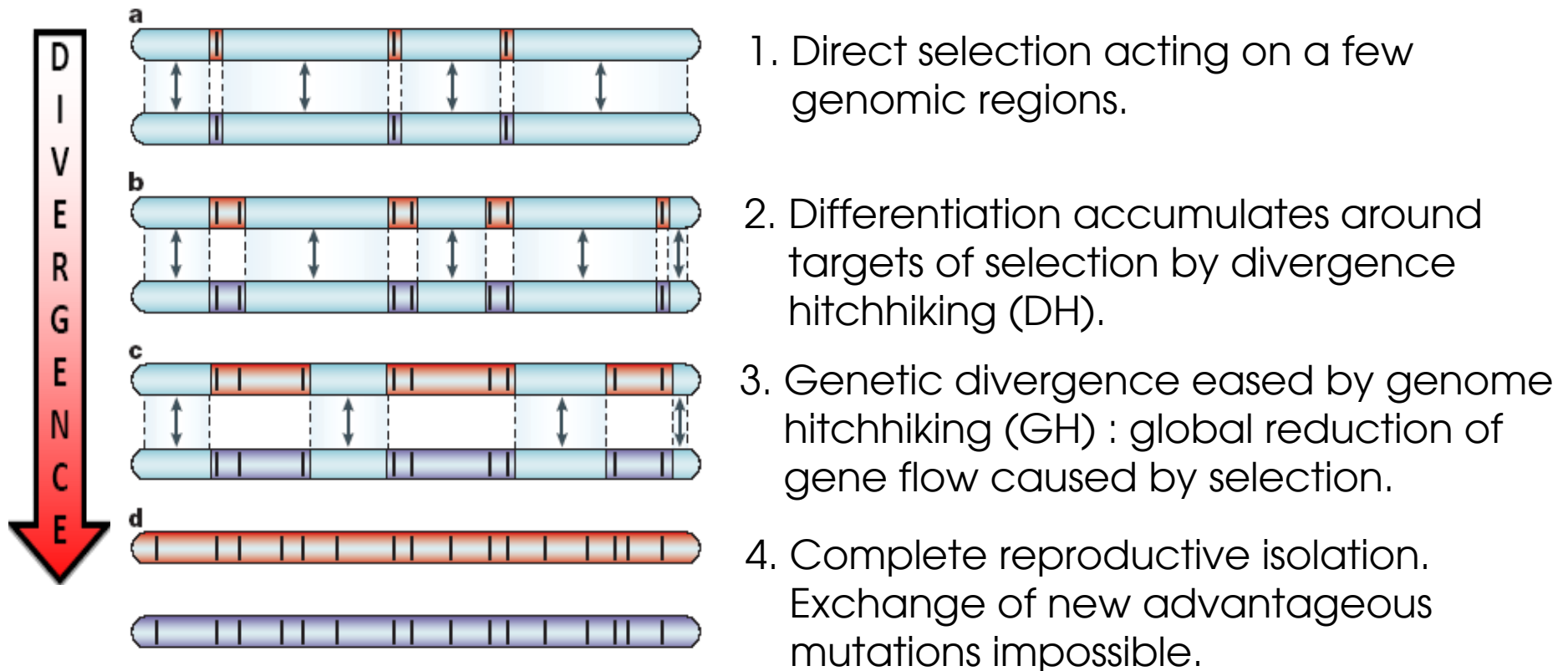
(Nosil & Feder 2011)

The unfolding of genomic divergence during ecological speciation

About the patterns of genomic divergence :

1. How many genomic regions differentiate during ecological speciation ?

2. How large are regions of divergence in the genome ?

3. Are regions of divergence concentrated on a few regions or widely spread ?

4. What types of genes tend to be differentiated ?

The unfolding of genomic divergence during ecological speciation

The genic view of speciation (*Wu 2001*)

1. Direct selection acting on a few genomic regions.

2. Differentiation accumulates around targets of selection by divergence hitchhiking (DH).

3. Genetic divergence eased by genome hitchhiking (GH) : global reduction of gene flow caused by selection.

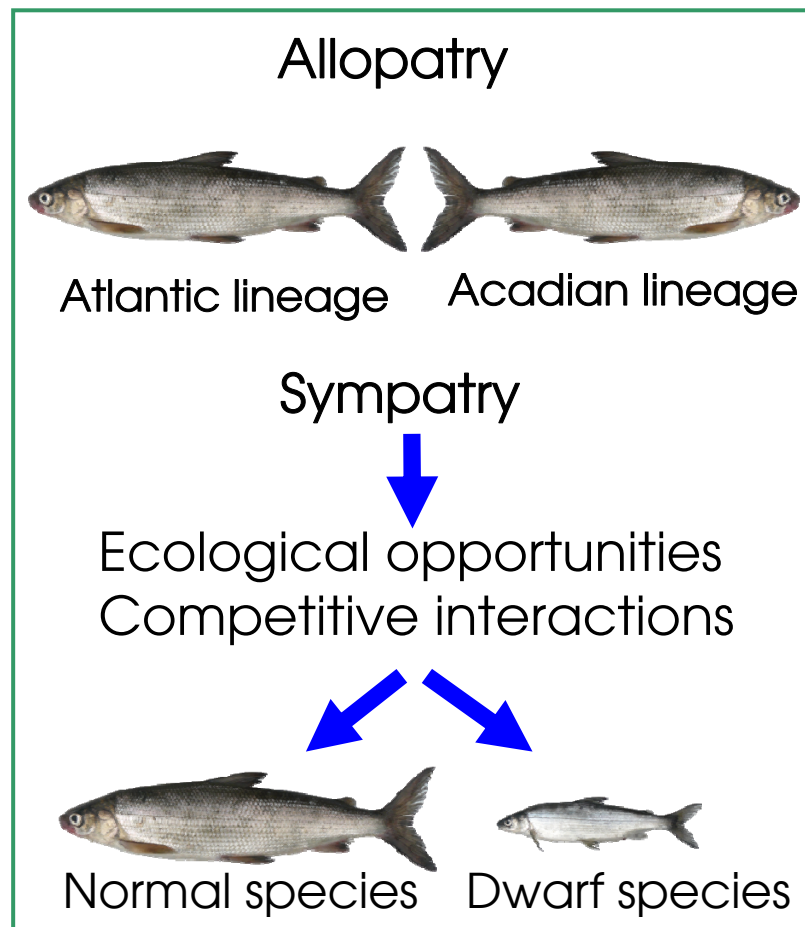4. Complete reproductive isolation. Exchange of new advantageous mutations impossible.

More ecologically diverged populations should have more and larger genomic regions (DH) and be more genetically differentiated overall (GH)

The unfolding of genomic divergence during ecological speciation

. Mainly addressed by comparing study systems potentially representing different stages of ecological speciation in different taxa.

  - Interpretations complicated by differences in methods, knowledge of natural and evolutionary history, type and number of markers used.

. <u>Ideally</u> :
  - Detailed analyses of genomic divergence between very closely related species spanning a continuum of speciation with well characterized ecology and evolutionary history.

