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Local Adaptation in Plants

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Introductory article

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Local adaptation reflects the fact that local populations tend to have a higher mean fitness in their native environment than in other environments and in other populations introduced in their home site. Starting in the 1920s a large number of reciprocal transplant and common garden experiments, as well as studies of populations along environmental clines, have demonstrated that local adaptation is widespread in plants. One remaining challenge is to understand how populations become locally adapted and to characterise the genes involved in this process. Theoretically, local selection at single loci will promote local adaptation and gene flow will decrease it. For quantitative traits, the situation is more complex, and strong local adaptation can even be established and maintained in the presence of higher gene flow. The genetic basis of local adaptation will evolve through time, and eventually trade-offs between alleles at a locus may occur in the different environments (antagonistic pleiotropy).

Introduction

The concept of local adaptation can be traced back as far as the beginning of the 1800s (Matthews, 1831 cited in Whitlock, 2015), if not earlier, but studies of local adaptation really started in earnest with the Swedish botanist Göte Turesson (1922). His main goal was to understand the variability of plant species in relation to their environment and, more specifically, whether this variation was hereditary. To that end, he cultivated a large number of individual plants collected in different habitats under the same environmental conditions. He did what we would call today a *common garden experiment*. The gist of what he found

is vividly demonstrated by another common garden experiment that Turesson installed in the 1930s, and that can, to this day, still be seen south of Uppsala (Sweden). Turesson planted birch trees that originated from different latitudes in Sweden. In the early fall, trees from northern latitudes will stop growing and shed their leaves while trees from the south will still bear green leaves (Figure 1). And the same would be true for their offspring: offspring from trees from northern latitudes will still stop growing and shed leaves much earlier than trees from more southern latitudes. In other words, many generations at high latitudes have selected for early growth cessation in the fall, while at more southern latitudes trees could grow longer without the risk of damage by early frost. Since the seminal work of Turesson, a large volume of studies has established that local adaptation is widespread in plants (~70% of the studies surveyed by Leimu and Fischer, 2008). For example, reciprocal transplant experiments by Clausen *et al.* (1940, 1948) constitute another landmark. In these experiments, individuals from at least two populations are reared in their respective native and non-native environments. A recent example of a reciprocal transplant experiment is the one carried out in the model plant *Arabidopsis thaliana*, where plants from northern Sweden were transplanted in central Italy, and vice versa (Ågren and Schemske, 2012). The experiment was monitored over 5 years, and in almost all cases the fitness of the local population was significantly higher than that of the non-local population. This last experiment was done on a continental scale, but studies also indicated that local adaptation could operate on smaller geographical scales, such as along altitudinal gradients across the western part of the Pyrenees Mountain range (Montesinos-Navarro *et al.*, 2011) and even at very local scales such as observed between polluted and non-polluted mine sites separated by a few hundred meters (Antonovics and Bradshaw, 1970). While all these experiments demonstrated the ubiquity of local adaptation, they did not, in themselves, shed light on the evolutionary forces that led to the establishment of local adaptation. Obviously, two forces that will play a major role in the establishment and maintenance of local adaptation are local selection, on one hand, and gene flow, on the other. Local selection will give rise to and maintain local adaptation, and gene flow will tend to erase it. If two habitats are different enough such that the selection is sufficiently divergent and strong in the two habitats, then natural selection will overcome the homogenising effect of gene flow and local adaptation will emerge. Or is it always so? To confirm our intuition, we will model it and see that, at least for simple cases, our intuition is

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Figure 1 Birch trees that originated from different latitudes in Sweden and were planted south of Uppsala in Central Sweden. In the early fall, trees from northern latitudes, on the left, stop growing and shed their leaves, while trees from the south, on the right, still bear green leaves. (Photo courtesy of Jon Ågren.)

indeed right. We will also see later on that, in plants where gene flow can be extensive and occur over vast distances, one can still obtain what seem, at first glance, paradoxical results, namely local adaptation despite gene flow. But before sketching basic models of local adaptation, we shall briefly review measures of local adaptation.

