

# Landscape genomics

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## Landscape genomics

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# Ten years of landscape genetics

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**Landscape genetics is now ten years old.** It has stimulated research into the effect of landscapes on evolutionary processes. This review describes the main topics that have contributed most significantly to the progress of landscape genetics, such as conceptual and methodological developments in spatial and temporal patterns of gene flow, seascape genetics, and landscape genomics.

discipline with a particular focus on potential applications in terms of adaptation to global change and the conservation of natural resources.

## Glossary

**Adaptation:** the process by which a population or a species globally or locally adapts to its environment. Adaptation refers to both the current state of being

Manel, S., & Holderegger, R. (2013). Ten years of landscape genetics. *Trends in Ecology & Evolution*, 28(10), 614–621. doi:10.1016/j.tree.2013.05.012

# 10 years after this paper was published



## Landscape genetics: combining landscape ecology and population genetics

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Manel, S. (2003). Landscape genetics: combining landscape ecology and population genetics. *Trends in Ecology & Evolution*, 18, 189–197. doi:10.1016/s0169-5347(03)00008-9

# Ten years of landscape genetics

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“... facilitating the integration of researchers in the fields of population genetics, landscape ecology, and spatial statistics “

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## Glossary

**Adaptation:** the process by which a population or a species globally or locally adapts to its environment. Adaptation refers to both the current state of being



“Landscape genetics [*during these 10 years*] has helped a move from the study of gene flow in a purely theoretical space characterized by geographical distances only, to the study of gene flow in heterogeneous and fragmented landscapes“

But before 2003, many studies moved “from the study of gene flow in a purely theoretical space characterized by geographical distances only” ...

34 years before in fact...

# Isozyme Genotype–Environment Relationships in Natural Populations of the Harvester Ant, *Pogonomyrmex barbatus*, from Texas

F. M. Johnson,<sup>1</sup> Henry E. Schaffer,<sup>2</sup> James E. Gillaspay,<sup>3</sup> and E. S. Rockwood<sup>4</sup>

Received 23 Dec. 1968—Final 19 April 1969

Three different allelic isozyme systems (two esterases, *ESH* and *ESR*, and a malic dehydrogenase, *MDH*) were analyzed in population samples of a species of ant, *Pogonomyrmex barbatus*, from Texas. Allelic frequencies were determined for several collection localities, and a number of significant differences were found. Principal component analysis was used to compare the patterns of variability of the allelic frequencies with environmental factors. Significant correlation was particularly evident with respect to weather and the pattern of variability in both esterases, and it is therefore suspected that natural selection is important in determining the allele frequency patterns. Observed and expected genotypic proportions were found in good agreement, generally, but in some localities homozygotes appeared in significantly greater numbers than expected. Heterotic selective maintenance was thus not indicated. Correlation found between patterns of variability in the enzyme systems themselves was consistent with the hypothesis that all three enzyme systems were affected by the environmental factors.

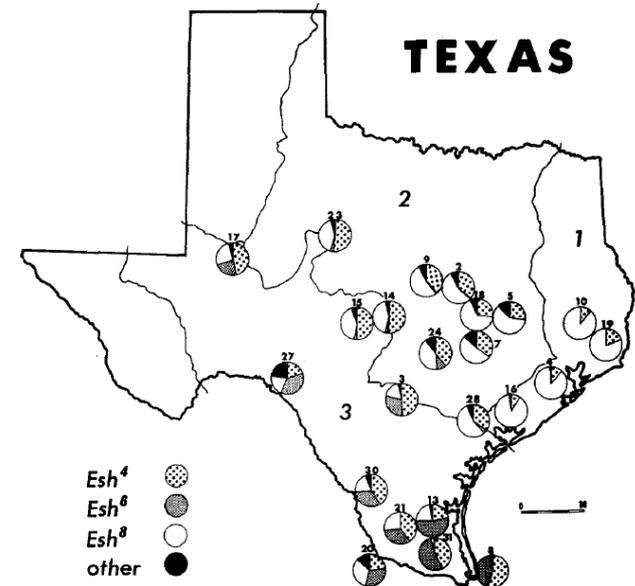


Fig. 4. Outline map of Texas showing *P. barbatus* *Esh* allele frequencies as parts of circles in various localities. Each allele is represented by a different kind of shading, except "other" is a group of low-frequency alleles. The three areas indicated by the numbers 1, 2, and 3 refer to plant life areas (see text), and the numbers above the circles identify the collection localities (see Table I). The distance scale is in U.S. statute miles.

