

Examples of landscape genomic studies

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Case studies

- Common frog in the Alps
- Pine weevil in Europe
- Goats in Europe/western asia
- *Biscutella laevigata* - Swiss Alps
- Cichlids in Lake Victoria



Common frog

Explorative Genome Scan to Detect Candidate Loci for Adaptation Along a Gradient of Altitude in the Common Frog (*Rana temporaria*)

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Today, with the rapid development of population genomics, the genetic basis of adaptation can be unraveled directly at the genome level, without any prerequisites about the selectively advantageous genes or traits. For nonmodel species, it is now possible to screen many markers randomly scattered across the genome and to distinguish between the neutral genetic background and outlier loci displaying an atypical behavior (e.g., a higher differentiation between populations). This study investigated the genetic frame of adaptation to a gradient of altitude in the common frog (*Rana temporaria*) by means of a genome scan based on 392 amplified fragment length polymorphism markers. Using two outlier detection methods never applied to dominant data so far, we sought for loci with a genetic differentiation diverging from neutral expectations when comparing populations from different altitudes. All the detected loci were sorted out according to their most probable cause for outlier behavior and classified as false positives, outliers due to local effects, or outliers associated with altitude. Altogether, eight good candidate loci were identified as potentially involved in adaptation to altitude because they were picked out in several independent interaltitude comparisons. This result illustrated the potential of genome-wide surveys to reveal selection signatures along selection gradients, where the association between environmental variables and fitness-related traits may be complex and/or cryptic. In this article, we also underlined the need for confirmation of the selection footprints for the outlier loci. Finally, we provided some preliminary insights into the genetic basis of adaptation along an altitudinal cline in the common frog.

Table 1
Location and Altitude of the Studied Populations

Population name	Site	Altitude	Longitude	Latitude	Number of individuals genotyped
Low 1	Saint-Rémy-de-Maurienne	425 m	6.2775E	45.3697N	34
Low 2	Cognin	438 m	5.8730E	45.5635N	28
Inter 1	Col de Plainpalais	1,074 m	6.0207E	45.6475N	30
Inter 2	Tignes	1,082 m	6.9022E	45.9522N	34
High 1	Lac des Aiguillettes	2,100 m	6.8106E	45.9249N	32
High 2	Lac des Tempêtes	2,130 m	6.5491E	45.6205N	32

Bonin, A., Taberlet, P., Miaud, C., & Pompanon, F. (2006). Explorative Genome Scan to Detect Candidate Loci for Adaptation Along a Gradient of Altitude in the Common Frog (*Rana temporaria*). *Molecular Biology and Evolution*, 23(4), 773–783.

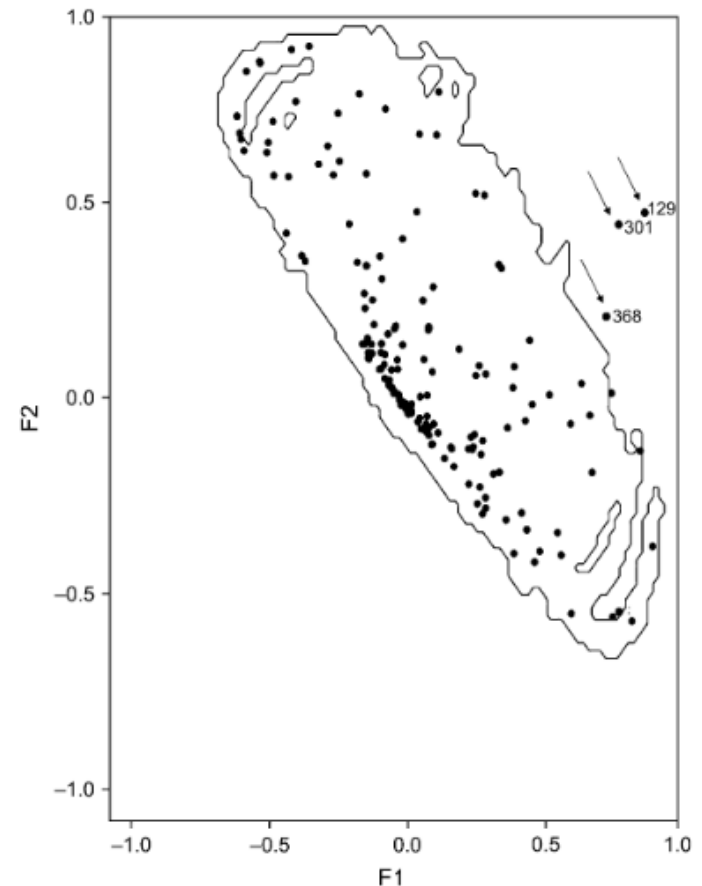
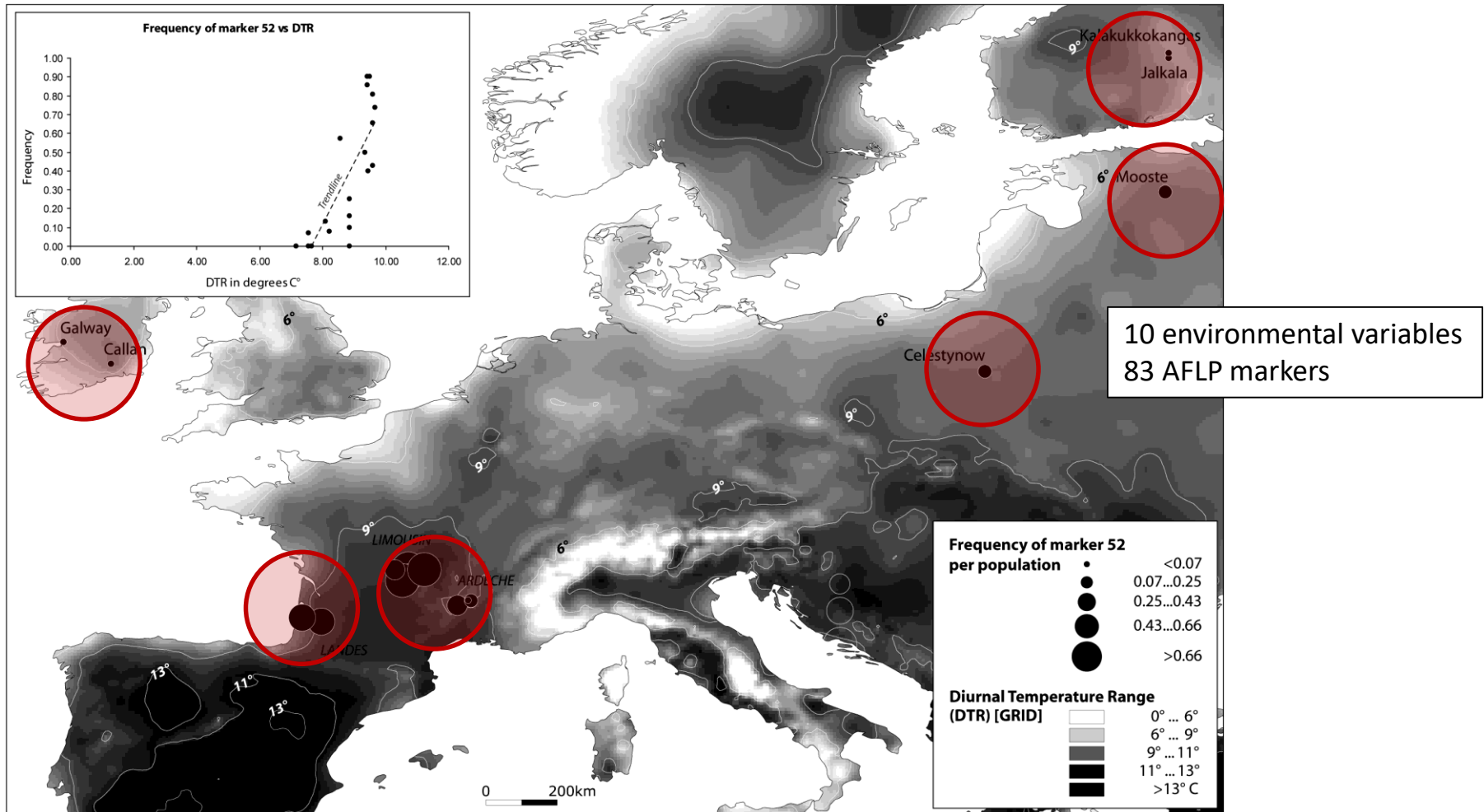


