Fundamentals of Evolution

EEEB G6110

Session 11: The Coalescent

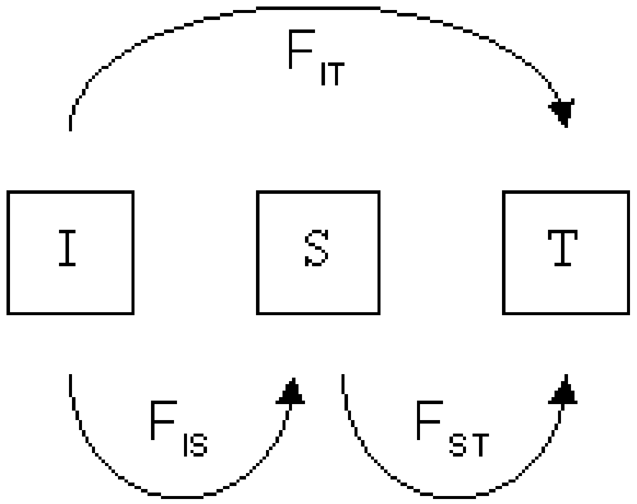
Today's topics

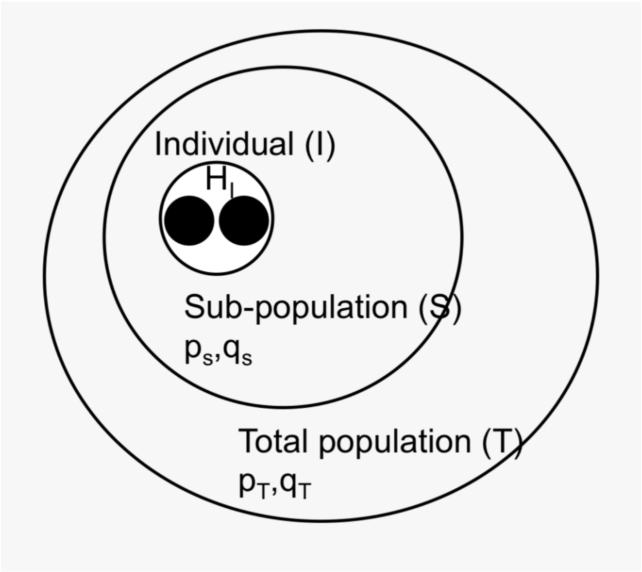
1. Recap (Fst, Wright-Fisher)
2. The coalescent
3. Coalescent simulations
4. Forward simulations
5. Readings

Wright's F-statistics

Measure an inbreeding coefficient (deviation of H from expected). Applied at different hierarchical grouping of alleles (e.g., individuals, subpopulations) these statistics can measure population structure.

The prob. two randomly sampled alleles are the same in an individual (compared to in a subpop or total), or that they are the same in one subpop (compared to the combination of two subpops).

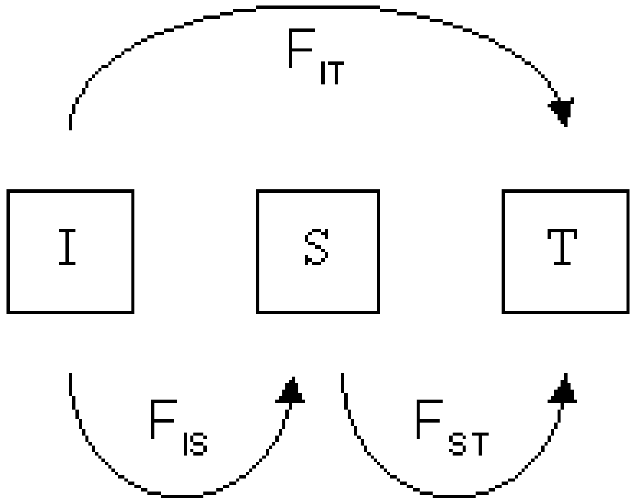


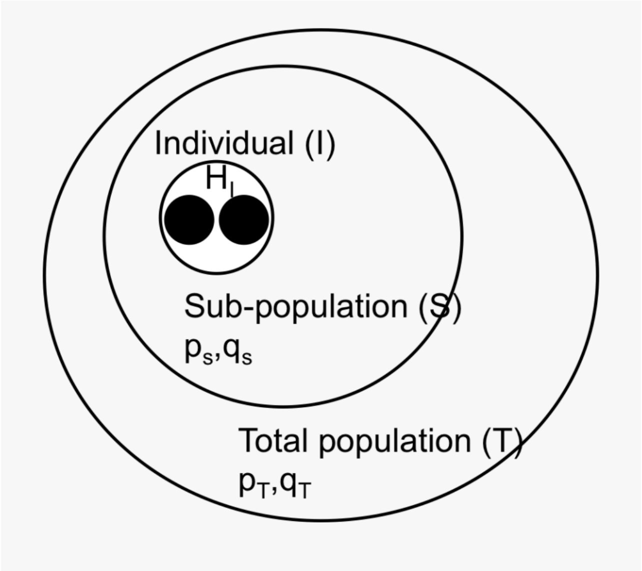


https://en.wikipedia.org/wiki/F-statistics

Wright's F-statistics

F_{ST} can be interpreted as a measure of population differentiation. If F_{ST} between two populations is 1 then they are *fixed* for different alleles (no variation is segregating in both populations).