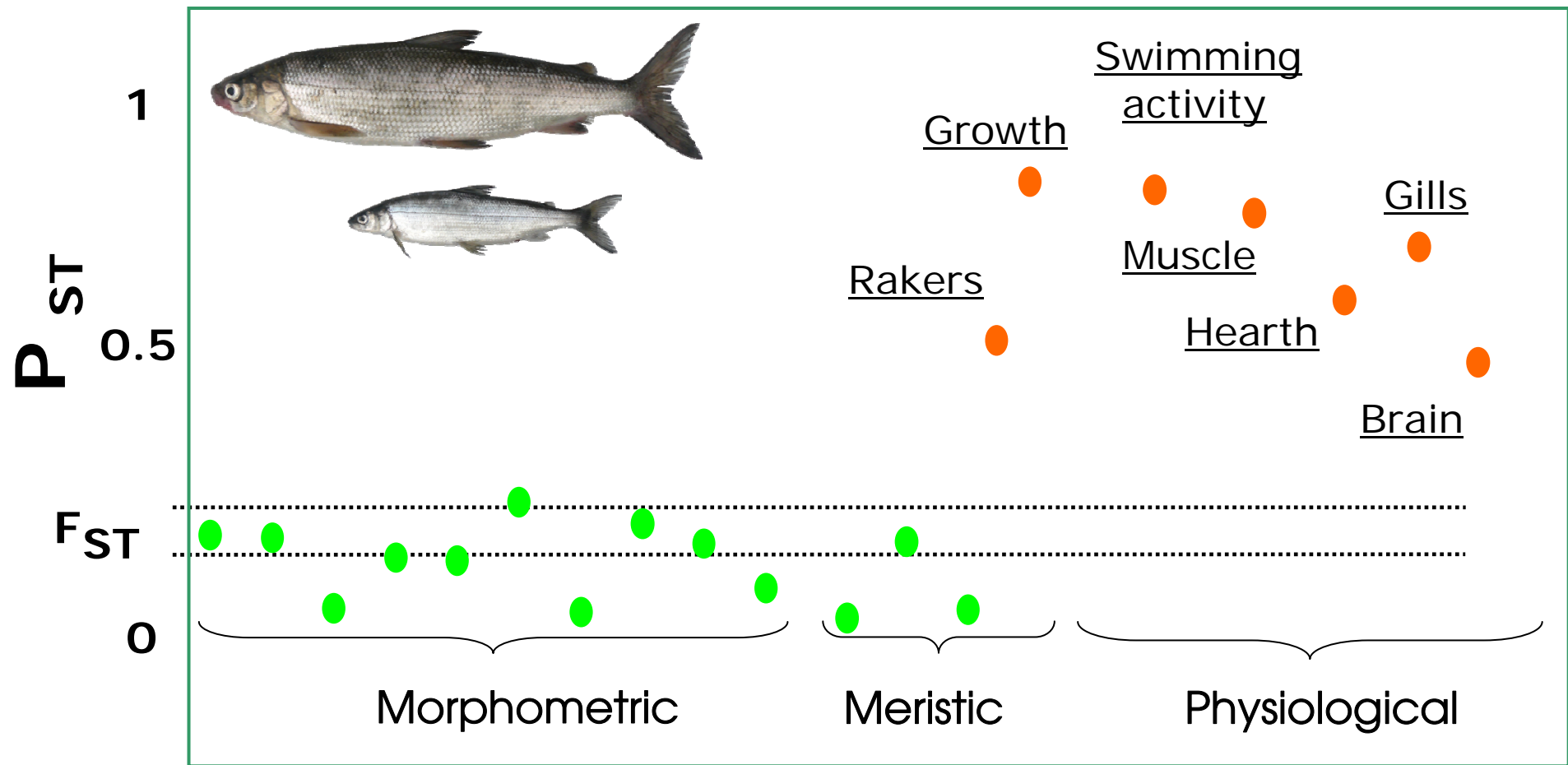# The unfolding of genomic divergence during ecological speciation

. <u>Whitefish as such an ideal model system:</u>

Allopatry

Atlantic lineage   Acadian lineage

Sympatry

Ecological opportunities
Competitive interactions

Normal species   Dwarf species

	Benthic	Limnetic
Habitat	Benthic	Planktonic
Life history	" K "	" r "
Bioenergetic efficiency	High	Low
Predation	Low	High

Life history trade-off between Growth/fecundity (Normal) vs. Survival (Dwarf) functions associated with occupying distinct niches

The unfolding of genomic divergence during ecological speciation

Bernatchez 2004 ; Rogers & Bernatchez 2005; Evans et al., in press.

