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## EVOLUTION

# The Genomic Basis of Local Climatic Adaptation

Outi Savolainen

Many plant populations are locally adapted and genetically differentiated for traits related to fitness, but the genetic basis of this adaptation remains poorly known. The best genomic resources for plants are available either for model species such as *Arabidopsis thaliana*, or for crop plants such as maize. In contrast, studies of fitness variation in natural conditions are spread over a large number of species with poorly understood genomes. Two reports in this issue, by Fournier-Level *et al.* on page 86 (1) and Hancock *et al.* on page 83 (2), report a major advance toward finding the genomic sites related to climatic adaptation in *A. thaliana* by combining genome-wide analysis of single-nucleotide polymorphism (SNP) and fitness estimates. Such information may eventually be used to better predict and manage climate change responses.

Reciprocal transplant experiments can verify that at each geographic site, the native population has higher fitness than any introduced population of that same species. Such experiments have detected strong signals of local adaptation, especially in species with large populations (3), such as forest trees (4), and in relatives of *A. thaliana* (5, 6). These findings imply that natural selection has been strong relative to genetic drift, and has caused genetic differentiation with respect to traits related to fitness. In small populations natural selection may be too weak, relative to genetic drift, for local adaptation to evolve (3).

In *A. thaliana* itself, the classical evidence for local adaptation is weaker. There are few reciprocal transplant experi-

ments, and correlations of putative adaptive phenotypes with latitude are lower (7) than in many other species (see the figure). DNA sequence variation analysis (8) and association studies (9) have provided some evidence of local adaptation. Range expansions, recolonizations, and bottlenecks can, however, also give rise to patterns suggestive of adaptation.

Scientists have previously searched for genetic variants for local adaptations in several plant species, but not with truly genome-wide approaches (5). The two studies in this issue relate SNP variations in extensive col-

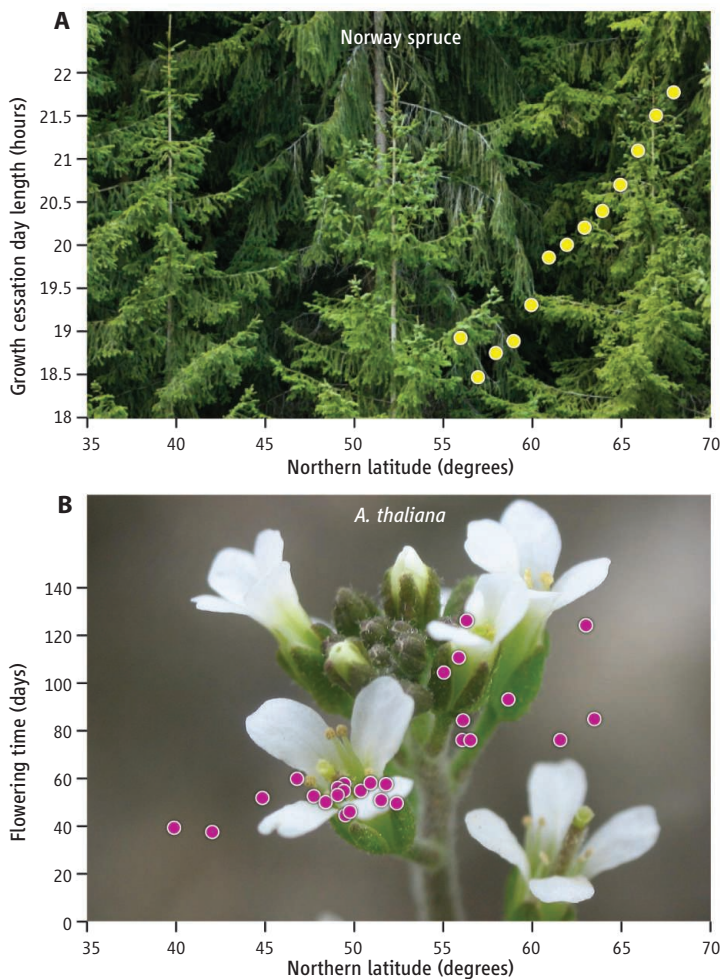
Studies of *Arabidopsis thaliana* help to identify the genomic sites associated with adaptation to local climatic conditions.

lections of *A. thaliana* to the climate at the location where each genotype was collected. Both studies also examine how the environmentally correlated SNPs relate to fitness data from the field experiments.

Fournier-Level *et al.* analyze data from field experiments in which about 150 distinct samples from different locations (accessions) were grown at four different field sites across Europe (10), and both survival and reproductive fitness were estimated. Among more than 200,000 genotyped SNPs, the authors identify SNPs that account for fitness

variation in the different field sites. In most cases, SNP variants favorable in one environment did not have deleterious effects in other environments—the SNPs associated with fitness occurred at different loci in different environments. This suggests that the mechanism of adaptation differs for different environments. Thus, natural selection (or plant breeders) can benefit from flexible responses based on different mechanisms across environments.