Johnson, F. M., Schaffer, H. E., Gillaspay, J. E., & Rockwood, E. S. (1969). Isozyme genotype-environment relationships in natural populations of the harvester ant, *Pogonomyrmex barbatus*, from Texas. *Biochemical Genetics*, 3(5), 429–450.

	Elevation	Rainfall	January temp.	July temp.	Growing season	
Elevation	1	-0.61516	-0.83986	0.30436	-0.68007	(4)
Rainfall		1	0.38927	-0.65243	-0.09021	
January temp.			1	-0.39250	0.80074	
July temp.				1	0.02764	
Growing season					1	



# ISOZYME ALLELIC FREQUENCIES RELATED TO SELECTION AND GENE-FLOW HYPOTHESES<sup>1</sup>

HENRY E. SCHAFFER AND F. M. JOHNSON

*Department of Genetics, North Carolina State University, Raleigh, North Carolina 27607*

Manuscript received September 24, 1973

Revised copy received January 29, 1974

## ABSTRACT

Significant correlations between allelic frequencies and environmental variables in a number of insect species have been demonstrated by multivariate techniques. Since many environmental variables show a strong relationship to geographic location and since gene flow between populations can also produce patterns of gene frequencies which are related to the geographic location, both selection and gene-flow hypotheses are consistent with the observed correlations. The genetic variables can be corrected for geographic location and so for linear gene-flow patterns. If, after correction, the genetic variables still show significant correlations with similarly corrected environmental variables, then these correlations are consistent with hypotheses of selection but not of gene flow. The data of JOHNSON and SCHAFFER (1973) have been reanalyzed using the method of canonical correlation after correction for geographical location by means of multiple regression. Five of the nine loci studied exhibit significant canonical correlations. These results, under the assumption of linear gene flow, support hypotheses of selective action of environmental variables in the genotype-environment relationships observed.

Schaffer, H. E., & Johnson, F. M. (1974). Isozyme Allelic Frequencies Related to Selection and Gene-Flow Hypotheses. *Genetics*, 77(1), 163–168.



*D. Melanogaster*

TABLE 1

*Analysis of genetic and environmental data with respect to geographical location*

Variable	No. of sites	R <sup>2</sup>	First canonical correlation
<i>EstC</i>	30	.65**	.66
<i>Est6</i>	42	.25**	.72**
<i>Adh</i> †	42	.88**	.43
<i>α-gpdh</i>	42	.23**	.72**
<i>Acph</i>	42	.18*	.62
<i>Odh</i>	41	.64**	.56*
<i>Mdh</i>	42	.12	.65**
<i>Pgm</i>	25	.36**	.82**
<i>Aph</i> ‡	14	.84**	.70
Elevation	42	.78**	
Avg. ppt.	42	.90**	
Avg. temp.	42	.99**	
Avg. midnight rel. humid.	42	.39**	
Avg. noon rel. humid.	42	.01	
Avg. wind speed	42	.31**	

For loci with multiple alleles the largest R<sup>2</sup> for regression on geographical location is given.  
\* p < .05; \*\* p < .01.

The canonical correlations are computed using the corrected data as described in the text.  
† Multiple correlation coefficient (R) for regression of corrected genetic data on environment is given instead of canonical correlation since only two alleles were found at this locus.  
‡ Not all environmental measurements included because of multiple collinearities.