Fig. 1—Example of interaltitude pairwise comparison performed with DetSel: plot of F_2 against F_1 estimates for the population pair Low 1/High 1. Each dot indicates an AFLP marker, and the line represents the 95% confidence envelope. Outlier loci are pointed out by arrows and referred to by numbers.

	Marker	301	320	214	357	357	184	179	265	328	180	250	354	233	368	228	266	385	386	3	271	248	58	62	46	39	16	243	347	364	390	24	10	165	200	17	237	97	52	307	334	371	12	169	94	120																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																								
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Pine weevil



Joost, S., Bonin, A., Bruford, M. W., Després, L., Conord, C., Erhardt, G., & Taberlet, P. (2007). A spatial analysis method (SAM) to detect candidate loci for selection: towards a landscape genomics approach to adaptation. *Molecular Ecology*, 16(18), 3955–3969.

Pine weevil

- 6 populations
- 367 weevils (larvae and adults)
- 10 environmental variables
 - Climate Research Unit (CRU), Norwich
- 83 AFLP markers
- Analyses with Fdist and Matsam
- Goal: detect signatures of selection

Genetic markers

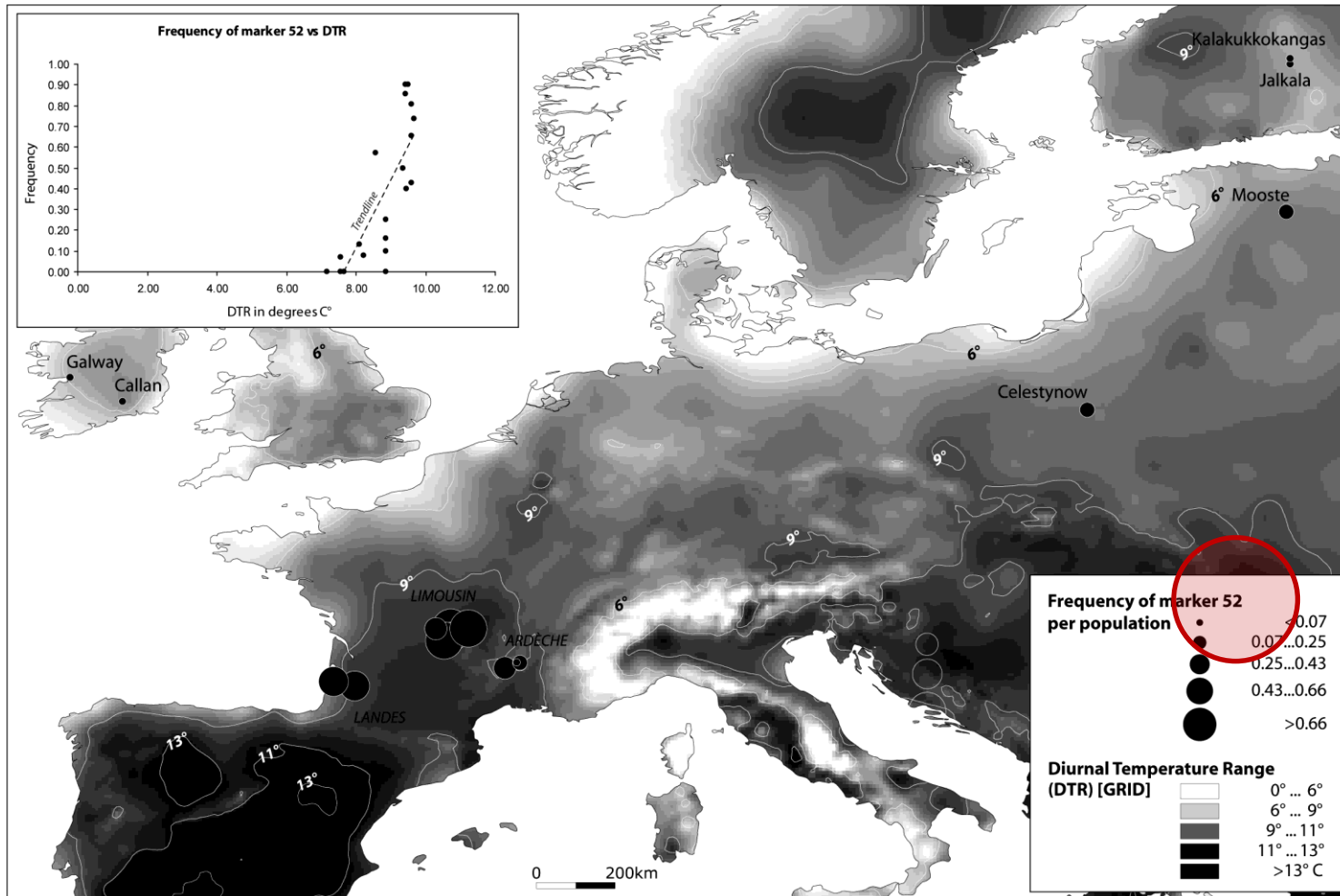
Variables environnementales

Genetic differentiation (FST)