Measuring Local Adaptation

Reciprocal transplant experiments certainly constitute one of the most effective ways to test for local adaptation, and it has often been used in plants since the seminal work of Clausen *et al.* (1940, 1948). A conceptual framework for the measurement of local adaptation was developed by Kawecki and Ebert (2004) and further extended by Blanquart *et al.* (2013). What a measure of local adaptation should quantify is the proportion of spatial variation in mean fitness (e.g. total seed yield) caused by adaptation to local conditions. Or, in other words, it should capture the interaction between genotypes and local environments. Kawecki and Ebert (2004) proposed two definitions of local adaptation when a sample of populations is considered (e.g. a pair of populations). First, in the ‘home vs. away’ (HA) definition, local adaptation can be measured as the difference between the mean fitness of a population at its home site and the average mean fitness of the population when transplanted to other sites. Second, in the ‘local vs. foreign’ (LF) definition, local adaptation is measured as the mean fitness of a focal population at home minus the average mean fitness of all other populations when transplanted into the focal patch. What these two definitions make clear is that local adaptation is not a property of a single population but of a group of populations located in different environments. As a matter of fact, one can also define local adaptation at the level of the total group of populations (metapopulation), simply as the difference between fitness of populations in their home sites and the fitness of populations away from their home sites, averaged over all populations in the metapopulation and over time (Blanquart *et al.*, 2013) (**Figure 2**). This third approach presents the appealing statistical property of

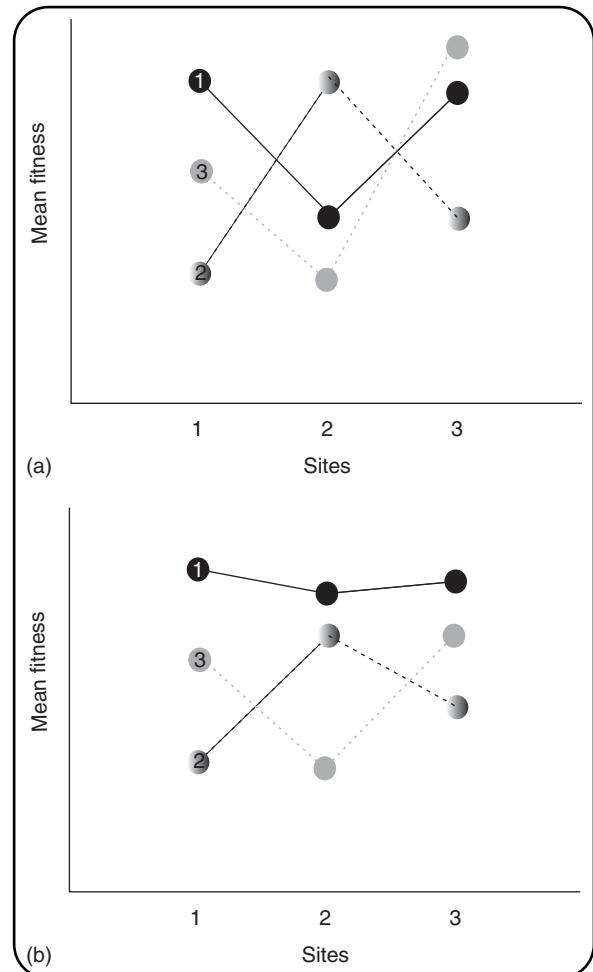


Figure 2 Mean fitness of three populations over three environmental sites. Populations 1, 2 and 3 originate from sites 1, 2 and 3, respectively. Each population was grown in its home site as well as in the two other populations' home sites. Local adaptation is defined as the difference between fitness of populations in their home sites and fitness of populations away from their home sites. In (a), the local population always has a higher fitness than the two others in its native environment. Then we say that the populations are locally adapted. In contrast, in (b) population 1 has the highest fitness over the three sites. The populations are not locally adapted.

removing the intrinsic habitat and population effects. Indeed, the HA definition depends on the habitat effect (some habitats are more productive than others), while the LF definition depends on population quality (some populations are more fit than others, less inbred, for instance). Reciprocal transplant experiments are very informative but are logically demanding and in some organisms hard to implement, and they are generally limited to a few populations. Alternatives that allow more easily the inclusion of a large number of populations are common garden studies and studies of environmental clines. One common difficulty with all experimental designs studying local adaptation is measuring fitness: estimating total seed numbers is seldom an easy task, especially in species with long reproductive spans.