The unfolding of genomic divergence during ecological speciation

Over-represented functional groups

Dwarf

Energetic metabolism

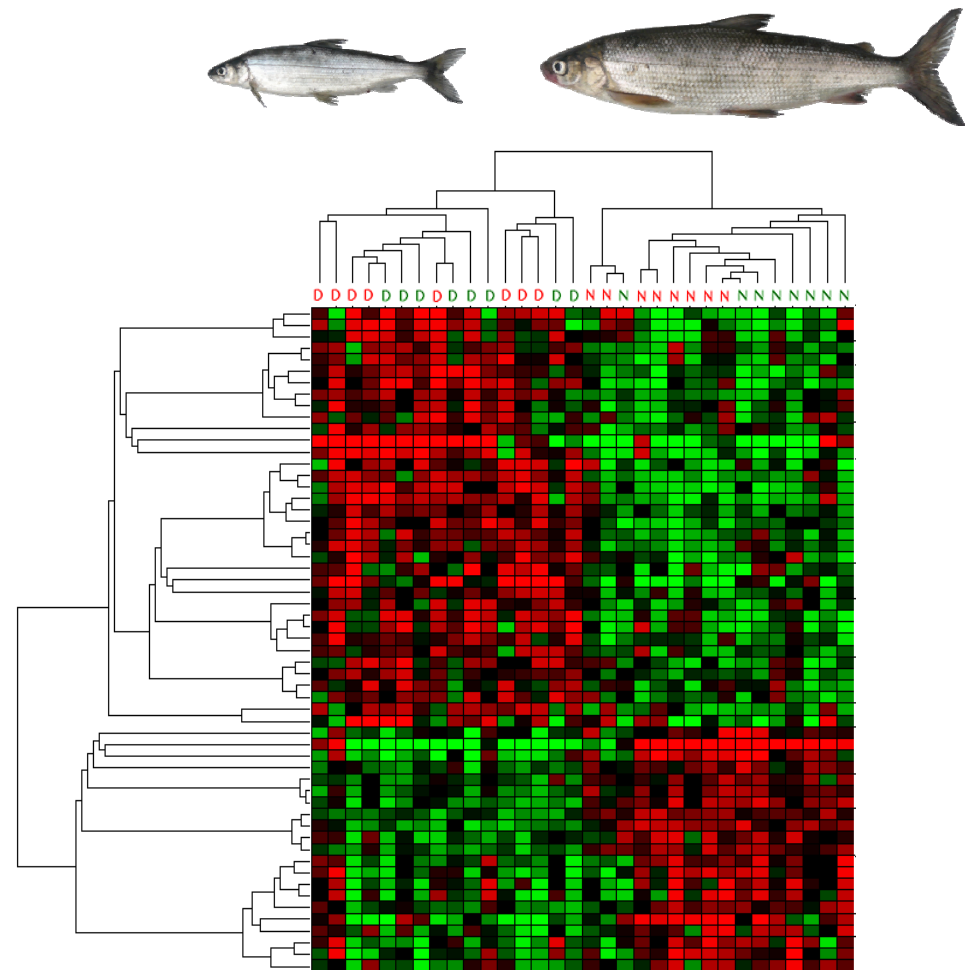Muscle contraction

Lipid metabolism

Detoxification

Survival functions

Normal

Cellular cycle/growth
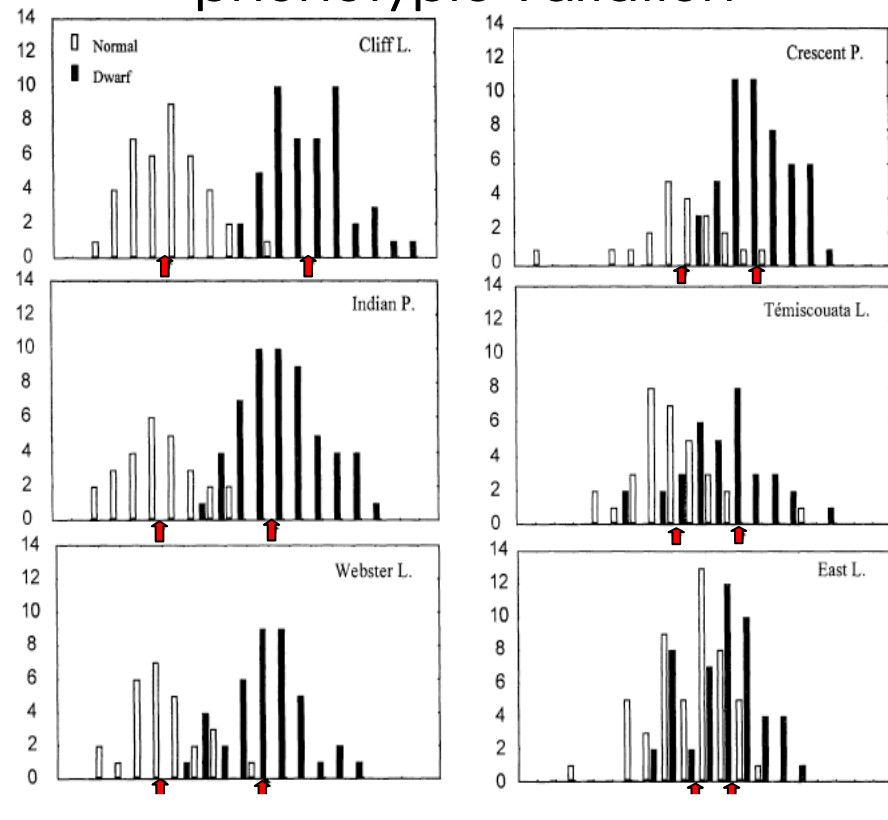
Protein synthesis

Growth functions

St-Cyr et al. 2008 ; Nolte et al. 2009; Jeukens et al. 2010
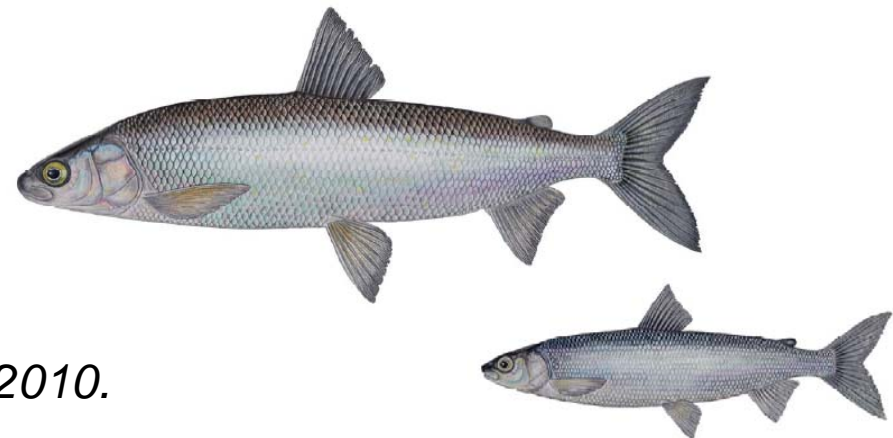
The unfolding of genomic divergence during ecological speciation

Gradient of phenotypic variation

Phenotypic gradient parallels ecological gradient

Landscape (biotic and abiotic) with higher potential for intra-population competition and more potential for distinct trophic niches associated with increased phenotypic divergence

*Lu & Bernatchez 1999 ; Landry et al. 2007; 2010.*

The unfolding of genomic divergence during ecological speciation

. <u>In this study... :</u>

. RAD genotype-by-sequencing approach to:

1 . Test the hypothesis that gradient of phenotypic and ecological divergence correlates with overall genetic divergence (GH).

2. Test the hypothesis that DH can drive the divergence of large (many cM) genomic regions.

3. Test whether divergence concentrated on a few regions or widely spread.

The unfolding of genomic divergence during ecological speciation
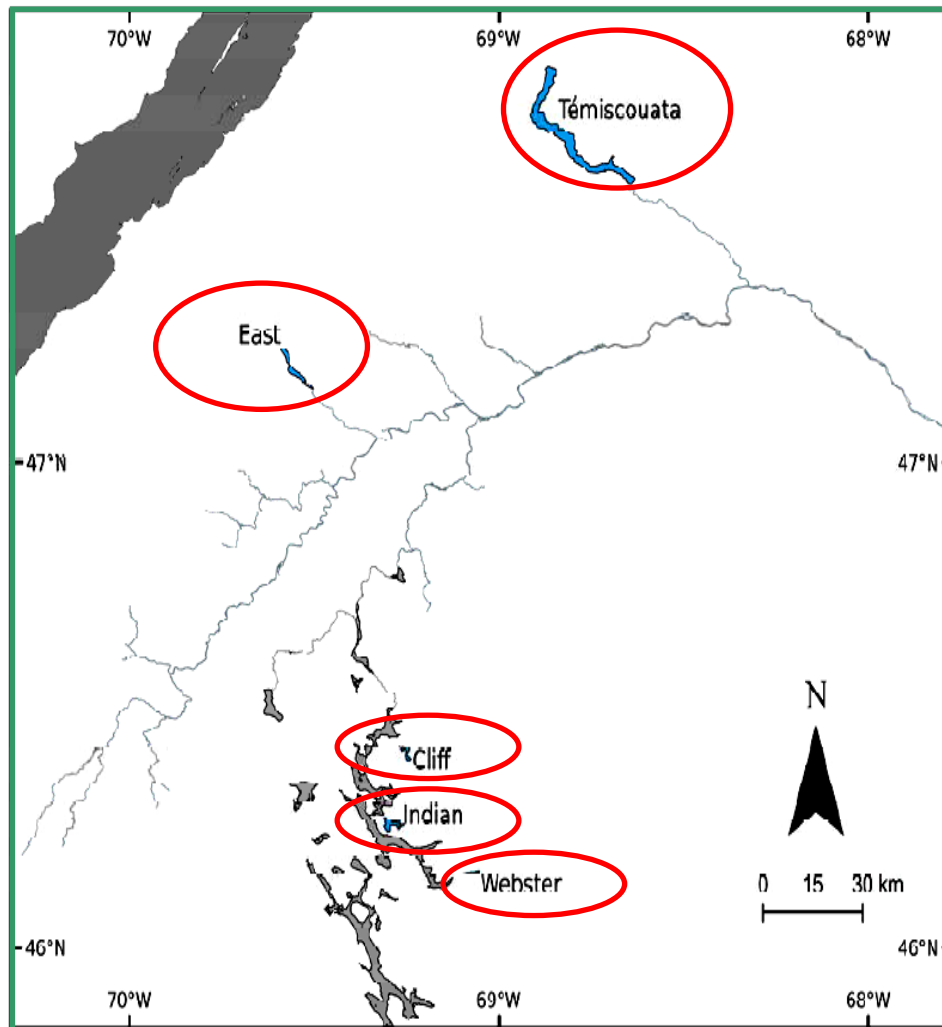
Natural populations :