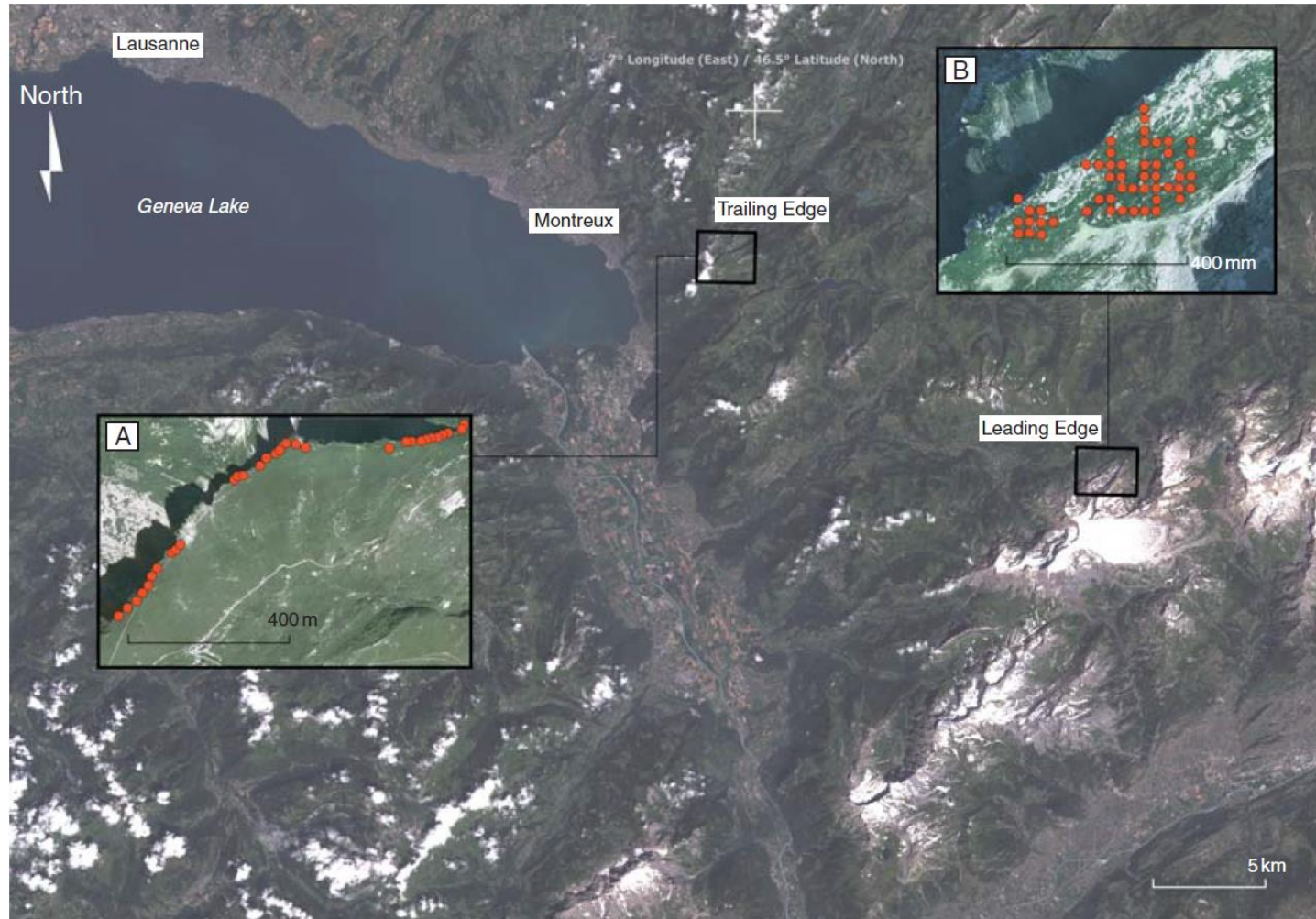
3 markers (38, 52, 63)
congruently identified by
both methods

Pine weevil: main result



Diurnal temperature range exerts a selective pressure on a given region of the genome

Biscutella laevigata (Swiss prealps)



Parisod, C., & Joost, S. (2010). Divergent selection in trailing- versus leading-edge populations of *Biscutella laevigata*. *Annals of Botany*, 105(4), 655–660. doi:10.1093/aob/mcq014



Biscutella laevigata (Swiss prealps)

	Trailing edge	Leading edge
Population's details		
Coordinates	6°58'/46°26'	7°12'/46°20'
Historical features	Refugial populations in the peripheral Alps (Parisod and Christin, 2008)	Expanding population in the central Alps (Parisod and Bonvin, 2008)
Spatial features	Linear (1000 × 25 m)	Two-dimensional (350 × 200 m)
Grid sampling	31 plots of 4 individuals	51 plots of 4 individuals
Environmental heterogeneity*		
DEM: altitude (m)	(1851–1990); significant SA up to 140 m	(2154–2298); significant SA up to 140 m
DDEG: degree-days during growing season (°d)	(1124–1260); significant SA up to 140 m	(839–921); significant SA up to 140 m
ETPT: daily average evapotranspiration (mm d ⁻¹)	(2.5–6.6); low or no SA	(2.1–5.6); low or no SA
PDAY: number of precipitation days (d)	(62.9–63.75); low or no SA	(43–43); low or no SA
SRAD: daily average radiation (kJ d ⁻¹)	(18057–75418); low or no SA	(17763–63928); low or no SA
Slope (°)	(2–69); low or no SA	(7–56); low or no SA
Genetic dataset		
Number of polymorphic AFLP bands	102	113
Error rate (number of replicates)	1.8 % (20)	2.4 % (10)

SHORT COMMUNICATION

Divergent selection in trailing- versus leading-edge populations of *Biscutella laevigata*

Christian Parisod^{1,*} and Stéphane Joost²

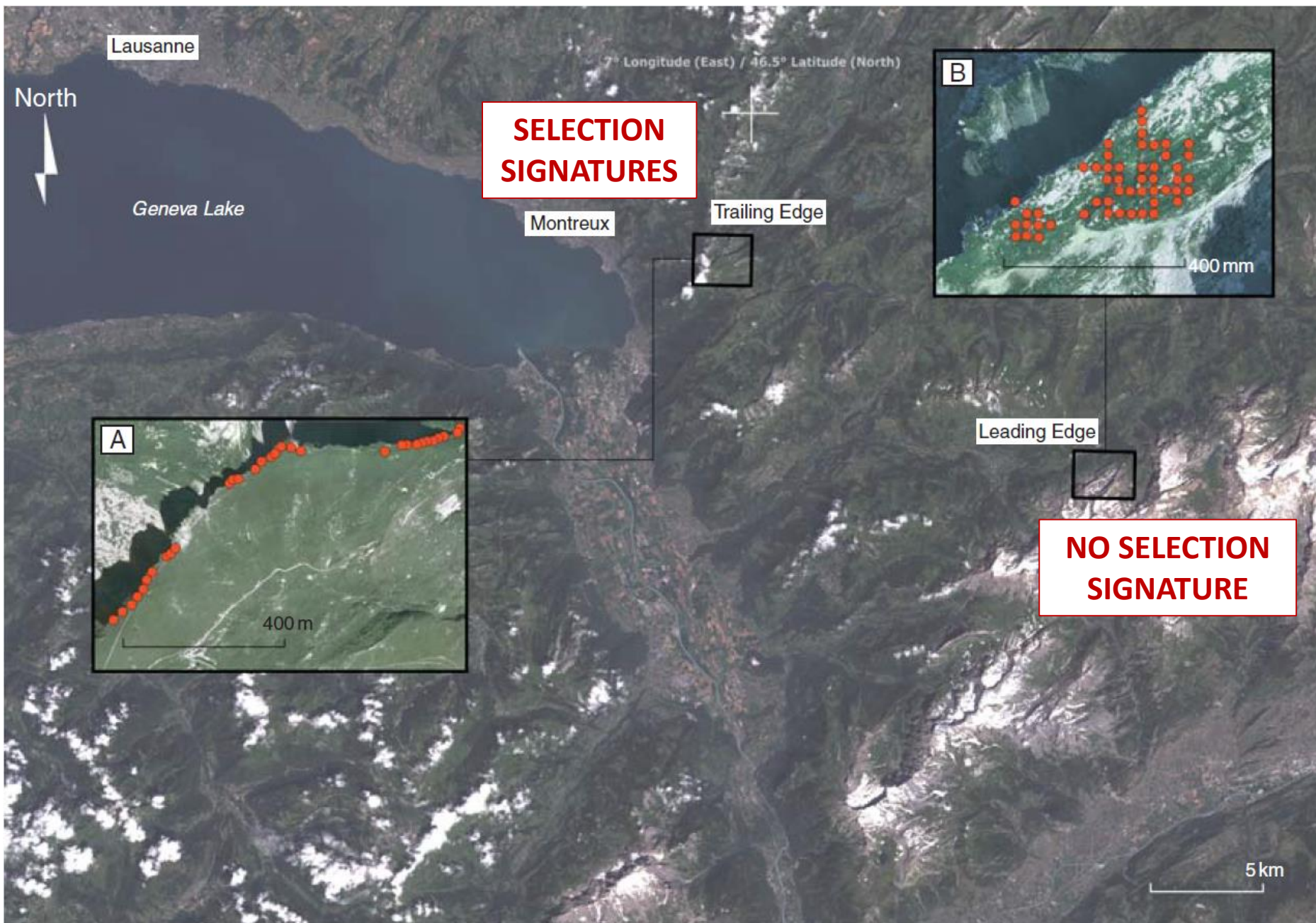
¹National Center for Biosystematics (NCB), Natural History Museum, University of Oslo, 0318 Oslo, Norway and ²GIS Research Laboratory (LASIG), School of Civil and Environmental Engineering (ENAC), Ecole Polytechnique Fédérale de Lausanne (EPFL), CH-1015 Lausanne, Switzerland