Hancock *et al.* examine climate associations of SNPs in a different set of accessions. They have correlated the genotypic data of more than 200,000 SNPs of nearly 1000 *A. thaliana* lines with the climatic data of the location where these plants were originally collected. Similar approaches have earlier detected loci related to climatic adaptation in humans (11) and forest trees (12). To confirm that the correlations of SNPs with climate variables are due to natural selection and not population history, Hancock *et al.* use two approaches. First, they show that nonsynonymous (that is, amino acid-changing) SNPs are enriched among the climate-correlated ones. Second, they demonstrate that the climate-related SNPs can account



**Adaptation with latitude.** (A) The day length below which seedlings of Norway spruce (*Picea abies*) will set bud in preparation for winter depends on latitude. Based on population data of Dormling (4). (B) The latitude dependence of how many days it takes after 4-week cold treatment for *A. thaliana* to flower is much less pronounced. Data on European accessions from (9), binned in groups of five based on latitude.

for some fitness variation in a field experiment in Lille, France.

Changing climates may require rapid adaptation. Adaptation based on selection on new mutations (species-wide or regionally limited selective sweeps) can be slowed down by the lack of suitable mutations, whereas selection on existing low- or intermediate frequency variants can be faster. Only selection on new mutations leaves a footprint of long tracks of correlated variants around the selected sites. Fournier *et al.* did not find such a signal, and conclude that selection has mostly been on existing variation. In contrast, Hancock *et al.* did identify this signal of selection on new mutations. These different findings remain to be explained. Recent genome-wide resequencing studies have shown that such selection on new mutations has been common in *Drosophila* (13) but not in the human lineage (14).

In addition to selection on individual loci, phenotypic data suggest that selection on quantitative traits is also important for local adaptation. Suitable methods need to be developed for finding the signals of this kind of selection in the genome (15).

Perhaps surprisingly, none of the top “climate adaptation” SNPs identified in (1) were close to the intensively studied flowering-time genes *FRI* and *FLC* (9). The role of these loci in governing fitness variation merits further study.

SNP-based studies cannot be used to examine all polymorphisms. The effects of the polymorphisms related to climate are only detected if they are correlated with the SNPs that were genotyped. As the *Arabidopsis* resequencing project (16) advances, these problems will be avoided. Improving genomic resources will also allow genome-wide studies of species with very strong sig-

nals of local adaptation.

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#### PHYSICS

## Toward Control of Large-Scale Quantum Computing

David P. DiVincenzo

During the past decade, a wide array of physical systems—atoms, semiconductors, and superconductors—have been used in experiments to create the basic components of quantum-information processing. Precision control over elementary quantum two-state systems (qubits) is now well advanced, and it is now possible to ask how a complete, functioning quantum computer with many qubits would really work. In this issue, two very different steps in this direction have been taken. On page 61, Mariantoni *et al.* (1) examine how the basic architectural elements of a stored-program computer, as articulated originally by von Neumann, can be achieved in the quantum setting. On page 57, Lanyon *et al.* (2) explore how a quantum computer can be programmed. Although the physical qubits used in each study are extremely different, both attack a device-independent question of system functionality.

A vision of the possible approaches to programming a quantum computer has emerged only very tentatively in the past

decade. Quantum computers will unquestionably be able someday to solve arithmetic problems that are so difficult that they are intractable for digital computing, most notably finding the prime number factors of large numbers. However, the scale of these problems in their interesting form (that is, exceeding what supercomputers could do), and the high precision of operation needed to solve them, points toward a machine containing millions of qubits.

Such large machines are many years away, so attention has focused in the near term on other problems, more directly connected to quantum physics, for which much smaller machines can be programmed to solve problems. Lanyon *et al.* present results on “digital quantum simulation,” as distinct from the less powerful technique of “analog quantum simulation.” The analog approach implies a direct emulation of the system to be simulated; the quantum processor is tailored to have, up to a scale, the same intra- and interqubit forces (i.e., described theoretically by the same type of Hamiltonian function) as the simulated system.

In the digital approach, the qubit Hamiltonian is fixed to be one of two (or several) optimized forms. The simulated Hamilto-

Basic quantum computing elements are combined to improve quantum simulations and to create a quantum version of a central processing unit.

nian is approximated by switching rapidly between these qubit Hamiltonians, so that the average effect is correct. Parallel parking provides a good analogy of the enhanced capability of this machine. An analog simulation that emulates moving forward and backward to park on the right can do only that operation. Digital simulation implies programmability; the car can also be parked to the left with a modified application of the same basic actions. Lanyon *et al.* used up to six qubits in an ion trap, with only one type of physical coupling between them mediated by quanta of collective ion vibrations. By successive alternation of interactions, they simulated the dynamical creation of entangled quantum states in small magnetic clusters with a variety of spin interactions.

Mariantoni *et al.* attacked the very different problem of machine architecture. The superconducting device toolkit has grown in recent years to include qubits of a wide variety of constructions and characteristics, and a quantum version of computer “busses” (a classical bus transfers data between computer components; quantum busses can be created from harmonic quantum systems based on superconducting electrical resonators). Can these devices be combined to take

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