

NEWS AND VIEWS

MEETING REVIEW

Adaptive landscape genetics: pitfalls and benefitsCHRISTIAN PARISOD* and ROLF
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Landscape genetics offers a promising framework for assessing the interactions between the environment and adaptive genetic variation in natural populations. A recent workshop held at the University of Neuchâtel brought together leading experts in this field to address current insights and future research directions in adaptive landscape genetics. Considerable amounts of genetic and/or environmental data can now be collected, but the forthcoming challenge is to do more with such manna. This requires a markedly better understanding of the genetic variation that is adaptive and prompts for advances in information management together with the development of a balance between theory and data. Moreover, showing the links between landscapes and adaptive genetic variation will ultimately move the field beyond association studies.

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Understanding adaptation in natural populations and under natural conditions is one of the main aims of landscape genetics. Landscape genetics thus explores the interactions between environmental factors and adaptive genetic variation (Manel *et al.* 2010a; Holderegger *et al.* 2011). Corresponding studies have typically identified loci of adaptive relevance or linked to adaptive genomic regions by showing higher than expected differentiation (i.e. outlier loci) and/or presenting outstanding associations of alleles frequencies with environmental features. Latest trends in this research area were discussed at the workshop 'adaptive landscape genetics' (University of Neuchâtel, 7–8 February 2012). The major objectives of this

workshop were to highlight recent progresses in (i) genomic technologies; (ii) environmental data acquisition; and (iii) methods to associate genetic with environmental data to pave the way towards reliable assessment of adaptive genetic variation and selective factors in natural landscapes. Fostering exchanges between leading scientists having complementary expertise, this workshop illustrated the 'deluge' of genetic data now accessible and put forward that a comparable fast development in landscape characterization also produces a plethora of environmental data. While allowing new avenues of analyses, these amounts of information also cause substantial challenges in data management and information when deducing adaptive processes from landscape genetics patterns.

Landscape genetics is now in a phase where the production of genetic data increases exponentially. Pierre Taberlet (CNRS Grenoble, France) compared the multitude of available sequencing platforms (next-generation sequencing) and concluded that the number of currently achievable sequences is surely matching demanding needs in the field. For instance, the personal MiSeq sequencer from Illumina produces up to 7 Gb of 2 × 250 bp reads within a few hours, allowing researchers to efficiently decipher genome-wide variation in most organisms. Currently, a critical issue is to decide on the most efficient strategy to genotype individuals from natural populations and to profitably exploit resulting data. AFLP-based genome scans have been widely used so far and the parallel sequencing of AFLP fragments offers a suitable option to deepen such work (Paris & Despres 2012). Although producing SNPs through a suite of enigmatic technical steps, RAD sequencing is currently popular and provides useful information at the population level (Rowe *et al.* 2011). Noticeably, Martin Fischer (ETH Zurich, Switzerland) demonstrated that genome resequencing (i.e. the sequencing and assembly of large pieces of chromosomes at the individual level) is now reachable for reasonably sized projects. Producing millions of SNPs for later analysis at the population level, genome resequencing has great potential to pull the field towards 'adaptive landscape genomics'.

Beholding such luxuriant data, one should, however, not be tempted to neglect the bioinformatic defiance behind the formidable promises. In particular, Malika Ainouche (University of Rennes, France) illustrated the numerous challenges faced when exploring the genome of a nonmodel species. Phylogenetic proximity to well-assembled and annotated reference genomes certainly helps gaining insight into genome architecture and sequence function. Nevertheless, it should be kept in mind that all taxa present genome variation and significant sequence redundancy (e.g. paralogs, palaeologs, homoeologs) that may blur interpretation (Chelaifa *et al.* 2010). In addition to such

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complexity, we are still far from understanding how genetic variation along pathways impacts on ecologically relevant phenotypes and, for instance, to what extent epigenetic variation determines long-term trait evolution. In this context, David Neale (UC Davis, USA) highlighted the complementary use of QTL mapping and sequencing of underlying genes at the population level to understand the molecular basis of adaptation to environmental heterogeneity (Eckert *et al.* 2010; Neale & Kremer 2011). It is clear that the genetic approaches to explore adaptive variation in natural populations are dramatically changing, from traditional studies analysing a few anonymous loci (microsatellites, AFLP) towards genome-wide data assessing thousands or millions of SNPs even in nonmodel species. To make the best of such advances, corresponding progress in complementary research areas is needed.