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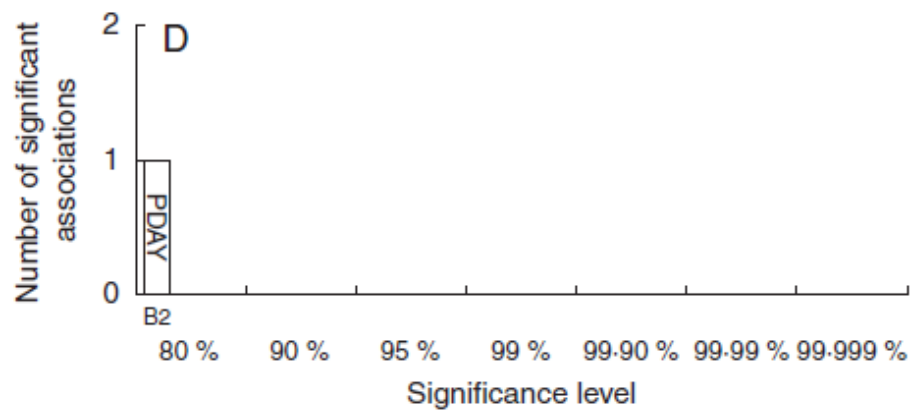
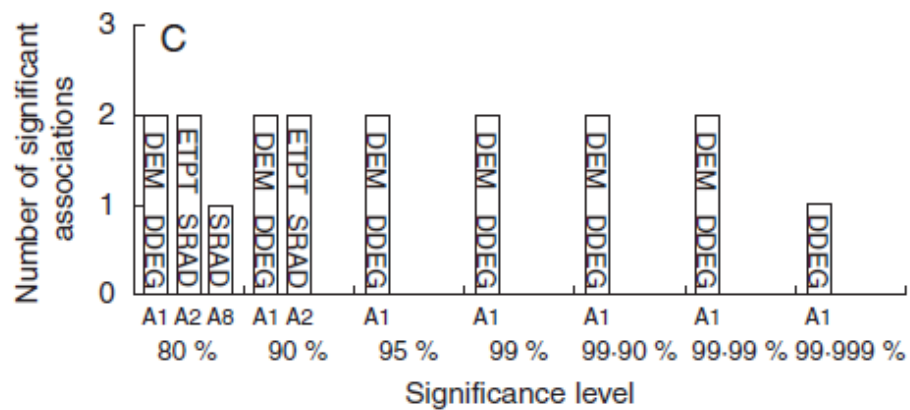
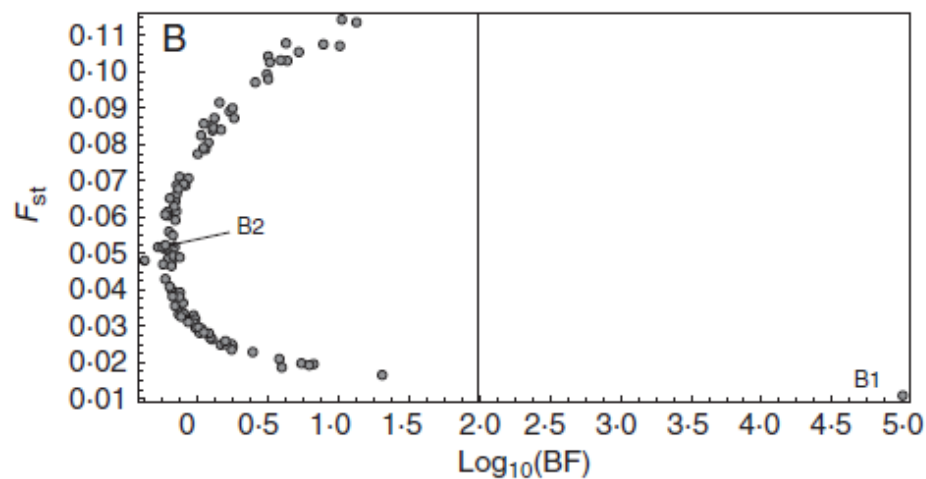
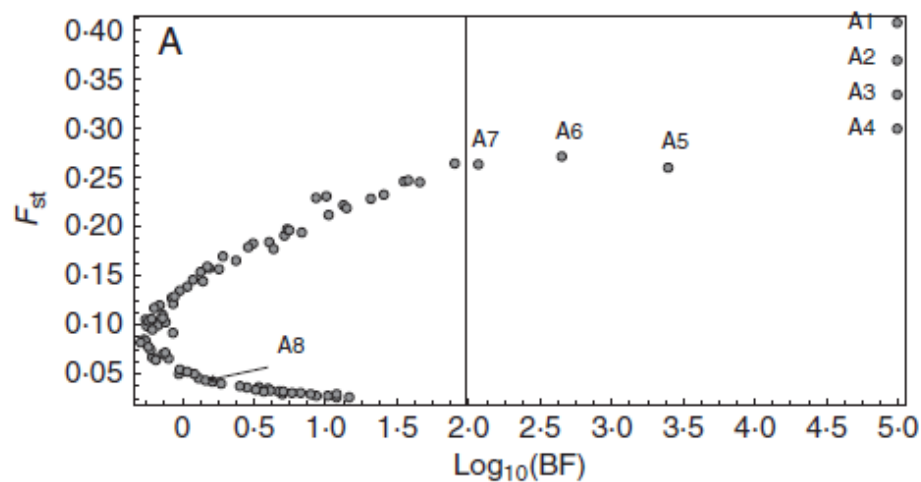
- **Background and Aims** Knowledge on how climate-induced range shifts might affect natural selection is crucial to understand the evolution of species ranges.
- **Methods** Using historical demographic perspectives gathered from regional-scale phylogeography on the alpine herb *Biscutella laevigata*, indirect inferences on gene flow and signature of selection based on AFLP genotyping were compared between local populations persisting at the trailing edge and expanding at the leading edge.
- **Key Results** Spatial autocorrelation revealed that gene flow was two times more restricted at the trailing edge and genome scans indicated divergent selection in this persisting population. In contrast, no pattern of selection emerged in the expanding population at the leading edge.
- **Conclusions** Historical effects may determine different architecture of genetic variation and selective patterns within local populations, what is arguably important to understand evolutionary processes acting across the species ranges.