The Genetics of Local Adaptation: Models

From a theoretical point of view, the question is to determine the conditions under which polymorphism can be maintained in a spatially heterogeneous environment. A key ingredient is the existence of spatially heterogeneous selective pressure favouring locally specialised genotypes, which is balanced by other evolutionary forces such as migration and random genetic drift. See also: [Drift: Introduction](#)

Single locus

To keep things simple, let us assume first a haploid two-patch model with reciprocal migration, where m_1 is the migration rate from patch 1 to patch 2 and m_2 is the migration rate from patch 2 to patch 1. Each of the patches is large enough so we can ignore random genetic drift, the random change in allele frequencies due to sampling. Consider a single locus with two alleles A1 and A2 and assume that A1 is favoured in patch 1, whereas it is selected against in patch 2 and the opposite is true for allele A2 (A2 is selected against in patch 1 and favoured in patch 2). If we call s_1 and s_2 the selection coefficient of A1 in patches 1 and 2, respectively, then they are of opposite sign. Bulmer (1972) showed that polymorphism would be maintained if

$$\frac{m_1}{s_1} + \frac{m_2}{s_2} < 1$$

So, local adaptation will depend on the relative strength of selection and migration. For instance, if migration is very strong compared to selection, one of the two alleles will disappear. If, on the other hand, selection is strong compared to migration, the two alleles will be maintained, A1 being favoured in patch 1 and A2 in patch 2. Of course, without migration A1 will fix in patch 1 and A2 will fix in patch 2. If the two patches are of finite size, then random genetic drift will reduce the potential for the maintenance of polymorphism and the effect of drift will be particularly potent when selection and migration balance each other (Yeaman and Otto, 2011).

Quantitative traits

Most traits that influence fitness, for instance growth cessation in trees as in our birch example above, are controlled by a large number of genes, many of which can have a weak effect on the trait. These traits are called ‘quantitative traits’ or also ‘complex traits’. Local adaptation for quantitative traits will also depend on a balance between migration and selection, but the dynamics will be more complex than in the simple one-locus model described above. Modelling local adaptation for quantitative traits is more difficult, and we will not get into the details of the models; but instead, we will simply outline some of the most striking conclusions (Le Corre and Kremer, 2003, 2012; Berg and Coop, 2014; Yeaman, 2015). First, local adaptation for these traits does not depend upon strong differences in allele frequencies at the genes controlling the trait variation but, instead, can result from

small coordinated changes at a large number of genes (**Figure 3**). Second, and as a consequence, local adaptation for quantitative traits can be maintained in the face of important gene flow.

In summary, the differentiation observed at single loci or at quantitative trait will be the result of a highly dynamic process, and therefore we would expect to observe a large range of different cases, depending on the species under consideration, its demographic history and the suite of environments and selection pressures under which this history unfolded.

The Genetic Basis of Local Adaptation: Data

Questions related to the genetic basis of local adaptation are of two kinds: general questions attached to most quantitative traits (see also: [Genomic Studies of Adaptation in Natural Populations](#)) and questions more specifically associated to local adaptation. Questions related to the genetic architecture of the trait, such as number of loci and distribution of their effects, belong to the first category. A question that is more specific to local adaptation is whether trade-offs exist at the level of the loci controlling the trait under local adaptation. Under antagonistic pleiotropy, local adaptation results from allelic trade-offs at individual loci, with local alleles being favoured in the local environment and detrimental elsewhere. In contrast, under conditional neutrality, local alleles are favoured in their native environment but are selectively neutral elsewhere.

Information on the genetic basis of local adaptation can be direct, when fitness (or a trait related to it) is assessed, or indirect, when it is not. In the latter, the evidence for the contribution of a given gene to local adaptation is generally based on (1) a higher level of divergence at the gene between populations than the level of divergence expected under a given demographic model, and (2) a correlation between differences in allele frequencies among populations at that gene and some environmental variables. We will start by reviewing the direct evidence.

Direct evidence

Reciprocal transplant experiments are one of the main sources of direct evidence of local adaptation in plants. The main approach to unravel the genetic architecture of local adaptation has been quantitative trait locus (QTL) mapping, which is based on the joint analysis of phenotypes and genotypes. For instance, let us consider the case of the yellow monkeyflower (*Mimulus guttatus*) populations growing along the Pacific Coast of North America. The inland annual ecological races are locally adapted to summer drought and flower early, whereas coastal perennial ecological races are adapted to persistent summer fog and cooler temperatures and grow to a much larger size before flowering. They are also adapted to oceanic salt spray (Hall and Willis, 2006; Lowry *et al.*, 2008, 2009). To investigate the genetic basis of local adaptation in these two ecological races, Willis and co-workers (Hall and Willis, 2006; Hall *et al.*, 2010) created recombinant inbred lines (RILs) by crossing an inland individual and a coastal one. The resulting individuals are heterozygotes that are then selfed to