. 5 dwarf – normal pairs

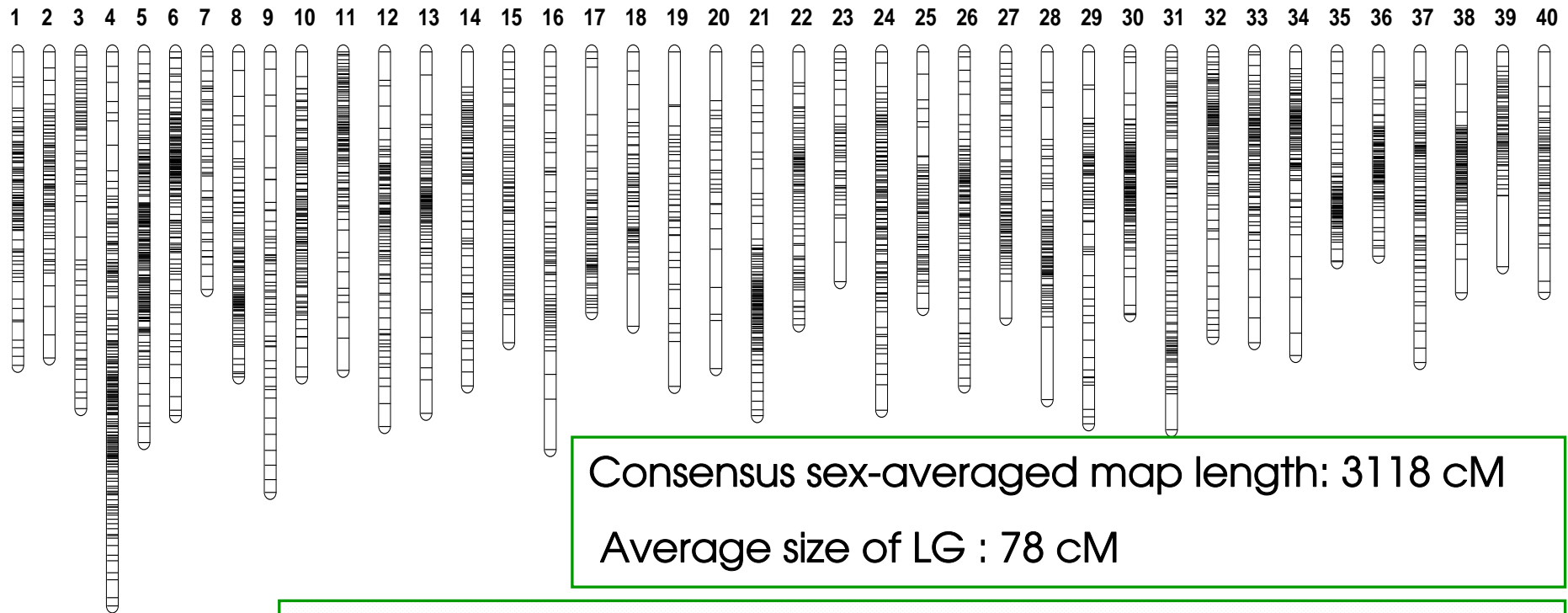 (20 fish each = 200 fish)

Mapping family :

. 102 BC progeny

. Synteny with zebrafish

RAD sequencing :

. 4887 segregating SNP

  in both map and wild fish

I. Gradient of overall genetic vs. phenotypic / ecological divergence

SNP discovery and genetic mapping using sequenced RAD Tags

Consensus sex-averaged map length: 3118 cM

Average size of LG : 78 cM

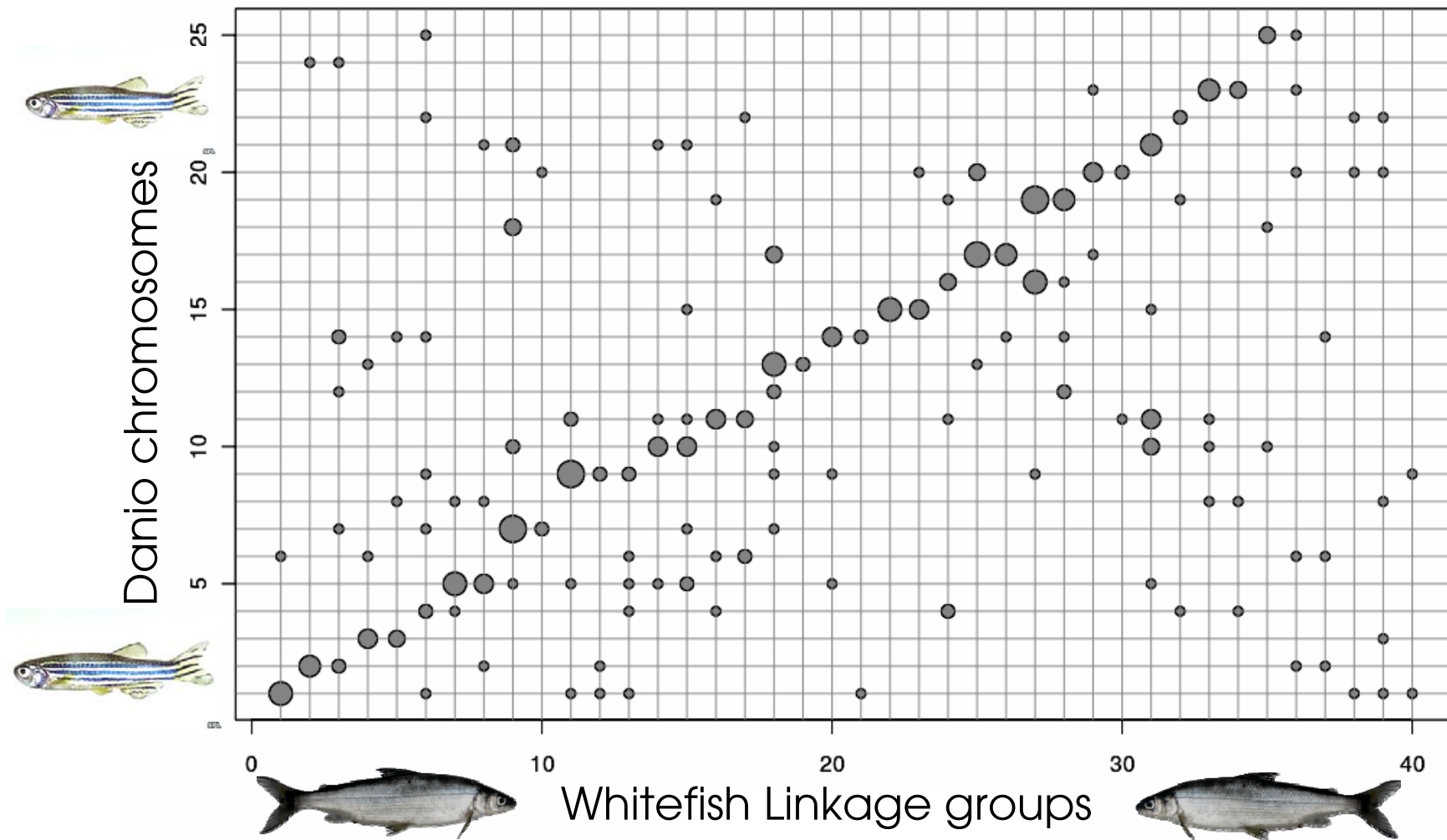4887 mappable SNPs genotyped in 102 progeny from one backcross
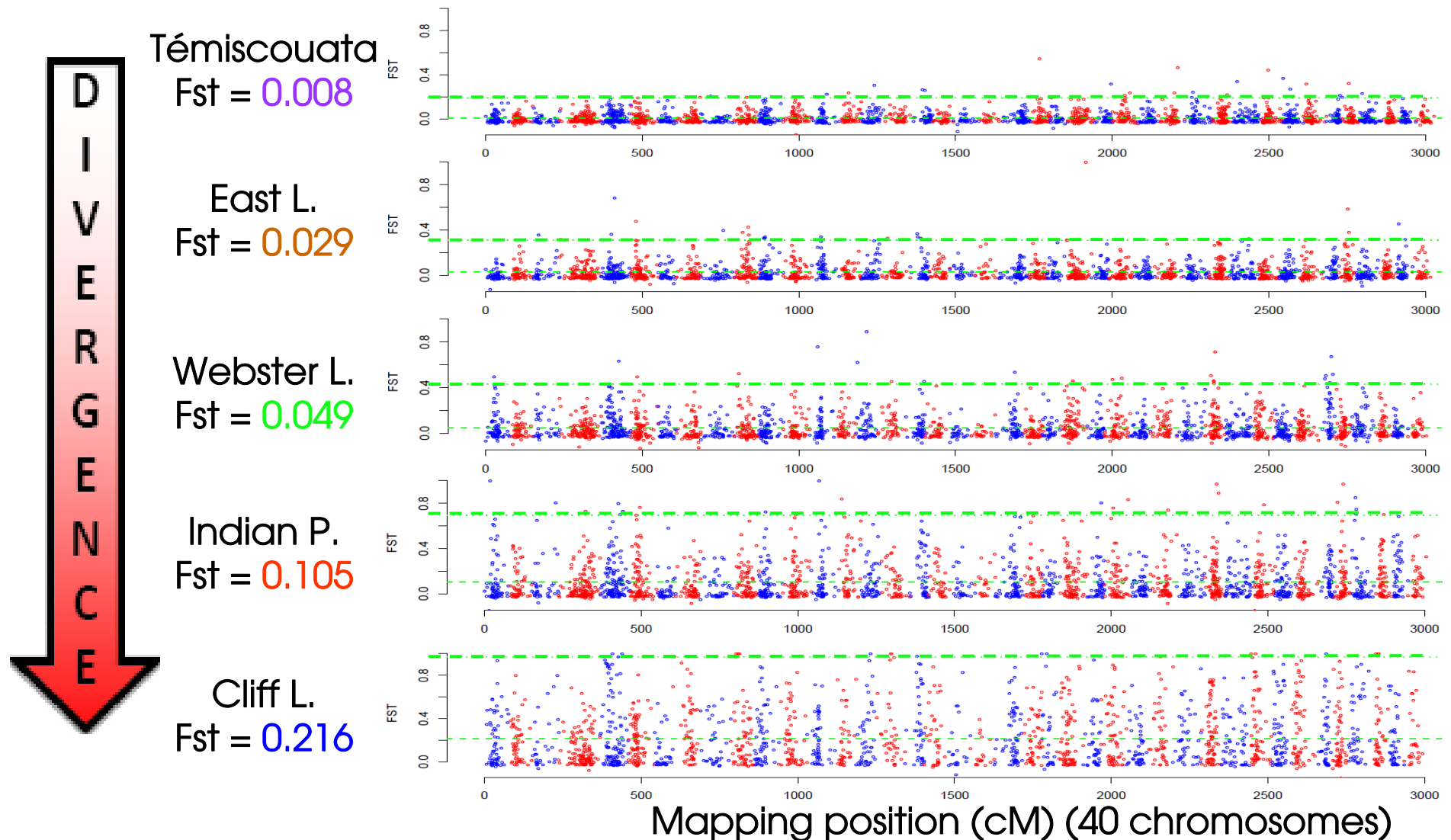
40/40 linkage groups identified