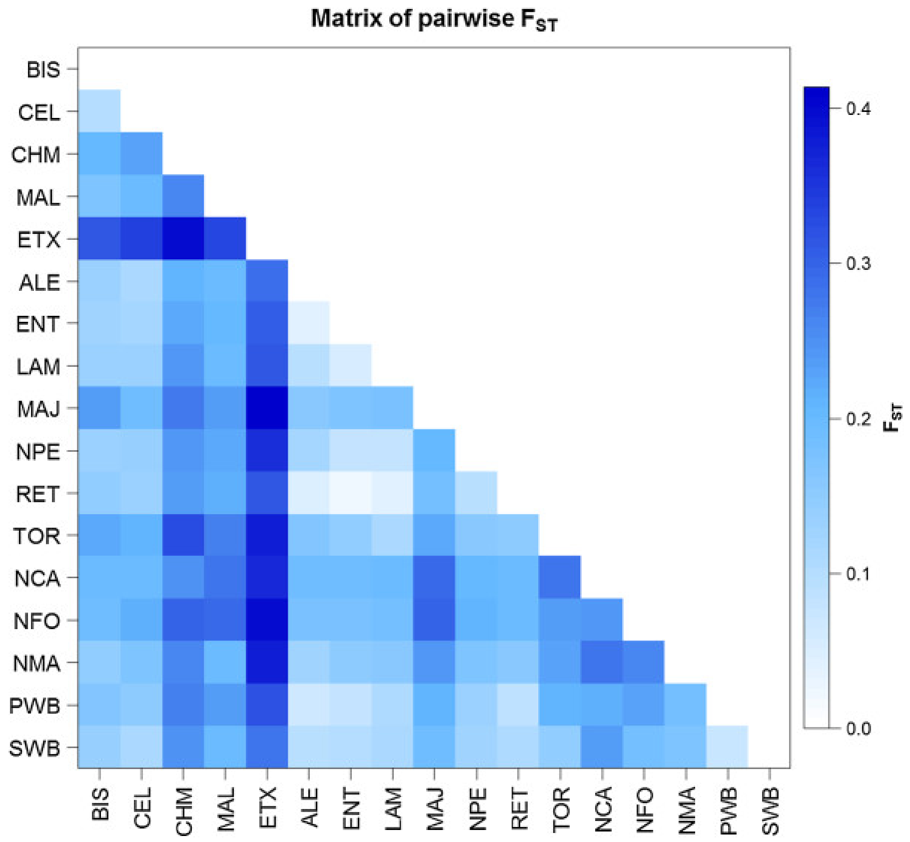




https://en.wikipedia.org/wiki/F-statistics

Wright's F-statistics (F_{ST})

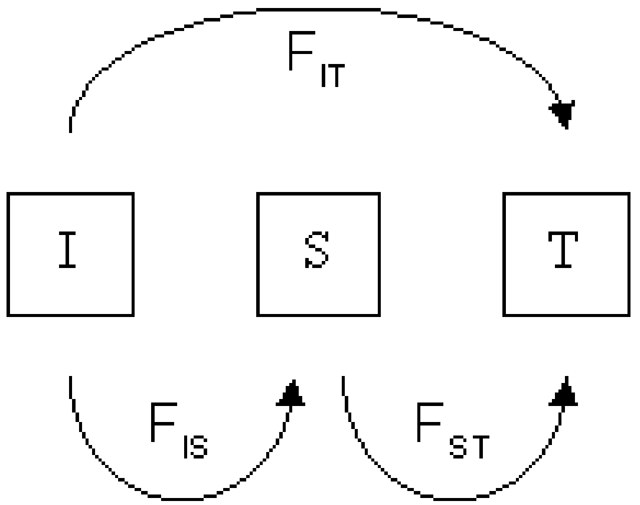
Although F_{ST} is formally describe as partitioning variance relative to the *total population*, in practice we are often interested in *pairwise* F_{ST} as a measure of differentiation between two populations. This is simply done by re-defining what we mean by the *total population*.

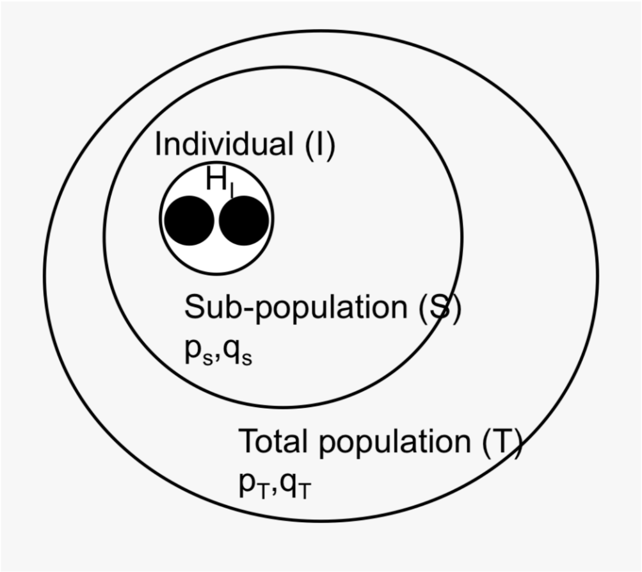


source

F_{ST} Readings (review paper)

F_{ST} can be defined and measured in several ways. The measure itself is informative, and it also can set a benchmark against which to test hypotheses about selection or introgressive gene flow.





“Genetics in Geographically Structured Populations: Defining, Estimating and Interpreting FST.”

F_{ST} Readings (empirical papers)

“Genome-Wide Patterns of Divergence and Gene Flow across a Butterfly Radiation.”

"Population Genomics of Parallel Adaptation in Threespine Stickleback using Sequenced RAD Tags"

F_{ST} Readings (empirical papers)

What is so interesting about the Heliconius butterfly radiation?

Do Heliconius populations form *good* taxa (identifiable by geography + morphology)?

What types of F_{ST} patterns do the authors observe? And what do they conclude from these?

"Genome-Wide Patterns of Divergence and Gene Flow across a Butterfly Radiation."

F_{ST} Readings (empirical papers)

There are many examples of phenotypic convergence in Heliconius between closely related and distantly related species and populations.