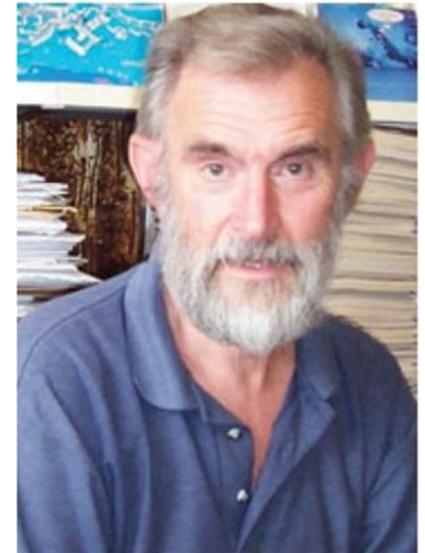
# Godfrey M Hewitt (1940–2013): highlights in *Heredity* from a career in evolutionary genetics

RA Nichols<sup>1</sup>, RK Butlin<sup>2</sup> and MW Bruford<sup>3</sup>

*Heredity* (2013) **110**, 405–406; doi:10.1038/hdy.2013.30

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During his career, Godfrey Hewitt, who died in February of this year, and whose impact on evolutionary biology in Europe has been well documented (Butlin *et al.*, 2006), published a remarkable 44 papers in *Heredity*. He also directly collaborated with and scientifically influenced the current and previous two Editors-in-Chief of the journal. In this brief article, we pay tribute to his immense scientific contribution by each summarising one of his *Heredity* papers. In doing so, we aim to highlight not only different aspects of his work and the diversity of his scientific interests, but also his pioneering approach to placing genetic diversity in the context of spatio-temporal processes, integrating an understanding of the ecology, landscape and history of the organisms he studied, and, most importantly, of how these factors interact to provide the myriad of genetic patterns that have been uncovered during the last few decades.



# Origins of molecular ecology

Hewitt GM (1975) A sex chromosome hybrid zone in the grasshopper *Podisma pedestris*. *Heredity* 35: 375–387.

Two chromosome types (XO and neoXY form) in the Southern French Alps.

The two **spatial distributions** are separated by geographic barriers such as **high mountain ridges** and **lowlands**.

**Genetic dynamics of hybrid zones** and the biogeography of this situation.

Such chromosomal races frequent event in relatively immobile species that are subjected to isolation and expansion by major climatic and **ecological changes**



areas 1 to 6 where the XO and neoXY distributions approach closely to each other, and in some cases produce hybrid populations.

*Area 1.* A mixed population was located 3 km west of the village of Barles (Route N100A) near the Bergerie de Chine. This sample contained 2 XO males and 9 XY males, 5  $\widehat{XA}:\widehat{XA}$  females and 1  $\widehat{XA}:\widehat{XA}$  female hybrid. This population seemed well established. To the south and east the