Density: 1.56 marker per cM (or 122 markers per LG)

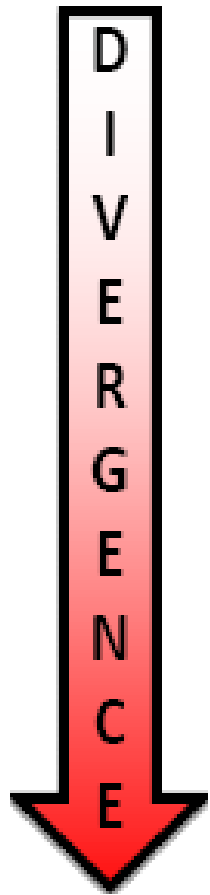# I. Gradient of overall genetic vs. phenotypic / ecological divergence

A partially conserved synteny with the Zebrafish genome

I. Gradient of overall genetic vs. phenotypic / ecological divergence

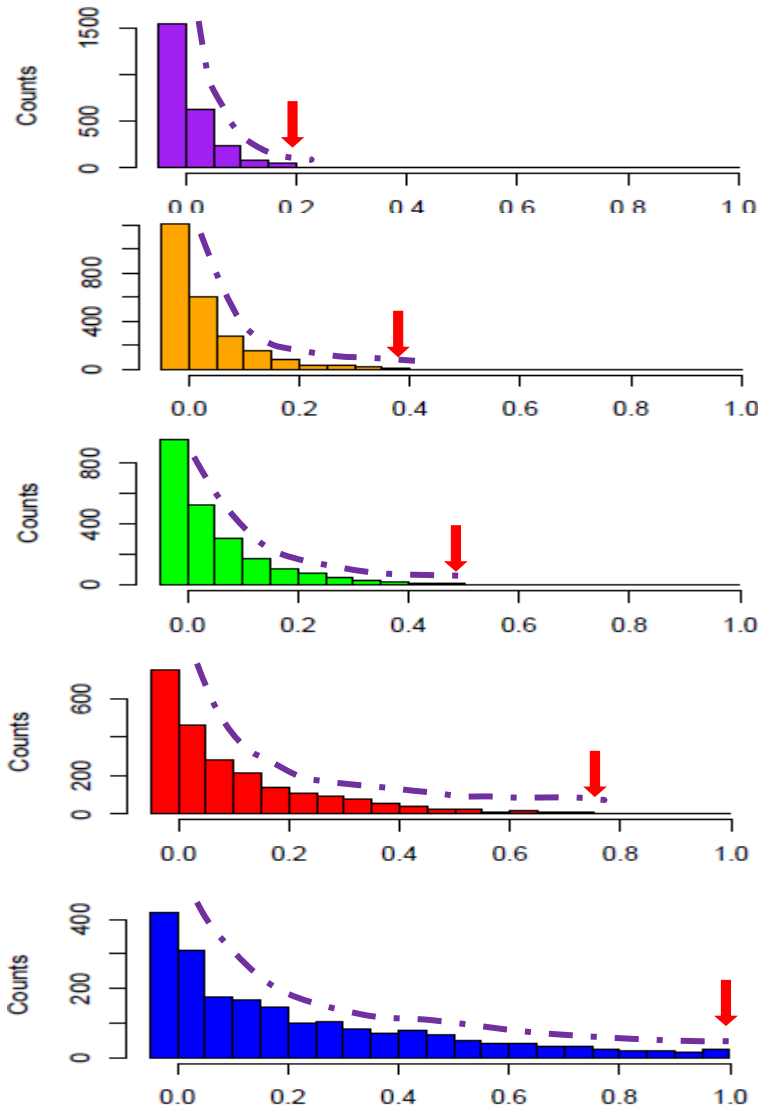# I. Gradient of overall genetic vs. phenotypic / ecological divergence