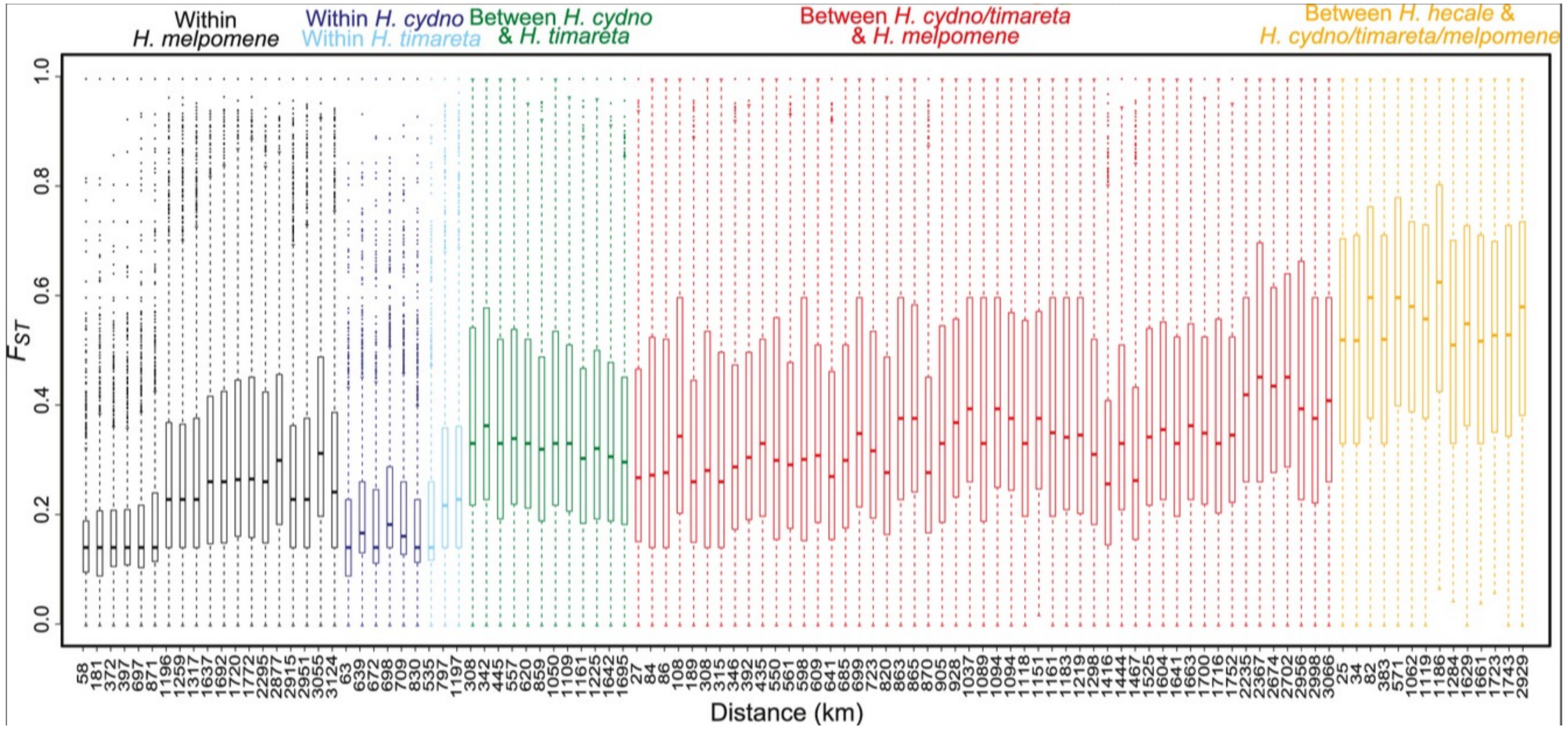
Here the authors focus on *H. cyndo* and *H. melpomene* which co-occur broadly, rarely hybridize, but may have experienced adaptive introgression.

To what extent do color patterns reflect independent evolution versus retention of ancestral alleles, versus introgressed exchange of alleles? Genome-wide F_{ST} can shed some light.

“Genome-Wide Patterns of Divergence and Gene Flow across a Butterfly Radiation.”

F_{ST} Readings (empirical papers)

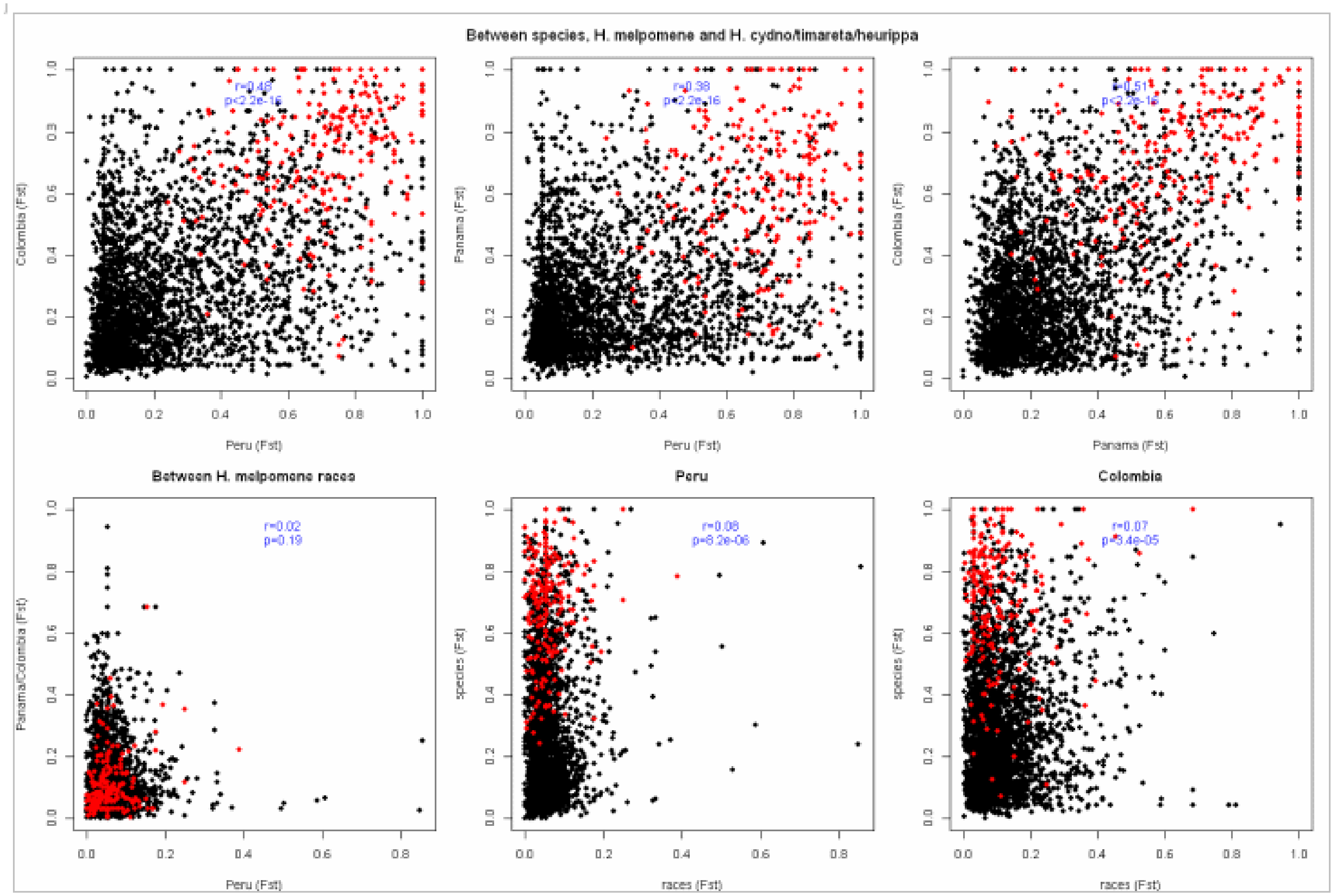
Genome-wide pairwise F_{ST}. Populations showed increasing divergence with increasing geographic distance, as well as increases with taxonomic distance (Fig. 3). In addition, correlation between all pop distances with geography (mantel P=0.003).