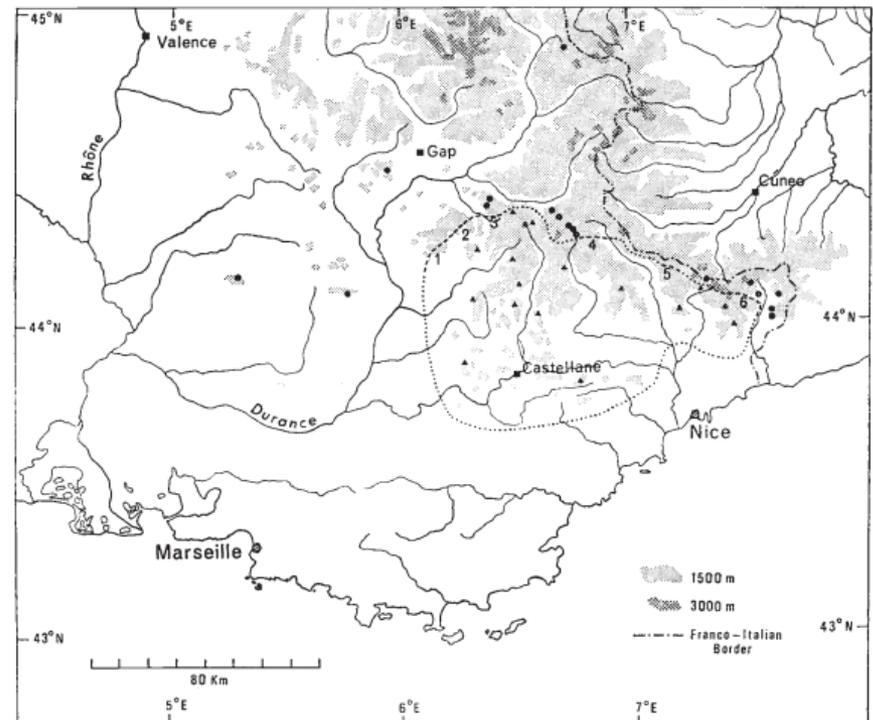


FIG. 8.—A map of the Southern European Alps showing the distribution of the XO (circles) and neoXY (triangles) races of *Podisma pedestris* in this region. Where the neoXY distribution line is more heavily dashed, the juxtosition of the two races is accurately determined.

# A review of «paleo-landscape genetics» contributions

*Ann. Rev. Ecol. Syst.* 1976, 7:1–32  
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## GENETIC POLYMORPHISM IN HETEROGENEOUS ENVIRONMENTS<sup>1,2</sup>

*Philip W. Hedrick, Michael E. Ginevan, and Evelyn P. Ewing*  
Division of Biological Sciences, University of Kansas, Lawrence, Kansas 66045

## GENETIC-ENVIRONMENT ASSOCIATIONS

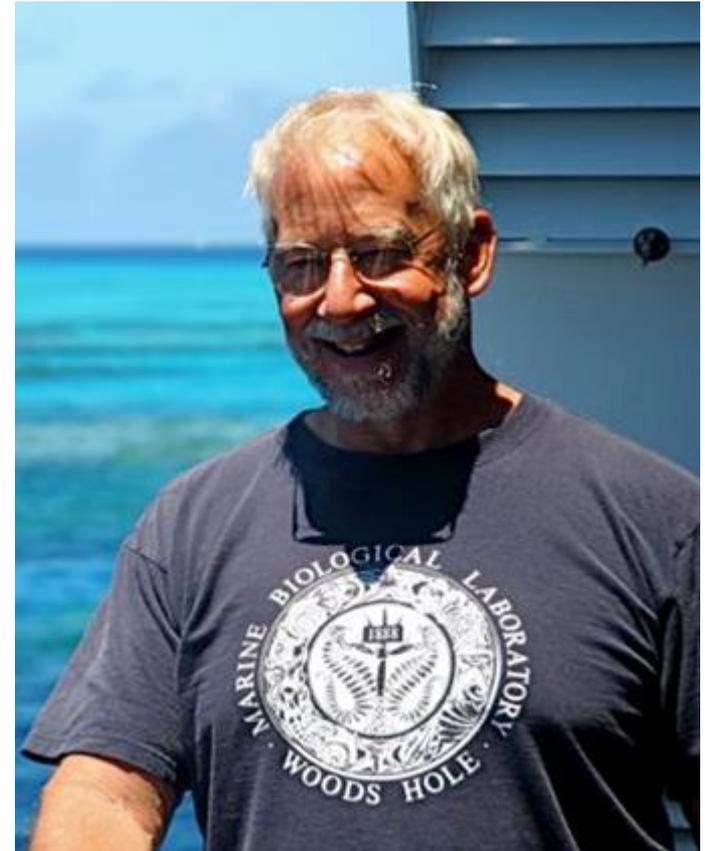
There are a number of examples of associations between particular genotypes and environmental parameters. Such an association of course does not mean that the genetic pattern is the result of the environmental factor unless additional evidence supports a cause-effect relationship. Some efforts have been made (29, 169) to eliminate nonselective causes such as genetic drift or gene flow as explanations for genetic-environmental associations as seen in clines of gene frequency. In general, the examples we discuss are ones in which there is supportive evidence to demonstrate that different selective pressures are actually operating in different environments. Most of the examples are related to spatial heterogeneity in the environment, primarily because fewer polymorphisms associated with temporal differences have been documented. It is not clear whether this is because fewer temporal-based polymorphisms actually exist, or because they are more difficult to document, or both.