I. Gradient of overall genetic vs. phenotypic / ecological divergence
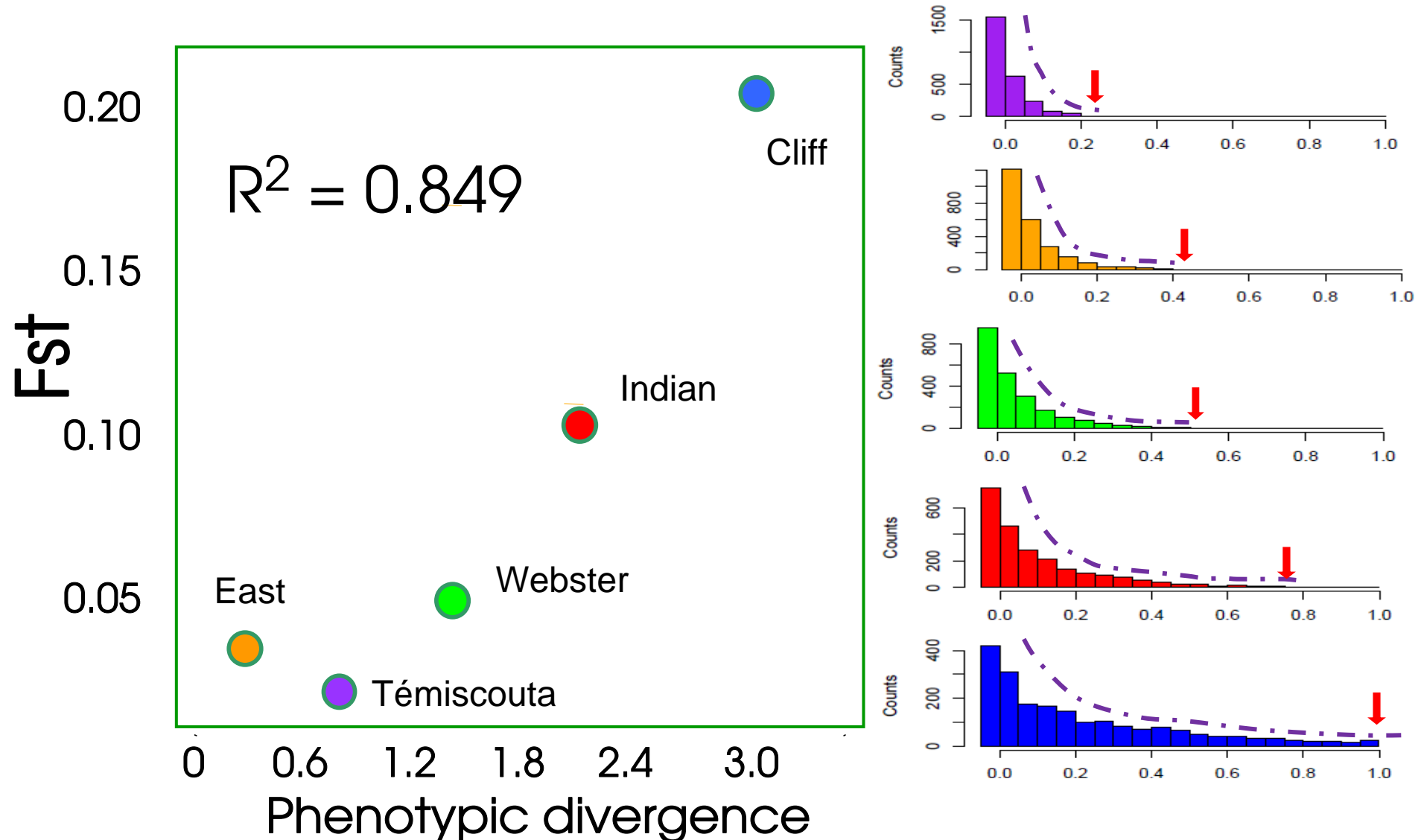
2. Can DH drive the divergence of large genomic regions ?
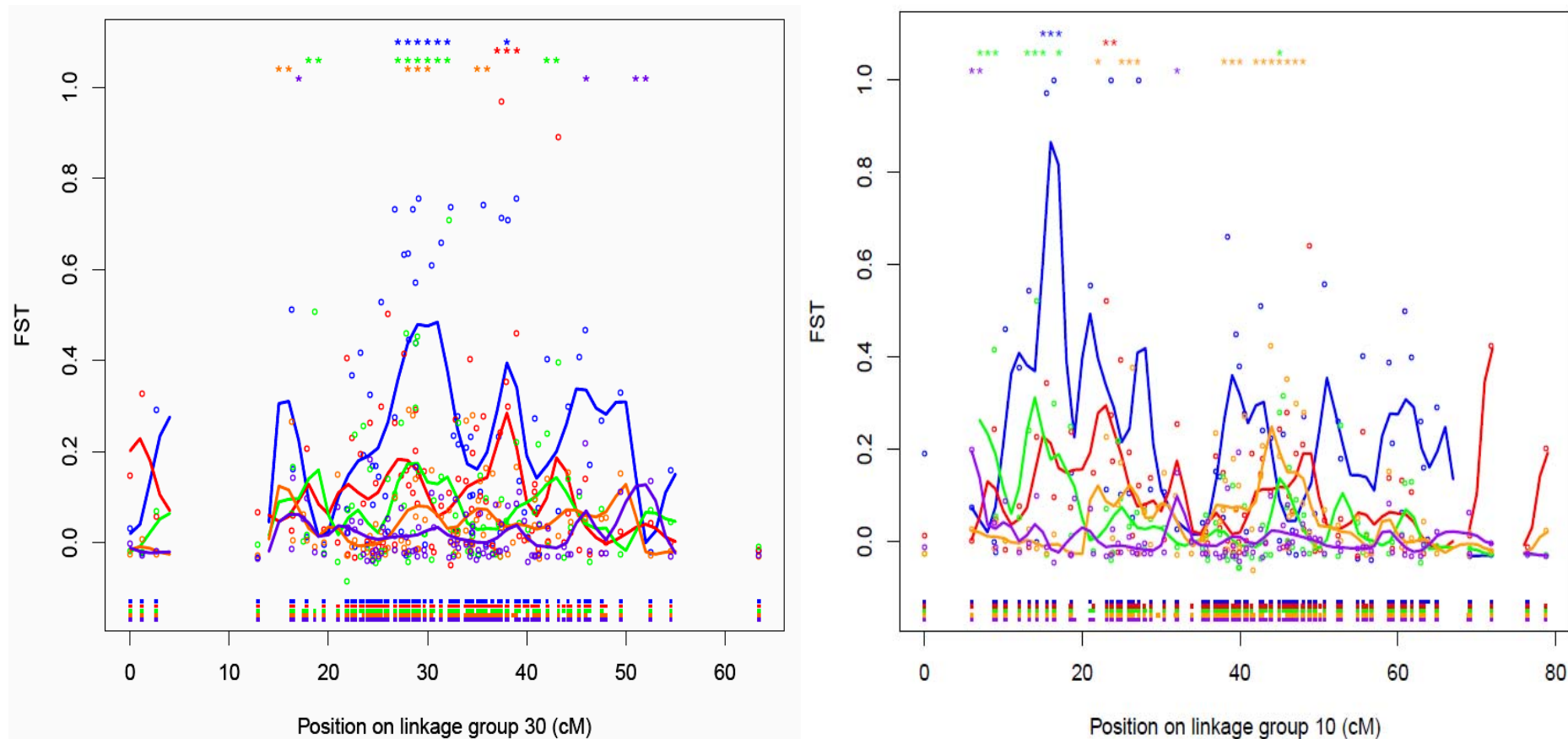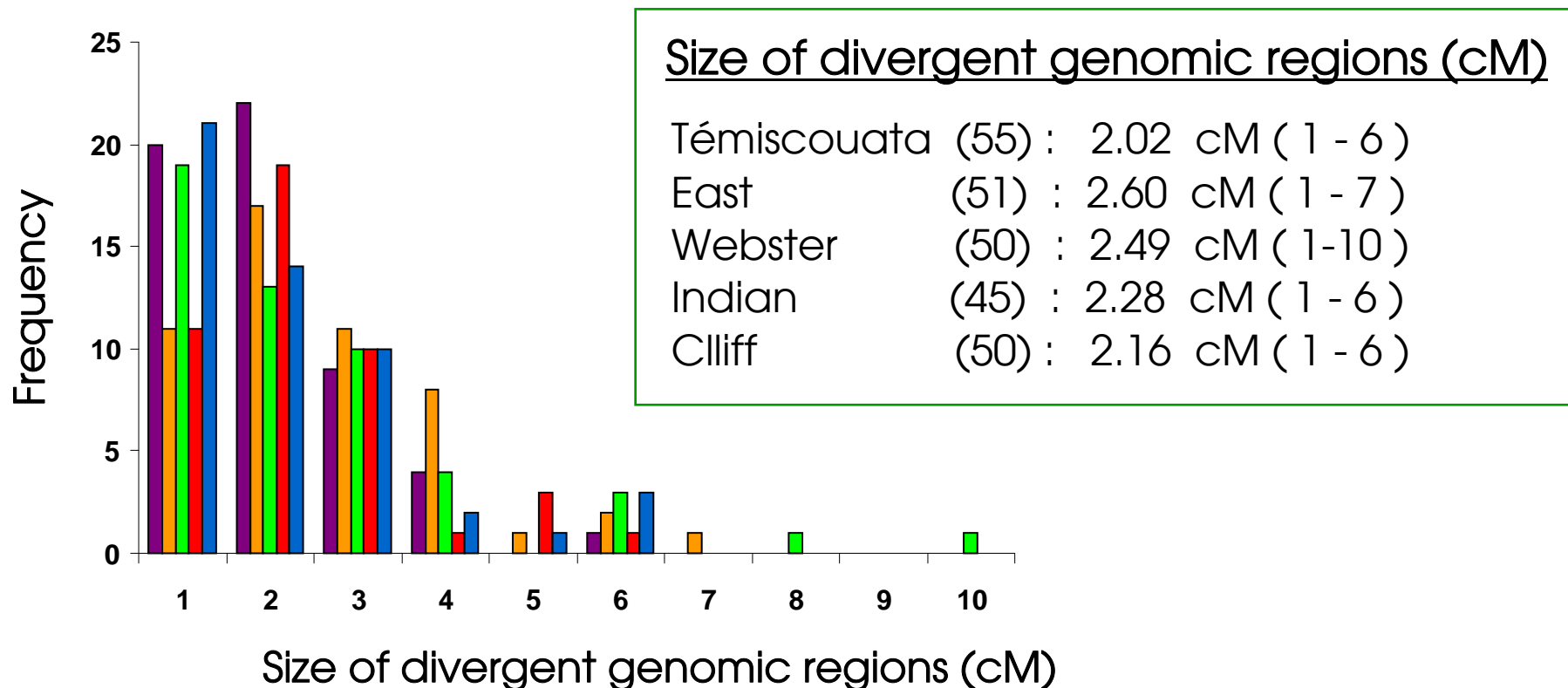
Kernel smoothing sliding window analysis:

Divergence tested every 1cM (boostrap resampling, $p < 0.05$)

Position on linkage group 30 (cM)

Position on linkage group 10 (cM)

2. Can DH drive the divergence of large genomic regions ?

. **Sliding window analysis:**
  number of 1cM regions > 95% permutated SNP

Size of divergent genomic regions (cM)

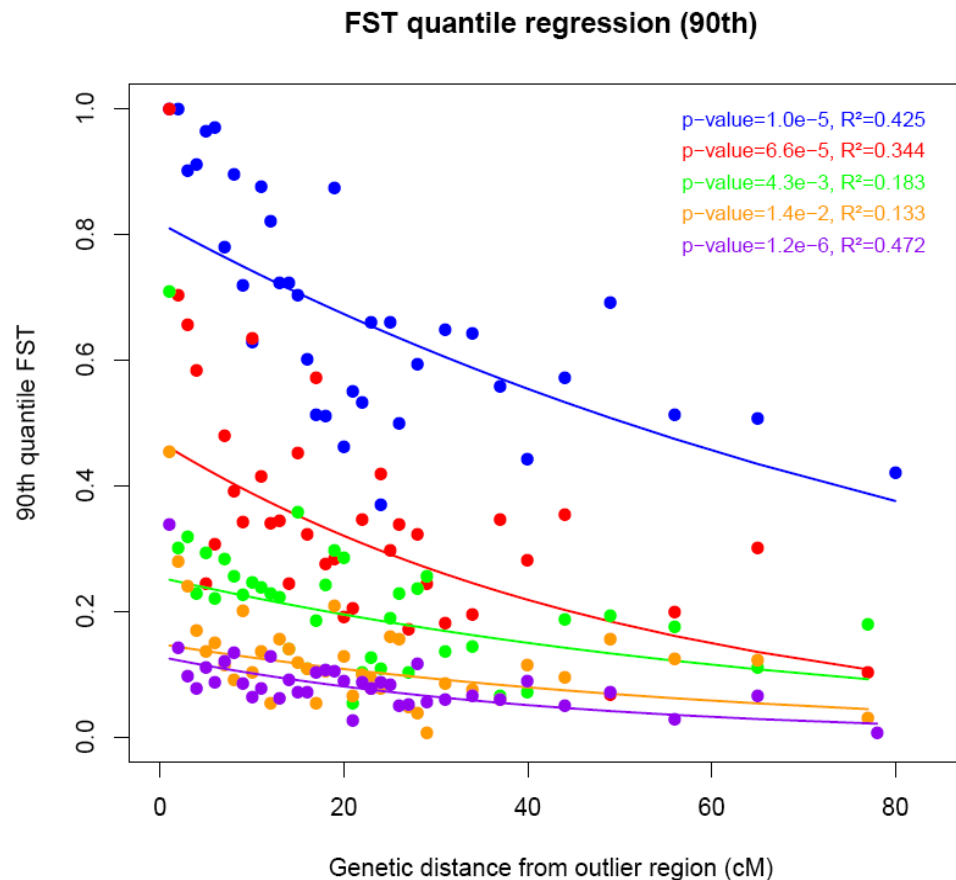|		
Témiscouata	(55) :	2.02 cM (1 - 6)
East	(51) :	2.60 cM (1 - 7)
Webster	(50) :	2.49 cM (1-10)
Indian	(45) :	2.28 cM (1 - 6)
Clliff	(50) :	2.16 cM (1 - 6)

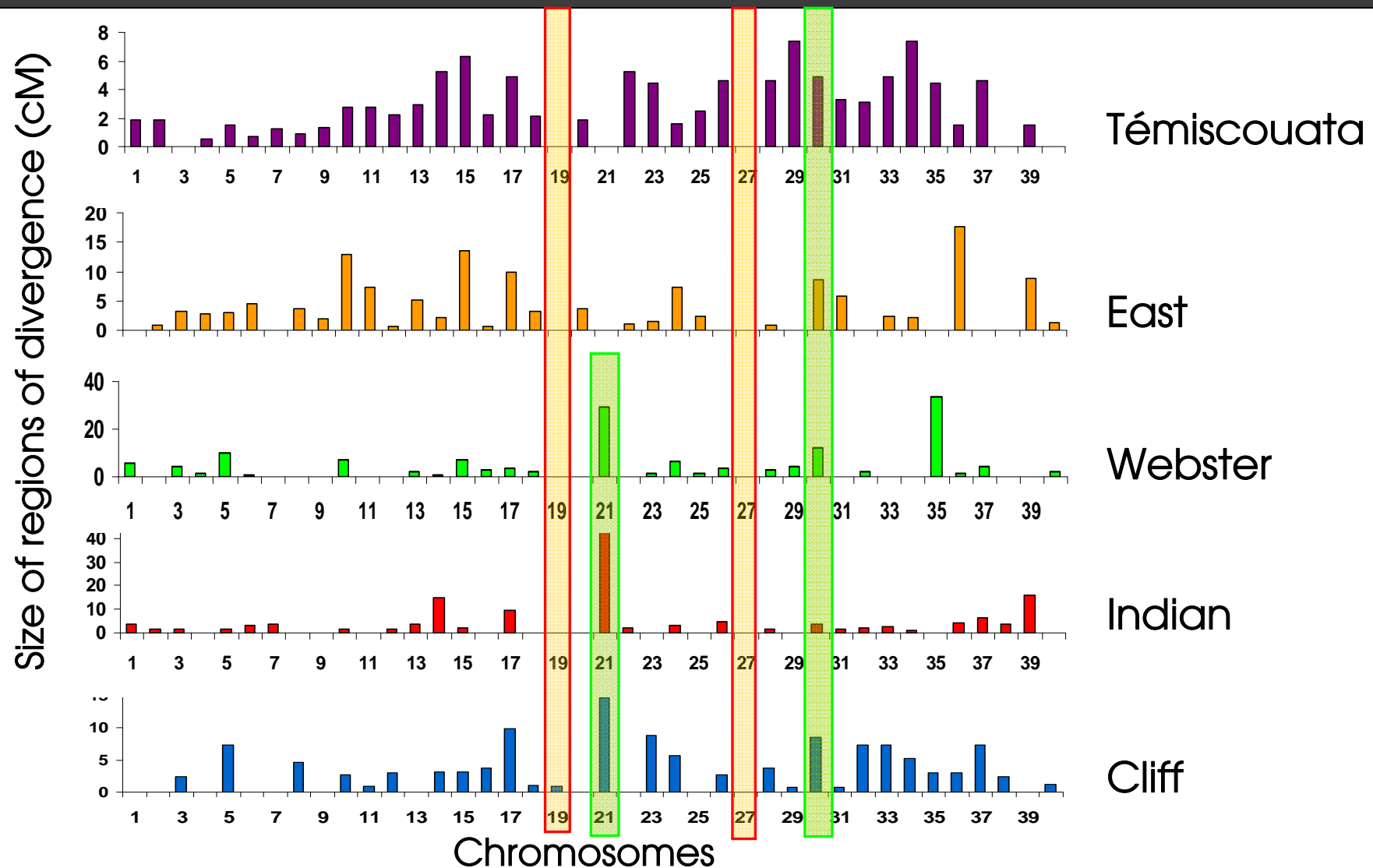Size of divergent genomic regions (cM)