“Genome-Wide Patterns of Divergence and Gene Flow across a Butterfly Radiation.”

F_{ST} Readings (empirical papers)

per-locus pairwise F_{ST}. Sympatric species pairs show correlated regions of high FST.

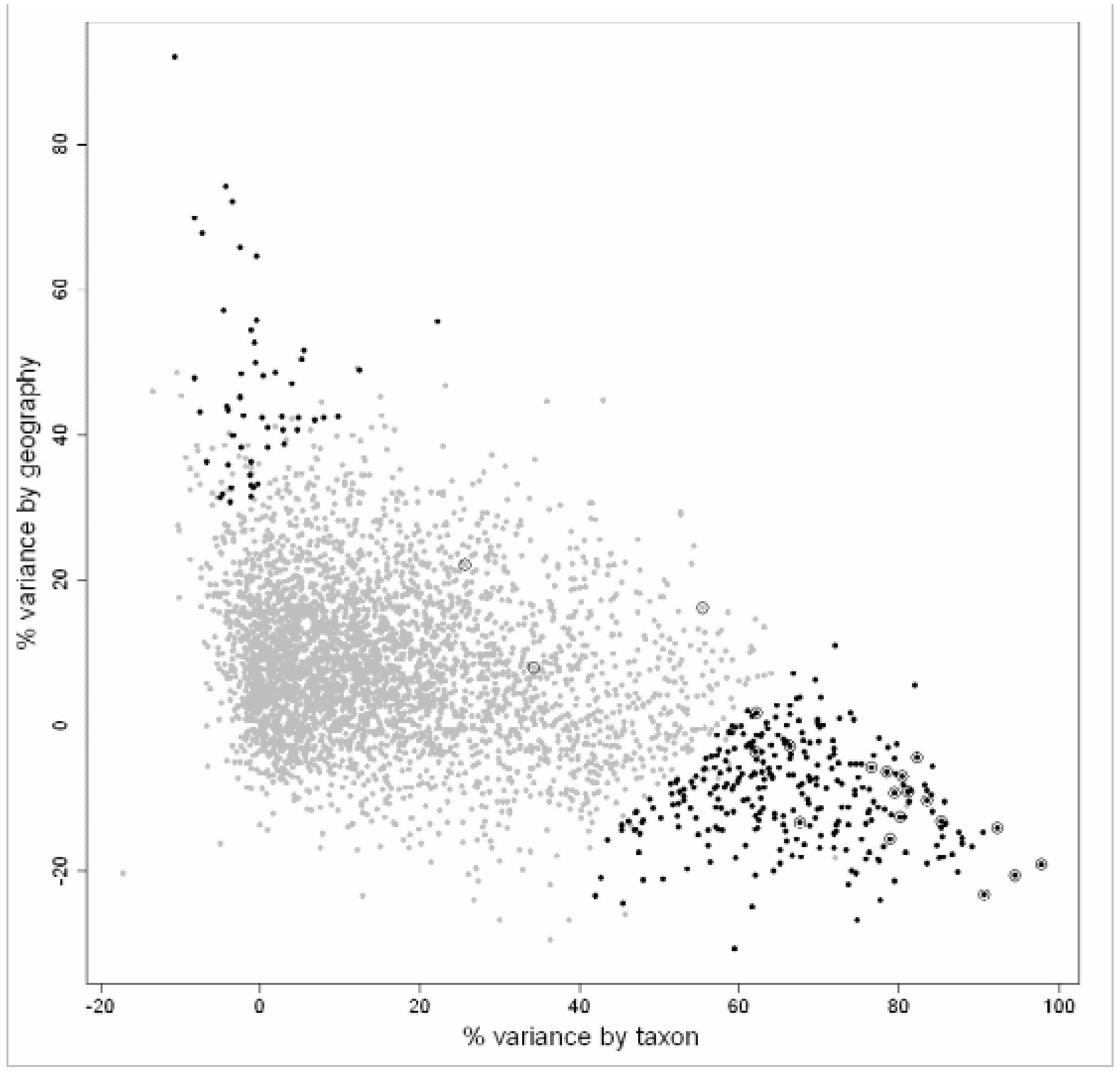


SI Figure 3. Comparisons of F_{ST} values calculated for all RAD tags in different population and species pairs. Red points are those identified in AMOVAs as being more strongly associated with taxon than geography.

"Genome-Wide Patterns of Divergence and Gene Flow across a Butterfly Radiation."

F_{ST} Readings (empirical papers)

Association with geography, taxon, and color pattern. Analysis of Molecular Variance.