Key words: Amplified fragment length polymorphism, *Biscutella laevigata* (Brassicaceae), gene flow, genome scan, landscape genetics, range margins, selection, species range shift.

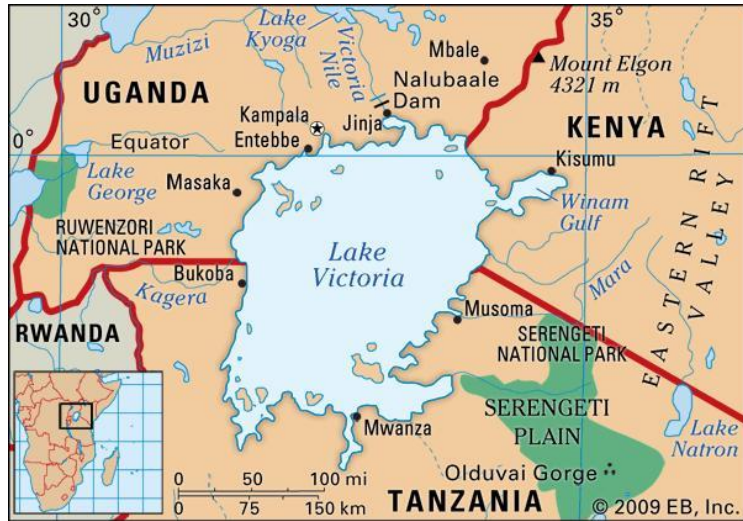


Trailing edge

Leading edge



Cichlids in the lake Victoria



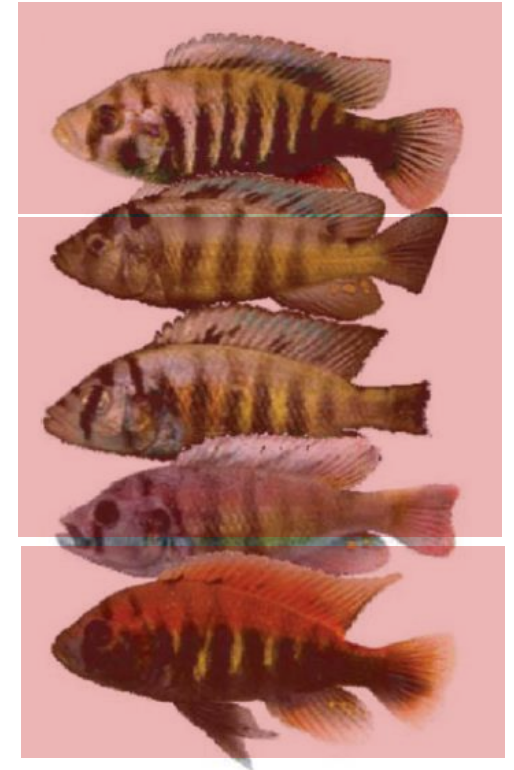
Joost, S., Kalbermatten, M., Bezault, E., & Seehausen, O. (2012). Use of Qualitative Environmental and Phenotypic Variables in the Context of Allele Distribution Models: Detecting Signatures of Selection in the Genome of Lake Victoria Cichlids. In F. Pompanon & A. Bonin (Eds.), *Data Production and Analysis in Population Genomics* (pp. 295–314). Humana Press.

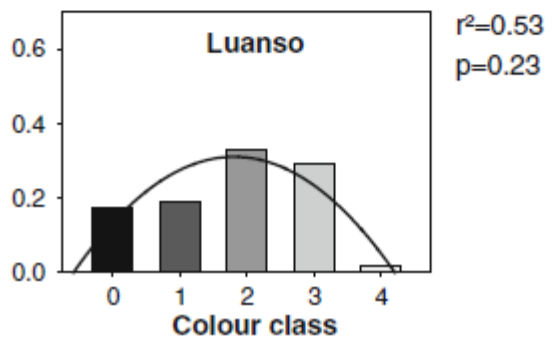
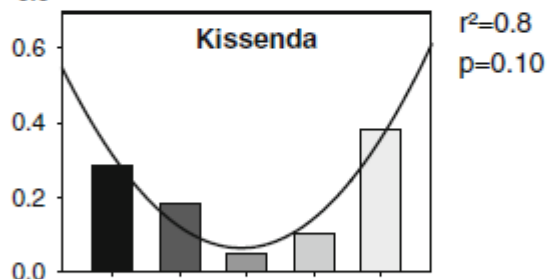
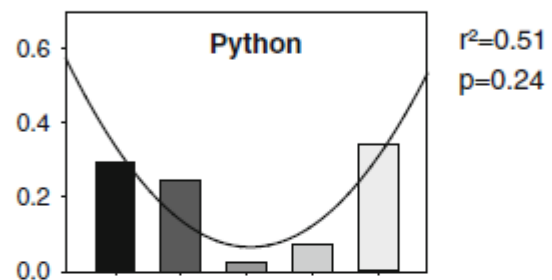
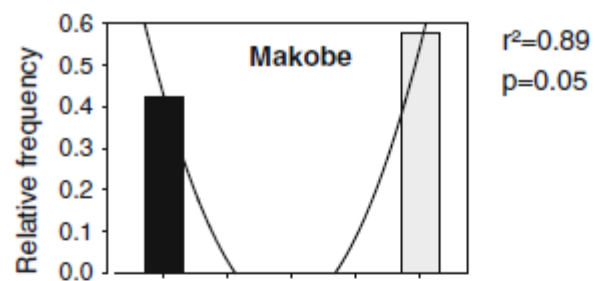
Why Lake Victoria?