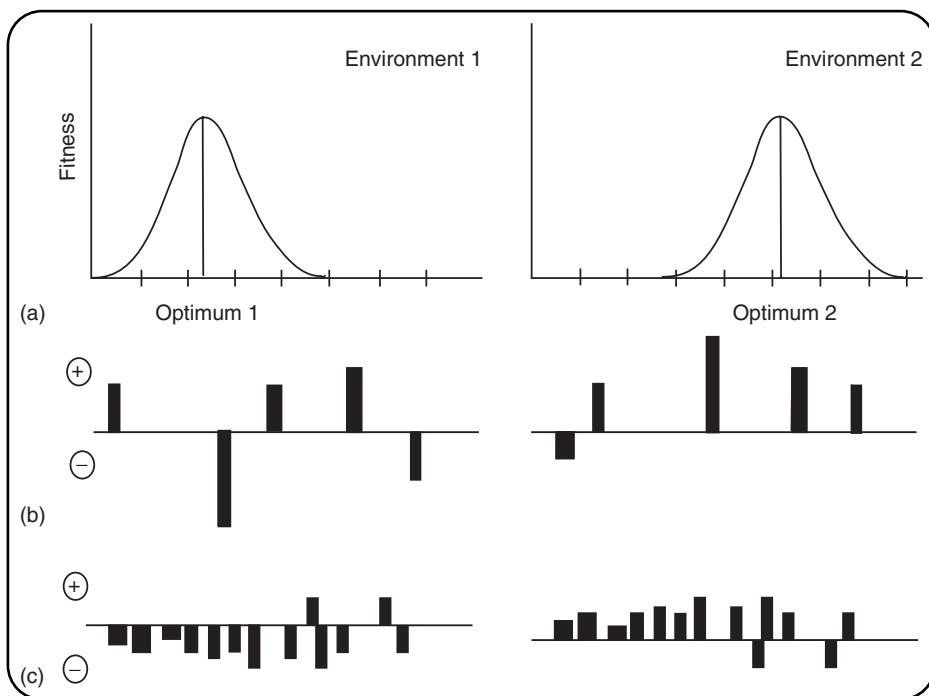


Figure 3 Genetic basis of local adaptation. (a) Fitness has different optima in Environment 1 and Environment 2. (b, c) Under each graph, we have represented the genome and the location of the loci contributing to fitness. The horizontal line represents a chromosome. The vertical bars are the loci contributing to fitness, and their length is proportional to the effect of a given locus on fitness. The effect can be positive (above the vertical line) or negative (below the vertical line). In case (b), local adaptation is due to a few loci with large effects. Some loci are common to both environments and others are specific to a given environment. In contrast, in case (c), local adaptation is due to coordinated changes at a large number of loci, each with a small effect. Theoretical work suggests that the latter is more likely if there is gene flow between the two environments.

produce individual RILs with different mixtures of the parental genomes in a homozygous state. To avoid inbreeding depression, these RILs were backcrossed to the parents before being installed in the field, both at coastal and inland sites, thereby creating a reciprocal transplant experiment. They identified 19 QTLs, each of small effect, affecting one or more of the 16 traits measured in the two environments. Overall, non-overlapping sets of loci were involved in local adaptation to different habitats, and the only evidence of trade-offs was when closely related fitness traits were examined. This is, however, in contrast to results obtained in *A. thaliana* (Oakley *et al.*, 2014), where a similar scheme was used to compare local adaptation between populations from northern Sweden and Central Italy: in that case, antagonistic pleiotropy was observed at a QTL for freezing tolerance. Finally, in *Boechera*, a relative of *A. thaliana*, both trade-offs and conditional neutrality contributed to local adaptation (Anderson *et al.*, 2013). It is not straightforward to compare the various experiments and come to a general conclusion, since they differ in a large number of parameters and also because we still lack a strong theoretical underpinning. However, recent theoretical progress based on Fisher geometric model with two optima (Martin and Lenormand, 2015) brings some new insights. In particular, their model predicts that the strength of fitness trade-offs should increase as adaptation proceeds. In experimental populations of *Pseudomonas fluorescens* selected in different environments, specialisation evolves because beneficial mutations

have increasingly antagonistic effects in alternative environments (Schick *et al.*, 2015). Experimental evolution might be hard to implement in plants due to their long generation time, but to get a better understanding of the evolution of trade-offs, it would seem particularly fruitful to test for the presence of trade-offs between populations at different stage of divergence, other factors being otherwise similar.