Hedrick PW, Ginevan ME, Ewing EP (1976) Genetic polymorphism in heterogeneous environments. *Annual Review of Ecology and Systematics*, 7, 1–32.

# ...and also...

Mitton et al. (6) first had the idea to correlate the frequency of alleles with an environmental variable (elevation) to look for a signature of selection in ponderosa pine. They detected significant association between gene frequencies and slopes of different aspects. In another paper also dedicated to ponderosa pine, Mitton et al. (7) discovered that excess of heterozygosity was associated with xeric habitats. Then, Stutz and Mitton (8) applied the same approach to Engelmann spruce and showed that natural selection was varying with soil moisture. At the beginning of the 2000s, Joshi et al. (9) and Skøt et al. (10) implemented such association studies on a broad scale to study adaptation in common plant species. But until then, the number of loci considered remained very low, for instance six AFLP loci analyzed together with temperature data in Skøt et al. in 2002 (10). A few years later, Joost (11) contrasted a higher

6. Mitton JB, Linhart YB, Hamrick JL, Beckman JS (1977) Observations on genetic structure and mating system of ponderosa pine in Colorado Front Range. *Theor Appl Genet* 51:5–13
7. Mitton JB, Sturgeon KB, Davis ML (1980) Genetic differentiation in ponderosa pine along a steep elevational gradient. *Silvae Genet* 29:100–103
8. Stutz HP, Mitton JB (1988) Genetic variation in *Engelmann spruce* associated with variation in soil moisture. *Arctic Alpine Res* 20: 461–465
9. Joshi J, Schmid B, Caldeira MC et al (2001) Local adaptation enhances performance of common plant species. *Ecol Lett* 4:536–544
10. Skøt L, Hamilton NRS, Mizen S, Chorlton KH, Thomas ID (2002) Molecular genecology of temperature response in *Lolium perenne*: 2. association of AFLP markers with ecogeography. *Mol Ecol* 11:1865–1876



**Low number of loci considered, for instance 6 AFLP loci analyzed together with temperature data in Skøt et al. in 2002**

# 1980's

- Recognition of the importance of the interaction between the genome and the environment to better understand evolution (Berry, 1989)
- Connecting genetics and ecology (Jelinski, 1997)

*Berry, R.J., (1989) Ecology : where genes and geography meet, Journal of Animal Ecology, 58:733-759.*

- David Galbraith proposed «to *place genetic diversity information into a spatial framework*» in 1995
- Natural Resources DNA Profiling and Forensic Centre in Peterborough (Canada)
- They were the first to have systematically used GIS to analyze the geographical distribution of genetic markers
- Galbraith and White: “spatial issues in genetics (...) solely deal with geographical structuring and with effects on populations of reduced gene flow (...) due to fragmentation of the landscape. Much more is required to be known about genetic processes in landscapes”.
- Then GIS were used to try to separate the effects of natural selection from the ones of genetic drift, and many landscape genetics studies (**many reports**) were applied to the Canadian’s fauna since the second part of the 1990s.
- Several studies corresponding to the definition proposed by Galbraith have been achieved, but **without referring to the *landscape genetics* designation.**

*Secchi, E.R, Wang, J.Y, Murray, B.W., Rocha-Campos, C.C., and White, B.N. (1999). Population differentiation in the franciscana (*Pontoporia blainvillei*) from two geographic locations of Brazil as determined by mitochondrial control region sequences. Canadian Journal of Zoology 76: 1622-1627.*