- The cichlid flock in this lake is one of the most explosive examples of adaptive radiation
- Where more than 500 species have evolved during the last 15,000 years.
- The repetitive occurrence of the same adaptively important traits in unrelated taxa
- Lake Victoria flock is an ideal model system for studying adaptation

Pundamilia pundamilia & *Pundamilia nyererei*

- 2 sympatric sister species inhabiting the shores of rocky islands, widely distributed in the lake
- Differ in male nuptial coloration, in feeding ecology, depth distribution, photic environment, visual pigment, female mating preference for male nuptial coloration
- However such divergences appear only in near islands with high water transparency,
- Whereas in near islands with low water transparency, genetic differentiation is reduced or absent and intermediate color phenotypes are common or even dominate





Water Transparency

Sampling

- Along the Mwanza Gulf, Southern part of the lake
- Rocky islands show a continuous gradient of water clarity, from turbid in the South to clear in the North
- Associated with an increased heterogeneity of the light environment
- Populations of *Pundamilia* exhibit different stages of speciation along this gradient
- 4 replicate pairs of divergent *Pundamilia* populations along this speciation transect
- 234 individuals
- 520 AFLP loci



Qualitative environmental variables

- Matsam improvement in order to support qualitative environmental predictors
- To permit the identification of associations between genomic variation and individual phenotypes
- Allowing the detection of loci involved in the genetic architecture of polymorphic characters

Methods

- Dfdist, Bayescan and Matsam
- Identification of signatures of divergent selection between the two *Pundamilia* species (or eco-morphs)
- Analyses:
 - (a) independently within each replicate pair of divergent populations (at the island level) to detect outlier loci within each of the four study islands
 - (b) across all island populations grouped by color-morph (i.e. blue *P. pundamillia* vs . red *P. nyererei*) to detect global outliers over the entire study area.

Methods	F_{ST} -outlier approach		Logistic regression
Software	DFDIST	BAYESCAN	MATSAM
<i>Analysis parameters</i>			
Detection thresholds			
Significant	$P < 0.01$	$\log_{10}(\text{BF}) \geq 1$ (equivalent $P < 0.24$)	$P < 0.05$
Marginally significant	$P < 0.05$	$\log_{10}(\text{BF}) \geq 0.5$ (equivalent $P < 0.09$)	$P < 0.1$
Additional detection parameters	Sequential background F_{ST} estimate	F_{IS} was estimated from microsatellites	Detection with both Wald and G-tests
<i>Sample set and test variables</i>			
- Comparison tests	Separately within each island and across all islands populations ($n = 5$ tests in total)		
- Sample sets	The two groups of extreme morphotypes (excluding intermediate phenotypes)		All individuals (including intermediate)
- Analyzed variables	Species (based on color phenotype)		Species and color (habitat, depth, morphometrics)
<i>Results</i>			
Loci detection			
- per method (signif. + marg. signif.)	49 (17 + 32)	15 (8 + 7)	21 (11 + 10)
- with outlier methods	49		
- with the three methods	55		
Repeated detection			
- between pairs of populations	2	1	1
- across populations	11	5	5
- between DFDIST and BAYESCAN	15 (31%)		
- between DFDIST and MATSAM	15 (27%)		
- between BAYESCAN and MATSAM	11 (44%)		

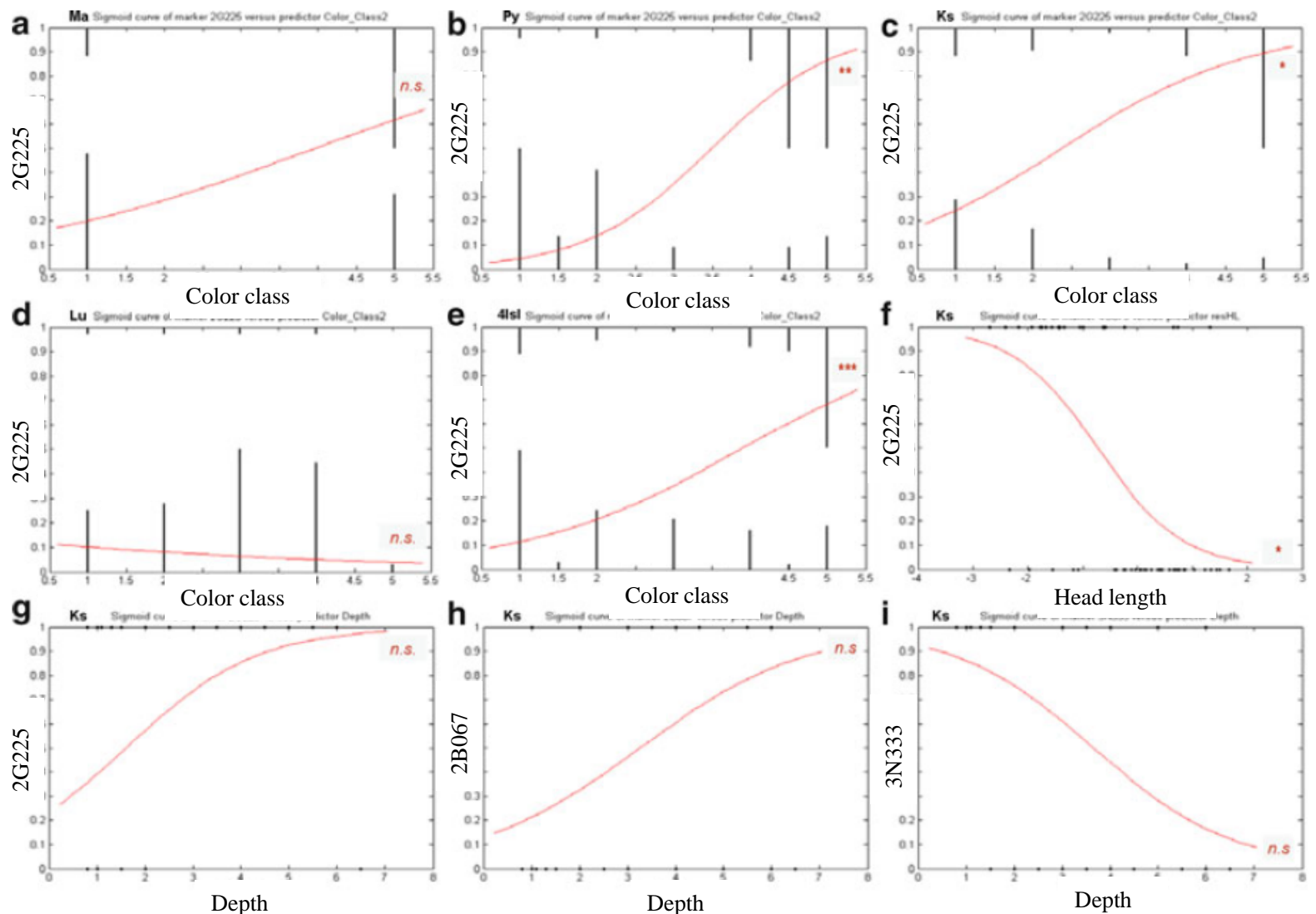


Fig. 4. Representation of different models of logistic regression to investigate association between locus genotype and phenotypic variables conducted with **MATSAM**; (a–e) test of association between genotype at locus 2G225 and individual color-score (considered as ordinal variable, ranging from 1 to 5) estimated independently within each island and across all islands; then within Kissenda Island populations, (f) test of association between genotype at locus 2G225 and a morphometric variable divergent between eco-morphs, the head length (HL), and (g–i) test of association between genotype at three loci (2G225, 2B067, and 3N333) and habitat depth. Respective levels of significance of the association are indicated for each model (*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, applying Bonferroni correction; n.s. nonsignificant).