Common gardens are another important source of information on the genetic basis of local adaptation. Common gardens have a long history in forestry where they are also called ‘provenance tests’ and have been used to identify the best seed sources for breeding. They have, however, generally been limited to phenotypic measurements. This is, however, changing with the availability of thousands of genetic markers. The first genome-wide study on *A. thaliana* characterised fitness and trait variation of hundreds of accessions at several field sites and genotyped $\sim 250\,000$ single-nucleotide polymorphisms (SNPs). Alleles that confer higher fitness in northern or southern Europe were slightly more common in the north or in the south, respectively. Antagonistic pleiotropy was rare, as few SNPs had fitness effects at multiple experimental sites. The same set of common garden experiments also allowed modelling of the influence of different flowering time loci in field conditions (Fournier-Level *et al.*, 2011). These and other experiments on *A. thaliana* have emphasised the importance of field studies, the conclusions

of which can substantially differ from those of studies under laboratory conditions.

Finally, the analysis of phenotypic and genotypic variation along clines has also provided important insights into the genetic control of local adaptation. Studies of clinal variation generally combine sampling along an environmental or geographical variable (e.g. photoperiod or temperature, latitude or altitude), phenotyping the plants in one or many common gardens, and genotyping them. Genotypic data are used to associate phenotypic and genotypic variations but also to account for population genetic structure, which can create clinal pattern similar to adaptive ones. For example, Scandinavia was recolonised after the Last Glacial Maximum from two main directions. This has created a strong population genetic structure in many species with a contact zone around latitude 64N. Hence clinal relationship between allele frequencies and latitude can have a purely demographic origin and not necessarily be adaptive. As we saw above, forest trees show strong latitudinal clines in growth cessation. To identify loci associated to growth cessation in spruce, Chen *et al.* (2012, 2014) studied two parallel clines, a Norway spruce (*Picea abies*) cline in Scandinavia and a Siberian spruce (*Picea obovata*) cline in Siberia. Because spruce species have very large genomes that had not yet been sequenced at the time, they focused on a set of candidate genes, that is, genes for which an association with growth cessation is likely. Because growth cessation was already known to be under the control of photoperiod, candidate genes were primarily chosen among homologues of genes from the photoperiodic pathway and the circadian clock in *A. thaliana*. They also sequenced genes *a priori* not related to growth cessation in order to characterise the population genetics structure. Finally, they grew seedlings under controlled conditions with a day length decreasing each week in order to imitate a growth season. Time of growth cessation and expression of some of the most promising candidate genes were then measured. In both species, growth cessation and allele frequencies at some of the candidate genes exhibited a clear latitudinal gradient. One of the candidate genes exhibiting clinal variation and evidence of selection was FTL2, whose homologue plays a crucial role in the integration of photoperiodic signals in *A. thaliana*. FTL2 was also more highly expressed at high latitudes than at lower ones. Finally, a transformation experiment demonstrated that its overexpression in Norway spruce indeed leads to growth cessation and bud set (Karlgren *et al.*, 2013). So, in spruces at least, it seems that differentiation for growth cessation is due to rather strong differentiation at a few loci and, most likely, low differentiation at many loci, still to be identified.

Indirect evidence

F_{ST} outliers

Suppose that we have one population that splits into two subpopulations. Unless they are connected through high gene flow, the two populations will drift apart and eventually will lose all genetic variation (at least in the absence of mutations). Wright's fixation index, F_{ST} (Wright, 1949) is a relative measure of the amount of random genetic drift experienced by the two populations since they diverged: if the two populations reach fixation of different

alleles, then $F_{ST} = 1$, and if the populations are connected by extensive gene flow and behave like a random mating population, then $F_{ST} = 0$. Random drift being a random process, there will of course be a large variation around the average F_{ST} value. Lewontin and Krakauer (1973) proposed a method based on F_{ST} to find the genes under local adaptation. The basic idea is that the F_{ST} value of genes that are under differential selection in different populations should be outliers when compared to the F_{ST} values of genes that have simply been affected by random genetic drift and migration. The statistical method initially proposed by Lewontin and Krakauer (1973) to detect outliers had some important caveats, but many methods have since been developed to detect F_{ST} outliers (see Whitlock and Lotterhos, 2015 for a recent method and for comparison with other methods). This F_{ST} outlier approach has been extensively used and tens of loci have been claimed to be under local selection in various plant species, though in most cases the studies were not followed by tests of the impact of those loci on fitness or on its components. So in most cases, these loci are only candidate loci of local adaptation. It is important to test those, since F_{ST} outlier detection methods have been plagued with high false-positive rates. Also, Savolainen *et al.* (2013) suggested that appropriate study design, including, for instance, negative and positive control loci, and careful sampling of populations could lead to more confidence in the results of F_{ST} outlier studies.