Progresses of landscape  
genetics during the last 14 years

# A toolbox for genetic connectivity analysis

- Landscape genetics provides tools to correlate the spatial heterogeneity of landscapes with estimates of gene flow
- Mantel tests to relate a matrix of genetic distances between individuals or populations to matrices of geographical or landscape distances (e.g. based on least-cost paths)
- *!! Non-independence between the response and predictor variables, the degrees of freedom are not known, methods to select the best model (AIC) are not valid !!*
- *Raufaste, N. and Rousset, F. (2001) Are partial Mantel tests adequate? Evolution 55, 1703–1705*

# Scale

- **Temporal**-scale effects
- The effects of **spatial** scale on genetic patterns have only recently been tackled
- Researchers have found that distinct landscape effects are often detected only up to certain distances

# GIS

- Geographic information systems (GISs) facilitate the interpretation of results and communication with practitioners
- The use of geo-referenced genetic data within a GIS is a prerequisite for spatial-based analysis of spatial ecological processes
- One important application of GIS in landscape genetics is the **overlay** of land use, land cover, ... with genetic groups or genetic boundaries
- **Database** is key together with computer science issues given that big data are available
- **Spatial statistics**



# Simple Rules for an Efficient Use of Geographic Information Systems in Molecular Ecology

Kevin Leempoel<sup>1\*</sup>, Solange Duruz<sup>1</sup>, Estelle Rochat<sup>1</sup>, Ivo Widmer<sup>1</sup>,  
Pablo Orozco-terWengel<sup>2</sup> and Stéphane Joost<sup>1</sup>

<sup>1</sup> Laboratory of Geographic Information Systems (LASIG), School of Architecture, Civil and Environmental Engineering (ENAC), Ecole Polytechnique Fédérale de Lausanne (EPFL), Lausanne, Switzerland, <sup>2</sup> Biomedical Science, Cardiff University, Cardiff, UK

Geographic Information Systems (GIS) are becoming increasingly popular in the context of molecular ecology and conservation biology thanks to their display options efficiency, flexibility and management of geodata. Indeed, spatial data for wildlife and livestock species is becoming a trend with many researchers publishing genomic data that is specifically suitable for landscape studies. GIS uniquely reveal the possibility to overlay genetic information with environmental data and, as such, allow us to locate and analyze genetic boundaries of various plant and animal species or to study gene-environment associations (GEA). This means that, using GIS, we can potentially identify the genetic bases of species adaptation to particular geographic conditions or to climate change. However, many biologists are not familiar with the use of GIS and underlying concepts and thus experience difficulties in finding relevant information and instructions on how to use them. In this paper, we illustrate the power of free and open source GIS approaches and provide essential information for their successful application in molecular ecology. First, we introduce key concepts related to GIS that are too often overlooked in the

## OPEN ACCESS

### Edited by:

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Institute of Ecology, Mexico

# Seascape genetics

- Marine ecosystems have been largely understudied in landscape genetics
- “Seascape genetics would gain from using more large-scale sampling to capture wide-ranging patterns of connectivity”
- Seascape genetics “would gain from being more aware of the progress being made in terrestrial landscape genetics»

# Landscape genomics

- A powerful tool for studying adaptive genetic variation
- Specific landscape genomic approaches have also been developed that directly correlate allele frequencies with environment factors
- One important point is the need to account for genetic structure and/or demographic effects