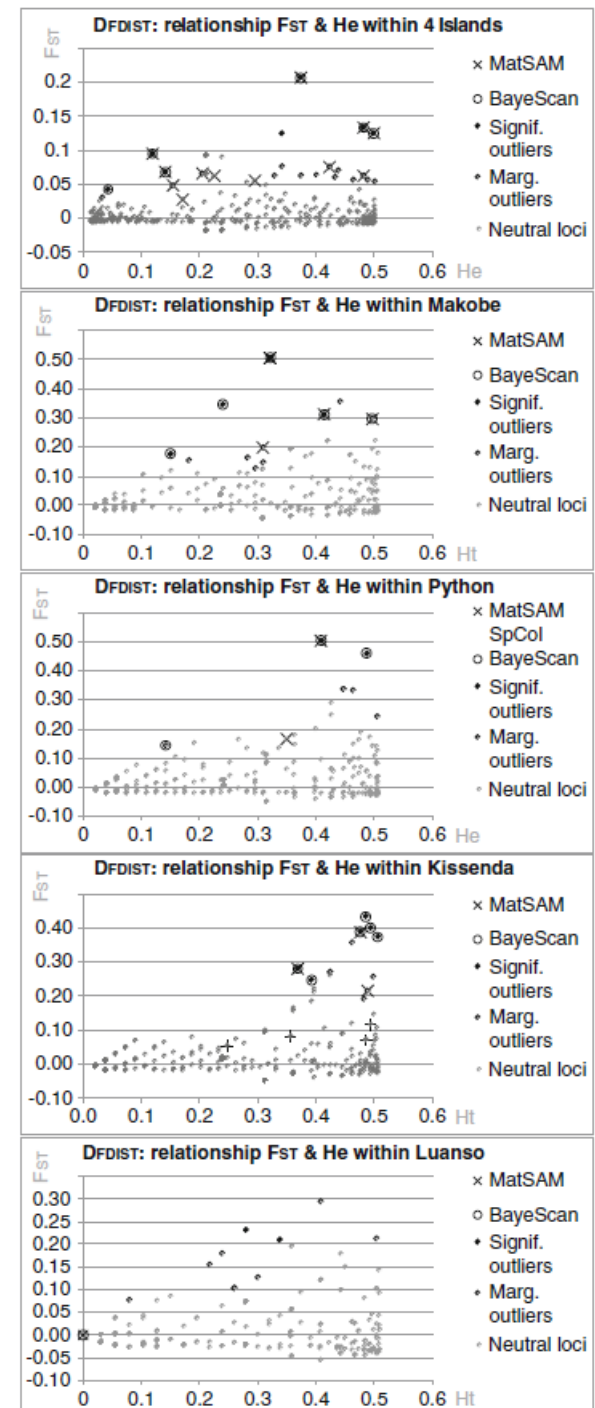
Table 3
Summary of environmental characteristics at the four islands along the Mwanza gulf transect, number of sampled individuals for each island, estimators of genetic diversity and differentiation, and number of potentially divergent loci detected by each method as well as by all three methods, and finally estimate of the fraction of genomic loci under selection

Locality	Makobe	Python	Kissenda	Luanso	All_Islands	Total
Code	Ma	Py	Ks	Lu	2Col	Loci
<i>Islands environmental characteristics</i>						
Water transparency ^a	225 ± 67	96 ± 21	78 ± 24	50 ± 10	—	
Light slope ^b	8 × 10 ⁻³	7.6 × 10 ⁻²	7.9 × 10 ⁻²	9.6 × 10 ⁻²	—	
<i>Sample sets (number of individuals)</i>						
<i>Pundamilia nyererei</i>	34	30	29	26	119	
<i>Pundamilia pundamilia</i>	25	26	28	14	93	
Intermediate	0	1	3	18	22	
Island community	59	57	60	58	234	
<i>Genetic diversity and differentiation</i>						
Number of polymorphic loci (<i>P</i> < 0.99)	382	394	334	308	369	520
<i>Detected divergent loci</i>						
Dfdist	12	7	12	10	21	49
BayeScan	6	3	6	0	6	15
MATSAM	5	2	8 (+4)	0	12	21
Across all methods	12	8	13 (+4)	10	24	55
Percentage of divergent loci	2.31%	1.54%	2.5% (3.27%)	1.92%	4.62%	11%

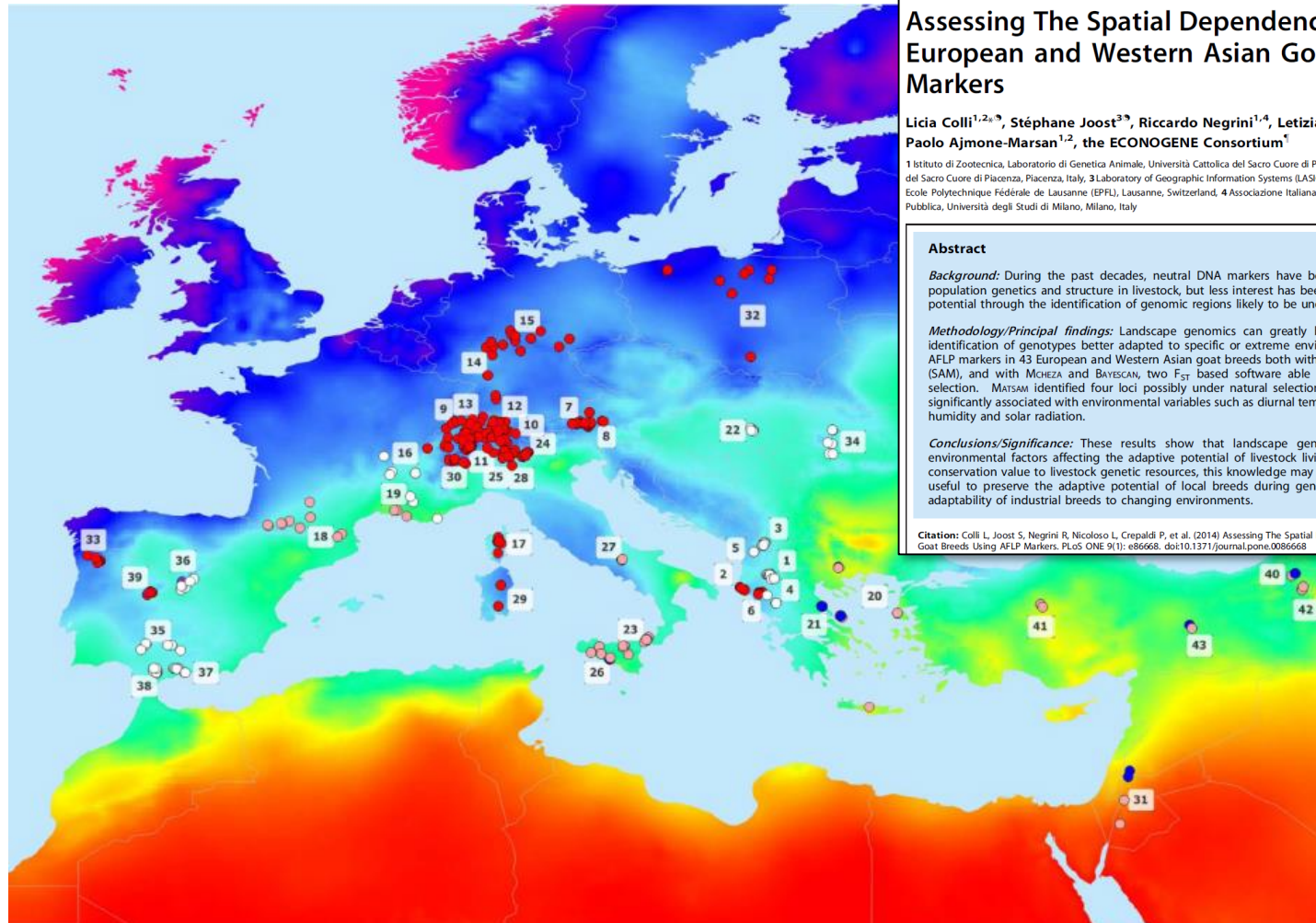
^aSecchi depth in centimeters

^bThe light slope is the steepness of the light gradient. It is calculated by regressing the transmittance orange ratio against the mean distance (in meters) from the shore, measured along the lake floor in transects