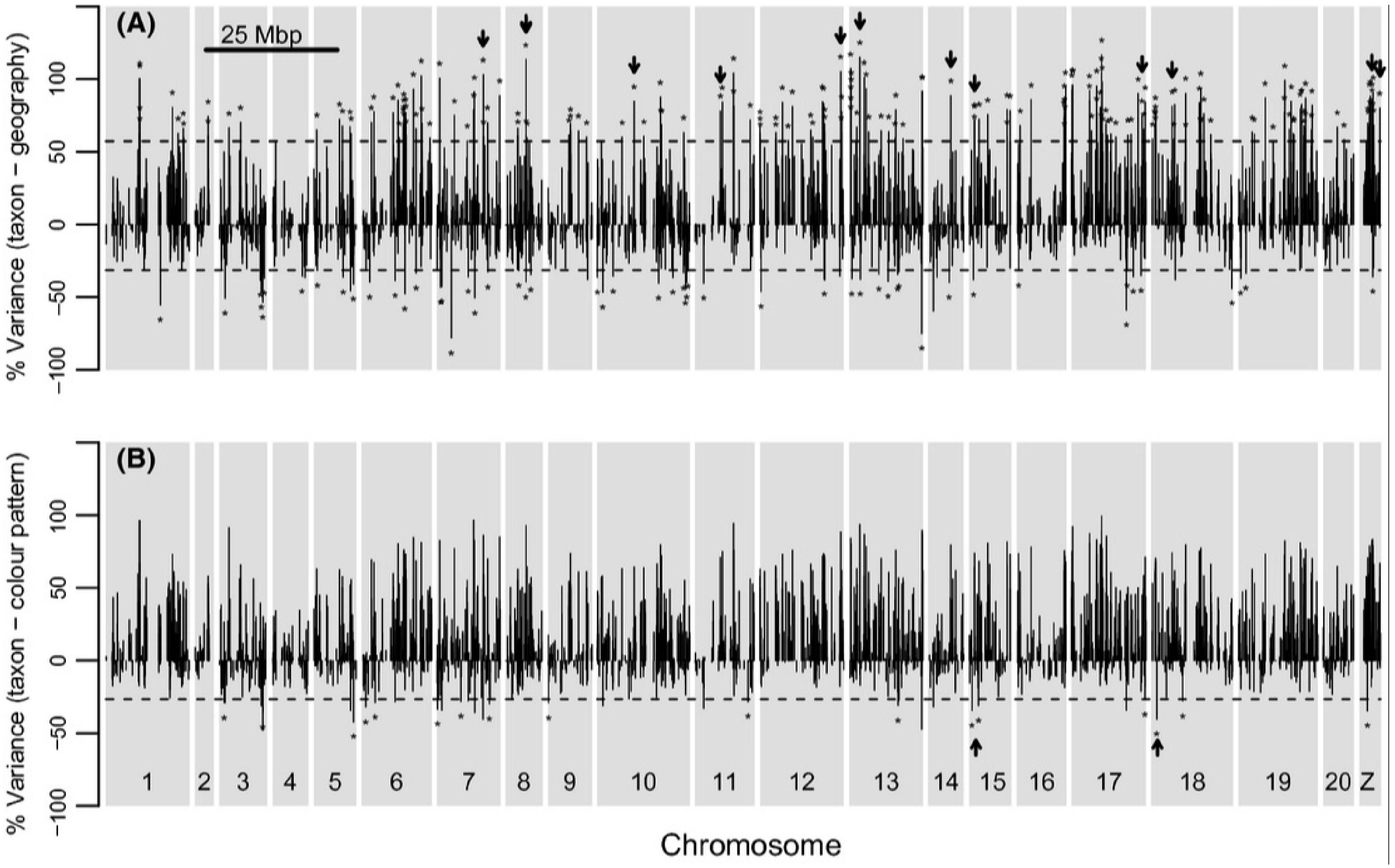


SI Figure 5. AMOVA associations with taxon (*H. cyndo/melpomene*) and geography. Black points are those identified as being significantly more highly associated with one or other variable. Circled points are loci that are outliers in all F_{ST} comparisons between sympatric sister species.

“Genome-Wide Patterns of Divergence and Gene Flow across a Butterfly Radiation.”

F_{ST} Readings (empirical papers)

Association with geography, taxon, and color pattern. Analysis of Molecular Variance.



“Genome-Wide Patterns of Divergence and Gene Flow across a Butterfly Radiation.”

F_{ST} Readings (empirical papers)

"If the loci most strongly associated with 'taxon' are those under **divergent selection**, these should also be loci with high FST in sympatric mel v. cydo/tim pairs. ... The 21 loci that are FST outliers do appear as outliers in AMOVA."

"Convergent wing color patterning may be controlled by loci that are **introgressed** between taxa. Fourteen loci were found to be more strongly associated with color pattern than taxon or geography (Fig. 4B). Two of these are known to be associated with wing color."

“Genome-Wide Patterns of Divergence and Gene Flow across a Butterfly Radiation.”

F_{ST} Readings (empirical papers)

Population Genomics of Parallel Adaptation in Threespine Stickleback using Sequenced RAD Tags

F_{ST} Readings (empirical papers)

What is so interesting about threespine Sticklebacks?

What are the relationships of sampled populations in this study?

What types of F_{ST} patterns do the authors observe? And what do they conclude from these?

Population Genomics of Parallel Adaptation in Threespine Stickleback using Sequenced RAD Tags

F_{ST} Readings (empirical papers)

There are many examples of phenotypic convergence in sticklebacks that have adapted recently to freshwater lakes from marine environment.

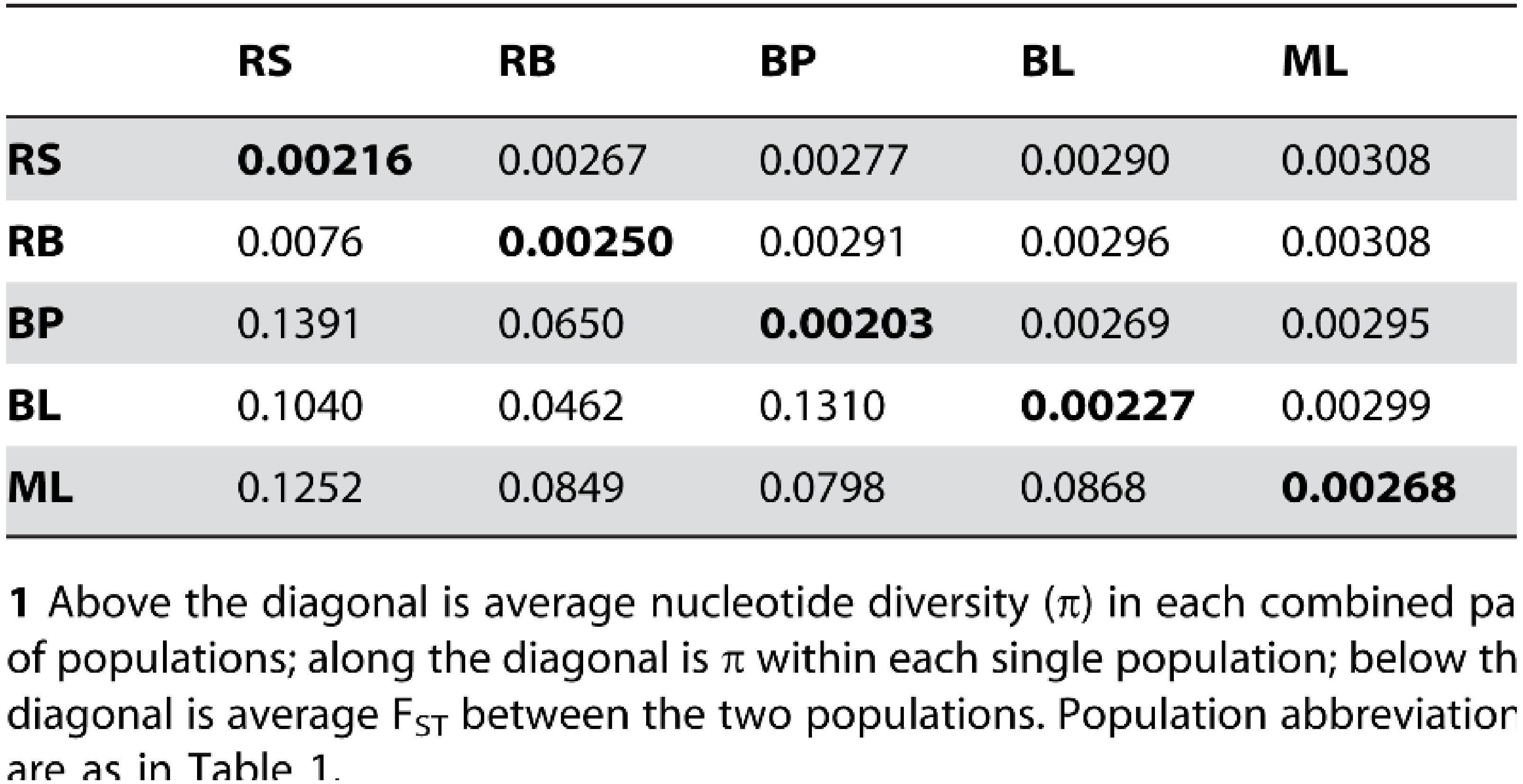
Genetic diversity and differentiation statistics support the repeated colonization of small freshwater pops from a large marine population.