Frequency

2. Can DH drive the divergence of large genomic regions ?

.<u>**Sliding window analysis:**</u>
Fst of 90% quantile SNP vs. chromosomal distance from outlier regions

FST quantile regression (90th)

p-value=1.0e-5, R²=0.425
p-value=6.6e-5, R²=0.344
p-value=4.3e-3, R²=0.183
p-value=1.4e-2, R²=0.133
p-value=1.2e-6, R²=0.472

90th quantile FST

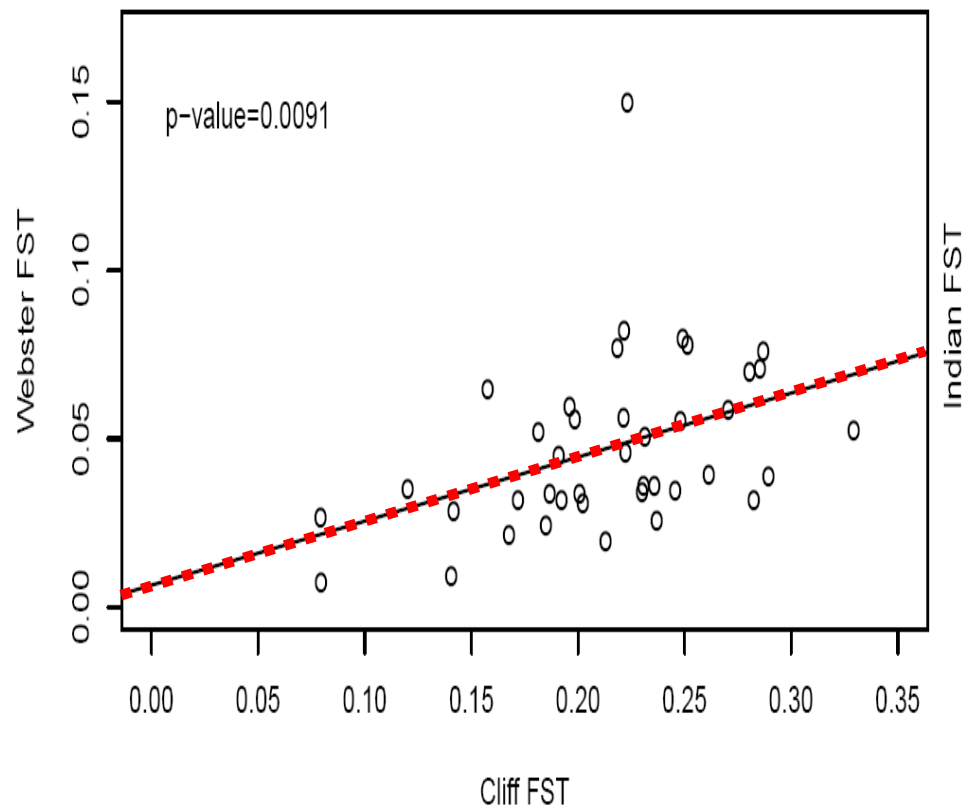Genetic distance from outlier region (cM)

3. Are regions of divergence concentrated on a few regions ?
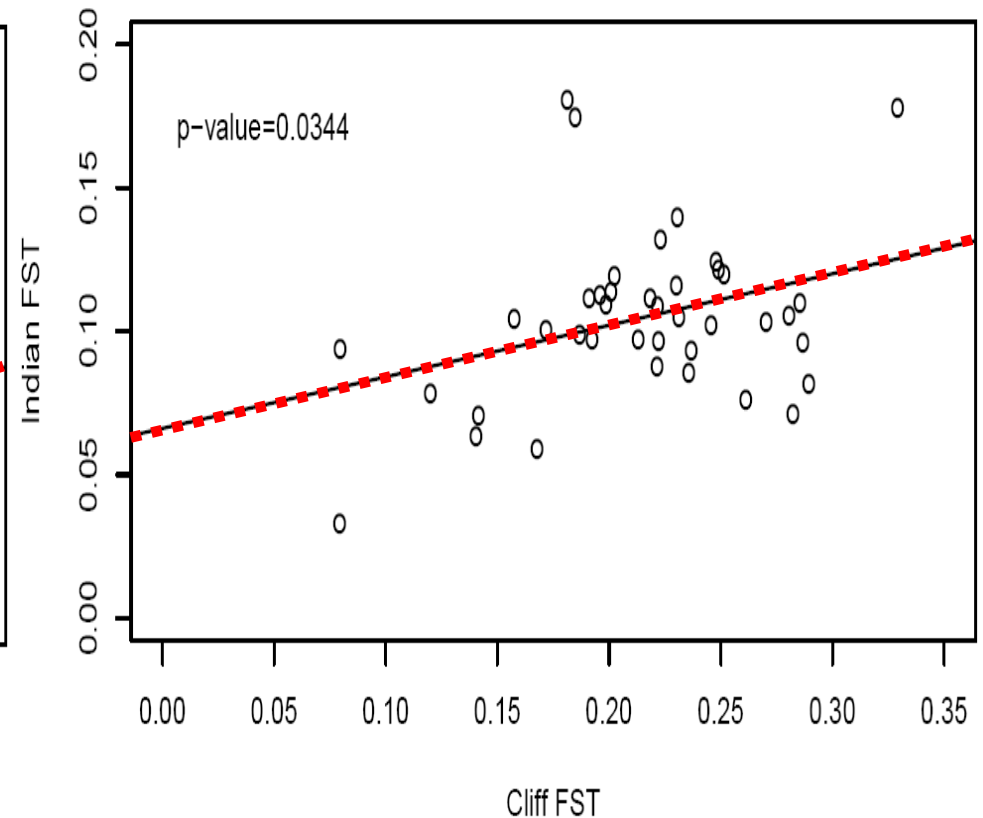
3. Are regions of divergence concentrated on a few regions ?

Pairwise chromosomal F_{st} :

Mean LG FST: Cliff/Webster   **Mean LG FST: Cliff/Indian**

Summary :

1 . Continuum of overall genetic divergence between
   dwarf and normal whitefish which correlates
   with adaptive phenotypic divergence.
   Intensity of selection imposed by biotic and abiotic landscape
   drives the extent of Global hitchhiking (GH).

2 . Divergence hitchhiking can drive the divergence
    of "large" genomic regions (at least up to 10cM).

3 . Divergence is widely spread over chromosomes
   but chromosome-specific effect and
   partially parallel only.
   Parallel phenotypic evolution not accompanied
   by strong genomic parallelism.

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