# Conclusion

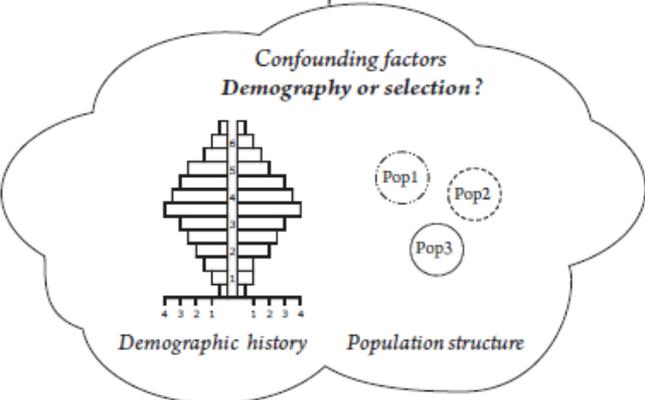
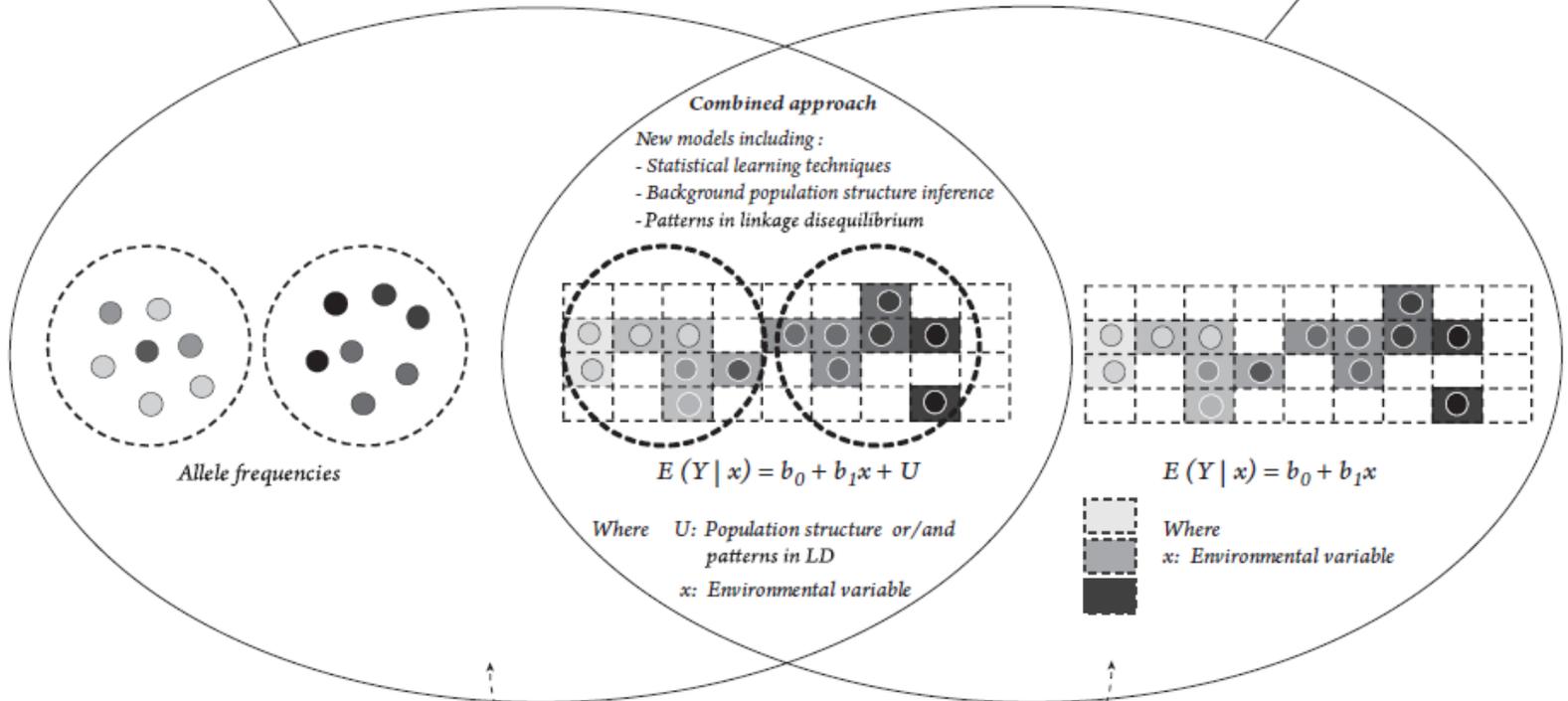
- The virtue of the landscape genetics' paper of 2003: it has increased general awareness of the important effects that spatial patterns of landscape elements and environmental factors exert on neutral and adaptive genetic variation
- Landscape genomics contributes to our understanding of the nature of genes involved in local adaptation to environmental heterogeneity
- Landscape genomics has still to proceed from identifying the genomic regions under selection to characterizing the underlying genes, understanding genome architecture and ecological functions as well as their interactions.