FST scans reveal evidence of balancing and divergent selection, often in parallel but not always among freshwater pops.

Population Genomics of Parallel Adaptation in Threespine Stickleback using Sequenced RAD Tags

F_{ST} Readings (empirical papers)

Marine populations have little differentiation even over large geographic distance, while marine/fresh or fresh/fresh FST shows much larger differentiation.



	RS	RB	BP	BL	ML
RS	**0.00216**	0.00267	0.00277	0.00290	0.00308
RB	0.0076	**0.00250**	0.00291	0.00296	0.00308
BP	0.1391	0.0650	**0.00203**	0.00269	0.00295
BL	0.1040	0.0462	0.1310	**0.00227**	0.00299
ML	0.1252	0.0849	0.0798	0.0868	**0.00268**

1 Above the diagonal is average nucleotide diversity (π) in each combined pa
of populations; along the diagonal is π within each single population; below th
diagonal is average F_{ST} between the two populations. Population abbreviatio
are as in Table 1.

Population Genomics of Parallel Adaptation in Threespine Stickleback using Sequenced RAD Tags

F_{ST} Readings (empirical papers)

Genetic diversity and heterozygosity vary considerably across the genome.

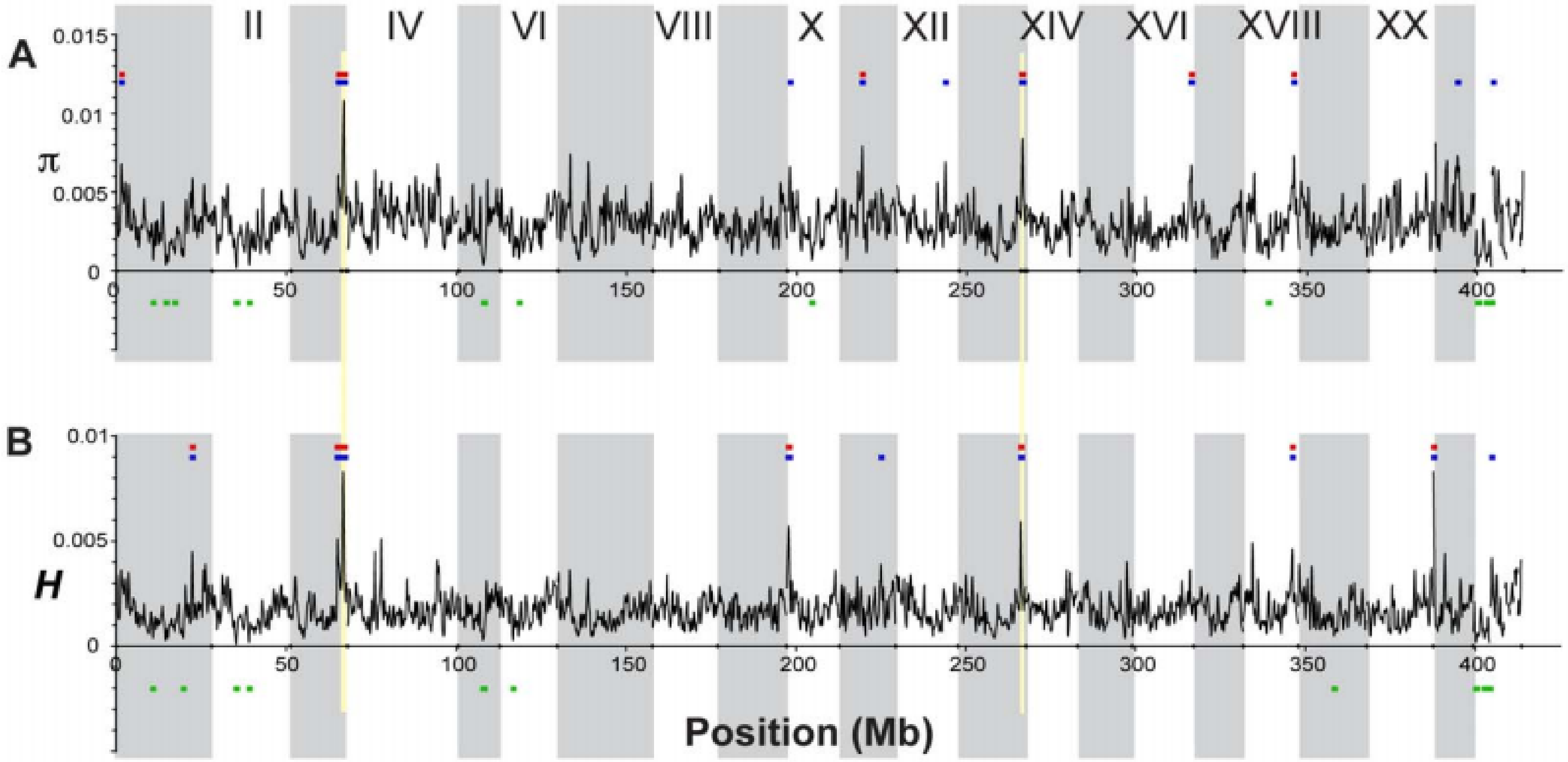


Figure 4. Genome-wide patterns of nucleotide diversity. Each plot shows a smoothed distribution of the statistical measure across the genome (black lines). Colored bars above and below the distributions indicate regions of significantly elevated ($p \le 10^{-5}$, blue; $p \le 10^{-7}$, red) and reduced ($p \le 10^{-5}$, green) values, assessed by bootstrap resampling. Vertical shading indicates the 21 linkage groups and the unassembled scaffolds greater than 1 Mb in length, and gold shading indicates two regions showing evidence of balancing selection as discussed in the text. (A) Nucleotide diversity (π) across all five stickleback populations sampled. (B) Heterozygosity (*H*) across all five populations.
doi:10.1371/journal.pgen.1000862.g004