- High proportion of genomic loci exhibiting both a signature of selection and association with divergent color-morph characters (73% of significant and marginally significant loci)
- Suggests a predominant action of selection on male nuptial coloration in the divergence between *P. pundamilia* and *P. nyererei*



Goats in Europe and western asia



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Assessing The Spatial Dependence of Adaptive Loci in 43 European and Western Asian Goat Breeds Using AFLP Markers

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Abstract

Background: During the past decades, neutral DNA markers have been extensively employed to study demography, population genetics and structure in livestock, but less interest has been devoted to the evaluation of livestock adaptive potential through the identification of genomic regions likely to be under natural selection.

Methodology/Principal findings: Landscape genomics can greatly benefit the entire livestock system through the identification of genotypes better adapted to specific or extreme environmental conditions. Therefore we analyzed 101 AFLP markers in 43 European and Western Asian goat breeds both with MATSAM software, based on a correlative approach (SAM), and with MCEZA and BAYESCAN, two F_{ST} based software able to detect markers carrying signatures of natural selection. MATSAM identified four loci possibly under natural selection – also confirmed by F_{ST} -outlier methods – and significantly associated with environmental variables such as diurnal temperature range, frequency of precipitation, relative humidity and solar radiation.

Conclusions/Significance: These results show that landscape genomics can provide useful information on the environmental factors affecting the adaptive potential of livestock living in specific climatic conditions. Besides adding conservation value to livestock genetic resources, this knowledge may lead to the development of novel molecular tools useful to preserve the adaptive potential of local breeds during genetic improvement programs, and to increase the adaptability of industrial breeds to changing environments.

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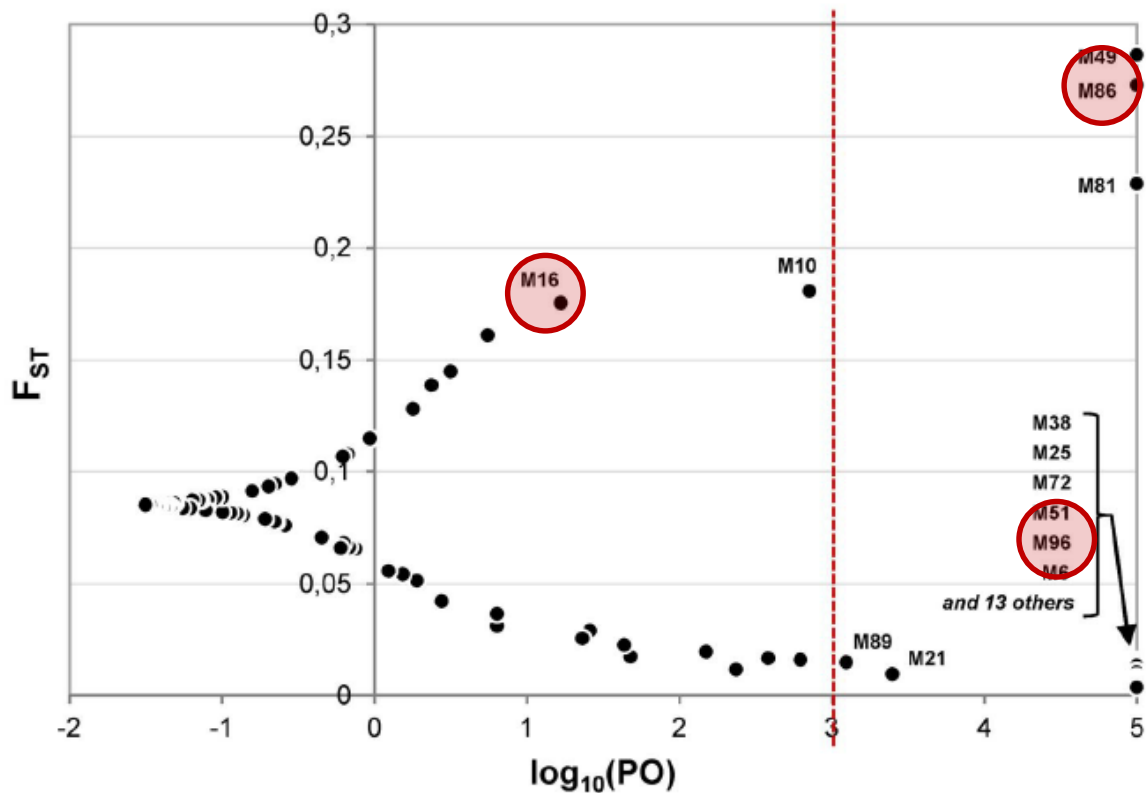
- 43 European and Southwestern Asian goat breeds
- 1239 animals
- Environmental variables
 - Altitude (SRTM30, NASA)
 - Climate Research Unit (CRU), Norwich
 - Yearly mean + monthly values for each variable
- 101 AFLP markers
- Analyses with Bayescan, Mcheza and Matsam
- Goal: detect signatures of selection and analyse their spatial dependence

Sampling: simple constraints

- The sampling strategy = balanced effort of collecting information from a list of selected key breeds
- While ensuring spatial representativeness to prevent from over-representing any environmental condition
- Blood samples were collected from 1'239 animals belonging to 43 European and Southwestern Asian goat breeds
- Between 28 and 33 unrelated individuals were sampled in 10 farms covering the area of origin and the present distribution of breeds
- A maximum of 3 individuals per farm were sampled to reduce the relatedness among animals and to increase the breed representativeness

Marker	Frequency of the marker among all animals (% values)	PP BayeScan	Fst	Diurnal Temperature Range					Ground frost			Temperature				Frequency of precipitation				Relative humidity					Solar radiation					Total
				dtrjun	dtrsep	dthroct	dtrnov	dtryear	frsjan	frsfeb	frsdec	tmpjan	tmpfeb	tmpnov	tmpdec	rdojul	rdosep	rdooct	rdonov	rehjul	rehsep	rehoct	sunmar	sunapr	sunjun	sunaug	sunsep	sunoct	sunyear	
M86	11,05	1,000	0,147	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	2
M16	91,90	1,000	0,161	1	1	1	1	1	0	0	0	0	0	0	0	0	1	1	1	0	1	1	0	1	1	1	1	1	1	16
M96	60,47	1,000	0,117	0	0	0	0	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	8
M89	60,97	0,999	0,121	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2

Significance level, Bonferroni correction included: 8.31E-17



Spatial dependence of M86