# Conclusion

- Big data and the key role of computer science
- Bioinformatics
- Collaboration, interdisciplinary teams
- Landscape genomics: where molecular ecology, environmental engineering (drones) Geo-environmental sciences and bioinformatics meet
- Integrate theoretical population genetics

**Theoretical Population Genetics** seeks to explain why allele frequencies differ between populations

**Landscape Genomics** attempts to explain the pattern of spatial genetic variation in relation to local adaptation to the environment



# MOLECULAR ECOLOGY

Molecular Ecology (2013) 22, 3659–3665

## NEWS AND VIEWS

### MEETING REVIEW

## Uncovering the genetic basis of adaptive change: on the intersection of landscape genomics and theoretical population genetics

STÉPHANE JOOST,\* SÉVERINE VUILLEUMIER,† JEFFREY D. JENSEN,‡§ SEAN SCHOVILLE,¶ KEVIN LEEMPOEL,\* SYLVIE STUCKI,\* IVO WIDMER,\* CHRISTELLE MELODELIMA,\*\* JONATHAN ROLLAND†† and STÉPHANIE MANEL‡‡§§

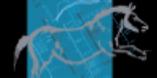
→ Detect patterns of linkage disequilibrium

This overview of theoretical population genetics' and landscape genomics' strengths and drawbacks highlights the need for further integration of these disciplines (see Fig. 1). Indeed, decisive advantages would result in a combined approach able to capitalize mainly on the robust theoretical framework of theoretical population genetics, on the incorporation of the effect of landscape spatial heterogeneity at multiple scales and on fast computation of large genomic data sets. Interestingly, analytical frameworks recently implemented and simultaneously based on mutational frequencies, ecological modelling and statistical learning techniques appear effective (Frichot *et al.* 2013; Guillot 2012). The correlative framework is thus probably flexible enough to move a step forward and to integrate recent statistical developments from population genetics, thus taking advantage of progress towards differentiating selection from demography.

# Landscape epigenomics

ANIMAL GENETICS

Immunogenetics, Molecular Genetics  
and Functional Genomics



doi: 10.1111/age.12731

## Genome-wide differential DNA methylation in tropically adapted Creole cattle and their Iberian ancestors

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\*School of Biosciences, Cardiff University, Cathays Park, Cardiff, CF10 3AX, UK. <sup>†</sup>Corporación Colombiana De Investigación Agropecuaria (Corpoica), Centro de Investigaciones Tibaitatá, km 14 via Bogotá, 250047 Mosquera, Colombia. <sup>‡</sup>Sustainable Places Research Institute, Cardiff University, Cardiff, CF10 3BA, UK.

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### Summary

Enhancing climate resilience and sustainable production for animals in harsh environments are important goals for the livestock industry given the predicted impacts of climate change. Rapid adaptation to extreme climatic conditions has already been imposed on livestock species, including those exported after Columbus's arrival in the Americas. We compared the methylomes of two Creole cattle breeds living in tropical environments with their putative Spanish ancestors to understand the epigenetic mechanisms underlying rapid adaptation of a domestic species to a new and more physiologically challenging environment. Reduced representation bisulfite sequencing was used to assess differences in methylation in Creole and Spanish samples and revealed 334 differentially methylated regions using high stringency parameters ( $P$ -value  $<0.01$ ,  $\geq 4$  CpGs within a distance of 200 bp, mean