Correlation with environmental variables

Another approach that has been extremely popular since it was launched (Coop *et al.*, 2010) is the estimation of correlations between allele frequencies and environmental variables. The principle of these studies is straightforward but, like F_{ST} outlier methods, one of the main challenges has been to control for false positives created by population genetic structure: if environment and population genetic structure co-vary, correlation between allele frequencies and environmental variables could be falsely attributed to a causal relationship between the two (Rellstab *et al.*, 2015). This often happens when populations colonise new areas – environmental gradients are parallel with the direction of migration. Hancock *et al.* (2011) used a large set of *A. thaliana* populations to test for correlation between genome-wide SNPs and a large array of environmental variables ranging from aridity to daylength. They observed significant correlations between numerous SNPs and environmental variables. To test whether the detected SNPs were indeed related to fitness, they tested their ability to predict the relative fitness of 147 *A. thaliana* accessions planted in the fall in a common garden in Lille, France. More specifically, they “identified alleles that are more common within a window of climate similar to Lille’s”. Then, they asked whether the count of these alleles could predict relative fitness, as measured by total silique (fruit) length among the accessions. They indeed found a strong correlation between the number of favoured alleles and fitness. This last confirmation step is, unfortunately, often missing.

To conclude, outliers and correlation methods are certainly promising but, as stressed by Savolainen *et al.* (2013) and, in the case of F_{ST} outliers by Whitlock and Lotterhos (2015), they

should be ‘only one step in the process of inferring which genes are responsible for local adaptation.’

Theoretical and Practical Implications

Beyond local adaptation: ecological speciation?

If disruptive selection and local adaptation between different habitats are strong, migration and reproduction between individuals from different habitats may be deleterious. This raises the question whether the process of local adaptation could eventually lead to the formation of reproductive barriers and speciation. Such an ecological speciation process thus requires a form of association (genetic linkage or pleiotropy) between ecologically selected traits and traits involved in reproductive isolation. Under this scenario, speciation thus occurs as a by-product of adaptive divergence between contrasted habitats. Although some examples have been well described, the importance of this mechanism is debated, and whether the genetic changes associated to local adaptation are, in themselves, leading to reproductive isolation remain to be demonstrated.

Local adaptation in practice: plant breeding and conservation strategies

The study of local adaptation also plays a central role in plant breeding and conservation biology. Throughout the history of cultivated plants, local adaptation has occurred in different contexts. At the beginning, the domestication process itself involved adaptation to new human-managed environments. For example, in many plants, especially cereals and legumes, traits favouring seed of fruit dispersal were selected against under cultivation, while there are key components of plant fitness in the wild. During the spread from their centre of origin, crops have also been locally adapting to many conditions (climate, soils, agricultural practices, human uses, etc.), leading to the formation of the so-called landraces. Although plant breeders may not in general talk explicitly of local adaptation, concepts in plant breeding such as genotype–environment interactions, genotypic stability and specific or general adaptability are closely related to local adaptation and have played a key role in plant breeding and beyond. For example, Finlay and Wilkinson (1963) proposed to use the mean yield of all varieties at each site as a measure of the environment in the sites at which the varieties are compared; varieties that are specifically adapted to good or poor sites and those showing general adaptability may then be identified. This is, indeed, very close to the measures of local adaptation that were discussed above. Likewise, foresters have been conducting common garden experiments (also called provenance tests) for 200 years to identify the best seed sources, which have often been found to be local or close to local populations.

In conservation biology, proposals to conserve local populations are generally based, implicitly or explicitly, on the assumption that native populations are locally adapted. However, under

certain conditions, small isolated populations can also benefit from bringing new genetic variation from other populations. So the cost–benefit balance between connecting populations and disrupting local adaptation must be properly evaluated to take informed conservation decision. Finally, maintaining local adaptation in the face of climate change is a concern and an active area of research. In many plant and animal species, evolution of local adaptation has always been a component of range changes. Whether they can adapt will depend on the availability of genetic variation in relevant traits but also critically on many ecological constraints (Shaw and Etterson, 2012; Alberto *et al.*, 2013).

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