Population Genomics of Parallel Adaptation in Threespine Stickleback using Sequenced RAD Tags

F_{ST} Readings (empirical papers)

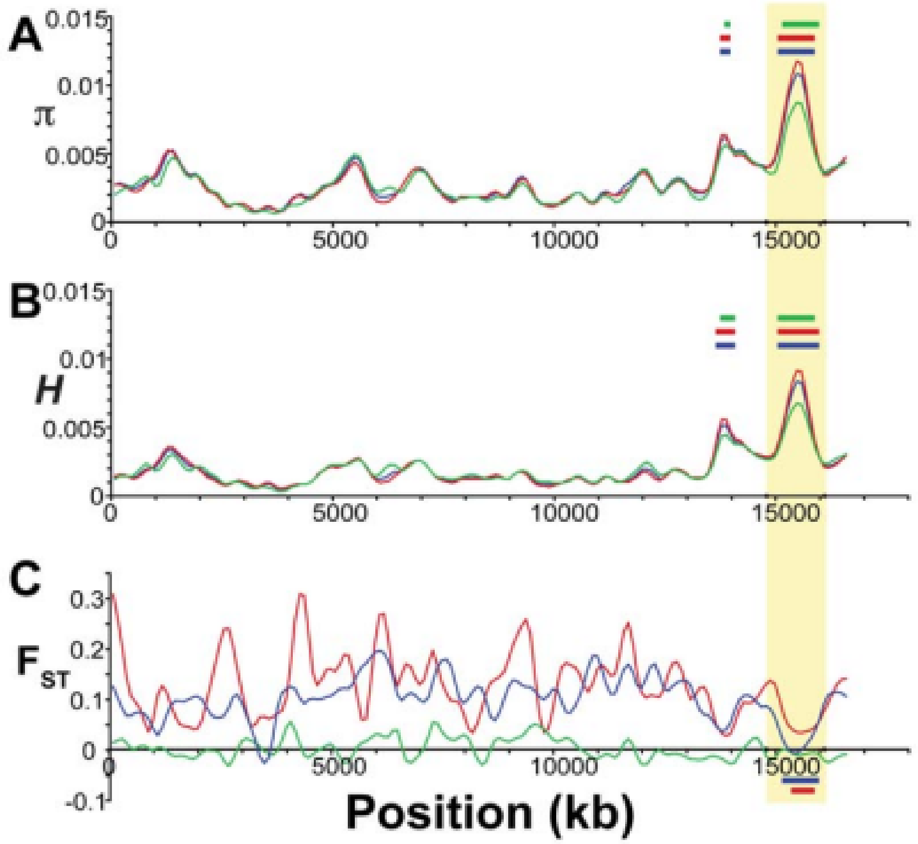
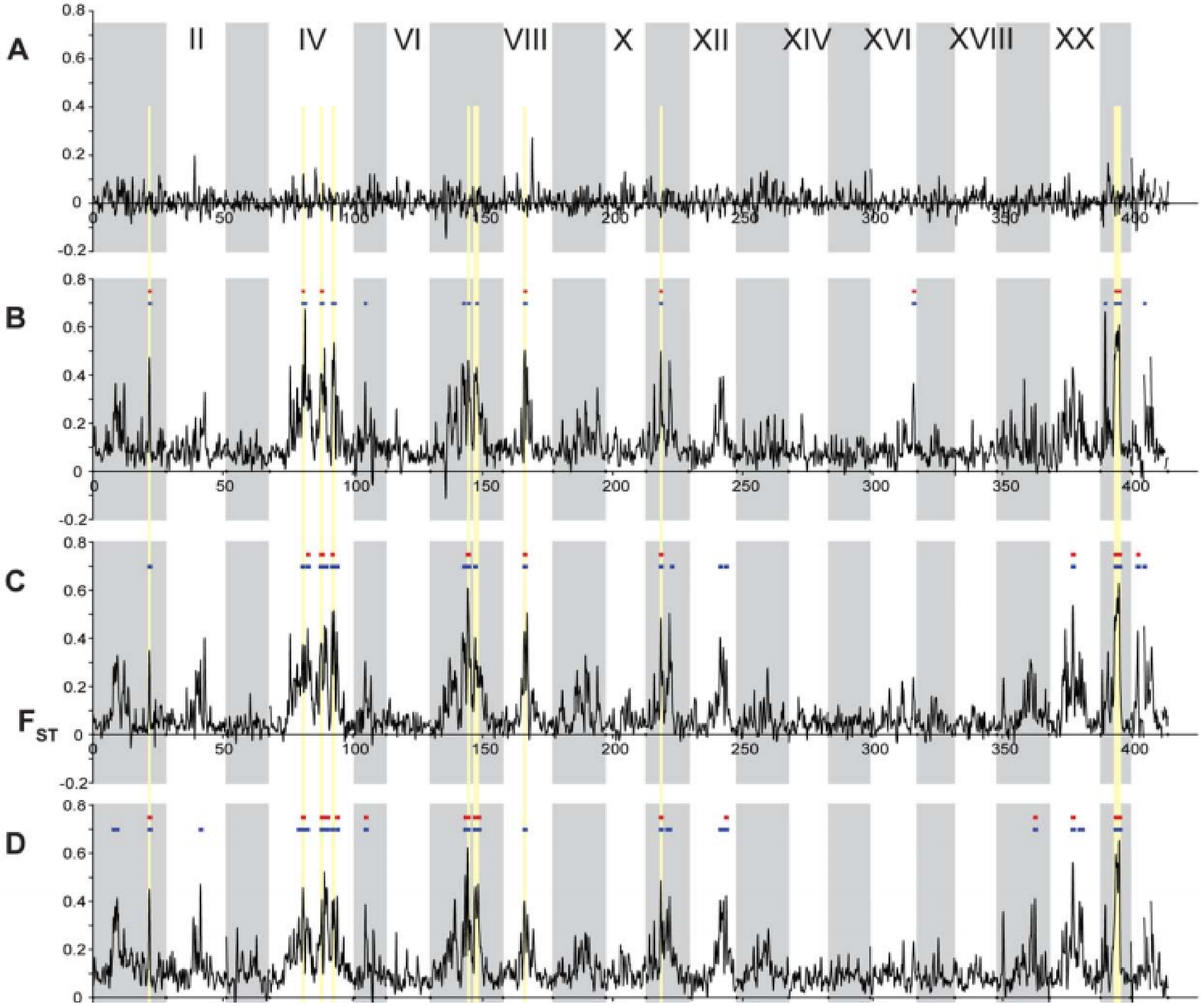


Figure 5. Evidence for balancing selection on Linkage Group III. Population genetic measures plotted along Linkage Group III. (A) Nucleotide diversity (π) and (B) heterozygosity (*H*) across all five (blue), the three freshwater (red), and the two oceanic (green) populations. (C) Population differentiation (F_{ST}) between oceanic and freshwater (blue), among freshwater (red), and between oceanic (green) populations. Colored bars indicate significant ($p \leq 10^{-5}$) regions of elevated (above the plots) or reduced (below the plots) values of each statistic for the corresponding set of populations. Vertical yellow shading indicates the region of putative balancing selection used for candidate gene annotation.