Researchers in landscape genetics may be aware that environmental characterization also launched a 'next-generation sensing' revolution, offering a wave of ecological data (Porter *et al.* 2012). Christophe Randin (University of Basel, Switzerland) gave an overview of these developments and showed that measures derived directly from topography and land cover may be close to the real world, but that topoclimatic factors generated through the spatial interpolation of information from dispersed weather stations may be short of the desired accuracy for specific studies (Pearman *et al.* 2008). Another issue of major interest for landscape genetics is the use of environmental data at an optimal spatial resolution (Lassueur *et al.* 2006). For instance, freely available WorldClim data offer averaged estimates of climatic factors within 1 km², which may fail to match the resolution needed to detect local adaptation. Therefore, empirical downscaling techniques based on topographic constraining can be used to provide data at a finer resolution, but may thereby introduce potential bias deserving further attention. Finally, the display of environmental sensors over a region of interest and at a spatial resolution fitting the needs of fine-scale projects (Parisod & Joost 2010) is now achievable. Future studies in landscape genetics can thus base on a broad diversity of available resources and/or can profitably produce suitable data at a pace corresponding to the production of genetic information.

To reliably detect adaptive genetic variation across the landscape, we have to overcome challenges in spatial analysis of adaptive loci. As exemplified in most of the studies presented during the workshop, a crucial first step is to apply a strong sampling design that encompasses optimal geographic scale(s), allowing to improve the signal to noise ratio and to tease apart spatial dependency from spatial autocorrelation. Christian Lexer (University of Fribourg, Switzerland) described how admixture mapping could be profitably used to detect loci under selection in situations where locally adapted individuals exchange genes (Buerkle & Lexer 2008; De Carvalho *et al.* 2010). Felix Gugerli (WSL Birmensdorf, Switzerland) further presented work relying on statistical techniques such as Moran's eigenvector maps and generalized estimating equations to associate AFLP loci with environmental factors while taking 'space' into account (Manel

et al. 2010b; Poncet *et al.* 2010). Populations sampled at multiple geographic scales showed specific loci consistently associated with the same ecological factors, supporting an adaptive interpretation. Independent validation and proof of function usually remain out of reach for such studies, but would be needed before concluding on the adaptive relevance of loci.

Analysing adaptive instead of neutral genetic variation adds challenges as the genetic mechanisms of adaptation are complex and still poorly known for most organisms (McNiven *et al.* 2011). For instance, it should be emphasized that outlier loci, even those showing strong association with environmental heterogeneity, may map to loci causing endogenous incompatibilities rather than genes underlying local adaptation to exogenous factors (Bierne *et al.* 2011). Accordingly, this meeting highlighted how important it is for adaptive landscape genetics to link theoretical and empirical approaches. As stressed by Frederic Guillaume (ETH Zurich, Switzerland), the interplay between gene flow, heterogeneity of selection and genetic correlations among adaptive traits influence local adaptation over spatial gradients encompassing multiple ecological conditions. He also pointed to the need to recognize adaptive variation in a multivariate rather than univariate context (Guillaume 2011). Although few individual-based simulation tools allow exploring the interactions between neutral and selective processes (but see Landguth *et al.* 2012), analysing adaptive variation in a demographically explicit context will be highly valuable. In particular, Laurent Excoffier (University of Bern, Switzerland) gave striking examples of patterns of neutral genetic variation that could be mistakenly interpreted as showing the signs of adaptation. Range expansion into previously unoccupied environments can drive the surfing of nonadaptive mutations over large areas, while the colonization of already occupied territories can produce asymmetrical introgression and local surfing following interbreeding (Excoffier & Ray 2008). Accordingly, neutral processes can lead to the differential success of genes in space and time, resulting in patterns of genetic variation mimicking signatures of selection (Excoffier *et al.* 2009). This urges researchers in adaptive landscape genetics to carefully interpret their results, because, in many cases, it remains unclear how adaptive patterns may be reliably distinguished from neutral patterns.

The rapid production of sufficient data with recent technologies—be it landscape or genetics—may no longer be a bottleneck in adaptive landscape genetics. However, data collection is far ahead of information management (transport/storage, quality control and gap filling, analysis and interpretation; Baraniuk 2011). The required database curation for massive data sets now needs to be automated and thus depends on reliable bioinformatic pipelines if one wants to reach scientifically meaningful, better founded and novel conclusions (do 'more with more'). Collaborative work in the future will meet these technical needs, but we shall certainly further cultivate a balance between theory and data. This meeting helped in identifying relevant challenges towards a consistent assessment of adaptive genetic variation in empirical surveys. In particular, we need to further understand how the actual landscape reflects the

'adaptive landscape', and how it shapes genetic variation in natural populations. This would also move the field of adaptive landscape genetics beyond association studies. Finally, it is worth noting that even correlations based on massive data sets must ultimately be rigorously tested with field manipulations and experiments, which will hardly become high throughput.

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C.P. is interested in the impact of genome variation on adaptation and speciation. R.H. is generally interested in landscape genetics and its application to conservation management.

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