Population Genomics of Parallel Adaptation in Threespine Stickleback using Sequenced RAD Tags

F_{ST} Readings (empirical papers)



Population Genomics of Parallel Adaptation in Threespine Stickleback using Sequenced RAD Tags

F_{ST} Readings (empirical papers)

Despite the phenotypic divergence of freshwater pops, a huge amount of genetic variation is still shared among all populations (no windows reach FST=1).

The regions of highest differentiation are shared among most freshwater-marine comparisons, showing *convergence* at the genetic level. Similar regions responding to directional selection.

Private alleles are greater in marine than freshwater, supporting that fresh is a subset of marine. However, some high Fst (f/m) regions are associated with private alleles in freshwater. These are likely low freq alleles in marine that were unsamples but maintained by balancing selection or gene flow.

Population Genomics of Parallel Adaptation in Threespine Stickleback using Sequenced RAD Tags

Wright-Fisher Model

Each generation randomly sample alleles from the parental generation. By incorporating a finite population size (N) into our sampling probabilities we can estimate the expected change in allele frequencies due to drift.

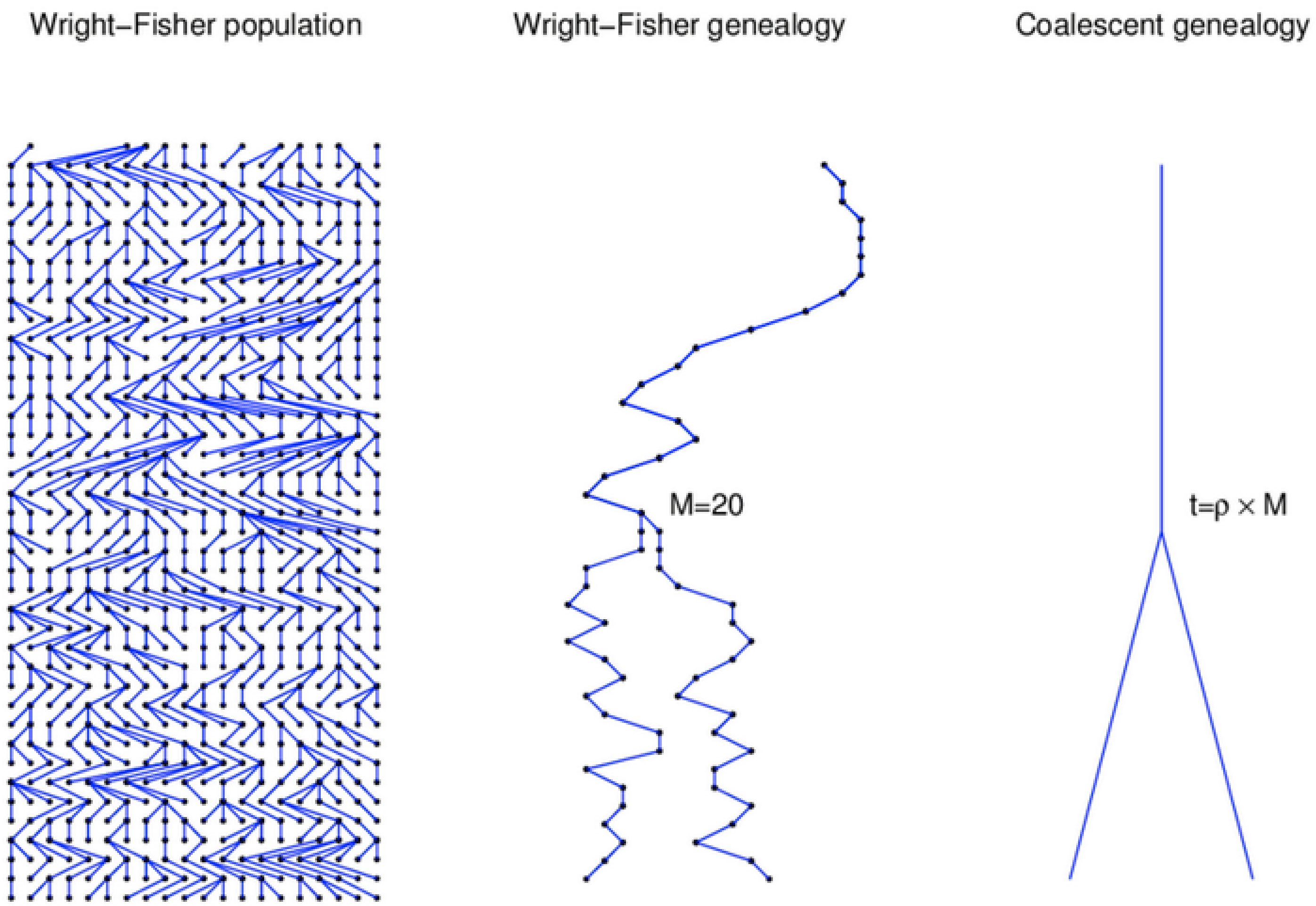
A discrete time model in which each generation is composed of 2N copies of each gene. Each subsequent generation 2N new copies are randomly drawn from the previous generation. The probability of obtaining k copies the next generation is:

$$\binom{2N}{k} p^k (1-p)^{2N-k}$$

https://en.wikipedia.org/wiki/Genetic_drift#Wright.E2.80.93Fisher_model

Wright-Fisher Model

A neutral evolutionary process (no selection) can be modeled using the WF model in which allele frequencies change over time by genetic drift.



Source: Alexei Drummond

Reading for next session

Read both of these:

Gene tree discordance, phylogenetic inference and the multispecies coalescent

Inferring the Joint Demographic History of Multiple Populations from Multidimensional SNP Frequency Data